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Seasonal flight activity and the length of the generation period of selected Noctuidae (Lepidoptera) – extent and causes of variation

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Abstract

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The variability in the timing of spells of flight activity was monitored in 25 monovoltine and 10 bivoltine species of Noctuidae (Lepidoptera) by evaluating their catches in a light trap operated nightly from April to November 1967–1995. We determined the day when 50% of the individuals of a particular generation were caught, $T_{0.5}$. The intraspecific ranges of variability in $T_{0.5}$ were 9 to 37 days, 29 to 41 days and 25 to 53 days in the monovoltine and the first and second generations of the bivoltine species, respectively. Annual changes in $T_{0.5}$ were strongly correlated between species whose flight activity occurred during a similar period of the season. For bivoltine species, the abundance and $T_{0.5}$ of the first and second generations were correlated. We calculated, for each species and generation, the length of the generation period (GP), i.e., the time from $T_{0.5}$ of generation n to $T_{0.5}$ of generation n+1. This quantity was then converted to the sum of degree-days above 10.7 °C (the thermal threshold for the development of Noctuidae) accumulated under natural conditions. The temporal sequences of these recalculated lengths of the GP were significantly correlated in 91% of the pairs of monovoltine species and in 98% of the pairs of first-generation bivoltine species. The correlations between the lengths of the GP confirmed that temperature determines the periodicity of flight activity, but this effect is modified by photoperiod.

Keywords

abundance, annual, changes, light trap, moths, temperature

Introduction

In insects, the seasonal dynamics and changes in the abundance (assessed by changes in activity) of species during the growing season fluctuate in successive years. The study of the course of these changes in population density and their causes constitutes an important part of the ecology of insect populations (Danilevskii, 1965; Tauber et al., 1986). Such studies require obtaining accurate records of seasonal changes in species abundance. However, long-term documentation of changes in abundance is challenging in terms of choosing a suitable object, place and time of observation, especially in terms of the presence and working capacities of the observers. These difficulties

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can be eliminated by using automated and standardized methods of collection that allow continuous sampling and facilitate the work of the observers. A suitable method for monitoring the abundance of flying adults of nocturnal insects is light traps of various constructions (Taylor and French, 1974), and a taxonomic order that can be successfully studied in this way is Lepidoptera (Raimondo et al., 2004; Merckx and Slade, 2014; Wölfling et al., 2016). This method relies on the well-established fact that Lepidoptera with nocturnal flight activity fly towards a light source (Wigglesworth, 1939; Williams, 1939). Such studies provide much information about changes in the abundance of species (number of individuals caught during a period of collecting activity) and contribute to the study of the causes of these changes (Honek et al., 2023).

While considerable attention has been given to annual changes in the abundance of Lepidoptera species, little attention has been given to the variability in their seasonal activity. This is probably because the monitoring of seasonal activity is demanding, as it is necessary to operate the traps and record the results (species identity and individual counts) frequently, preferably at one-day intervals. The national phytosanitary services of different countries are important collectors of this type of data (Devetak et al., 2014; Keszthelyi et al., 2016; Hrubesova et al., 2023). However, the methodology used by these organizations (efficiency of traps and lengths of sampling intervals) often does not allow a detailed study of the seasonal activity of monitored species. In our study, we used a 29-year series of noctuid moth (Lepidoptera) captures in a light trap located in Prague (Central Europe). These data are particularly suitable for studying the seasonal activity of species since the moths were collected during the entire growing season at daily intervals.

We determined peaks of flight activity in 25 monovoltine (one generation per year) species and 10 bivoltine (two generations per year) species that were sufficiently abundant to enable determination the seasonal dynamics of their flight. The scope was to compare the annual variability in the timing of the peak of flight activity and determine the length of the generation period, i.e., the period that elapsed from a certain phase of the life cycle of generation n to the same phase of the life cycle of the following generation, n+1 relative to calendar time and thermal time which is a measure of the speed of life processes of exothermic organisms (Trudgill et al., 2005). After establishing that annual differences in thermal time were closely related to the variability in the length of the generation period, we investigated the factors that influenced the association between temperature accumulation and the length of the generation period of the species.

Materials and methods

Study site

The light trap was set up in Prague (Czech Republic), at 50.0863058N, 14.3018056E, and 340 m asl. It was placed in an 80 × 250 m garden planted with various ornamental coniferous and deciduous trees. This park was surrounded by experimental plots and production fields at a distance of 500–2,000 m and by sparse residential buildings with gardens at greater distances.

Light trap

The trap was designed and constructed by Dr. Ivo Novák (Novak, 1983). It consisted of a 250-W mercury vapour lamp placed 8 m above ground level on the southern-facing wall of a building. Its light was projected onto a 1 × 1.2 m white panel. A grid of thin wires, stretched 7 mm apart, was placed approximately 20 cm before the white panel and charged with a 2,000–3,000 V/2 mA electric current. Insects flying to the light source and white panel were knocked down by electric shock into a glass bottle where they were killed by chloroform vapour.

Sampling

The study took place between 1967 and 1995. Every year, the trap was run nightly, from sunset to sunrise, from the beginning of March to the end of November. Insect catches that accumulated during one night, sometimes on two consecutive nights, and, rarely, on three consecutive nights combined were processed. Catches accumulated over multiple nights because of the absence of staff operating the light trap. All individuals of the family Noctuidae were manually selected from among the catches and identified to species, and the number of individuals of each species was recorded. Thirteen species economically important in agriculture were monitored for the entire 29-year period; for the other species, data were available for the periods 1967–1976 and 1980–1995 (26 years).

Seasonal dynamics of flight activity

Twenty-five abundant monovoltine species (Table 1) and 10 abundant bivoltine species (Table 2) were included in the study. Included were species whose maximum annual catch over the period of the study was >100 individuals. Migrant species were excluded from the analysis. For each species in each year, its abundance (N, sum of individuals caught in a given year) and seasonal flight activity, i.e., the number of individuals caught each day (daily catch), were determined. When the moths in traps were accumulated over two or three nights, the daily catches were calculated as the cumulative total divided by number of days over which this total was cumulated. Then, for each calendar day, the total number of individuals caught since the beginning of the year was calculated. Using this time series, calendar dates were identified on which 50% ($T_{0.5}$) of the total number of individuals caught in a given year were collected (Fazekas 1997). The date when $T_{0.5}$ was reached was designated the “median day of seasonal flight activity” or “the peak of flight activity” of the species. For each species, the arithmetic average of $T_{0.5}$ in all observation years was calculated, which was termed the average median day

Table 1. Abundance (sum of individuals caught in a year) and median day of seasonal flight activity of monovoltine species (ranked in order of their seasonal activity according to mean $T_{0.5}$)

Species	Ny	Ni			$T_{0.5}$			
		Mean ± SE	Min	Max	Mean ± SE	Min	Max	Dif
Cerastis rubricosa (D. & Sch. 1775) *)	25	53 ± 5.7	5	110	124 ± 5.3	115	135	20
Apamea anceps (D. & Sch. 1775)	29	316 ± 4.5	91	908	166 ± 7.5	148	179	31
Apamea sordens (Hufnagel, 1766)	29	207 ± 24.4	29	606	169 ± 6.9	153	183	30
Oligia strigilis (Linnaeus, 1758)	26	904 ± 110.3	152	2,318	178 ± 8.3	159	190	31
Agrotis exclamationis (Linnaeus, 1758)	29	3,806 ± 367.8	1,302	9,907	180 ± 8.1	160	191	31
Axylia putris (Linnaeus, 1761)	26	988 ± 123.4	97	2,513	181 ± 8.1	163	194	31
Hoplodrina octogenaria (Goeze, 1781)	26	883 ± 67.0	258	1,554	193 ± 7.8	179	208	29
Caradrina morpheus (Hufnagel, 1766)	26	554 ± 57.2	64	1,353	193 ± 7.4	181	210	29
Mamestra persicariae (Linnaeus, 1761)	26	488 ± 70.4	38	1,372	193 ± 6.6	184	210	26
Xestia ditrapezium (D. & Sch. 1775)	26	426 ± 56.6	40	1,046	195 ± 7.7	182	211	29
Lacanobia oleracea (Linnaeus, 1758)	29	326 ± 41.0	68	1,093	196 ± 9.3	178	215	37
Pyrrhia umbra (Hufnagel, 1766)	26	167 ± 20.5	23	499	196 ± 6.8	181	215	34
Apamea lithoxylaea (D. & Sch. 1775)	26	197 ± 31.1	12	698	198 ± 7.2	187	215	28
Mythimna conigera (D. & Sch. 1775)	26	211 ± 21.1	26	454	198 ± 5.7	189	213	24
Apamea monoglypha (Hufnagel, 1766)	29	329 ± 48.6	97	1,423	199 ± 7.4	185	215	30
Mythimna ferrago (Fabricius, 1787)	26	387 ± 41.2	91	906	200 ± 6.5	187	215	28
Hoplodrina blanda (D. & Sch. 1775)	26	473 ± 45.5	129	981	208 ± 5.1	196	217	21
Amphipoea fucosa (Freyer, 1830)	26	807 ± 140.9	105	2,865	210 ± 8.2	198	228	30
Mespamea secalis (Linnaeus, 1758)	29	302 ± 33.0	65	797	213 ± 5.4	204	223	19
Mesoligia furuncula (D. & Sch. 1775)	26	137 ± 14.2	27	269	220 ± 6.8	209	235	26
Luperina testacea (D. & Sch. 1775)	26	65 ± 7.1	24	164	233 ± 5.7	223	245	22
Amphipyra tragopogonis (Clerck, 1759)	26	53 ± 6.2	13	150	239 ± 8.8	223	255	32
Xestia xanthographa (D. & Sch. 1775)	26	232 ± 38.7	31	815	242 ± 2.9	237	248	11
Tholera decimalis (Poda, 1761)	26	39 ± 3.9	13	104	244 ± 2.0	240	249	9
Agrochola litura (Linnaeus, 1761)	26	92 ± 7.9	38	168	266 ± 3.9	257	272	15

Ny – number of years for which data are available, Ni – sum of individuals caught in a year, $T_{0.5}$ – median day of seasonal flight activity, Mean ± SE – mean ± standard error, Min – minimum, Max – maximum, Dif – difference between maximum and minimum (provided for $T_{0.5}$ only). *) D. & Sch. = Denis & Schiffermüller.

of flight activity (a $T_{0.5}$). For species with two generations per year, the periods when the first and the second generations were active were separated first. The dividing line between the two generations was set in the middle of the break period between the flight activity of the first generation and that of the second generation. $T_{0.5}$ was calculated separately for each generation. We then calculated, for each species and generation, the length of the generation period (GP), i.e., the number of days that elapsed from $T_{0.5}$ of generation n to $T_{0.5}$ of generation n+1. This quantity was converted to thermal time, sum of degree-days accumulated during this period. The relative size of the range of minimum and maximum lengths of the generation period of a particular species was calculated as GPrange = (GPmax – GPmin) / GPaverage × 100, where GPrange is the range indicated as a percentage of GPaverage, GPmax is the maximum GP, GPmin is the minimum GP, and GPaverage is the arithmetic mean of all the GP values accumulated over the study period. This study compares the average values of GPrange (±SE) for groups of species and expresses GP length using either calendar days or degree-days.

Evaluating the variability in the day of median flight activity and generation period

The tightness of the relationship between $T_{0.5}$ and the GP of species was calculated using the correlations for all combinations of series of degree-days summed up from the beginning of the year until $T_{0.5}$ was reached or for the entire duration of the GP (hereinafter referred to as the "$T_{0.5}$ series" or "sum of dd series"). For the monovoltine species, there were 300 combinations of species pairs; for the first-generation bivoltine species, there were 45 combinations of species pairs; for the connections between the monovoltine and first-generation bivoltine species, there were 250 combinations of species pairs. To include only positive values in the calculations, the correlations were expressed as the coefficient of determination (squared correlation coefficient, R^2). Thermal data (average daily temperatures) were obtained from Station Praha Ruzyně of the Czech Hydrometeorological Institute (50.1003N, 14.2555E, altitude 364 m asl) located 3.6 km from the light trap. All calculations were performed via SigmaStat® 3.5 software (SYSTAT SOFTWARE Inc., 2006).

Thermal requirements for the development of species

In exotherm animals, the rate of development is dependent on temperature. A species has its lower development threshold (LDT), which is the temperature below which ontogenetic development does not take place and the rate of development is zero. To measure the duration of ontogenetic development, the length of a period can be expressed as "thermal time", which is the sum of positive differences

Table 2. Abundance (the number of individuals caught in a year, N) and median time of flight activity $T_{0.5}$ (Julian day, D) of the first and second generations of bivoltine species (listed in alphabetic order)

Species		First generation				Second generation			Correlation	
		Mean ± SE	Min	Max		Mean ± SE	Min	Max	R^2	P
Abundance										
	Ny	N	N	N	Ny	N	N	N		
Acronicta rumicis (Linnaeus, 1758)	26	35.3 ± 4.1	8	87	26	157.8 ± 20.51	30	504	0.2401	0.0110
Agrotis segetum (D. & Sch. 1775)	29	307.1 ± 56.3	45	1,653	29	215.8 ± 61.76	1	1,740	0.0001	0.9690
Diachrysia chrysitis (Linnaeus, 1758)	29	164.7 ± 15.4	45	392	29	156.9 ± 18.56	19	420	0.1756	0.0238
Discestra trifolii (Hufnagel, 1766)	29	75.5 ± 11.4	12	300	29	605.2 ± 95.01	77	2,067	0.1552	0.0345
Hoplodrina ambigua (D. & Sch. 1775)	26	214.6 ± 37.8	6	731	26	895.2 ± 189.09	18	4,203	0.3003	0.0038
Lacanobia suasa (D. & Sch. 1775)	29	80.9 ± 13.6	8	285	29	561.9 ± 93.84	20	2,186	0.5198	1.03E-05
Mythimna albipuncta (D. & Sch. 1775)	26	189.8 ± 40.1	20	832	26	711.3 ± 145.38	67	3,155	0.7921	1.16E-09
Mythimna l-album (Linnaeus, 1758)	28	28.6 ± 4.2	0	76	29	80.9 ± 11.05	1	227	0.1600	0.0347
Mythimna pallens (Linnaeus, 1758)	26	637.3 ± 174.8	49	4,658	26	833.2 ± 146.83	34	3,289	0.0408	0.3230
Ochropleura plecta (Linnaeus, 1761)	29	375.3 ± 55.4	33	1,201	29	305.5 ± 58.64	9	1,375	0.3080	0.0018
Median time of flight activity (T0.5)										
	Ny	D	D	D	Ny	N	N	N		
Acronicta rumicis (Linnaeus, 1758)	26	140.5 ± 1.71	125	164	26	215.9 ± 1.48	203	232	0.4410	0.0243
Agrotis segetum (D. & Sch. 1775)	29	172.9 ± 1.51	157	186	29	244.7 ± 1.83	223	262	0.3580	0.0568
Diachrysia chrysitis (Linnaeus, 1758)	29	172.3 ± 1.38	157	186	29	232.3 ± 1.48	219	249	0.5430	0.0023
Discestra trifolii (Hufnagel, 1766)	25	148.8 ± 1.43	136	167	29	216.4 ± 1.25	204	228	0.2310	0.2270
Hoplodrina ambigua (D. & Sch. 1775)	29	167.8 ± 1.39	153	183	26	240.0 ± 1.58	227	255	0.7780	2.93E-06
Lacanobia suasa (D. & Sch. 1775)	29	157.1 ± 1.53	143	177	29	225.4 ± 1.23	215	244	0.1570	0.4170
Mythimna albipuncta (D. & Sch. 1775)	29	161.8 ± 1.24	147	175	26	236.1 ± 1.62	221	250	0.6780	0.0001
Mythimna l-album (Linnaeus, 1758)	29	186.9 ± 1.84	169	204	25	259.7 ± 1.69	239	280	0.5100	0.0092
Mythimna pallens (Linnaeus, 1758)	26	183.1 ± 2.30	151	204	26	238.3 ± 1.75	215	256	0.5380	0.0046
Ochropleura plecta (Linnaeus, 1761)	27	176.1 ± 1.29	160	191	29	223.1 ± 1.13	210	235	0.1230	0.5250

Ny – number of years for which data are available (it may differ between the first and second generations because in some years, the catch of the first generation was not sufficiently numerous to reliably determine $T_{0.5}$). Mean ± SE – mean ± standard error, Min – minimum, Max – maximum. Correlation – correlation of the data of abundance or median time of flight activity for the first and second generations, R^2 – coefficient of determination, P – significance of R^2 (correlation is significant if $P < 0.05$).

between the average daily temperature and the LDT set in degree-days. Thermal time can be used to measure any time period including time required for termination of individual ontogenetic development, sum of effective temperatures (SET). In this study we deal with thermal time that elapsed from the commencement of the studied period (beginning of the year, oviposition) to the peak of flight activity $T_{0.5}$. Thermal requirements for development are not known for the individual species included in this study. Therefore, we assumed that the species included in this study and belonging to the Noctuidae are sufficiently closely related to have similar thermal requirements (Jarosik et al., 2011). From a set of published data for 49 populations of 12 Noctuidae species living in temperate climatic zone (summarized in Honek and Kocourek, 1990; Honek, 1996) lower development threshold (LDT) was set to 10.7 ± 0.26 °C and the sum of effective temperatures for preimaginal development (SET) equal to 486 ± 31.1 degree-days. This LDT was used to calculate daily effective temperatures (parts of average daily temperatures that are ≥LDT) and their sums accumulated in individual years. Data on the average daily temperature were taken from the Station Praha Ruzyně of the Czech Hydrometeorological Institute (50.1003N, 14.2555E, altitude 364 m asl) located 3.6 km from the light trap.

Results

Variation in seasonal flight activity

First, we studied the annual differences in calendar dates of flight activity. For the 25 monovoltine species, the average median day of seasonal flight activity (a $T_{0.5}$) was set between Julian Day 124 (2 May) in *Cerastis rubricosa* and Julian Day 266 (21 September) in *Agrochola litura* (Table 1). There was a large intraspecific annual variability in the median day of seasonal flight activity ($T_{0.5}$): the smallest difference (9 days, 27 August to 5 September) between the earliest $T_{0.5}$ and the latest $T_{0.5}$ was found in *Tholera decimalis*, and the largest difference (37 days, 26 June to 2 August) was found in *Lacanobia oleracea*.

The $T_{0.5}$ values were significantly correlated for some species pairs (Fig. 1). Among 201 pairs of species whose a $T_{0.5}$ differed by less than 40 days, i.e., when the flight activity of these species fell into a similar period of the year (Fig. 2A), the correlation between their $T_{0.5}$ series was not significant for only 35 (17.4%) species pairs. For 99 species pairs in which the difference between their a $T_{0.5}$ was greater than 40 days (Fig. 2A), a significant correlation between their $T_{0.5}$ series was found for only 3 pairs of species. There were also important seasonal differences in the correlation of the $T_{0.5}$ series (Fig. 2B). Strong correlations were found among pairs of species whose a $T_{0.5}$ was between 14 June and 7 August. For 10 bivoltine species (Table 2), the average median day of seasonal flight activity (a $T_{0.5}$) of the first generation ranged between Julian days 141 (21 May) in *Acronicta rumicis* and 187 (5 July) in *Mythimna l-album*, and the a $T_{0.5}$ values of the second generation of bivoltine species ranged between Julian Day 216 (3 August) in *A. rumicis* and Julian Day 260 (16 September) in *M. l-album* (Table 2).

We tested the dependence of the abundance (N) and

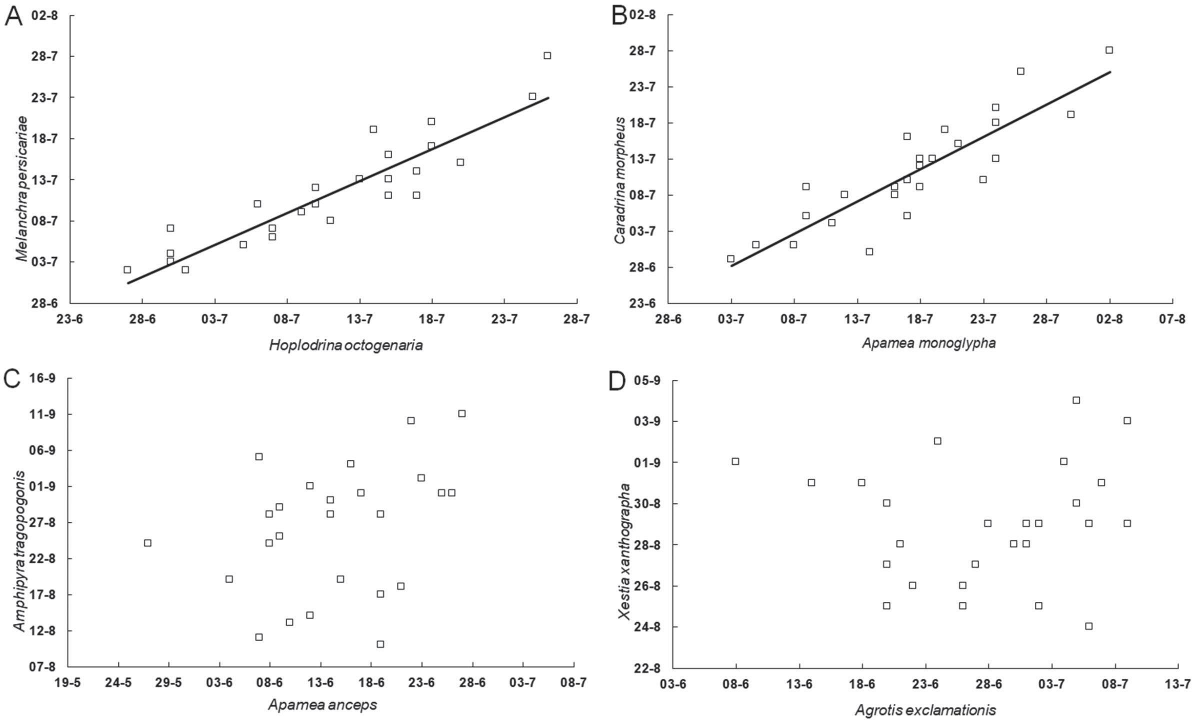

Fig. 1. Examples of significant (above) and nonsignificant (below) correlations between the median period $T_{0.5}$ of species pairs. The squares indicate $T_{0.5}$ in particular years of the study. A – *Melanchra persicariae* vs. *Hoplodrina octogenaria* (a = 0.7741, b = 43.969, R^2 = 0.8371), B – *Caradrina morpheus* vs. *Apamea monoglypha* (a = 0.8950, b = 14.594, R^2 = 0.7728), C – *Amphipyra tragopogonis* vs. *Apamea anceps* (a = 0.423, b = 168.7, R^2 = 0.1332), D – *Xestia xanthographa vs. Agrotis exclamationis* (a = 0.0219, b = 238.0, R^2 = 0.0037).

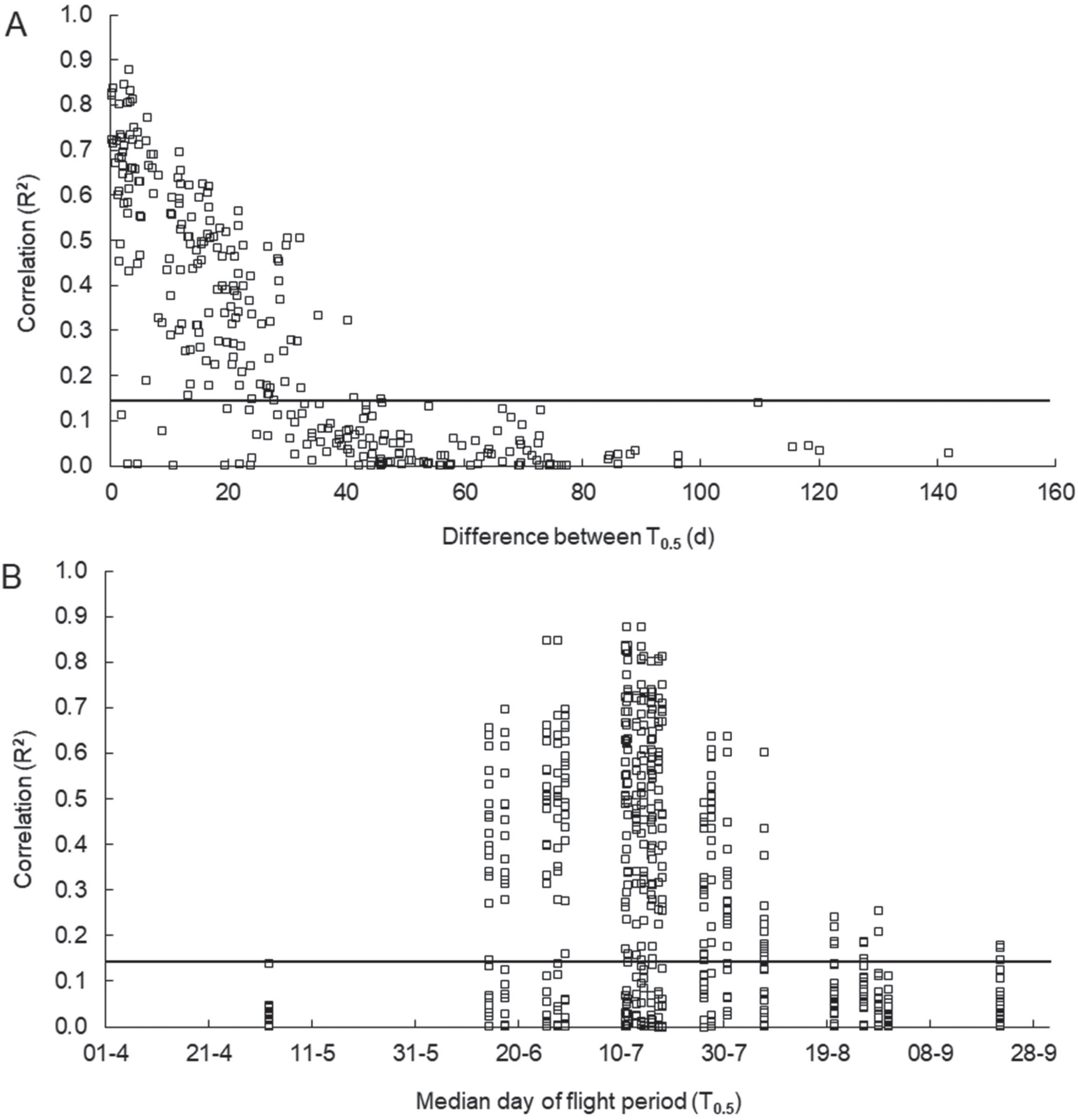

Fig. 2. Correlations between the $T_{0.5}$ of the monovoltine species pairs and the flight periods of these species. A – Correlations (R^2) between the median day of the flight period ($T_{0.5}$) of species pairs plotted against the difference between the a $T_{0.5}$ of these species. B – Correlations (R^2) of the median day of the flight period ($T_{0.5}$) of species pairs plotted against the a $T_{0.5}$ of one of these species (this means that symbols representing correlations for a particular moth species (ordinate) make up a column placed at the date of a $T_{0.5}$ of this species (abscissa)). In both panels, the horizontal line indicates the critical value of $P = 0.05$ for R^2.

median day of flight activity ($T_{0.5}$) of the second generation on the same parameters as those of the first generation. A significant correlation between the abundances of the second and first generations was found for 9 species, and a significant correlation between the $T_{0.5}$ values of the second and first generations was found for 7 of the 10 studied species (Table 2, Fig. 3). Thus, in most bivoltine species, the timing of flight activity of the first generation determines the same qualities as those of the second generation.

Length of the generation period

We calculated the length of the generation period (GP), i.e., the time (number of days) elapsed from $T_{0.5}$ of generation n to $T_{0.5}$ of generation n+1. In calendar time, the temporal sequences of the GP values were significantly correlated for some species pairs (Fig. 4). The degree of GP correlation was high only among species whose flight activity took place during a similar period of the year. Among the monovoltine species (Fig. 4), there was a high proportion of significant correlations (153 of 171 cases, 89.5%) among the GP sequences, which belonged to 19 species whose a $T_{0.5}$ (see Table 1) was between 14 June and 7 August.

After converting calendar days to thermal time (the sum of degree-days accumulated during the GP period), the proportion of significant interspecific correlations of the GP series revealed that, in most species, there was con-

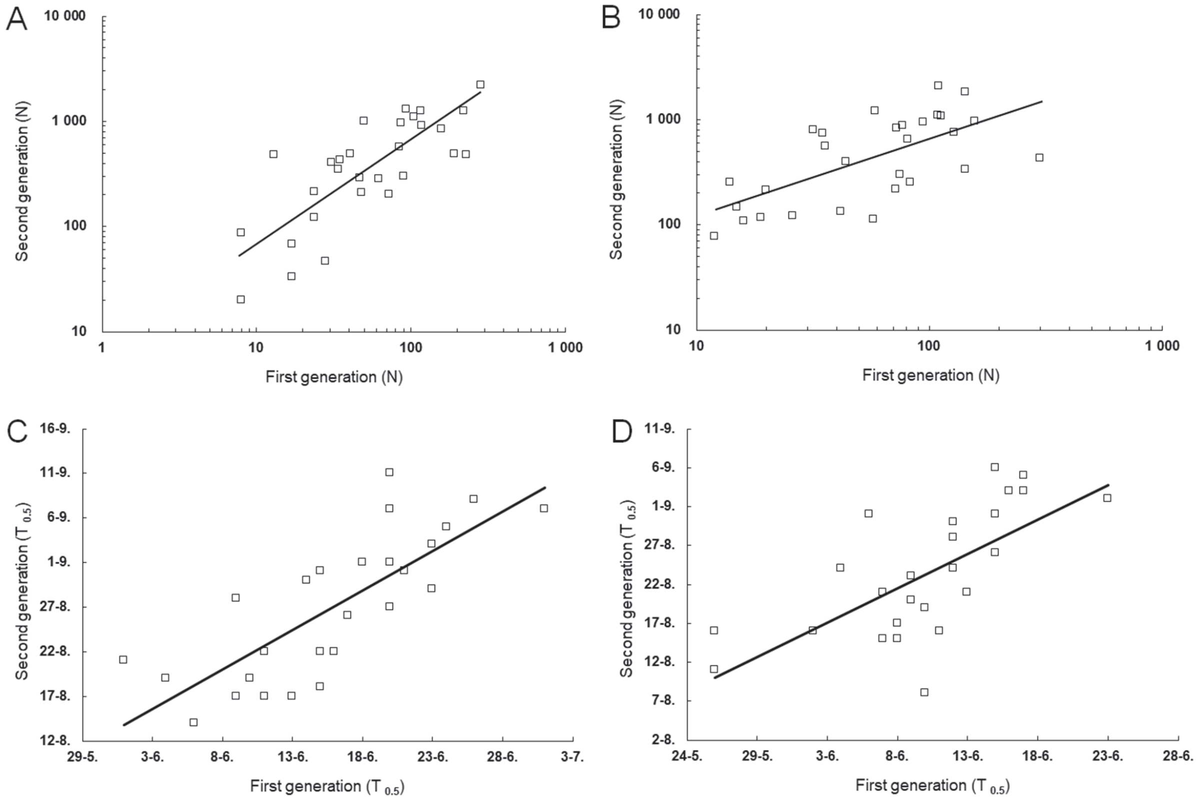

Fig. 3. Examples of significant relationships between the abundance (N, log-transformed) of the second and first generations of bivoltine species (Panels A and B) and between the median day of flight activity ($T_{0.5}$) of the second generation and the $T_{0.5}$ of the first generation of bivoltine species (Panels C and D). A – abundance of *Lacanobia suasa* (a = 0.925, b = 0.935, $R^2 = 0.597$, F = 40.048, $P < 0.001$); B – abundance of *Discestra trifolii* (a = 0.728, b = 1.347, $R^2 = 0.423$, F = 19.812, $P < 0.001$); C – median day of flight activity of *Hoplodrina ambigua* (a = 0.888, b = 90.996, $R^2 = 0.605$, F = 36.741, $P < 0.001$); D – median day of flight activity of *Mythimna albipuncta* (a = 0.885, b = 92.918, $R^2 = 0.460$, F = 20.460, $P < 0.001$).

siderable similarity between the series of GP length (Fig. 4). After transformation, for most species pairs, there was a statistically significant correlation between the lengths of the GP expressed in degree-days and in calendar days, but for some pairs of species, there was a statistically significant correlation only for the lengths of the GP expressed in degree-days (Fig. 5). For 25 monovoltine species, the lengths of the GP expressed in degree-days were significantly correlated for 274 pairs of species, i.e., in 91.3% of the 300 possible combinations of species pairs (Table 3). The correlation between the GPs of the first generation of bivoltine species and monovoltine species was significant in 229 (91.6%) of the 250 possible cases. The correlation between the GPs of the first generation of bivoltine species was significant in 44 (97.8%) of the 45 possible cases.

We compared the overwintering generations, i.e., the monovoltine species and the first generation of the bivoltine species, in which the generation period included both the later part of year n and the early part of year n+1, during which the generation lived. The range of intraspecific variability (Table 4) in the length of the GP (in calendar time) was from 9 days in *T. decimalis* to 48 days in *Apamea monoglypha*. The minimum lengths of the GP in particular species varied between 335 and 361 days, and the maximum lengths varied between 370 and 391 days. It is not surprising that in monovoltine species, after 23–28 years of observation, the average length of the GP approached 365 days (fluctuating between 364.2 days in *Mesoligia furuncula* and 365.5 days in *Amphipyra tragopogonis*). This length is close to the duration of one year (set at 365 days in our calculations), as it must be in monovoltine species. The relative range of the minimum and maximum lengths of the GP in individual species varied on average by 10.2 ± 0.67% of the average length of the GP. The range of variability in the length of the GP expressed in thermal time varied from 355 dd for *A. tragopogonis* to 551 dd for *C. rubricosa*. The minimum duration of the GP ranged between 541 dd in *Mesapamea secalis* and 657 dd in *Mythimna conigera*, and the maximum length ranged between 981 dd in *A. tragopogonis* and 1,114 dd in *Pyrrhia umbra*. The relative range of the minimum and maximum lengths of the GP in individual species varied on average by 56.7 ± 1.08% of the average length of the GP. This value was thus greater than that when the GP was expressed in calendar days.

In the second generation of bivoltine species (Table 5), the range of variability in the length of the GP varied from 24 days in *Ochropleura plecta* to 53 days in *Lacanobia suasa*. The minimum length of the GP for individual species varied between 125 days in *Hoplodrina ambigua* and 221 days in *A. segetum* and the maximum length varied between 164 days in *H. ambigua* and 256 days in

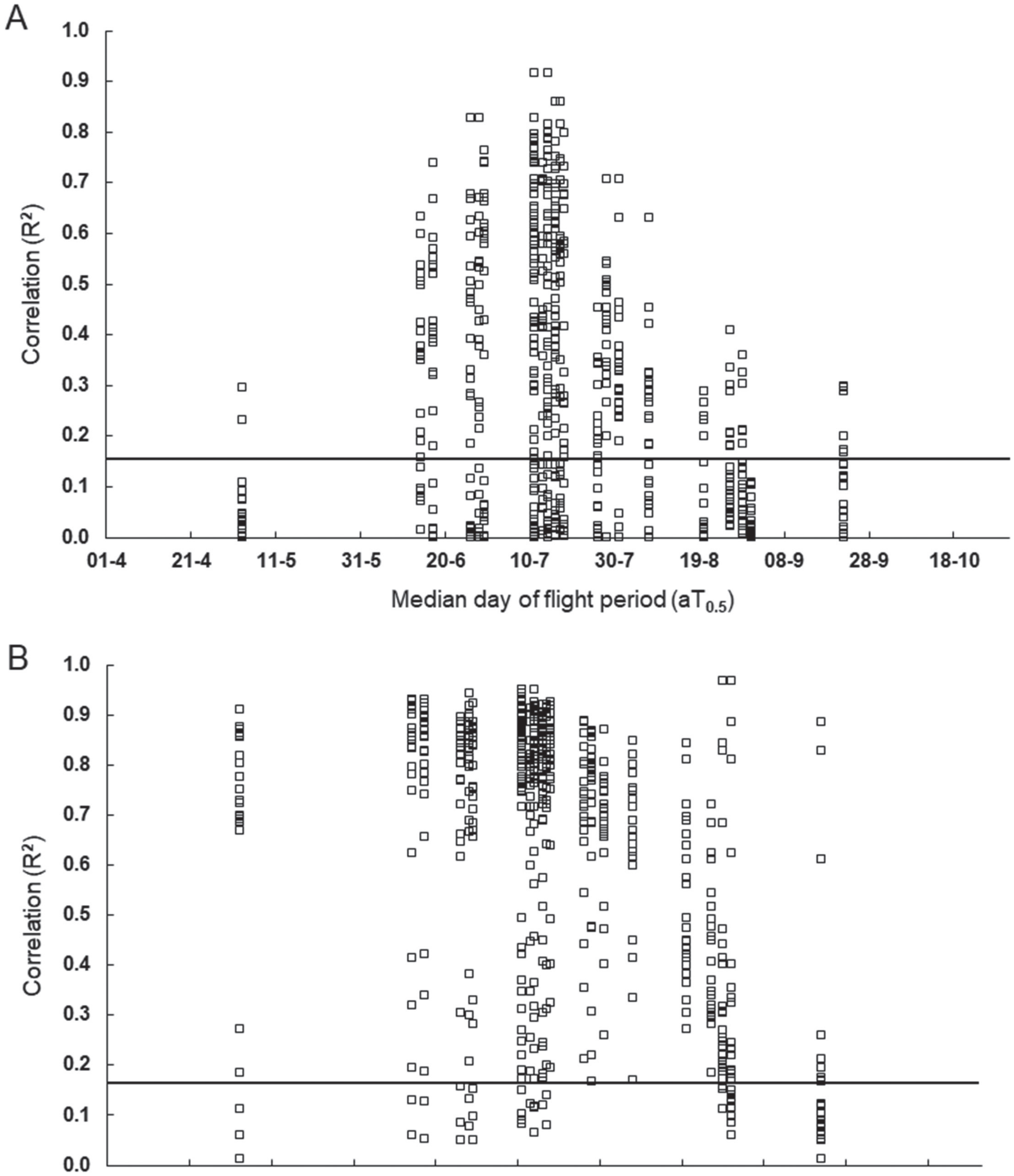

Fig. 4. Correlations between the lengths of the generation period (GP) of pairs of monovoltine species plotted against the a $T_{0.5}$ value of one of these species. A – length of the GP in calendar time. B – length of the GP in thermal time. The symbols representing correlations for a particular moth species (ordinate) make up a column placed at the date of a $T_{0.5}$ for that species (abscissa). The horizontal line indicates the critical value of $P = 0.05$ for R^2. Note: Each correlation value for two species (a and b) is indicated twice in the figure, once in the column showing data for species a and once in the column representing species b; i.e., the two tick marks indicating the correlation have different positions relative to the abscissa and the same position relative to the ordinate.

D. chrysitis. The range of the minimum and maximum lengths of the GP for individual species varied on average by 17.9 ± 2.03% of the average duration of the GP for the given species. The range of intraspecific variability in GPs expressed in thermal time varied between 190 dd in *A. rumicis* and 412 dd in *M. pallens*. The minimum duration of the GP varied between 106 dd in *O. plecta* and 350 dd in *M. albipuncta*, and the maximum length varied between 444 dd in *O. plecta* and 654 dd in *H. ambigua*. The range of the minimum and maximum lengths of the GP for individual species varied on average by 71.4 ± 6.38% of the average length of the GP for the species.

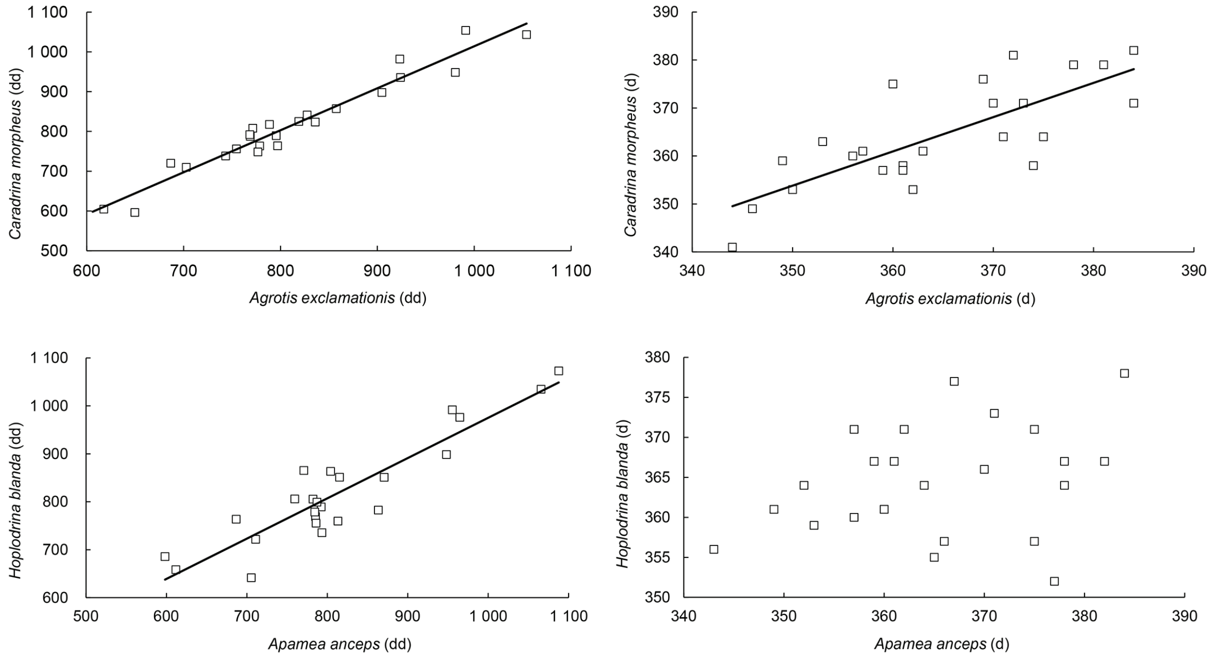

Fig. 5. Correlations between the lengths of the generation period (GP) in selected species pairs. Top: *Caradrina morpheus* vs. *Agrotis exclamationis*, species for which there is a statistically significant correlation between the lengths of the GP expressed in both degree-days and calendar days (left – degree-days (dd) $y = 1.0564x - 42.217$, $R^2 = 0.9442$; right – calendar days (d) $y = 0.1977x - 42.216$, $R^2 = 0.6021$). Bottom: *Hoplodrina blanda* vs. *Apamea anceps*, species for which there is a statistically significant correlation between the lengths of the GP expressed in degree-days but not in calendar days (left – degree-days (dd) $y = 0.8401x + 134.95$, $R^2 = 0.8347$; right – calendar days (d) $y = 0.1977x + 292.2$, $R^2 = 0.097$).

Table 3. Correlation between the lengths of the generation period of pairs of monovoltine species (Monovoltine vs. monovoltine), pairs of monovoltine and first generation of bivoltine species (Monovoltine vs. bivoltine 1st gen.), and pairs of first generation and second generation of bivoltine species (Bivoltine 1st gen. vs. bivoltine 2nd gen.) calculated using thermal time (Degree-days) and calendar time (Calendar days)

	Monovoltine vs. monovoltine			Monovoltine vs. bivoltine 1st gen.			Bivoltine 1st gen. vs. bivoltine 2nd gen.		
	Total	Significant		Total	Significant		Total	Significant	
	N_T	N_S	Pc	N_T	N_S	Pc	N_T	N_S	Pc
Degree days	300	274	91.3	250	229	91.6	45	44	97.8
Calendar days	300	178	59.3	250	84	33.6	45	37	82.2

Total – total number (N_T) of possible correlations between species pairs. Significant – number of significant correlations between species pairs (N_S) and the percentage of significant correlations from the total number of possible correlations (Pc) ($Pc = N_S/N_T \times 100$).

Discussion

A considerable amount of data has been obtained on the annual variability in the abundance of Noctuidae species, i.e., the number of individuals of a species caught in light traps per year (Meszaros, 1979; Spitzer et al., 1984; Spitzer and Lepš, 1988; Guo et al., 2020). Although many studies have addressed the effects of environmental factors on the timing of flight activity (Nowinszky, 2008; Altermatt, 2012; Sharma et al., 2017; Duraimurugan, 2018; Larsen et al., 2022), the annual variability in the median day of flight activity ($T_{0.5}$) has been less studied. The periods of flight activity of noctuid species have been known for a long time (Spuler, 1908), with a precision of approximately ten days (Koch, 1988); however, few studies have accurately determined the variability in $T_{0.5}$. According to a 14-year study of *Xestia c-nigrum*, the range of variation in $T_{0.5}$ was 16 days in the first generation and 22 days in the second generation (Tsutsui and Hayakawa, 1991). In an 11-year study of the flight activity of nine noctuid species, Ayre and Lamb (1990) reported less extensive variability in T0.5, from 3 to 9 days. We found (i) significant annual variability in the median time of flight activity ($T_{0.5}$) within species and (ii) a correlation between the $T_{0.5}$ values but only in species whose flight activity falls into the same period of the season.

Significant progress was made in terms of the transformation of the results, which considered the entire length

Table 4. Length of generation period (GP) of monovoltine species (time elapsed from $T_{0.5}$ of year n to $T_{0.5}$ of year n+1) in calendar days and degree days (N – number of GP)

	N	Calendar days X ± SE	Min	Max	Range	Degree days X ± SE	Min	Max	Range
Agrochola litura	24	365.1 ± 1.19	356	375	19	822.2 ± 21.45	599.9	1,038.0	438.1
Agrotis exclamationis	28	365.0 ± 2.28	344	384	40	793.6 ± 22.21	606.2	1,054.0	447.8
Amphipoea fucosa	24	364.3 ± 2.43	342	387	45	819.3 ± 23.91	594.0	1,100.9	506.9
Amphipyra tragopogonis	24	365.5 ± 2.55	343	386	43	825.5 ± 23.03	625.9	981.0	355.1
Apamea anceps	28	365.4 ± 1.99	343	384	41	796.9 ± 23.99	598.2	1,087.7	489.5
Apamea lithoxylaea	24	364.5 ± 2.17	339	385	46	819.0 ± 22.92	596.1	1,072.4	476.3
Apamea monoglypha	28	365.0 ± 2.11	343	391	48	794.1 ± 22.27	622.3	1,037.2	414.9
Apamea sordens	28	364.9 ± 2.06	343	382	39	794.5 ± 23.44	590.9	1,068.5	477.6
Axylia putris	24	364.7 ± 2.51	338	385	47	814.1 ± 24.37	584.2	1,077.2	493.0
Caradrina morpheus	24	364.3 ± 2.21	341	382	41	816.9 ± 23.78	596.3	1,054.1	457.8
Cerastis rubricosa	23	365.5 ± 1.55	353	379	26	806.7 ± 26.02	542.7	1,093.9	551.2
Hoplodrina blanda	24	364.4 ± 1.40	352	378	26	819.0 ± 22.81	641.6	1,073.0	431.4
Hoplodrina octogenaria	24	364.2 ± 2.26	339	381	42	816.1 ± 24.77	593.5	1,090.7	497.2
Lacanobia oleracea	28	365.0 ± 2.81	335	382	47	794.8 ± 24.37	595.0	1,080.7	485.7
Luperina testacea	24	364.6 ± 1.83	347	377	30	821.1 ± 23.80	589.1	1,030.3	441.2
Mamestra persicariae	24	364.6 ± 1.93	341	380	39	820.2 ± 25.33	604.7	1,093.1	488.4
Mesoligia furuncula	24	364.2 ± 1.95	349	390	41	812.7 ± 21.12	640.7	1,088.0	447.3
Mespamea secalis	28	365.0 ± 1.45	347	382	35	790.3 ± 21.10	541.4	1,028.1	486.7
Mythimna conigera	24	364.5 ± 1.55	345	375	30	819.0 ± 23.12	657.1	1,063.3	406.2
Mythimna ferrago	24	364.4 ± 1.58	343	377	34	819.0 ± 23.06	639.8	1,072.4	432.6
Oligia strigilis	24	364.4 ± 2.63	342	385	43	811.1 ± 21.64	599.9	1,070.4	470.5
Pyrrhia umbra	24	364.4 ± 1.73	341	380	39	818.4 ± 24.36	618.0	1,103.6	485.6
Tholera decimalis	24	365.3 ± 0.46	361	370	9	824.2 ± 23.91	589.1	1,032.0	442.9
Xestia ditrapezium	24	364.8 ± 2.28	337	383	46	821.8 ± 25.44	579.1	1,070.5	491.4
Xestia xanthographa	24	364.7 ± 0.79	358	370	12	822.2 ± 21.86	584.1	984.2	400.1

Table 5. Length of generation period (GP) of 1st generation and 2nd generation of bivoltine species (time elapsed from $T_{0.5}$ of generation n to $T_{0.5}$ of generation n+1) in calendar days and degree days (N – number of GP)

	N	Calendar days X ± SE	Min	Max	Range	Degree days X ± SE	Min	Max	Range
1st generation									
Acronicta rumicis	24	240.0 ± 1.58	227	255	28	370.7 ± 19.33	247.7	599.1	351.4
Agrotis segetum	28	172.9 ± 1.51	157	186	29	317.1 ± 11.58	178.6	465.6	287.0
Diachrysia chrysitis	28	157.1 ± 1.53	143	177	34	391.3 ± 17.92	248.4	663.8	415.4
Discestra trifolii	28	259.7 ± 1.69	239	280	41	382.6 ± 18.35	193.9	636.0	442.1
Hoplodrina ambigua	24	225.4 ± 1.23	215	244	29	316.5 ± 14.56	181.7	483.0	301.3
Lacanobia suasa	28	244.7 ± 1.83	223	262	39	356.8 ± 16.03	245.5	583.4	337.9
Mythimna albipuncta	24	232.3 ± 1.48	219	249	30	310.6 ± 15.41	159.7	523.0	363.3
Mythimna l-album	23	172.3 ± 1.38	157	186	29	355.2 ± 14.68	232.2	510.6	278.4
Mythimna pallens	24	167.8 ± 1.39	153	183	30	421.4 ± 16.18	288.4	597.8	309.4
Ochropleura plecta	28	186.9 ± 1.84	169	204	35	463.2 ± 15.46	264.7	658.2	393.5
2nd generation									
Acronicta rumicis	26	148.8 ± 1.43	136	167	31	443.5 ± 8.22	337.4	527.1	189.7
Agrotis segetum	29	236.1 ± 1.62	221	250	29	479.2 ± 15.24	319.0	613.0	294.0
Diachrysia chrysitis	29	238.3 ± 1.75	215	256	41	404.1 ± 13.32	157.1	523.7	366.6
Discestra trifolii	29	171.7 ± 2.80	153	185	32	416.4 ± 12.85	311.2	568.1	256.9
Hoplodrina ambigua	26	140.5 ± 1.71	125	164	39	500.1 ± 13.19	329.4	654.3	324.9
Lacanobia suasa	29	183.1 ± 2.30	151	204	53	440.3 ± 13.19	282.8	561.5	278.7
Mythimna albipuncta	26	176.1 ± 1.29	160	191	31	506.2 ± 12.40	350.2	650.5	300.3
Mythimna l-album	25	215.9 ± 1.48	203	232	29	469.9 ± 16.69	320.1	623.2	303.1
Mythimna pallens	26	223.1 ± 1.13	210	235	25	396.3 ± 17.11	135.1	547.4	412.3
Ochropleura plecta	29	216.4 ± 1.25	204	228	24	332.8 ± 14.95	105.7	443.5	337.8

of the generation period, i.e., the interval starting from T0.5 of year n and ending at $T_{0.5}$ of year n+1. The conversion of the length of the generation period from calendar to thermal time, which scales the rate of development of exothermic organisms and determines the speed (Honek and Kocourek, 1990; Honek, 1996; Bues and Poitout, 1980; Kitajima et al., 2016; Moon et al., 2022) and plasticity (Lee and Roh, 2010; Degut et al. 2022) of ontogenetic development can also be considered a progress.

After the transformation, the lengths of the generation period were more closely correlated. If the length of the generation period is expressed in calendar days, this synchronicity of flight activity is not evident. This is because the length (number of days) of the generation period also includes the span of the cold winter period when ontogenetic development does not occur and whose length varies from year to year. Therefore, the proportion of correlated pairs of species was low (178 out of 300 possible pairs, i.e., 59.3%). An even lower proportion of correlated pairs of species was found when 25 monovoltine species were compared with the first generation of 10 bivoltine species (84 out of 250 possible pairs, i.e., 33.6%). This is because the first generation of bivoltine species has less time to develop than monovoltine species, as two generations develop in one year in bivoltine species.

The recalculation of the calendar time to thermal time erases, from the time period of preimaginal and teneral development, periods of calendar time when ontogenetic development does not occur. The recalculation evened out the differences between cold and warm weather and, in this way, compensated for differences in the number of calendar days needed to complete development. Species share approximately identical thermal conditions, and their generation periods were correlated. Correlations between the above combinations of pairs of monovoltine species and the first generation of bivoltine species thus became significant in 91–98% of cases. The thermal time, which is the determinant of the duration of the generation period of a species, is best suited to describe the correlation of the series of degree-day sums of species.

The temperature is not the only factor determining the length of the GP or the timing of $T_{0.5}$. In monovoltine species, the GP expressed in thermal time was excessively long compared to the sum of effective temperatures needed for ontogenetic development of noctuid species (SET = 486 dd). In all the cases (species × year combinations), the GP expressed in thermal time was 1.1–2.1 times longer than the thermal sum calculated for Noctuidae using laboratory experiments. Even more interesting was the case of bivoltine species. For these species, the thermal time (the sum of temperatures) available under natural conditions was usually shorter than the SET value calculated for ontogenetic development. In the first generation, the thermal time "provided by nature" (i.e. the sum of degree-days calculated for the first generation using temperature data for the period between $T_{0.5}$ in year n and $T_{0.5}$ in year n+1) was, in most cases, lower than the SET needed for ontogenetic development. In two species, *A. segetum* and *H. ambigua*, the lengths of the GP in nature did not reach the needed 486 dd in any year. In other species, it was only in one year to up to ten years (on average, in 10.5 ± 3.30% of species × year combinations) when the thermal time calculated for the generation period was longer than 486 dd, i.e., long enough for preimaginal development to take place. For its development, the second generation had a slightly wider thermal horizon. For only one species, *O. plecta*, the "naturally provided" thermal time did not reach the 486 dd needed for the development of Noctuidae in any year. For the other species, the required amount of thermal time was achieved only in some years, namely, in three (for *D. chrysitis*) to sixteen (for *M. albipuncta*) years.

The inconsistency between the thermal conditions available for species in nature and their temperature requirements for ontogenetic development may be solved in two ways. First, we may allow for the possibility of error in the estimation of temperature requirements. This can occur in several ways: (i) Owing to the distorting influence of fluctuating temperatures on the summation of effective temperatures. If we use the "triangle method of degree-day accumulation" (Bryant et al., 1998) and take not only the average but also the minimum and maximum daily temperatures when calculating the sum of the effective temperatures, the sum of the effective temperatures will increase significantly. (ii) By choosing a different method of calculating LDT values from experimental data on the length of development at constant temperatures. In our studies (Honek and Kocourek, 1990; Honek, 1996), we used a linear model that provided the best estimate of the LDT for recalculating published data on development length (Honek et al., 2014). Recalculation using nonlinear methods will provide different results, the applicability of which would have to be tested (Régnier et al., 2022). The correct choice of LDT is very important because a 1 °C shift in estimation can cause differences in the SET of tens to hundreds of degree-days. (iii) Selection of inappropriate set of species to calculate the LDT and SET typical for Noctuidae. In our study, the selection of species used for the calculation was limited by published data (summarized in Honek and Kocourek, 1990; Honek, 1996). Data for the species included in this study are not available. Better information about the effects of temperature on the rate of development of these species could lead to improved study results.

The second possibility is to consider the mechanisms by which insects can regulate the effect of temperature on the rate and length of development. Regarding the reduction in the thermal sum available for monovoltine species, the obvious mechanism is the induction of dormancy (Danilevskii, 1965; Beck, 1968). Induction of dormancy by photoperiod (Lees, 1955; Saunders, 2020) interrupts growth and ontogenetic development even at high temperatures favourable for ontogenetic development. In Central Europe, diapause induction adjusts temperature effects so that a monovoltine cycle is achieved.

It is more difficult to explain the discrepancy between the low sum of temperatures accumulated under natural conditions and high temperature requirements for the ontogenetic development of species. The body temperature of ectothermic animals can increase as a result of thermoregulatory behaviour (May, 1979). Thermoregulation is widespread in Lepidoptera (Hill et al., 2021) and is used to increase (Ayres and Scriber, 1994; Bardoloi and Hazarika, 1994; Bryant et al., 1998; Moore et al., 2023) or decrease (Frears et al., 1997) body temperature. It is possible that thermoregulatory behaviour also contributes to the synchronization of the generation periods of species.

In our study, we showed that temperature has a decisive effect on the length of the generation period (GP) and on the timing of median day of flight activity ($T_{0.5}$). In addition to temperature, the timing of seasonal flight activity is influenced by other factors that deserve further investigation.

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