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Using thermal time to predict the timing of flight activity in Noctuidae (Lepidoptera) species: Calculation and verification of forecast methods

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Abstract: From 1967 to 1995, the flight activity of 25 monovoltine species of moths (Noctuidae, Lepidoptera) was monitored via a light trap located in Prague (50.09 N, 14.30 E). For each species, the day when half of the individuals were caught (peak of flight activity, PFA) was specified each year. This study addresses a method of predicting the calendar date of the PFA via thermal time. We determined a base temperature of +6 °C, at which the differences between the predicted and actual dates of the PFA were minimal. For each species and each year, the sum of the degree days exceeding the base temperature from January 1 to the date of the PFA (SumT) was determined, and the average SumT throughout the study was calculated. Each year, the predicted date of the PFA is the date when the average SumT was achieved. Sixty-five percent of the predicted PFA dates fell within ±5 days of the actual date of the PFA. Shifts in the magnitude and direction of the difference between the actual and predicted PFAs affecting concurrently all species were caused by the thermal conditions of the year.

Keywords: base temperature; peak flight activity; prediction; thermal time

Temperature controls ectothermic organisms' rate of life processes (Trudgill et al. 2005). In insects, the metabolic rate relies on body temperature, which largely depends on the ambient temperature (Heinrich 1993). The temperature controls the timing of reproduction and life manifestations, ensuring their successful course, including flight activity. In Lepidoptera, flight activity secures the selection of a partner and the search for oviposition sites. The period of flight activity therefore immediately precedes (Ge et al. 2021) or coincides (Jiang et al. 2010) with the period of mating and oviposition.

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Before reaching the reproduction stage, an individual passes through a sequence of developmental processes, the duration of which is determined by the rate of metabolism, which largely depends on body temperature. Since body temperature reflects ambient temperature, reproduction and flight activity timing are confined to a defined period during the vegetative season.

In Lepidoptera, flight activity can be observed conveniently. Considerable attention has been given to Noctuidae, moths, whose flight activity has been studied for over two hundred years. This long-standing interest was sparked and sustained by the aesthetic qualities of moths. Their attractive appearance stimulated collectors and students of their systematics and life histories. The period of flight activity of individual species was generally known more than a hundred years ago (Spuler 1908), with an accuracy of approximately 10 days (Koch 1988). The flight activity of a monovoltine moth species has a standard course. From the moment when the flying individuals appear for the first time in the season, their numbers increase, peak for a short period, and finally decrease. In a graphical representation, flight activity is hill-shaped when the number of flying individuals is plotted against the time axis.

Light traps are suitable for monitoring flying adults of nocturnal insects (Taylor & French 1974). Lepidoptera is a taxonomic group that can be successfully studied this way (Raimondo et al. 2004). The advantage of light traps is that they are easy to use, which enables their continuous operation during the entire growing season. They are therefore routinely used by phytosanitary services (Meszaros et al. 1979) and research organisations (Altermatt et al. 2009; Hrubešová et al. 2023). Light traps are successfully used to determine the peak of flight activity (Jermy 1974).

In our earlier work, we studied the timing of flight activity of 25 monovoltine species in the family Noctuidae. This study was based on a twenty-nine-year series (1967–1995) of catches of Noctuidae species in light traps. The date of the peak of flight activity, i.e., the day when half (50%) of the individuals caught in a given year occurred, differed considerably across years. For some species, this date fluctuated within a range of up to 30 days. As expected, the cause of these fluctuations was differences in thermal conditions over the years. The annual variation in ambient temperature explained a significant proportion of the variance in the calendar date of the peak of flight activity.

Because temperature is an important factor in the timing of moth flight activity, it can also be used for prediction (Jarvis & Brindley 1965). For 25 species of the Noctuidae family, we investigated the possibility of predicting the calendar date of peak flight activity via temperature data measured via the standard meteorological method.

MATERIAL AND METHODS

Light trap. The light trap was located at 50.086 N, 14.302 E and 340 m asl in an 80 × 250 m garden with various ornamental coniferous and deciduous trees. Experimental plots and production fields surrounded the garden at distances of 500–2 000 m. Even farther away, the surroundings consisted of sparse residential buildings with gardens. The light trap was designed and constructed by Ivo Novák. The description of the trap (Novák 1983) also provides an illustration and details of its construction and maintenance. It consisted of a 250 W mercury vapour lamp placed 8 m above ground level on the southern-facing wall of a building. The 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 the white panel were knocked down by an electric shock into a glass bottle, where they were killed by chloroform vapour. The conditions and operation of the trap were regularly checked, and the trap was maintained in flawless condition throughout the entire period of the study.

Sampling and determination of the flight activity of moths. The moths were sampled between 1967 and 1995. The trap was run nightly every year, from sunset to sunrise, from the beginning of March to the end of November. The insects that accumulated during one night, sometimes on two consecutive nights, and, rarely, on three consecutive nights, were processed. All individuals of the family Noctuidae were manually selected from among the caught insects, identified to species according to their phenotypic appearance (Spuler 1908), and the number of individuals of each species was recorded. The species *Mesapamea secalis* (L.) and *Mesapamea secalella* (Remm)

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were not distinguished at the time of the study, and we recorded a mixture of both species as one species (*M. se*calis). This confusion may have influenced the results. *Mesapamea secalis* and *M. secalella* can only be distinguished by their copulatory organs. Analysis of *Mesapamea* specimens collected by our light trap in the early 1990s showed that *M. secalella* constituted only a small fraction of the *Mesapamea* material. Therefore, the bias in the results was probably not significant.

This study is based on data from twenty-five abundant monovoltine noctuid species (Table 1). Six of these species were monitored for the entire 29 year period; for the other species, data were available from 1967–1976 and 1980–1995 (26 years). The number of individuals caught each night (calendar day) was determined for each species. Then, for each calendar day, the sum of individuals caught from the beginning of the year until this calendar day was calculated. Using this time series of cumulative numbers of individuals, a calendar date was identified on which 50% of the individuals of a species caught in a given year were collected. This date was designated the peak of flight activity (PFA), and the calendar date when this peak occurred was designated the actual date (AD), of the peak of flight activity. The number of individuals of a species caught in a year is called "abundance". Data on average abundance over the study period and average date of the PFA over the study period were published in Honěk et al. (2025).

Determining the base temperature. The extent of variation in Dif (the number of days elapsed between the actual and predicted dates of the PFA) varies depending on the value of the base temperature, Tb, which was selected. As a base temperature, Tb, we selected the temperature for which the annual variation in Dif in a species was minimal.

Specifically, to investigate the difference between the actual and predicted dates of peak of flight activity, the base temperature Tb was determined empirically via the following procedure: *(i)* For a selected species of Noctuidae, we tentatively chose the base temperature value (Tb). *(ii)* Using this temperature Tb, we determined the sum of degree days from January 1 until reaching the PFA called actual (SumT), i.e., the sum of positive values of the differences between the average daily temperature and the base temperature Tb, which elapsed from the beginning of the period of prediction until the peak of flight activity (PFA). *(iii)* We calculated the arithmetic mean of actual SumT from all years during the observation period, and this value was set as the predicted SumT. *(iv)* For each year of observation, we calculated the difference Dif between the predicted SumT and the actual SumT observed in that year. *(v)* We calculated the average value as the arithmetic mean of the differences established in individual years (Dif).

To select the optimum Tb (i.e., Tb in which the average value of Dif was minimal), we used tentatively chosen values of Tb increasing in 1 °C increments from 0–12 °C. We determine which value of Tb is the average value of Dif at the minimum. This value of Tb was then adopted as the optimum value of the base temperature Tb for the selected species.

Predicting the peak of the seasonal flight activity. The basis for the prediction was the determination of the length of the thermal time (sum of degree days above the base temperature Tb). As the beginning of the period for which the temperature summation was made, two different time points were chosen: temperatures were summed from (a) the beginning of the calendar year (January 1) or from (b) the peak of flight activity PFA of the maternal generation.

For each year of observation, the sum of the effective temperatures (SumT) was accumulated from the beginning of the period for which the thermal time (a measure of the duration of a period expressed in degree days) was summed to the day of the peak of flight activity. The arithmetic mean (XSumT) of the values of SumT for all years of observation was subsequently calculated. We used the following procedure: *(i)* For each year of observation, the sum of effective temperatures (SumT) accumulated from the day of the beginning of the period for which the thermal time was summed to the day of the peak of flight activity was determined. *(ii)* Then, the XSumT values of SumT for all years of observation were calculated. *(iii)* For each year of observation, the calendar date was determined when the thermal time reached the value of XSumT. This date is the predicted date of the seasonal flight activity predicted date (PD) peak. *(iv)* Then, the Dif, i.e., the number of days between the actual date of the peak of seasonal flight activity AD and the predicted date of the peak of seasonal flight activity PD (Dif = AD – PD), was calculated. These calculations were performed for each species and for both monitored periods, i.e., the period (a) beginning from the start of the year (January 1) and the period (b) beginning from the moment of peak flight activity PFA of the maternal generation (i.e., AD

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Table 1. Actual and predicted dates of the peak flight activity PFA calculated via prediction starting from January 1

		Actual date (Julian day)			Actual degree days			Predicted date (Julian day)				
	N	Mean ± SE	Min	Max	Mean ± SE	Min	Max	Min	Max	Dif –	Dif +	Dif X ± SE
Cerastis rubricosa (D. & Sch., 1775)	25	124 ± 1.1	115	135	130.6 ± 8.61	51.2	247.3	102	147	–20	+20	6.7 ± 1.22
Apamea anceps (D. & Sch., 1775)	29	166 ± 1.4	148	179	454.3 ± 9.63	361.9	569.7	149	186	–12	+15	4.0 ± 0.76
Apamea sordens (Hufnagel, 1766)	29	169 ± 1.3	153	183	483.6 ± 8.53	378.6	566.2	152	189	–6	+16	3.4 ± 0.60
Oligia strigilis (Linnaeus, 1758)	26	178 ± 1.6	159	190	569.3 ± 9.55	468.9	669.4	159	200	–7	+13	3.7 ± 0.52
Agrotis exclamationis (Linnaeus, 1758)	29	180 ± 1.5	160	191	592.3 ± 9.73	468.9	688.7	161	203	–8	+16	4.2 ± 0.63
Axylia putris (Linnaeus, 1761)	26	181 ± 1.6	163	194	613.8 ± 1.31	496.0	747.1	162	206	–10	+16	4.3 ± 0.80
Hoplodrina octogenaria (Goeze, 1781)	26	193 ± 1.5	179	208	748.2 ± 2.18	646.4	862.7	179	216	–11	+8	4.5 ± 0.47
Caradrina morpheus (Hufnagel, 1766)	26	193 ± 1.5	181	210	753.0 ± 8.88	674.3	833.6	180	217	–5	+8	3.0 ± 0.40
Mamestra persicariae (Linnaeus, 1761)	26	193 ± 1.3	184	210	752.9 ± 0.54	669.6	891.4	180	217	–9	+8	3.6 ± 0.48
Xestia ditrapezium (D. & Sch., 1775)	26	195 ± 1.5	182	211	778.7 ± 14.12	686.7	938.3	182	218	–10	+10	4.9 ± 0.55
Lacanobia oleracea (Linnaeus, 1758)	29	196 ± 1.7	178	215	783.3 ± 13.07	630.0	911.7	183	219	–9	+19	5.0 ± 0.72
Pyrrhia umbra (Hufnagel, 1766)	26	196 ± 1.3	181	215	790.8 ± 12.40	673.9	897.4	183	219	–7	+10	4.2 ± 0.56
Apamea lithoxylaea (D. & Sch., 1775)	26	198 ± 1.4	187	215	810.1 ± 10.83	693.8	918.3	184	221	–7	+11	3.8 ± 0.55
Mythimna conigera (D. & Sch., 1775)	26	198 ± 1.1	189	213	811.0 ± 11.91	675.6	897.4	185	221	–6	+13	4.0 ± 0.60
Apamea monoglypha (Hufnagel, 1766)	29	199 ± 1.4	185	215	818.8 ± 11.34	717.7	928.3	185	221	–8	+12	4.1 ± 0.64
Mythimna ferrago (Fabricius, 1787)	26	200 ± 1.3	187	215	837.6 ± 13.29	669.6	958.4	186	223	–6	+16	4.3 ± 0.72
Hoplodrina blanda (D. & Sch., 1775)	26	208 ± 1.0	196	217	930.0 ± 13.23	768.4	1 053.4	197	232	–12	+18	4.6 ± 0.88
Amphipoea fucosa (Freyer, 1830)	26	210 ± 1.6	198	228	948.3 ± 10.96	864.5	1 060.3	198	233	–10	+7	3.4 ± 0.51
Mesapamea secalis (Linnaeus, 1758)	29	213 ± 1.0	204	223	975.7 ± 13.63	819.3	1 111.1	200	237	–12	+16	4.8 ± 0.84
Mesoligia furuncula (D. & Sch., 1775)	26	220 ± 1.3	209	235	1 080.3 ± 14.56	918.1	1 297.1	207	250	–17	+20	4.7 ± 1.00
Luperina testacea (D. & Sch., 1775)	26	233 ± 1.1	223	245	1 243.4 ± 20.39	1 029.5	1 388.5	215	278	–12	+35	8.9 ± 1.45
Amphipyra tragopogonis (Clerck, 1759)	26	239 ± 1.7	223	255	1 296.5 ± 26.47	1 006.2	1 522.1	218	321	–22	+80	13.8 ± 2.94
Xestia xanthographa (D. & Sch. , 1775)	26	242 ± 0.6	237	248	1 329.2 ± 22.21	1 066.3	1 556.0	220	283	–20	+41	7.7 ± 1.84
Tholera decimalis (Poda, 1761)	26	244 ± 0.4	240	249	1 346.6 ± 25.15	1 029.5	1 610.9	221	286	–24	+45	9.2 ± 1.94
Agrochola litura (Linnaeus, 1761)	26	266 ± 0.8	257	272	1 520.9 ± 26.39	1 192.7	1 800.6	237	338	–31	+79	15.6 ± 3.75

N – number of seasons included in the study; actual – actual terms of the PFA; date (Julian day) – dates of PFA in calendar dates (Julian days), average date of PFA (Mean ± SE), earliest date of PFA (Min), and latest date of PFA (Max); degree days – terms of the PFA in sums of degree days; average date of the PFA (Mean ± SE), earliest date of the PFA (Min), and latest date of the PFA (Max); predicted – predicted terms of the PFA; date (Julian day) – earliest predicted date of the PFA (Min), latest predicted date of the PFA (Max); Dif- – maximum negative difference between the actual and predicted terms of the PFA; Dif+ – maximum positive difference between the actual and predicted terms of the PFA; DifX ± SE – arithmetic mean of the absolute values of the difference between the actual date of the PFA and the predicted date of the PFA; data in columns are from the Actual/Date (Julian day); the species are arranged by their peak of flight activity PFA

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of the maternal generation). *(v)* The mean Dif, which is the arithmetic mean of the square root of the absolute values of Dif for individual years of observation [i.e., mean Dif = sum $\sqrt{(|AD - PD|)}/n$; where n is number of years], was subsequently calculated for each species. The square root (AD – PD) was used so that extreme values of Dif minimally distorted the arithmetic mean.

Statistical procedures. Where appropriate, the data were fitted by a linear function ($y = ax + b$). The annual variability in the direction and magnitude of the differences between the predicted PFA values and actual PFA values was tested via Kruskal-Wallis one-way analysis of variance on ranks, where the differences were the response variable and the years of observation were the factor. The contrasts between the average Dif calculated via thermal sums starting from January 1 and the average Dif calculated via thermal sums starting from the peak of flight activity of the maternal generation were tested via the Mann-Whitney rank sum test, where the differences were the response variable and methods of calculation (terms of the start of the sum of the temperatures) were the factor. All calculations were performed via SigmaStat (version 3.5).

RESULTS

Determining the base temperature value. The problem of how the variability of Dif depends on the selected value of Tb was investigated in detail in two species, *Agrotis exclamationis* with PFA in the early season (mean AD at Julian Day 180, i.e., June 28) and *Mesapamea secalis* with PFA in the advanced season (mean AD at Julian Day 213, i.e., July 31) (Figure 1). The minimum variation in Dif was established at Tb = 7 °C in *A. exclamationis* and at Tb = 6 °C in *M. secalis*. For the combined data of both species, the variation in Dif was lowest when Tb = 6 °C. The value of 6 °C was therefore chosen as the optimum Tb value. The adequacy of Tb = 6 °C for the other species included in this study was tested via a simplified method. The variability of Tb was calculated via three values: Tb = 4 °C, Tb = 6 °C and Tb = 8 °C. The variation in Dif was the lowest for all the tested species when Tb = 6 °C was used (data not shown). This confirmed the previous conclusion, and the value of Tb = 6 °C was confirmed as the base temperature that can be used for calculating the predicted date (PD) of the peak of flight activity.

Prediction of the date of the PFA via the summation of effective temperatures starting from the beginning of the calendar year (January 1). The average absolute values of the difference (DifX) between the actual (AD) and predicted (PD) dates of peak flight activity (PFA) were calculated for each of the studied species (Table 1). They ranged from 3.0 ± 0.40 days in *Caradrina morpheus* to 15.6 ± 3.75 days in *Agrochola litura*. From the total number of 661 forecasts of the date of the

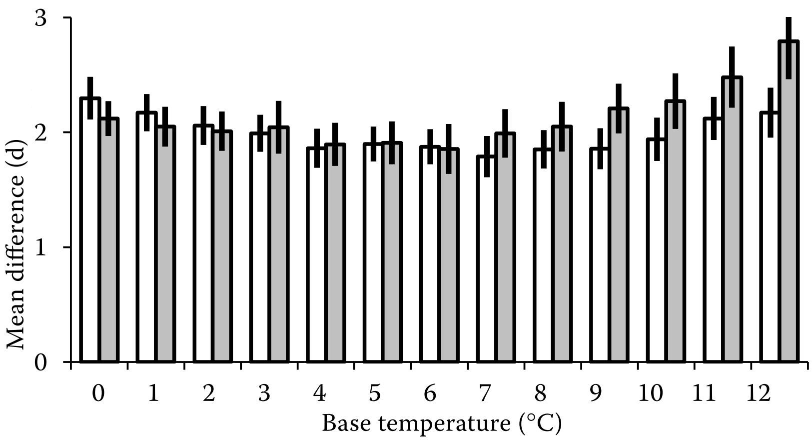

Figure 1. Effect of base temperature on the annual variation in the predicted date of peak flight activity
Ordinate: arithmetic means of differences between actual date (AD) and predicted date (PD) of the peak of flight activity in years of observation (indicated as the square root of the absolute value of differences AD–PD); error bars indicate the standard deviation of the mean; Abscissa: base temperatures (0 °C to 12 °C), which were used for the calculation of the predicted date of the peak of flight activity; the open columns represent *Agrotis exclamationis*, and the shaded columns represent *Mesapamea secalis*

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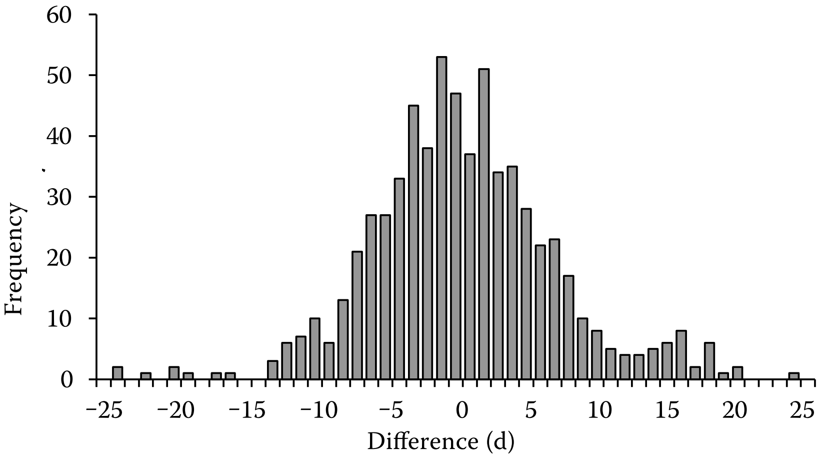

Figure 2. Frequency distributions of the differences between the actual date (AD) and the predicted date (PD) of the peak of flight activity

Cumulative data for all species and all years of observation; ordinate: number of cases with a particular difference in AD–PD; abscissa: magnitude of difference in AD–PD (number of days); extreme values of differences (>25 days) are not shown

peak of flight activity, in 428 (64.8%) forecasts, the predicted date ranged between –5 days and +5 days from the actual date of peak flight activity. In contrast, in 585 (88.5%) forecasts, the predicted date ranged between –10 days and +10 days from the actual date of peak flight activity (Figure 2).

Low values of the average Dif were established in species flying in late spring (the earliest *Apamea anceps*, average date of PFA on Julian Day 166, i.e., June 14, average Dif = 4.0 ± 0.76 days) and early and mid-summer (the latest *Mesoligia furuncula*, average date of PFA on Julian Day 220, i.e., August 7, average Dif = 4.7 ± 1.00 days) (Figure 3). Greater average differences in Dif were found for species that flew before and after this period. For *Cerastis rubricosa*, with an average PFA date of Julian Day 122, i.e., May 3, the average difference was 6.7 ± 1.22 days. In *Luperina testacea*, with an average date of PFA on Julian Day 233, i.e., August 20, the average Dif was 8.9 ± 1.45 days;

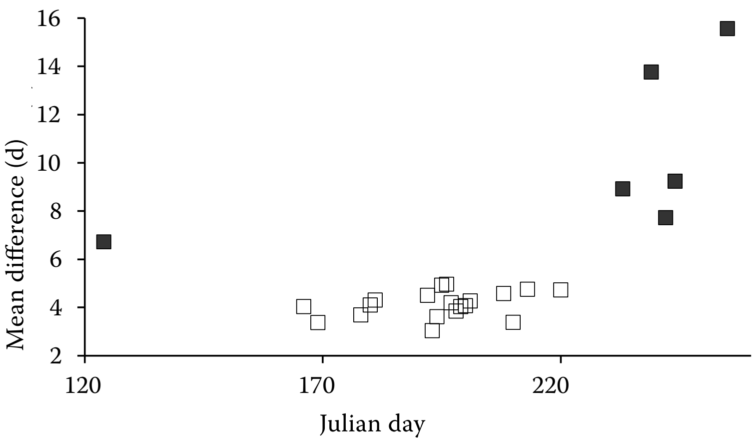

Figure 3. Effect of the timing of flight activity on the difference between the actual date (AD) and the predicted date (PD) of the peak of flight activity (PFA)

Ordinate: arithmetic mean of absolute values of differences between the actual date and the predicted date of flight activity; abscissa: average date of peak flight activity of a species (Julian day, calculated for the entire observation period); closed symbols: *Agrochola litura*, *Amphipyra tragopogonis*, *Cerastis rubricosa*, *Luperina testacea*, *Mesoligia furuncula*, *Tholera decimalis*, and *Xestia xanthographa*; open symbols: other species (listed in Table 1); the figure shows that predictions of the date of the PFA of early spring and late summer flying species (closed symbols) are less precise than predictions of the PFA of species that fly in late spring to mid-summer (open symbols)

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in *Agrochola litura*, with an average date of PFA on Julian Day 266, i.e., September 22, the average Dif was 15.6 ± 3.75 days. Reliable predictions of the date of PFA were thus obtained for species whose PFA ranged from mid-June to mid-August.

For species whose date of peak flight activity was "reliably" predicted, the maximum negative difference (Dif) between the actual and predicted dates of peak flight activity (Dif = AD – PD) ranged from –6 days (in *Apamea sordens*) to –17 days (in *Mesol-*

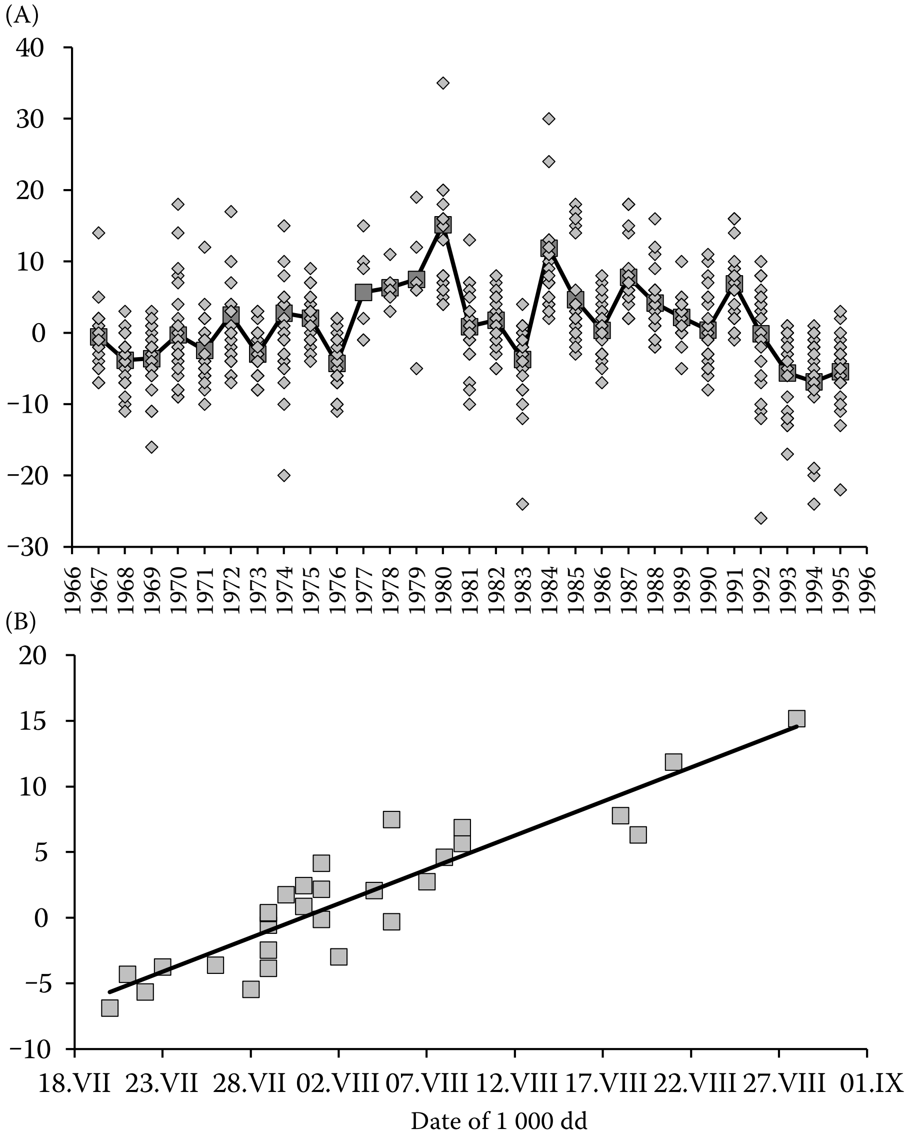

Figure 4. Annual variability in differences between the actual date (AD) and the predicted date (PD) of peak flight activity

(A) – annual variation in AD – PD differences between years of observation (1967–1995). Ordinate: magnitude of differences (number of days) between the AD (value of AD set at 0) and the PD of the peak of flight activity of a particular species included in the study; abscissa: years of observation; each year, each species is represented by one difference value, and positive values indicate cases (species × year combinations) when PD > AD, i.e., the actual date of the PFA occurred earlier than the predicted date of the PFA; negative values indicate cases (species × year combinations) when PD < AD, i.e., the actual date of the PFA occurred later than the predicted date of the PFA; shaded squares and heavy lines indicate the annual means of the differences in AD–PD

(B) – variations in the differences between the actual date and the predicted date of peak flight activity in relation to the thermal conditions of the year; ordinate: annual means of differences in AD–PD (days, bold symbols in figure A); abscissa: date in which (in this year) the thermal sum of degree days above Tb = 6 °C reached 1 000 dd (a = 0.5187, b = 110.3, R^2 = 0.832, P < 0.001); dd – the thermal sum of degree days

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igia furuncula), which means that the peak of flight activity was predicted to occur 6 to 17 days earlier than it occurred. The maximum positive differences between the actual and predicted dates of peak flight activity ranged from +7 days (in *Amphipoea fucosa*) to +20 (in *Mesoligia furuncula*) days, which means that the peak of flight activity was predicted to occur 7 to 20 days later than it occurred.

The sets of Dif values for a single investigated species calculated for a particular year in our study were not distributed symmetrically around the actual date of peak flight activity. This means that in some years, Dif values deviated systematically in a negative sense, i.e., the predicted peak flight activity dates were consistently earlier than the actual date of the peak of flight activity. In some other years, Dif values deviated systematically in a positive sense (i.e., the predicted peak flight activity dates were consistently later than the actual date of the peak of flight activity). The values of average annual Dif differed ($P_{\text{Kruskal-Wallis}} < 0.001$) in particular years from zero (i.e., the value that is expected

Table 2. Actual and predicted dates of peak flight activity—prediction starting from the peak flight activity of the maternal generation

		Actual degree – days			Predicted date (Julian day)					
	N	Mean ± SE	Min	Max	Mean ± SE	Min	Max	Dif–	Dif+	Dif X ± SE
Cerastis rubricosa (D. & Sch.)	23	1 680 ± 30.9	1 387	1 996	129 ± 4.8	88	161	–40	38	17.8 ± 2.70
Apamea anceps (D. & Sch.)	28	1 654 ± 32.7	1 366	2 088	167 ± 3.6	120	196	–32	59	15.2 ± 2.45
Apamea sordens (Hufnagel)	28	1 649 ± 30.8	1 314	1 924	170 ± 3.3	127	197	–34	32	14.1 ± 1.88
Oligia strigilis (Linnaeus)	24	1 672 ± 28.8	1 379	1 917	177 ± 3.0	137	201	–28	26	10.8 ± 1.58
Agrotis exclamationis (Linnaeus)	28	1 649 ± 30.7	1 305	1 933	181 ± 3.1	139	210	–38	31	12.4 ± 1.85
Axylia putris (Linnaeus)	24	1 676 ± 33.6	1 345	1 933	180 ± 3.0	141	207	–32	23	11.9 ± 1.61
Hoplodrina octogenaria (Goeze)	24	1 676 ± 33.8	1 355	2 043	193 ± 3.1	150	217	–31	32	10.6 ± 1.98
Caradrina morpheus (Hufnagel)	24	1 677 ± 32.0	1 376	2 017	193 ± 2.9	155	217	–29	26	10.7 ± 1.74
Mamestra persicariae (Linnaeus)	24	1 682 ± 33.5	1 376	2 075	194 ± 3.0	157	222	–36	30	11.0 ± 2.04
Xestia ditrapezium (D. & Sch.)	24	1 684 ± 33.0	1 332	2 043	196 ± 2.7	171	217	–33	28	10.5 ± 1.75
Lacanobia oleracea (Linnaeus)	28	1 650 ± 34.2	1 237	2 057	198 ± 2.9	154	224	–44	28	11.9 ± 1.92
Pyrrhia umbra (Hufnagel)	24	1 679 ± 31.7	1 389	2 015	196 ± 3.0	153	221	–28	32	10.4 ± 1.75
Apamea lithoxylaea (D. & Sch.)	24	1 680 ± 30.4	1 358	1 979	198 ± 2.9	159	219	–30	31	10.3 ± 1.65
Mythimna conigera (D. & Sch.)	24	1 680 ± 29.2	1 447	2 014	199 ± 2.8	161	220	–24	29	9.5 ± 1.62
Apamea monoglypha (Hufnagel)	28	1 649 ± 28.9	1 340	1 986	200 ± 3.0	159	225	–32	26	11.0 ± 1.62
Mythimna ferrago (Fabricius)	24	1 679 ± 29.8	1 421	1 979	201 ± 3.0	159	225	–26	31	9.8 ± 1.75
Hoplodrina blanda (D. & Sch.)	24	1 680 ± 29.9	1 464	2 045	208 ± 2.7	182	233	–26	27	9.2 ± 1.61
Amphipoea fucosa (Freyer)	24	1 679 ± 32.5	1 371	2 087	210 ± 2.9	182	232	–27	28	9.4 ± 1.77
Mesapamea secalis (Linnaeus)	28	1 649 ± 27.7	1 291	1 919	214 ± 3.2	186	264	–43	27	10.3 ± 1.82
Mesoligia furuncula (D. & Sch.)	24	1 676 ± 27.7	1 432	2 046	220 ± 2.7	197	244	–19	31	8.0 ± 1.53
Luperina testacea (D. & Sch.)	24	1 683 ± 30.4	1 456	1 940	235 ± 2.9	211	263	–26	22	12.5 ± 1.45
Amphipyra tragopogonis (Clerck)	24	1 691 ± 30.0	1 418	1 959	240 ± 2.7	218	264	–32	27	11.3 ± 1.93
Xestia xanthographa (D. & Sch.)	24	1 684 ± 24.6	1 427	1 869	244 ± 3.0	224	279	–34	15	10.7 ± 1.76
Tholera decimalis (Poda)	24	1 689 ± 27.8	1 419	1 909	246 ± 3.2	226	285	–44	19	12.6 ± 2.07
Agrochola litura (Linnaeus)	14	1 686 ± 26.1	1 382	1 912	298 ± 5.5	274	355	–92	–10	33.4 ± 5.31

N – number of seasons included in the study; actual – actual terms of the PFA; degree days – terms of the PFA in sums of degree days, average date of the PFA (Mean±SE), earliest date of the PFA (Min), and latest date of the PFA (Max); predicted – predicted terms of the PFA; date (Julian day) – earliest predicted date of the PFA (Min), latest predicted date of the PFA (Max), (Dif–) – maximum negative difference between the actual and predicted terms of the PFA; Dif+ – maximum positive difference between the actual and predicted terms of the PFA; Dif X ± SE – arithmetic mean of the absolute values of the difference between the actual date of the PFA and the predicted date of the PFA; the species are arranged by their peak of flight activity PFA

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if Dif is not significantly positive or significantly negative) (Figure 4A). For example, a negative difference was established in 1976, 1983 and 1993–1995, whereas a positive difference was established in 1980, 1984, 1987 and 1991.

The annual average Dif values were correlated with the year's thermal conditions. When the date when the thermal sum of 1 000 degree days above the base temperature of 6 °C (Figure 4B) was reached was selected as the representative characteristic of the thermal conditions of a year, the values of average Dif were significantly correlated with the calendar date when this sum of degree days was reached (Figure 4B). This means that the colder the weather (the lower the average temperature) of the year was and, consequently, the later the thermal sum of 1 000 dd was reached, the more the predicted values of the average peak of flight activity lagged behind the actual values of the peak of flight activity.

Prediction of the date of the PFA via the summation of temperatures from the start of the development of the generation. The prediction based on the summation of temperatures starting from the PFA of the maternal generation, i.e., at the moment when the development of the generation for which the prediction was made began (Table 2), was less accurate than the prediction based on the summation of temperatures from January 1. The maximum negative differences between the predicted date of the peak of flight activity PD and the actual date of the peak of flight activity AD ranged from +15 days (*Xestia xanthographa*) to +59 days (*Apamea anceps*). The maximum positive differences between the predicted date and actual date of the peak of flight activity ranged from –19 days (*Mesoligia furuncula*) to –44 days (*Tholera decimalis*). In *Agrochola litura*, whose flight activity occurs in autumn, only negative differences were found between PD and AD, with a minimum of –10 days and a maximum of –92 days. This means that in this species, the predicted peak of flight activity PD was systematically set later than the actual peak of flight activity AD. Thus, e.g. the difference of AD – PD = –92 days arose between predicted date Julian day 355 (December 20) and actual date Julian day 263 (September 19). The overall average DifX (average difference between the actual and predicted dates of PFA for a particular species) calculated via the summation of temperatures from the start of the development of the generation (12.2 ± 0.97 days; the average of the values in the last column in Table 2) was significantly greater ($P_{\text{Mann-Whitney}} < 0.001$, *U statistic* = 47.000) than the average difference calculated via the summation of temperatures from January 1 (5.6 ± 0.64 days; the average of the values in the last column in Table 1).

DISCUSSION

Base temperature. The base temperature Tb applied in this work, 6 °C, was ascertained empirically as a base temperature suitable for comparing the range of variability of the differences between actual and predicted PFA data. It was chosen so that the intraspecific annual variation in Dif was minimal.

Using a temperature of 6 °C as the base temperature initially seems unusual. The temperature of 6 °C is much lower than the base temperature for developing the preimaginal stages of Noctuidae, as calculated from experimental data on the duration of preimaginal development at constant temperatures. Using published data on the effect of temperature on the rate of preimaginal development of Noctuidae, the base temperature was calculated at 10.6 °C (Honěk et al. 2025). The use of the base temperature Tb = +10.6 °C, a temperature that was determined based on the known physiological characteristics of Noctuidae species, led to a large range of variability in Dif, a range significantly greater than the range that we obtained using the base temperature Tb = +6 °C. The base temperature of +10.6 °C is called the lower development threshold (LDT) (Honěk & Kocourek 1990). LDT is a thermal limit below which no ontogenetic development occurs. A change in temperature below this limit should not affect the speed of life processes, including the timing of the ability to fly. However, the range of Dif variability, the difference between the actual and predicted dates of peak flight activity, changed when we calculated these differences using different Tb values between 0 °C and 10 °C, i.e., temperatures below the LDT.

There are several reasons why a temperature of 10.6 °C might not be appropriate for predicting the date of peak flight activity; for example, the difference between the temperature data available from public meteorological data sources, i.e., the air temperature recorded at a height of 2 m above the mowed ground surface, and the temper-

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ature experienced by individuals of a species living under natural conditions. The latter may differ because the eggs and caterpillars live in plant stands, where actual temperatures differ from values measured by standard meteorological temperature (Bonan 2002). The body temperature of caterpillars can be further adjusted, reduced (Moore 2023) or increased (Frears et al. 1997), by active thermoregulatory behaviour. The temperature of the upper layer of the soil, a place where most species included in this study pupated, differed significantly from the prevailing air temperatures at the same sites. Lepidopteran larvae select pupation sites based on soil temperature (Scarbrough et al. 1977; Thibout & Nowbahari 1987). These findings indicate that the air temperature may not be a good indicator of the body temperature of a species.

In contrast, the reasons why using base temperature Tb = +6 °C led to the optimum results, i.e., that the intraspecific variability of Dif was the lowest when this temperature was used, are unclear. Although we cannot answer this question, the suitability of this temperature as a base temperature for predicting peak flight activity was verified for the species and years included in our study. Therefore, we believe that this temperature (Tb = +6 °C) can be generally recommended for use in predicting the peak of flight activity in nocturnal Macrolepidoptera.

The term for starting the sum of the temperature. We studied two variants of the date of the beginning of temperature summation: (a) the beginning of the calendar year (January 1) and (b) the beginning of the ontogenetic development of the investigated generation (the peak of flight activity of the maternal generation in the preceding year). The term, which was used as the start of temperature summation, significantly affected the variation in the differences between the actual and predicted dates of the peak of flight activity. We found that variant (a) provided significantly more accurate predictions of the term of the PFA than did variant (b). This is because prediction via variant (a) is based on thermal data (sums of effective temperatures) belonging to only a fraction of the development period of an individual, i.e., the period from the end of winter dormancy (diapause) to the peak of flight activity of the monitored generation, whereas prediction via variant (b) takes advantage of thermal data for the entire period of preimaginal development. The reason for the greater accuracy of predictions using variant (a) of temperature summation is that monovoltine species spend the winter period in diapause, which, in all individuals of a species, is terminated at the same stage of ontogenetic development, From this term the photoperiod no longer affects the rate of development (Tauber et al. 1986), and the duration of ontogenetic development is controlled by temperature (Beck 1968). The prediction of the timing of the peak of flight activity via variant (a) is precise just because the duration of postdiapause development is determined almost exclusively by the ambient temperature.

Suppose we use variant (b), i.e., the method that starts the summation of temperatures from the beginning of the development of the investigated generation. In that case, we consider the sum of temperatures for the entire period of preimaginal development. We thus also include the temperatures accumulated in the year‘s final period when this generation began to develop in calculating the thermal sum. At this time, the course of development is influenced not only by temperature but also by photoperiod. The photoperiod controls the onset of diapause, which is induced before the end of the growing season. The temperature is still high enough for ontogenetic development (Tauber et al. 1986). However, after the photoperiodically controlled onset of dormancy, temperature no longer affects development. The sums of the temperatures accumulated during this (photoperiodically controlled) insensitivity to thermal conditions vary yearly. Annual differences in the magnitude of the sum of the temperatures accumulated during this period, when moths are insensitive to temperature conditions, decrease the accuracy of the prediction of the date of the PFA.

Importance of predicting the timing of flight activity. Some species included in the study (*Agrotis exclamationis*, *Agrotis segetum*, *Lacanobia oleracea*, *Mamestra brassicae*, *Apamea monoglypha*, *Apamea sordens*, and *Mamestra persicariae*) are important pests of crops in Central Europe (Miller 1956; Anonymous 2024) and Western Europe (Cayrol 1972). These species occur not only on cultivated land but also on areas of native vegetation locked in agricultural land (Novák 1992). The flight activity of a species is associated with oviposition and the beginning of the development of the next generation. Knowing the period of egg laying is important for the timing of crop protection

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measures because damage to crops caused by developing larvae occurs in the immediately following period. Therefore, predicting the timing of the peak of flight activity is important for planning and timing protection measures. The long-term prediction of moth flight activity complements forecasts based on signalisation warnings and the first catches of moths in light traps (Jermy 1974).

We demonstrated that for forecasting, it was possible to use temperature data measured by standard meteorological methods (average air temperature) and data on average temperature sums necessary to reach the peak of flight activity calculated in this study (Table 1). In most cases, these data enabled a reliable prediction of the timing of the peak of flight activity, i.e., a forecast with an accuracy of ±5 days from the actual date of the peak of flight activity. Satisfactory forecasts can be made for species whose peak flight activity occurs in late spring and early and mid-summer (approximately between June 1 and August 10).

Current climate change creates another problem in predicting flight activity: emergence or increase in the abundance of the second generation of moth species (Altermatt 2010; Kocsis & Hufnagel 2011; Esbjerg & Sigsgaard 2014). Some formerly monovoltine species now regularly have a second generation, e.g. *Agrotis exclamationis*, *Lacanobia oleracea* (Hrubešová et al. 2023) and *Pyrrhia umbra* (Patočka & Kulfan 2009). Consequences of the emergence of the second generation and prediction of its flight activity require further investigation.

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