

THE EFFECT OF TEMPERATURE ON FLIGHT INITIATION OF PINE PROCESSIONARY MOTH IN BULGARIA

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Abstract

The purpose of the present work is to study the temperature effect on the flight initiation of the *Thaumetopoea pityocampa*. Our results show that the flight initiation of males is at relatively lower temperatures than females. Also, the average temperature for the flight initiation of the summer form is lower than for the winter one. This indicates a better adaptability of the summer form to lower ambient temperatures which should favour its spread in habitats located at a higher altitude in the country.

Key words: temperature, flight, *Thaumetopoea pityocampa*, summer and winter form

Introduction. Global warming is causing changes in many insects' activity periods, distribution areas, and the growth rate of populations [1]. In response, the insects have evolved a wide range of physiological strategies that facilitate their adaptation to the environmental conditions. For example, adapting to global warming may lead to temporary shifts of the periods of activity with a rest through a diapause and/or an aestivation [2] as well as phenological alterations, mainly through the regulation of the diapause induction or a termination [3].

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The phenological variations relative to the climate variability have long been observed for *Thaumetopoea pityocampa* (Lepidoptera: Notodontidae) – one of the most dangerous insect pests in the pine ecosystems. *T. pityocampa*, commonly known as a pine processionary moth (PPM), is normally a univoltine species: the emergence of adults is in summer, the larval development is in winter, and the beginning of the processions is in spring. Due to the timing of the larval feeding period, the population with the presented life-cycle is called “winter”. The phenological variations of the PPM winter populations are well known. They are associated with the earlier flights of adults in the northern part of its range [4], as well as some atypical processions in the different bioclimatic regions. In 1997, an atypical population exhibiting a divergent phenology was discovered in National Forest Park of Leiria (Portugal), where it was sympatric with a winter population. This unique population reproduces in spring, the larval development is in summer – not winter, therefore it is called “summer” population [5]. An interesting literary fact is that in 1929–1930 first RUSSKOFF [6] and later in 1965 ZANKOV [7] reported a presence of atypical populations in Bulgaria, with the larval development in summer and processions before winter. The authors use the terms “summer form (SF)” and “winter form (WF)” instead of summer and winter population – the latter terms continue to be used in the scientific literature in the country [8]. In the pine forests of Bulgaria, the winter form is widespread unlike the summer one whose distribution is limited in the Rhodope Mts. In this mountainous region they co-exist with the winter one.

Besides the phenological differences, some phenotypic and ecological differentiations between the Portuguese summer and winter populations have also been evidenced [9–11]. Yet, the mechanisms leading to these phenological differences remain unknown. Nonetheless, each life stage of both populations is expected to face different environmental pressures to the climatic conditions. In this connection, the studies focused on the temperature effect on the flight activity of the PPM summer and winter populations are still limited. It is well known that the females from the winter population have a low flight activity at 14 °C [12] and the reproductive activity of the adults is hindered at temperatures above 22 °C [13]. Note that *T. pityocampa* adults are short-lived and they fly and mate at night when temperatures drop. The phenological difference argues the claim that the flight of summer population is hindered by the cold weather in spring, and the reproductive activity of winter population is affected by the warm weather in summer. These understudied relations motivate us to investigate the temperature effect on the flight initiation of the summer and winter form of *T. pityocampa* in Bulgaria.

We base our research on the assumption that the data is normally (Gaussian) or Kies style distributed. The wide use of the Gaussian distribution in various real life fields including biology makes it a natural choice. On the other hand, the Kies distribution has several advantages. The main of them is the finite domain. Other

useful features are its non-symmetry, the high possible mass in the tails, and its generally large flexibility. We cannot use directly the distribution proposed by Kies because its domain is the interval $[0, 1)$. Instead of the original distribution we use a shifted to an interval $[a, b)$ version introduced in KUMAR and DHARMAJA [14] and later precised by ZAEVSKI and KYURKCHIEV [15].

Material and methods. Sampling of material. The temperature impact on the flight initiation of 670 adults of *T. pityocampa* was studied: 327 of them originate from samples of the summer form, and 343 from the winter one. The samples (larvae and prepupae) were collected during the period February-April 2021 from five sites of *Pinus nigra* J.F.Arnold and *Pinus sylvestris* L. Three of them are occupied by the PPM summer form: the land of villages Dobrostan and Kandilka and the vicinity of the town of Dzhebel (the Rhodope Mts.), and two by the winter form: the region of towns of Radomir (Radomir Valley) and Gotse Delchev (Pirin Mt.).

Material examined:

Kandilka Vill. ($41^{\circ}24'23''\text{N}/23^{\circ}34'48''\text{E}$), 450 m a.l.s, date of coll. 27.02.2021. Collected individuals in the sample: 353 (86 overwintering larvae and 267 overwintering prepupae). Emerged adults: 152 (64 ♂, 88 ♀). Unemerged specimens: 201.

Dobrostan Vill. ($41^{\circ}54'10''\text{N}/24^{\circ}55'07''\text{E}$), 1100 m a.s.l., date of coll. 12.03.2021. Collected individuals in the sample: 257 (138 overwintering larvae and 119 overwintering prepupae). Emerged adults: 124 (50 ♂, 74 ♀). Unemerged specimens: 135.

The region of Dzhebel ($41^{\circ}28'16''\text{N}/25^{\circ}17'01''\text{E}$), 450 m a.l.s, date of coll. 28.02.2021. Collected individuals in the sample: 98 overwintering prepupae. Emerged adults: 51 (21 ♂, 30 ♀). Unemerged specimens: 50.

The region of Radomir ($42^{\circ}29'04''\text{N}/23^{\circ}02'32''\text{E}$), 670m a.l.s, date of coll. 26.04.2021. Collected individuals in the sample: 101 mature larvae in procession. Emerged adults: 87 (4 ♂, 46 ♀). Unemerged specimens: 14.

The region of Gotse Delchev ($41^{\circ}35'17''\text{N}/23^{\circ}44'24''\text{E}$), 554 m a.l.s, date of coll. 30.04.2021. Collected individuals in the sample: 415 mature larvae in procession. Emerged adults: 256 (145 ♂, 111 ♀). Unemerged specimens: 161.

In the laboratory of the Forest Research Institute – Sofia, all collected larvae and prepupae were placed in plastic containers ($40 \times 30 \times 20$ cm) with ventilation holes and a 5 cm layer of sand. The description of the applied methodology and rearing processes of the collected larvae and prepupae until they pupated, and of the pupae until the adults emerged, is presented in a previous research of ZAEMDZHIKOVA [16]. In this work the factors affecting the survival of the summer and winter forms are also discussed. For the purposes of the current study, we should clarify that all reared pupae were placed individually in tubes and counted daily for the adult emergence. The study was carried out in laboratory conditions at room temperature (without heating) – an average of 18°C and natural light.

To study the temperature effect on the flight initiation of the PPM adults we use data on daily average night air temperatures for Sofia region provided by the National Institute of Meteorology and Hydrology – Sofia.

Statistical analysis. We provide several statistical tests to analyze the empirical data. Note that the probability density function (PDF) cannot be extracted directly from the data, because it consists of many points with equal values. This leads to empirical PDFs with many peaks which will distort the real PDFs. Alternatively, we suggest the use of the cumulative distribution functions (CDF) associated with the empirical samples. We derive the CDF at a point x as the number of observations lower than x divided by the total observations' number. If the available values are r_i and N is their number, then we can write $F_{\text{empirical}}(x) = \# \{r_i < x\} / N$. We apply this method to all particular samples as well as to the aggregate data w.r.t. the gender, habitat, and phenological form. We investigate also the totally pooled data.

The next step is to extract the theoretical CDFs based on the normal or Kies distributions. Remind that the PDF and CDF of the latter one defined on the interval $[a, b]$ are

$$f(x) = \frac{\lambda \beta (b-a)(x-a)^{\beta-1} \exp\left(-\lambda \left(\frac{x-a}{b-x}\right)^{\beta}\right)}{(b-x)^{\beta+1}} I_{x \in (a,b)}$$

$$(1) \quad F(x) = 1 - \exp\left(-\lambda \left(\frac{x-a}{b-x}\right)^{\beta}\right).$$

We use the standard maximum likelihood estimation (MLE) method to derive the distributional parameters assuming that the Kies domain is $[10, 30]$, i.e. $a = 10$ and $b = 30$ – it is very unlikely for a butterfly to appear out of this range. The derived parameters for all habitats are presented in Table 1 – separately for the males, females, and for the joint data. The average log-MLE similarity coefficients, obtained as $\frac{1}{N} \sum_1^n \ln(f(r_i))$, are provided too. We can see that both distributions produce values near 2.5. Also, note that the rate coefficient λ for the Kies distribution is relatively low. The power coefficient β takes values near 1.5. We can see that the derived confidence intervals are relatively lower for the Kies estimations, as well as they are close to the mean for this distribution. Also, the asymmetry of the Kies distribution has a confirmation – the means are closer to the right endpoints of the confidence intervals. The unique exception is the male specimens from the Dobrostan areal.

Results. *Flight and temperature profile.* The duration of the flight periods of the PPM samples is plotted together with the air temperature profile of the regions in Fig. 1. The absolute flight period of each sample was determined by the dates of the first and last emerged insect. Figure 1A illustrates some differences between the summer and winter forms. It can be seen that the flight period of the summer form occurs from May to July and it is between mid-June to early August for the winter one. We also observe that the flight period of the SF coincides with the cool period in June, whereas the WF flight invariably occurs during the hottest time of the year in July.

Temperature effect on the flight initiation of PPM. Statistical results of the primary sample are given in Table 1 – separately for the males, females, and for the joint data. We present their mean, standard deviation, and 95% confidence intervals. Figure 1B-F is a graphical representation of Table 1. The solid lines are for the empirical CDFs. Their stair behaviour is due to the used methodology for the empirical observations. The dash-dotted lines are for the Gaussian CDFs, whereas the dashed ones are for the CDFs obtained through the Kies style distribution.

Our results show that the mean of the flight initiation temperature of the PPM adults was at 20 °C, except for Dobrostan sample – there it was av. 16 °C (Table 1, Fig. 1B-F). We also found that the temperatures for the flight initiation of the males are lower than for the females. The only exception is for the Radomir specimens for which both expected temperatures are approximately equal. We have to mention also another exception, namely the observations from Dobrostan – the temperature mean is significantly lower for the male specimens as well as for the females. The respected values are 14.6380 and 17.552 for the normal distribution and 14.6462 and 17.4617 for the Kies one, respectively. In addition, the standard deviations are significantly lower too – the Gaussian distribution generates 2.2022 for the males and 2.8069 for the females, whereas the Kies values are 2.3098 and 3.0255, respectively.

The aggregate results of the data are presented in Table 2 and Fig. 2. These results are aggregated as follows: 1) pooled samples of the summer and winter form, divided by sexes (Fig. 2 A, B); 2) total samples (males + females) within the summer and winter form (Fig. 2 C); 3) total samples from the general population, divided by sexes (Fig. 2 D). Summary results show the following differences:

In both phenological forms we find that the temperature for the flight initiation of the males are on average lower than for the females. In the summer form, the observed differences in the Gaussian mean values between sexes are: 18.17 °C (males) vs. 19.46 °C (females) and 18.29 °C (males) vs. 19.52 °C (females) for the Kies one (Fig. 2A). In the winter form these differences by the Gaussian and Kies distributions are 19.57 °C (males) vs. 20.46 °C (females) and 19.61 °C (males) vs. 20.51 °C (females) (Table 2, Fig. 2B), respectively.

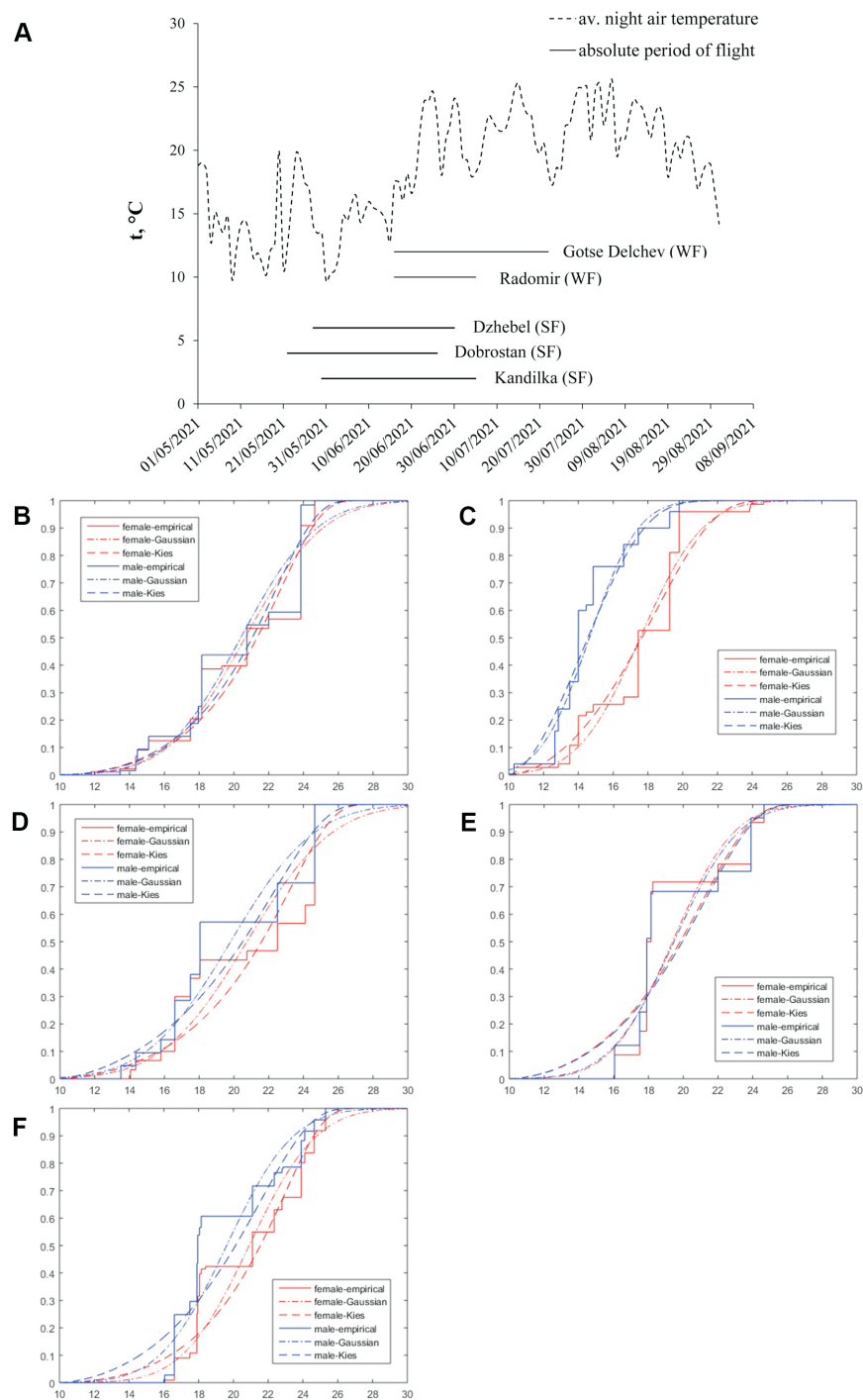


Fig. 1. (A) Comparison of the flight period w.r.t. the temperature profile. (B, C, D, E, F) CDF of the flight initiation temperature of *T. pityocampa*: (B) Kandilka (SF); (C) Dobrostan (SF); (D) Dzhebel (SF); (E) Radomir (WF); (F) Gotse Delchev (WF). On the x-axis is the av. night temperature

T a b l e 1
Parameters and moments

Sexes	Samples				
	Summer form			Winter form	
Male	Kandilka	Dobrostan	Dzhebel	Radomir	Gotse Delchev
Number of observations	64	50	21	41	145
Gaussian MLE result	2.6469	2.2084	2.7518	2.4869	2.5226
Gaussian mean	20.3914	14.6380	19.8119	19.3838	19.6107
Gaussian st. deviation (SD)	3.4144	2.2022	3.7919	2.9095	3.0151
Gaussian 95% CI (Confidence Interval)	(13.6993, 20.3914)	(10.3218, 18.9542)	(12.3800, 27.2438)	(13.7658, 25.1708)	(13.7012, 25.5203)
Kies MLE result	2.5331	2.2099	2.6971	2.5671	2.5949
Kies $-\lambda$	0.0013	0.0235	0.0058	0.0032	0.0036
Kies $-\beta$	1.7277	1.5539	1.3644	1.5897	1.5365
Kies mean	20.5125	14.6462	19.9571	19.5047	19.6463
Kies SD	3.2137	2.3098	3.8011	3.3549	3.4562
Kies 95% CI (Confidence Interval)	(13.0781, 25.2957)	(10.6760, 19.2660)	(11.7826, 25.8065)	(12.1984, 24.7848)	(12.1241, 25.0501)
Female	Kandilka	Dobrostan	Dzhebel	Radomir	Gotse Delchev
Number of observations	88	74	30	46	111
Gaussian MLE result	2.6681	2.4510	2.7711	2.4378	2.5269
Gaussian mean	20.6449	17.552	20.7500	19.4683	20.9081
Gaussian SD	3.4875	2.8069	3.8658	2.7699	3.0283
Gaussian 95% CI	(13.8096, 27.4802)	(12.0506, 23.0535)	(13.1732, 28.3269)	(13.9548, 24.8127)	(14.9728, 26.8434)
Kies MLE result	2.5349	2.4814	2.6268	2.5560	2.5011
Kies $-\lambda$	0.0013	0.0064	0.0025	0.0032	0.0011
Kies $-\beta$	1.7175	1.6040	1.5136	1.5968	1.7482
Kies mean	20.7602	17.4617	20.9395	19.3927	20.9676
Kies SD	3.2373	3.0255	3.5721	3.3323	3.1972
Kies 95% CI	(13.1963, 25.5145)	(11.4586, 22.7441)	(12.6811, 26.1244)	(12.1667, 24.6679)	(13.4135, 25.6107)
Total	Kandilka	Dobrostan	Dzhebel	Radomir	Gotse Delchev
Number of observations	152	124	51	87	256
Gaussian MLE result	2.6600	2.5006	2.7704	2.4616	2.5466
Gaussian mean	20.5382	16.3770	20.3638	19.4236	20.1732
Gaussian SD	3.4591	2.9497	3.8632	2.8368	3.0885
Gaussian 95% CI	(13.7584, 27.3179)	(10.5957, 22.1583)	(12.7920, 27.9355)	(13.8635, 24.9837)	(14.1198, 26.2266)
Kies MLE result	2.5354	2.4988	2.6643	2.5615	2.5738
Kies $-\lambda$	0.0013	0.0173	0.0037	0.0032	0.0024
Kies $-\beta$	1.7190	1.3979	1.4368	1.5931	1.5955
Kies mean	20.6556	16.3624	20.5338	19.4457	20.2223
Kies SD	3.2318	3.0784	3.6982	3.3435	3.4026
Kies 95% CI	(13.1381, 25.4288)	(10.8381, 22.1368)	(12.2380, 26.0302)	(12.1809, 24.7242)	(12.5526, 25.3712)

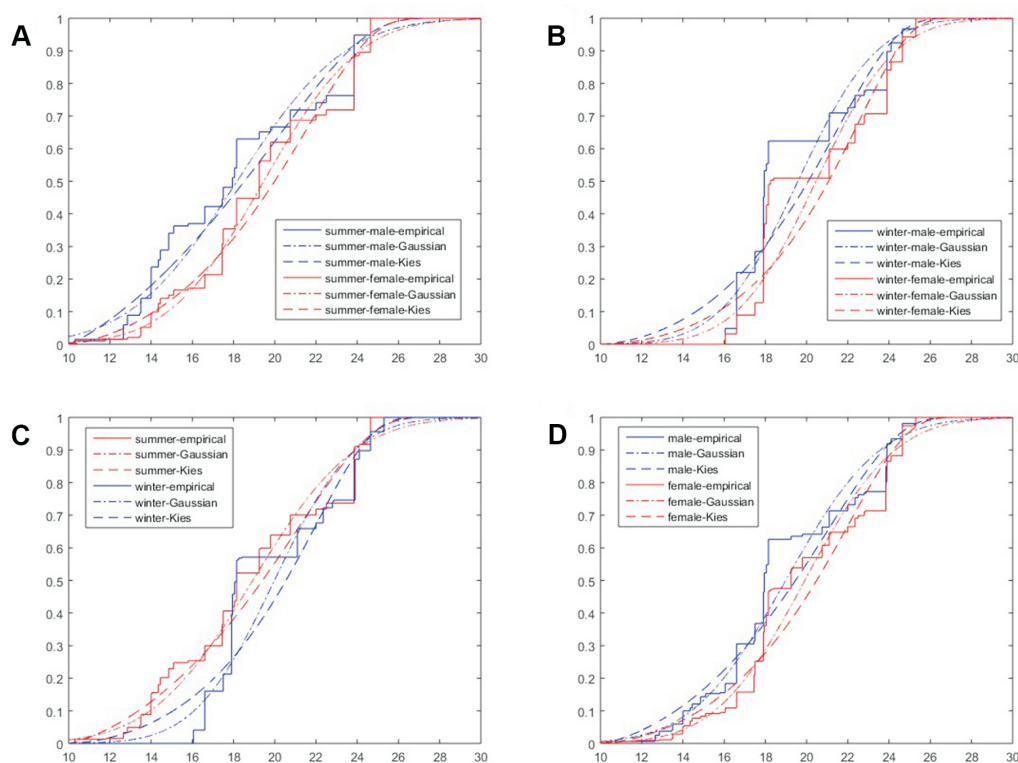


Fig. 2. CDF of the flight initiation temperatures of *T. pityocampa*: (A) pooled samples of the summer form, divided by sexes; (B) pooled samples of the winter form, divided by sexes; (C) total samples (males + females) within the summer and winter form; (D) total samples from the general population, divided by sexes. On the x-axis are presented av. night temperatures

The temperature for the flight initiation of the summer form is on average lower than for the winter one. This effect is also visible from the cumulative distributions in Fig. 2C. The observed differences in the means between the samples of summer and winter form are: 18.93 °C vs. 19.98 °C by the Gaussian distribution and 19.01 °C vs. 20.02 °C by the Kies one, respectively (Table 2).

Generally, regardless of the phenological differences, the temperature for the flight initiation of the PPM males was on average lower than for the females. The differences in the mean values by the Gaussian and Kies distribution are, respectively: 18.98 °C (males) vs. 19.91 °C (females) and 19.06 °C (males) vs. 19.96 °C (females) (Fig. 2D).

Temperature range for flight initiation. We find that the temperature range for the flight initiation of the summer form varies from 10 °C to 24.6 °C, and of the winter form from 16 to 26.3 °C. These intervals are constructed as the minimum and maximum recorded temperatures for the adult flights. The difference between the minimum flight temperature of the summer and winter form is very

T a b l e 2
Parameters and moments – aggregated data

Sexes	Pooled samples								
	Summer form			Winter form			Total		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
Number of observations	135	192	327	186	157	343	321	349	670
Gaussian MLE result	2.8337	2.7110	2.7790	2.5151	2.5292	2.5322	2.6936	2.6478	2.6790
Gaussian mean	18.1704	19.4693	18.9330	19.5793	20.4615	19.9831	18.9867	19.9157	19.4706
Gaussian SD	4.1156	3.6404	3.8966	2.9927	3.0353	3.0442	3.5773	3.4174	3.5256
Gaussian 95% CI (Confidence Interval)	(10.1038, 26.2369)	(12.3343, 26.6043)	(11.2959, 26.5701)	(13.7137, 25.4449)	(14.5125, 26.4105)	(14.0166, 25.9496)	(11.9753, 25.9982)	(13.2176, 26.6137)	(12.5606, 26.3806)
Kies MLE result	2.7608	2.6658	2.7186	2.5895	2.5433	2.5776	2.6839	2.6209	2.6587
Kies $-\lambda$	0.0198	0.0058	0.0104	0.0035	0.0017	0.0027	0.0081	0.0036	0.0055
Kies $-\beta$	1.1455	1.4054	1.2789	1.5465	1.6602	1.5838	1.3515	1.5049	1.4199
Kies mean	18.2986	19.5214	19.0140	19.6143	20.5110	20.0267	19.0613	19.9657	19.5325
Kies SD	4.0518	3.6791	3.8709	3.4363	3.3150	3.4088	3.7283	3.5380	3.6529
Kies 95% CI (Confidence Interval)	(10.7942, 25.2378)	(11.7316, 25.3288)	(11.2515, 25.3288)	(12.1362, 24.9955)	(12.8881, 25.4463)	(12.4238, 25.2418)	(11.4396, 25.1141)	(12.1790, 25.4016)	(11.7733, 25.2934)

significant – 10.3 °C for the summer form and 16 °C for the winter one. This difference is well seen from the empirical frequencies of the flights in Fig. 2C. In terms of the maximum temperature for the flight initiation, the difference between summer and winter forms was insignificant.

The temperature effect thresholds on the flight initiation. It is well known that the PPM females rarely fly below 14 °C. Regarding the winter form, this threshold is consistent with our results. We observed that the females of the winter form did not fly below 16 °C (Fig. 1E, F). By contrast, the females of the summer form can fly below 14 °C – their share in the samples varies between 2 and 5% (Kandilka and Dzhebel) to 10% (Dobrostan) (Fig. 1B, C, D). It is also known that temperatures above 22 °C can affect the reproductive activity of the PPM adults. Here, we observe that the share of took off adults above this threshold is low – av. 20% in the samples, as only in the Dobrostan sample it is 0%. In both phenological forms no flights were observed above 27 °C.

Discussion. Our summary results show that the flight initiation temperature of the *T. pityocampa* summer form was on average lower than that of the winter one. The fly of butterflies is initiated voluntarily when the body temperature is within a given range. These optimal temperatures typically vary between 28 and 38 °C [17]. In temperate-zone environments this is usually well above the ambient temperature. Since the body temperature depends on the environmental conditions, unfavourable ambient temperatures are expected to negatively affect the flight of adults by limiting their body temperature range. In the country, this should have a stronger effect on the summer form, whose flight is in the spring, and conversely, to have a weaker effect on the winter form, which is in the summer [18]. Hence, the observed temperature difference in the flight initiation of the *T. pityocampa* summer and winter form may indicate a better adaptability of the summer form to unfavourable ambient temperatures in spite that the adults manage to achieve the necessary optimal body temperature for a flight. This could also explain the observed difference in the minimum temperature for the flight initiation, which in the summer form is lower than in the winter one, respectively, 10 °C and 16 °C. Females of the *T. pityocampa* winter population are known to occur rarely at temperatures below 14 °C [12]. This temperature threshold limits their altitudinal distribution. This is in agreement with our results regarding the winter form. But not for the summer one, whose flight at temperatures below 14 °C is possible, although with a low intensity of 2 to 10%. A lowered left limit for the flight initiation of the summer form is likely to extend their upper limit of the country's distribution. This is consistent with the study of ZAEMDZHIKOVA et al. [19] according to which the summer form of PPM are located average higher than the winter form.

In this study was found that the temperature for flight initiation of *T. pityocampa* males was average lower than that for females. This may be attributed to the lower wing loading in males (i.e. body mass/wing area), which allows

flight at a lower wing beat frequency [20]. Although the wing beat frequency is temperature-dependent, MERCKX et al. [21] predict that males are able to fly at lower temperatures than females because males are able to generate a higher lift at low temperatures than females. But the flight is energetically costly. Assuming that the cost of flight can be reduced by flying in search of optimal conditions, the flight of females is expected to be limited and to occur under better environmental temperature conditions, which will favour their dispersal and reproduction.

Conclusions.

1. In Bulgaria, the temperature for the flight initiation of the summer form is on average lower than for the winter one.

2. In the present research we observe a significant difference in the minimum temperatures for the flight initiation in both phenological forms: 10 °C for the summer form vs. 16 °C for the winter one. On the other hand, the difference between the maximum temperatures is not so pronounced: 24.6 °C (summer form) and 26.3 °C (winter form).

3. The lower temperature for the flight initiation of the summer form may indicate a better adaptability to lower ambient temperatures. This could explain the observed on average higher altitude distribution of the summer form in the country than the winter one [19].

4. The temperature for the flight initiation of *T. pityocampa* males is on average lower than that for females.

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