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# The effect of weather variables on the flight activity of horseflies (Diptera: Tabanidae) in the continental climate of Hungary

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**Abstract** Although the tabanid species and populations occurring in eastern central Europe (Carpathian Basin) are thoroughly studied, there are only sporadic data about the influence of weather conditions on the abundance and activity of horseflies. To fill in this lack, in Hungary, we performed a 3-month summer survey of horsefly catches registering the weather parameters. Using common canopy traps and polarization liquid traps, we found the following: (i) rainfall, air

temperature, and sunshine were the three most important factors influencing the trapping number of tabanids. (ii) The effect of relative air humidity  $H$  on tabanids was indirect through the air temperature  $T$ :  $H \approx 35\%$  (corresponding to  $T \approx 32^\circ\text{C}$ ) was optimal for tabanid trapping, and tabanids were not captured for  $H \geq 80\%$  (corresponding to  $T \leq 18^\circ\text{C}$ ). (iii) A fast decrease in the air pressure enhanced the trapping number of both water-seeking and host-seeking horseflies. (iv) Wind velocities larger than 10 km/h reduced drastically the number of trapped tabanids. Our data presented here may serve as a reference for further investigations of the effect of climate change on tabanids in Europe.

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Tabanid trap

## Introduction

Horseflies (Diptera: Tabanidae) can be found in different climates, from the tropics (Wolda 1978) through temperate areas (Foil and Hogsette 1994; Krcmar and Maric 2006) to desert oases (Wilkerson and Fairchild 1984), as well as at different altitudes (Cárdenas et al. 2013). As female tabanids need blood meal for their egg-production, they attack mammals including humans for blood (Thomas 1973; Lehane 2005). Besides causing economical losses with their nuisance behavior, tabanids are known as vectors of blood-dwelling pathogens of several animal and human diseases (e.g., tularemia, anaplasmosis, hog cholera, equine infectious anemia, filariasis, anthrax, Lyme disease), and they induce allergic reactions in the host when sucking blood (Foil 1989; Luger 1990; Maat-Bleeker and van Bronswijk 1995; Veer et al. 2002; Lehane 2005; Hornok et al. 2007). The etiologic agents

of the above-mentioned diseases, like *Francisella tularensis* subspecies *holarctica*, *Anaplasma marginale*, *Anaplasma ovis*, classical swine fever virus, and equine infectious anemia virus have occurred in Hungary and caused isolated illnesses or sporadic outbreaks (Gyuranecz et al. 2012; Hornok et al. 2014).

As one of the consequences of climate change, the shift of the transmission areas of mosquitos was observed by several studies (Gething et al. 2005; Romo and Tylianakis 2013; Townroe and Callaghan 2014). The studies on the distribution of vector arthropods became especially intense after Tiger mosquito (*Aedes albopictus*) populations had been established in Europe and caused chikungunya virus outbreak in Italy in the summer of 2007 (Fischer et al. 2013). Based on the predicted climate change scenarios, most of Europe could become a favorable habitat for *A. albopictus* in the next decades (ECDC 2009). A similar prediction has been presented about the spread of ticks and tick-borne diseases (EFSA 2010). Unlike in the case of mosquitos and ticks, the possible effects of climate change on the tabanid-transmitted zoonotic agents have not been elucidated yet.

Except for a few crepuscular or nocturnal tabanid species, most of them are active only at daytime, in bright sunshine (Roberts 1974; Burnett and Hays 1974). Their life cycle, especially in the larval stage, closely depends on bodies of water, mud of lake bottoms, or wet soil of shorelines (Goodwin and Drees 1996). The different species of horseflies are adapted well to a wide range of climatic conditions. In tropical/megathermal climates, where rainfall is very frequent, and both the average air temperature and relative air humidity are constantly high (>18 °C and >80 %, respectively), most horseflies are active throughout the year, but their daily and seasonal flight activity varies from species to species (Oliveira et al. 2007). Strickman and Hagan (1986), for example, reported that in the subtropic climate of Paraguay, the tabanid species *Chrysops variegatus* was present during the entire year, and the fluctuation of its activity by 89 % depended on the temperature, humidity, and wind. In the temperate zone, horseflies are active only on warm, sunny days, generally during the summer (Wyniger 1953; Middlekauff and Lane 1980; Chvála and Jezek 1997). Climatic conditions, such as temperature, humidity, atmospheric pressure, wind speed, and cloud coverage of the sky, strongly influence the daily activity of adult horseflies (Burnett and Hays 1974; Dale and Axtell 1975; Baldacchino et al. 2014a). Higher air temperature generally accelerates flight activity, while higher wind speed reduces it (Baldacchino et al. 2013, 2014b). Furthermore, low (<18 °C) temperature may be a limiting factor for tabanid flight (Amano 1985).

The Carpathian Basin, where Hungary and some areas of surrounding countries are located, belongs to a region of warm

summer continental/microthermal climate according to the Köppen-Geiger climate classification (Belda et al. 2014). This climate zone has four seasons and it is characterized by an average temperature more than 10 °C during at least 4 months of the year, and significant precipitations in all seasons. The tabanid species of this area have been described in detail: Parvu (2008) reported on 37 tabanid species in Romania. Dvorák (2011) identified 22 tabanid species at 6 locations in a relatively small mountainous area in the Czech Republic. Krcmar identified 22 and 26 species in 2 locations of eastern Croatia (Krcmar 2005) and 40 species in Serbia (Krcmar 2011). Krcmar et al. (2009) identified 22 tabanid species in the Drava and Danube river floodplain near the Hungarian border. In Hungary, 59 Tabanidae species and varieties are known (Majer 2001). Although the tabanid species and populations in the Carpathian Basin were thoroughly studied, these reports included only very few observations about the connection between weather conditions and flight activity. Hackenberger et al. (2009) found differences in the sensitivity of horseflies to the air temperature, wind, and humidity between the Mediterranean and the continental microclimate of a hill. Krcmar (2005) observed during a whole swarming season that the seasonal meteorological variability that occurred from year to year had a significant influence on the maximal peaks of tabanid abundance.

In the absence of a comprehensive, whole-season survey in the Carpathian Basin on the influence of the continental/microthermal climate on tabanid activities, we performed a 3-month study of horsefly catches and registered the weather parameters simultaneously during an entire swarming season. Our goal was to determine the weather variables that influence the trapping numbers of water-seeking and host-finding, female and male horseflies. Recently, Herczeg et al. (2014) reported on the seasonality and daily activity of male and female tabanid flies monitored by canopy traps and polarization traps. Our present work reports about other results of the same tabanid survey, concentrating on the meteorological parameters influencing tabanid catches.

## Materials and methods

### Site of tabanid monitoring

Our tabanid monitoring was performed between 2 June and 28 August 2013 on a horse farm at Szokolya (47° 52' N, 19° 00' E), northern Hungary, at an altitude of 260 m, 8 km from the Danube river. In this area and climate horseflies are present once a year, generally between the beginning of June and the end of August (Kriska et al. 2009; Horváth et al. 2010a,b).



## Applied tabanid traps

For the monitoring polarization liquid traps (Blahó et al. 2012a, b; Egri Á et al. 2012, p. 12) and conventional Manitoba-type (ball-and-hood), canopy traps (Muirhead-Thomson 1991) were used simultaneously. These trap types were used because polarization liquid traps attract both male and female polarotactic, water-seeking tabanid flies, while canopy traps capture almost exclusively host-seeking female tabanids (Egri et al. 2013). Two canopy traps were placed 10 m far from each other on the ground (in an area that was protected from farm animals by a fence), and two liquid traps were placed under them, separately. The horizontally polarizing liquid trap enhances the tabanid-capturing efficiency of the classic canopy trap (Egri et al. 2013). The liquids of the traps were changed once in every 2 weeks on average, especially after rainy days, or when the vegetable oil layer became too viscous (due to intense sunshine) on the water surface. At the beginning of the monitoring period (from 2 to 24 June 2013), the liquid traps were checked twice a day: at 1300 h (= local summer time=GMT+2 h, where GMT is Greenwich Mean Time) and at 2000 h. After 25 June, when horseflies became more numerous, the traps were checked and the number of catches was registered hourly between 0800 and 2000 h every day till the end of the study (28 August 2013). If at least one horsefly was found in the traps at 2000 h, the traps were checked again at nightfall (between 2100 and 2130 h), and the captured horseflies were added to the previous catch. Trapped horseflies were removed from the traps during the inspections, and were collected in two plastic bottles filled with 70 % ethanol: one of the bottles, contained the horseflies, trapped till 1300 h, while the other bottle had the horseflies collected after 1300 h. Every day, a new pair of bottles was used. Thus, the hourly catch numbers were known every day, but the species could not be determined in situ. Taxonomical identifications were made only later in the laboratory, producing two data sets every day: the numbers and the species before and after 1300 h. The captured horseflies were identified (by sex and species) according to the taxonomic keys of Majer (1987). Further details of the used tabanid traps are published elsewhere (Herczeg et al. 2014).

## Registering the weather variables

The weather parameters were registered continuously by a Radio Weather Station (Conrad Electronic, equipment no: 672861, with USB and touchscreen, Supplementary Fig. S1A). The sensors of the weather station were installed 20 m away from the traps on a 2-m tall fence support (Supplementary Fig. S1B), because in meteorology this is the typical height of air temperature measurements. The nearest building with a reference room was 10 m away from the sensors, where a receiver unit of the

weather station registered the transmitted data in every 30 min, for 24 h a day simultaneously during the monitoring. The following weather parameters were registered: (i) temperature  $T$  (between  $-40$  and  $+65$  °C, accuracy  $\pm 0.1$  °C), (ii) relative air humidity  $H$  (from 10 to 99 %, accuracy  $\pm 5$  %), (iii) air pressure  $P$  (between 300 and 1100 hPa, accuracy  $\pm 3$  hPa), (iv) wind speed  $W$  (from 0 to 160 km/h, accuracy  $< \pm 10$  %), and (v) cumulative amount of rain (between 0 and 9999 mm, accuracy  $< \pm 10$  %). The manufacturer's calibration was used. The characteristic cloud coverage between 0800–1300 and 1300–2000 h was determined by a portable, automatic, imaging-polarimetric cloud detector (Estrato Research and Development Ltd., Budapest, Supplementary Fig. S1C).

## Correlations between weather parameters

As the weather parameters may be more or less dependent on one another, we examined the typical correlations using regression analysis with the Statistica 8.0 software. This software is designed for computing mathematical statistics including the Pearson's correlation coefficient based on the following formula:

$$r_{xy} = \frac{\sum_{i=1}^{i=n} (x_i - \langle x \rangle)(y_i - \langle y \rangle)}{(n-1)s_x s_y} \quad (1)$$

where  $x_i$  and  $y_i$  are values of the used variables,  $\langle x \rangle$  and  $\langle y \rangle$  are their averages,  $s_x$  and  $s_y$  are their standard deviations,  $n$  is the number of cases, and  $r$  is the correlation coefficient for  $x$  and  $y$ . As the weather parameters are measured on the statistical scale of interval or ratio, the prerequisites of a regression analysis are fulfilled. Because tabanids fly only during daylight hours, we compared only the hourly values of the weather parameters measured at daylight, between 0800 and 2000 h during our 88-day survey.

## Correlations between weather parameters and tabanid catches

Although the weather parameters were monitored in every 30 min day-and-night, the checking of the traps occurred hourly between 0800 and 2000 h. Therefore, only the data measured at the time of trap visit were taken into account to find correlations. For this analysis, the locally weighted scatterplot smoothing (LOESS) of R-graphics 3.1 software was used (R Development Core Team 2012). The Gaussian curve-fittings were checked by the residual errors (Supplementary Fig. S3), and according to their results, 0.5 span values were applied except the connection of wind speed  $W$  and trapping number, where the best fit was achieved at span = 0.7.

## Results

### Correlations between weather parameters

Supplementary Fig. S2 shows the original diagrams of the air temperature  $T$ , relative air humidity  $H$ , air pressure  $P$ , wind speed  $W$ , and amount of rain  $R$  registered during our 88-day summer survey. A strong negative correlation (with coefficients  $r_{TH} = -0.86$  and  $p < 0.05$ ) was found between the air temperature  $T$  and the relative air humidity  $H$  (Fig. 1). Thus, the higher the air temperature  $T$  was, the lower was the air humidity  $H$  (i.e., the drier was the air), as expected. Pairing of high temperature ( $T > 30^\circ\text{C}$ ) with high humidity ( $H > 80\%$ ) did not occur in the microclimate of our study site. Furthermore, we found no other significant correlations between the weather variables (temperature  $T$ , relative humidity  $H$ , air pressure  $P$ , wind speed  $W$ , amount of rain  $R$ ), that is, apart from  $T$  and  $H$ , they changed independently of one another (Table 1, Supplementary Fig. S3).

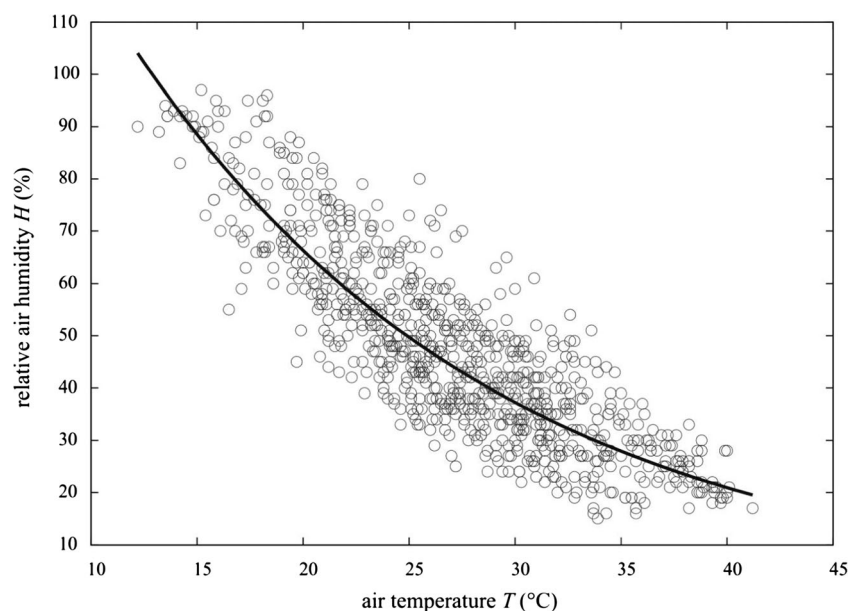
### Swarming periods of tabanid species

Our liquid traps and canopy traps caught a total of 5219 individuals of 16 species during the 3-month survey. The following 6 species predominated (with 4673 trapped individuals: 89.54 % of the total): *Atylotus loewianus* Villeneuve 1920 (1560: 29.89 %), *Tabanus tergustinus* Egger 1859 (1274: 24.41 %), *Tabanus bovinus* Linnaeus 1758 (753: 14.43 %), *Tabanus maculicornis* Zetterstedt 1842 (450: 8.62 %), *Tabanus bromius* Linnaeus 1758 (336: 6.44 %), and *Haematopota pluvialis* Linnaeus 1758 (300: 5.75 %). The representatives of the other 10 species occurred only in

small numbers, so their data were not evaluated. We mention here only their name, trapping number, and percentage: *Tabanus quatuornotatus* Meigen 1820 (144: 2.76 %), *Tabanus sudeticus* Zeller 1842 (144: 2.76 %), *Tabanus cordiger* Meigen 1820 (88: 1.69 %), *Tabanus autumnalis* Linnaeus 1761 (60: 1.15 %), *Tabanus unifasciatus* Loew 1858 (59: 1.13 %), *Tabanus glaucopsis* Meigen 1820 (24: 0.46 %), *Tabanus spectabilis* Loew 1858 (11: 0.21 %), *Haematopota italica* Meigen 1804 (7: 0.13 %), *Tabanus spodopterus* Meigen 1820 (5: 0.09 %), and *Atylotus fulvus* Meigen 1804 (4: 0.08 %).

In accordance with earlier observations at the same site (Egri et al. 2012, 2013), differences were found in the efficiency of the two types of tabanid traps: the liquid traps caught many more individuals of *A. loewianus*, *T. tergustinus*, *T. bromius*, and *T. maculicornis* than the canopy traps, while the canopy traps caught many more *T. bovinus* and *H. pluvialis* than the liquid traps (Table 2). Significantly, more females were caught than males for all species. Figure 2 shows the temporal change of the trapping numbers of the six most abundant species during our survey: The first *H. pluvialis* females were caught by the canopy traps in the first week of June after a rainy period in the end of May. Female *H. pluvialis* were present in the canopy traps continuously, but they appeared only very seldom in the liquid traps. Interestingly, neither the canopy traps nor the liquid traps caught male *H. pluvialis*. The first individuals of *T. tergustinus* and *T. bovinus* were caught by both trap types simultaneously with *H. pluvialis*. Similarly to *H. pluvialis*, the canopy traps caught practically only female *T. tergustinus* and *T. bovinus*, but the liquid traps captured also efficiently the males of the latter two species. The increase of the trapping number of *T. bromius*

**Fig. 1** Correlation between the air temperature  $T$  ( $^\circ\text{C}$ ) and the relative air humidity  $H$  (%) measured hourly at daylight between 2 June and 28 August 2013 during our 88-day tabanid survey. The continuous curve is fitted to the measured points



**Table 1** Values of the mean, standard deviation (SD), and correlation coefficient  $r$  of different weather parameters: air temperature  $T$ , relative air humidity  $H$ , air pressure  $P$ , wind speed  $W$  (number of samples  $n=1144$ )

	Mean	SD	$T$ (°C)	$H$ (%)	$P$ (hPa)	$W$ (km/h)
$T$ (°C)	27.2	5.86	$r=1.00$	$r=-0.86$ significant	$r=-0.17$ significant	$r=-0.11$ significant
$H$ (%)	47.2	18.1	$r=-0.86$ significant	$r=1.00$	$r=0.02$ not significant	$r=0.08$ significant
$P$ (hPa)	994	3.2	$r=-0.17$ significant	$r=0.02$ not significant	$r=1.00$	$r=0.02$ not significant
$W$ (km/h)	2.52	2.44	$r=-0.11$ significant	$r=0.08$ significant	$r=0.02$ not significant	$r=1.00$

Significant:  $p \leq 0.05$ , not significant:  $p > 0.05$  (according to Statistica 8.0). A strong negative correlation ( $r=-0.86$ ) was found between  $T$  and  $H$ . Between other weather variables, the correlation was weak or negligible

started in the third week of June, and the liquid traps proved to be much more effective than the canopy traps. The first captured individuals of *A. loewianus* and *T. maculicornis* appeared only in the first week of July, and they lasted for only a month. Although it had the shortest catch period, *A. loewianus* proved to be the most abundant species of the season, and as with *T. bromius*, the liquid traps were much more effective than the canopy traps.

In all cases, the rainfall and cloud coverage of the sky influenced strongly the trapping number of horseflies: the number of captured tabanids was reduced notably under overcast skies, and there was not any catch during rainfall. It should be noted that even a mild drizzle was enough to diminish the flight of tabanid flies.

#### Correlation between solar elevation and trapping number

Both the liquid traps (capturing water-seeking tabanids) and the canopy traps (capturing host-seeking tabanids) caught horseflies only in the daytime. The trapping numbers correlated well with the solar elevation (Fig. 3). Remarkably, both trap types were also effective at twilight, when the sun was at or just below the horizon.

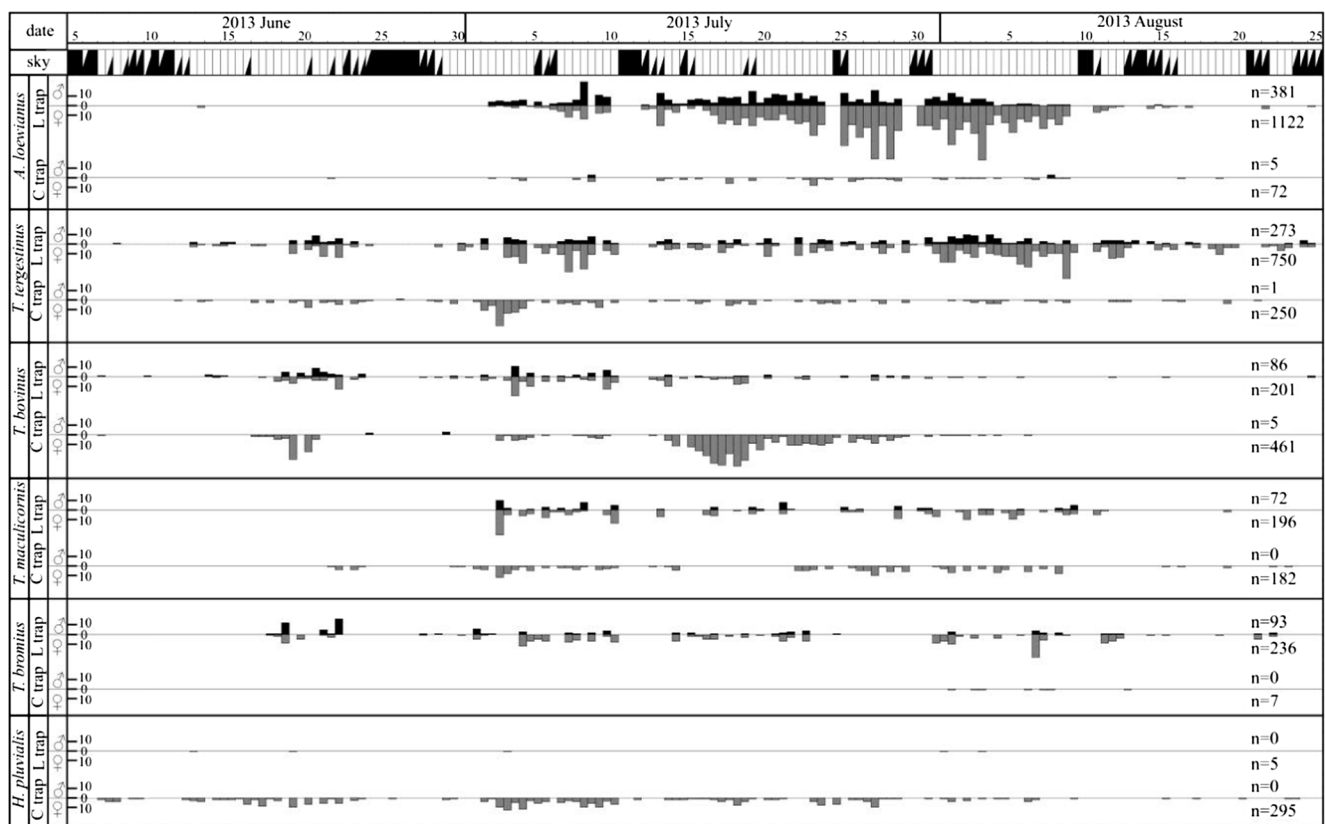
#### Effect of temperature on the trapping number

The presence of linearly polarized light is very important (being one of the main prerequisites of an efficient functioning of polarization insect traps), but not sufficient to induce the

**Table 2** Comparison of the trapping numbers of the six dominant tabanid species considering trap type ( $C$  canopy trap,  $L$  liquid trap) and sex ( $\sigma$  male,  $\varphi$  female)

Species	Comparison	$\chi^2$ Test result	Significance
<i>Atylotus loewianus</i>	( $C+L$ ) $\sigma$ versus ( $C+L$ ) $\varphi$	$\chi^2=413.2$ , $df=1$ , $p<0.0001$	Significant
	386 versus 1194		
	$C$ ( $\sigma+\varphi$ ) versus $L$ ( $\sigma+\varphi$ )	$\chi^2=1287$ , $df=1$ , $p<0.0001$	Significant
<i>Tabanus tergatus</i>	77 versus 1503		
	( $C+L$ ) $\sigma$ versus ( $C+L$ ) $\varphi$	$\chi^2=413.7$ , $df=1$ , $p<0.0001$	Significant
	274 versus 1000		
<i>Tabanus bovinus</i>	$C$ ( $\sigma+\varphi$ ) versus $L$ ( $\sigma+\varphi$ )	$\chi^2=467.8$ , $df=1$ , $p<0.0001$	Significant
	251 versus 1023		
	( $C+L$ ) $\sigma$ versus ( $C+L$ ) $\varphi$	$\chi^2=433.0$ , $df=1$ , $p<0.0001$	Significant
<i>Tabanus maculicornis</i>	91 versus 662		
	$C$ ( $\sigma+\varphi$ ) versus $L$ ( $\sigma+\varphi$ )	$\chi^2=42.6$ , $df=1$ , $p<0.0001$	Significant
	466 versus 287		
<i>Tabanus bromius</i>	( $C+L$ ) $\sigma$ versus ( $C+L$ ) $\varphi$	$\chi^2=208.1$ , $df=1$ , $p<0.0001$	Significant
	72 versus 378		
	$C$ ( $\sigma+\varphi$ ) versus $L$ ( $\sigma+\varphi$ )	$\chi^2=16.4$ , $df=1$ , $p<0.0001$	Significant
<i>Haematopota pluvialis</i>	182 versus 268		
	( $C+L$ ) $\sigma$ versus ( $C+L$ ) $\varphi$	$\chi^2=67.0$ , $df=1$ , $p<0.0001$	Significant
	93 versus 243		
<i>Haematopota pluvialis</i>	$C$ ( $\sigma+\varphi$ ) versus $L$ ( $\sigma+\varphi$ )	$\chi^2=308.6$ , $df=1$ , $p<0.0001$	Significant
	7 versus 329		
	( $C+L$ ) $\sigma$ versus ( $C+L$ ) $\varphi$	$\chi^2=300.0$ , $df=1$ , $p<0.0001$	Significant
<i>Haematopota pluvialis</i>	0 versus 300		
	$C$ ( $\sigma+\varphi$ ) versus $L$ ( $\sigma+\varphi$ )	$\chi^2=280.3$ , $df=1$ , $p<0.0001$	Significant
	295 versus 5		

All differences were significant (with  $p<0.0001$ )



**Fig. 2** The daily trapping numbers of the six dominant tabanid species as a function of the date of catching during our 88-day survey. *C* canopy trap (conventional Manitoba-type ball-and-hood trap), *L* polarization liquid

trap. ☐ percentage of cloud cover in the sky <10 % + sunshine, ☐ cloud cover 30–60 % + sunshine occasionally, ☐ cloud cover >90 % + no sunshine + no rain, ☐ cloud cover >90 % + rainfall

water- and/or host-seeking activity of horseflies. Figure 4 shows that tabanids were not caught early in the morning despite the fact that the sun was above the horizon. The first tabanids appeared in the traps only about after 0700–0800 h. This means that in tabanid trapping, the air temperature  $T$  is a more important factor than the sunlight: no individuals of any horsefly species were trapped if  $T < 18$  °C. We found that both trap types caught the most horseflies when  $T > 31$  °C, but the trapping number decreased for  $T > 35$  °C.

#### Effect of air humidity on the trapping number

The relative air humidity  $H$  in the temperate zone varies widely, but is closely related to the air temperature  $T$  in our microclimate. Because of this close correlation, the trapping number versus  $H$  (Fig. 5) reflects indirectly the effect of  $T$ . We found that the optimal  $H$  value for tabanid trapping was around 35 % (corresponding to an air temperature of 32 °C), and no individuals of any species were captured for  $H > 80$  % (corresponding to  $T \leq 18$  °C, Fig. 1).

#### Effect of air pressure on the trapping number

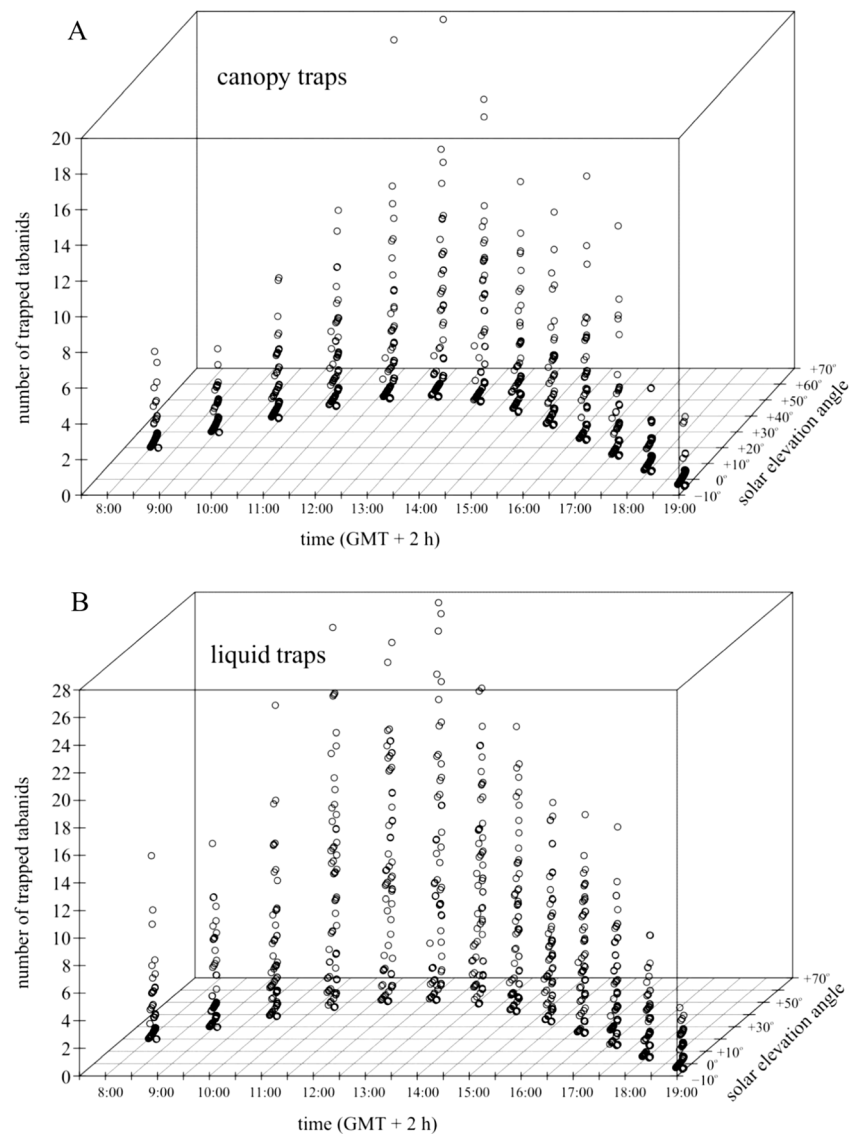
We found that the higher the air pressure  $P$  was, the more tabanids were trapped (Fig. 6a, b). It is also characteristic of this climate, that before the arrival of a cold front or a storm,  $P$  decreases quickly. We found that the more rapid the decrease of  $P$  was, the more water- and host-seeking horseflies were caught (Fig. 6c, d).

#### Effect of wind speed on the trapping number

If the values of  $T$ ,  $H$ , and  $P$  are suitable for tabanids, their flight is influenced by the wind velocity  $W$ . We obtained that the higher the  $W$  was, the less tabanids were trapped (Fig. 7). We found a gradual decrease of the trapping number as  $W$  increased. A threshold of  $W$  could not have been estimated because higher wind speeds (>15 km/h) occurred always together with storms, when both the low air temperature and/or the rainfall hindered the flight of horseflies.



**Fig. 3** Number of tabanids trapped by the canopy traps (a) and the liquid traps (b) as functions of time (GMT+2 h) and solar elevation angle during our survey

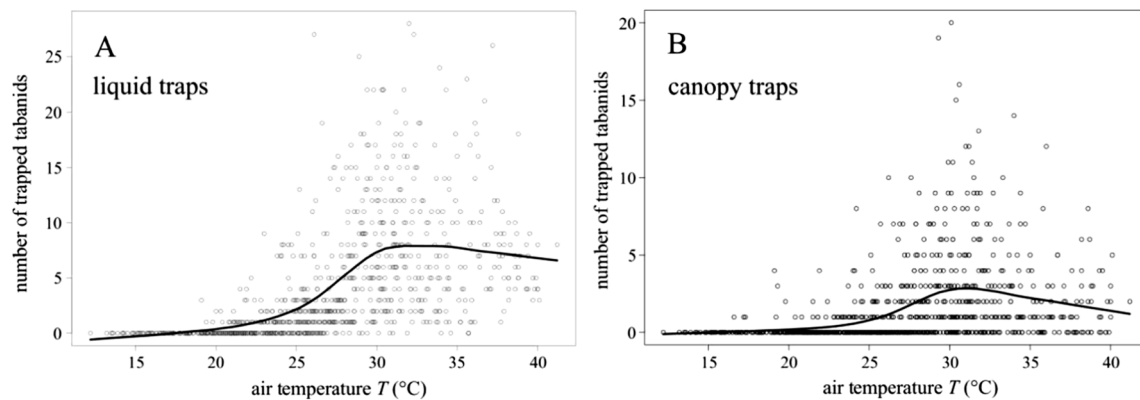


## Discussion

In our field experiment, we measured the trapping numbers (catches) of different tabanid species in order to study tabanid activity, the measure of which are the registered catches. The two trap types (polarization liquid trap capturing water-seeking male and female horseflies, and canopy trap catching host-seeking female horseflies) used in our 3-month tabanid survey caught 16 tabanid species from a fairly small area of a horse farm. Although these species are well-known and abundant during the summer in Hungary (Majer 2001) as well as in many other regions of the Carpathian Basin (Krcmar 2005, 2011; Parvu 2008; Krcmar et al. 2009; Dvorák 2011), the influence of the weather parameters on their seasonal and daily activity has not previously been studied in detail. Our results presented here partly fill in this lack of information.

Although the two types of traps used (liquid trap and Manitoba-type canopy trap, both reflecting strongly linearly polarized light) were variably efficient in the catching of different species and genders of horseflies, their effectiveness during daylight hours and at dusk shows that (i) the ability of horseflies to perceive linearly polarized light plays an important role in finding water or host, and (ii) even a low intensity of polarized light at dusk is enough for them to detect the target (water surface or host).

One of the main differences between the horseflies of the tropical/megathermal regions and those of the continental/microthermal areas is that the latter are not confronted with high relative air humidity and air temperature. All of the six dominant horsefly species of our survey showed a diurnal rhythm: they were captured only in the daytime. They were also sensitive to the temperature (confirming the findings of

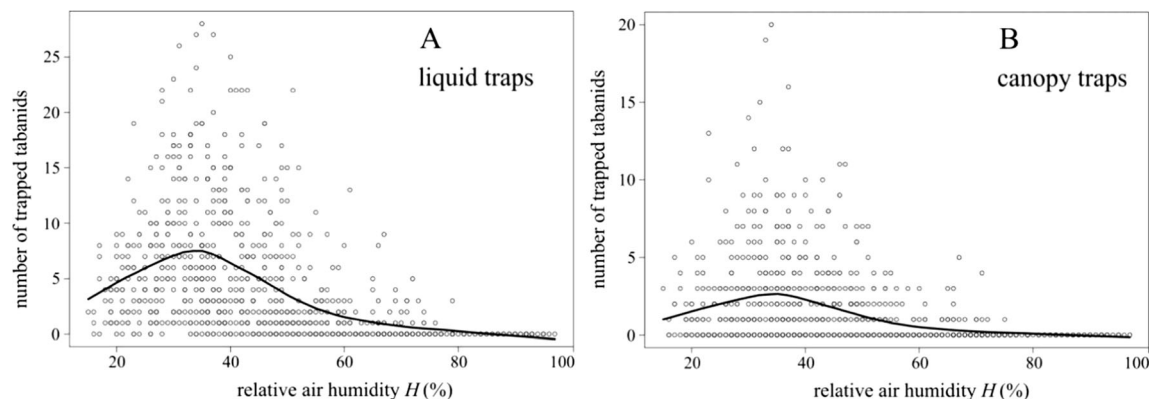


**Fig. 4** Number of tabanids trapped by the liquid traps (a) and the canopy traps (b) as a function of the air temperature  $T$  (°C) during our survey. The continuous curves are fitted to the measured points

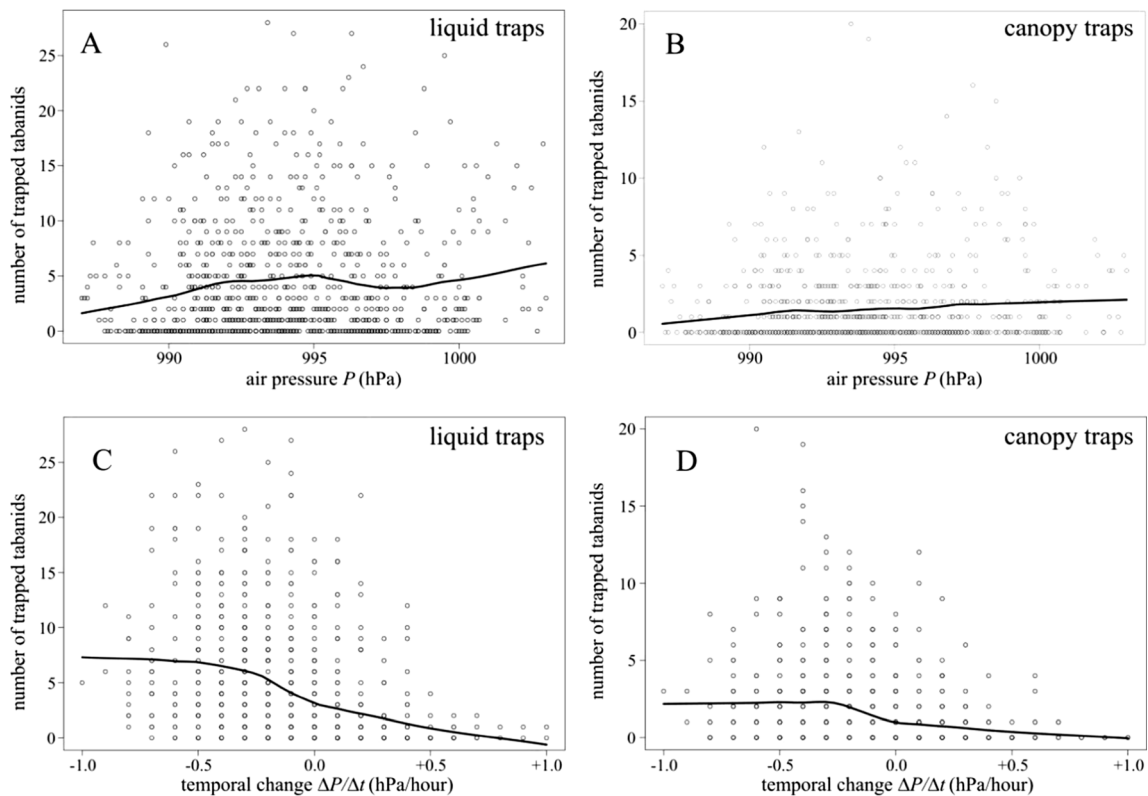
Amano 1985): they needed an ambient air temperature of at least 18 °C to fly. This temperature threshold corresponds to the minimum temperature required to activate the enzyme function and flight muscle fibers of horseflies (Pybus and Tragear 1975). We found that 31–35 °C is the optimal temperature range to catch tabanids with our traps. Higher temperatures caused a slight decrease in the trapping number. We cannot attribute this decrease solely to the failure of the flight muscles because Kohane and Watt (1999) and Josephson et al. (2000) have observed that the optimal frequency and power of isolated flight muscles increase as the temperature rises, peaking at about 39 °C.

As the peak air temperature (>30 °C) in Hungary during the summer months does not correspond to an elevated relative air humidity (the maximum of which is less than 80 % in this season), the investigated horsefly species have adapted to warm and dry weather conditions. In Hungary, the summer is generally characterized by moderate wind speeds (<10 km/h) and high air pressures, and only sudden thunderstorms interrupt the calm weather. During an impending storm, the air pressure  $P$  drops quickly (by  $|\Delta P|/\Delta t > 0.5$  hPa/h), and in our 88-day survey, we found that the activity (reflected by the trapping number) of both water-seeking and

host-seeking horseflies increased when such  $P$ -drops occurred prior to storms. In muscoid Diptera, Wellington (1946) found that their antennal arista function as a baroreceptor, which triggers their pre-thunderstorm flight. Dethier (1957) reviewed the physiological role of these sensors in the behavioral patterns of blood-sucking arthropods. We suppose that like the muscoid flies, tabanids may also have baroreceptors, with which they can sense the fast decrease in the air pressure prior to storms. The exact reasons for this remarkable phenomenon have not been revealed, but we imagine the following: (i) After storms, the meteorological conditions (below average air temperature, above average wind speed, and precipitation) can be disadvantageous for tabanid activities (e.g., host- and water-seeking flight, blood sucking, mate search, mating, egg laying) even for several days. Thus, it could be worth quickly performing these activities prior to a coming storm. (ii) Immediately before (thunder)storms/showers, the relative air humidity increases, which may be advantageous for the flight of certain tabanid species. Especially the small-bodied tabanids are more endangered by dehydration in warm air than larger ones. (iii) The blood sucking by female tabanids could be easier prior to storms, when the host animals move to shelters where they wait until the storm is over. Testing these ecological



**Fig. 5** Number of tabanids trapped by the liquid traps (a) and the canopy traps (b) as a function of the relative air humidity  $H$  (%) during our survey. The continuous curves are fitted to the measured points

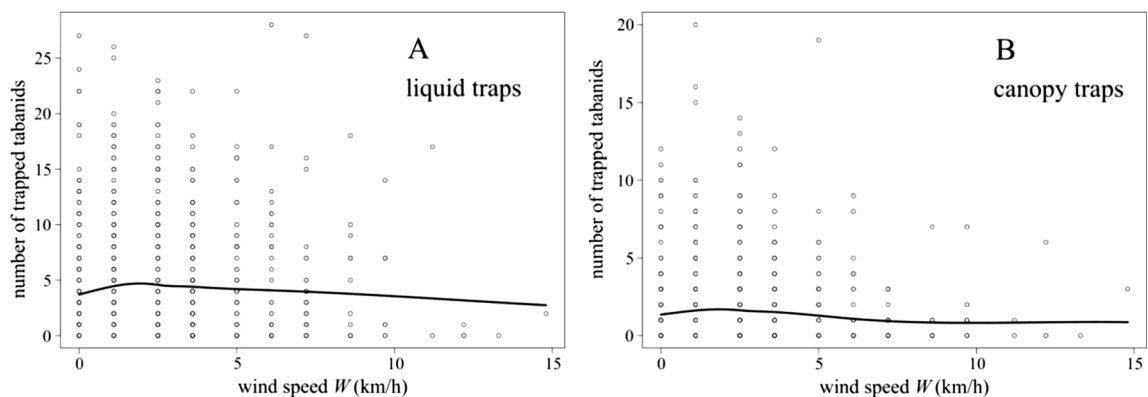


**Fig. 6** Number of tabanids trapped by the liquid traps (**a, c**) and the canopy traps (**b, d**) as a function of the air pressure  $P$  (hPa) (**a, b**) and the temporal change  $\Delta P/\Delta t$  (hPa/h) during our survey. The continuous curves are fitted to the measured points

hypotheses would be an interesting subject of future research.

As a consequence of the global climate change (global warming), an increase in the annual average air temperature and a decrease in the average amount of precipitation can be expected during the summer seasons of the next few decades in the Carpathian Basin (Bartholy et al. 2007). This climatic change may contribute to the appearance of new tabanid species in Europe, and changes in the seasonal and daily activities and abundance of horseflies. The geographical distribution and the temporal activity of many vectors (e.g., mosquitos, ticks) have been influenced by the effects of climate change (Garza

et al. 2014; Ogden et al. 2014). Like other parasites, tabanids can also appear and establish their populations in formerly uninfected areas, and they may introduce non-indigenous pathogens. Climate change may alter the host-vector interaction too. Tabanids are more active at higher air temperatures spending more time with blood sucking. For these reasons, females will lay more eggs and probably bigger populations of horseflies will attack animals and humans during the swarming periods. An increased frequency of blood sucking gives a higher chance for the transmission of causative agents. This may cause not only economical losses and health problems of livestock but also public health consequences,



**Fig. 7** Number of tabanids trapped by the liquid traps (**a**) and the canopy traps (**b**) as a function of the wind speed  $W$  (km/h) during our survey. The continuous curves are fitted to the measured points

depending on the pathogens. Climate change also alters the composition of plant ecosystems (Gehring et al. 2014) serving food for herbivores. This may influence the persistence of tabanid hosts. A more rainy weather, for example, results in more ponds, puddles, and mud, so the egg-laying areas of horseflies increase considerably. The follow-up study of the complex effects of the climate change on the activity and pathogen-transmission ability of tabanid flies could be performed by multinational research teams.

## Conclusions

Although the two trap types applied in our survey had different tabanid-capturing efficiencies considering species and sex, the effects of the weather parameters on tabanid abundance can be well monitored by these traps capturing differently motivated horseflies. We found that (i) rainfall, air temperature, and sunshine were the three most important factors influencing the trapping number of tabanids. (ii) The effect of relative air humidity  $H$  on tabanids was indirect through the air temperature  $T$ :  $H \approx 35\%$  (corresponding to  $T \approx 32^\circ\text{C}$ ) was optimal for tabanid trapping, and tabanids were not captured for  $H \geq 80\%$  (corresponding to  $T \leq 18^\circ\text{C}$ ). (iii) A fast decrease in the air pressure enhanced the trapping number of both water-seeking and host-seeking horseflies. (iv) Wind velocities larger than 10 km/h reduced drastically the number of trapped tabanids. Our data may serve as a reference for further investigations of the effect of climate change on the tabanid activity in Europe.

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