



# Atypical case of sex ratio disruption in Tabanidae collections with Malaise traps in Ecuadorian forests

Jaime Buestán<sup>1,2</sup> · Gabriel A. Brito Vera<sup>1,2,3</sup>

Received: 6 May 2024 / Accepted: 16 October 2024

© Plant Science and Biodiversity Centre, Slovak Academy of Sciences (SAS), Institute of Zoology, Slovak Academy of Sciences (SAS), Institute of Molecular Biology, Slovak Academy of Sciences (SAS) 2024

## Abstract

Male horseflies have low capture rates in Malaise traps, a widely documented pattern observed in numerous ecological studies. We present findings from a specific locality in Ecuador where a departure from this established pattern is observed. In this locality, males accounted for 59.14% of Tabanidae captures. The disruption in capture patterns observed using Malaise traps represents an uncommon feature in the scientific literature and during collections conducted over eight years in Ecuador. Despite the inherent limitations of Malaise traps in capturing male horseflies, it is possible that under specific conditions, such as the presence of optimal aggregation areas for horseflies, Malaise traps may enhance the capture efficiency of males. Additionally, we provide a detailed discussion on the disruption and disparity in capture sex proportions in Tabanidae, commonly reported in the scientific literature.

**Keywords** Male · Female · Tabanidae · Aggregation · Horse flies

## Introduction

Horseflies are dipterans that exhibit a pronounced sexual dimorphism with a remarkable separation of the eyes, which is a very characteristic morphological feature. This feature, known as holoptic (fused) eyes in males and dichoptic (separated) eyes in females, allows the sexes of horseflies to be clearly distinguished (Mullens 2019; do Carmo et al. 2022). Various techniques and tools based on intercepting and attracting flights are used to catch horseflies. These techniques include the use of traps such as Malaise, Manitoba, canopy, NZI, box traps, light traps, chemical attractants and reflective polarisation (Mihok 2002; Krolow et al. 2010; Mullens 2019; Horváth et al. 2020a, b). These different methodological approaches provide techniques for

capturing individuals and exploring diversity within this family. This also includes the investigation of ecological aspects such as behavior and diurnal periodicity (Altunsoy and Kılıç 2012; Herczeg et al. 2014; Buestán et al. 2024).

Malaise traps have demonstrated high efficacy in capturing female horseflies through flight interception, but not male horseflies. This phenomenon has been extensively documented across various geographical regions and ecological conditions (e.g., Krolow et al. 2017; Herczeg et al. 2018), with a few notable exceptions where male horseflies have been successfully collected (Rafael et al. 2021). Other alternative methods, such as deploying light traps above the canopy, offer clear advantages for catching male horseflies (Krolow et al. 2010), as do shiny black plastic oil traps (Krčmar 2013) and polarised reflective traps. The latter attract horseflies through positive polarotaxis because they mistake the reflection produced by the plate with the polarised light reflected by water bodies (Allan et al. 1987; Horváth et al. 2008, 2020a, b; Blaho et al. 2012). Despite the widespread use of Malaise traps, their tendency to catch a disproportionate number of females has led to a significant underrepresentation of males in entomological collections accounting for only 3.6% of specimens (Oliveira et al. 2023). This gender bias has resulted in a significant lack of male specimens in both museum collections and taxonomic

✉ Gabriel A. Brito Vera  
gabrielbrito1991@gmail.com

<sup>1</sup> Faculty of Natural Sciences, University of Guayaquil, Guayaquil, Ecuador

<sup>2</sup> Instituto Nacional de Biodiversidad (INABIO), Rumipamba 341 and Shyris Avenue, Quito, Ecuador

<sup>3</sup> Department of Ecology, Faculty of Biological Sciences, Pontifical Catholic University of Chile, 7820436 Santiago, Chile

records (Krolow et al. 2012). Remarkably, in Ecuador, over nearly five decades since the 1970s, reports of significant male horsefly capture using Malaise traps have been conspicuously absent. Thus, the identification of a disruption in this established pattern within an Andean locality prompted our investigation into the underlying hypotheses driving this variation.

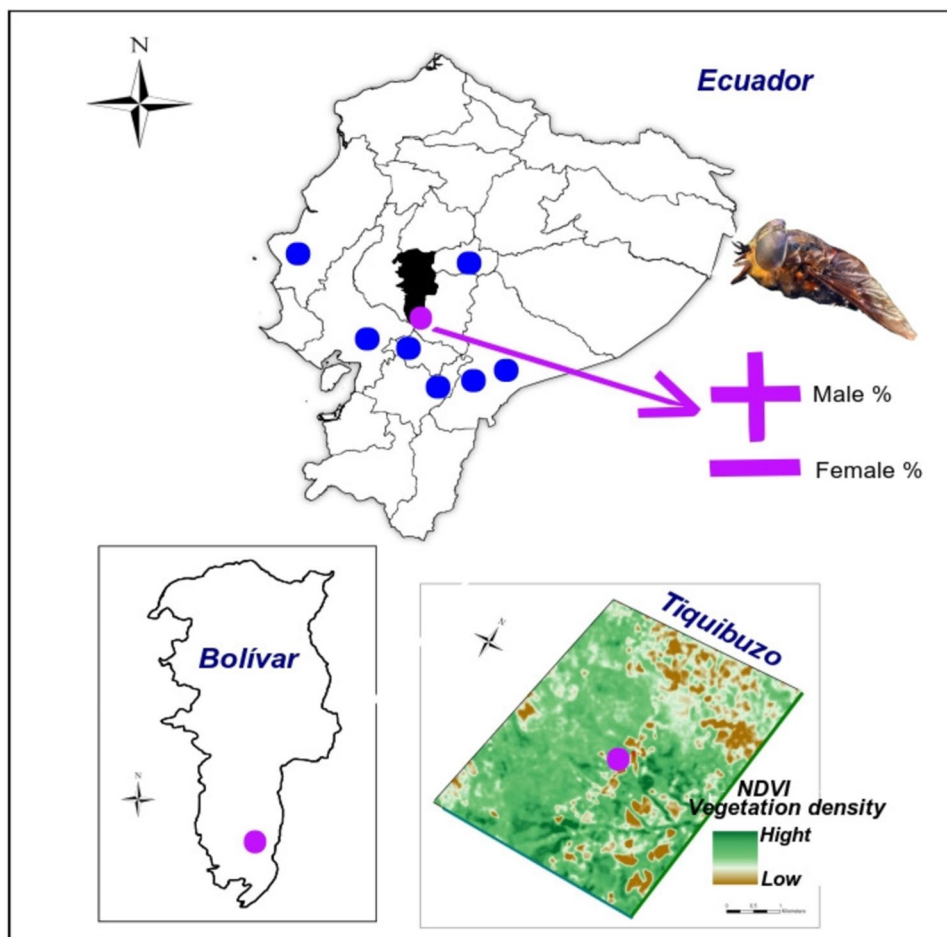
## Materials and methods

We conducted a routine preliminary collection in Tiquibuzo and when we observed an abundance of male horseflies, we intensified our collection efforts, which extended from May to December 2011. Three white Malaise traps were set during this period. The collections took place in a temperate forest area at coordinates 02°01'55.66"S and 79°05'51.44"W, 2300 m above sea level (Fig. 1). The forest is located in the western Andes, in Tiquibuzo, about 10 km from the canton Chillanes in the province of Bolívar, Ecuador. The traps were strategically placed along paths and clearings within the forest plot, maintaining an approximate distance of 60 m between each trap. The collected samples were taken daily

from the collection jars and stored in suitable plastic containers at the optimum temperature. Specimen identification and mounting were carried out at the former National Institute of Hygiene. The collection was then donated to the National Institute of Biodiversity (INABIO).

To compare the results in Tiquibuzo, we analyzed the information on the values and proportions between males and females from our collections between 2008 and 2018 at six other localities in Ecuador, including Galán Arriba, Manabí (01°20'30.69"S—80°40'39.63"W, 420 m a.s.l.); Soroche, Cañar (02°28'27.65"S—79°13'51.24"W); Bosque Protector Prosperina, Guayas (02°09'24"S—79°57'53"W, 210 m a.s.l.); Tinajillas, Morona Santiago (03°00'56"S—78°36'50"W, 2100 m a.s.l.); Maylas, Azuay (02°59'17"S—78°40'59"W, 3192 m a.s.l.); and Plan de Milagro, Morona Santiago (03°00'24.69"S – 78°17'27.20" W, 1100 m a.s.l.). We then standardized the data from the seven sampling sites due to the different temporal intensity of the sampling. To do this, we divided the number of females and males at each locality by the number of months of sampling to obtain the monthly number of females and males. These values were used to compare the collection frequency of females and males in the traps. First, we tested the homoscedasticity and

**Fig. 1** Map of the sampled locations in Ecuador (colored circles). The province of Bolívar is shown at the bottom of the figure. It also shows the study area of Tiquibuzo with NDVI vegetation gradients



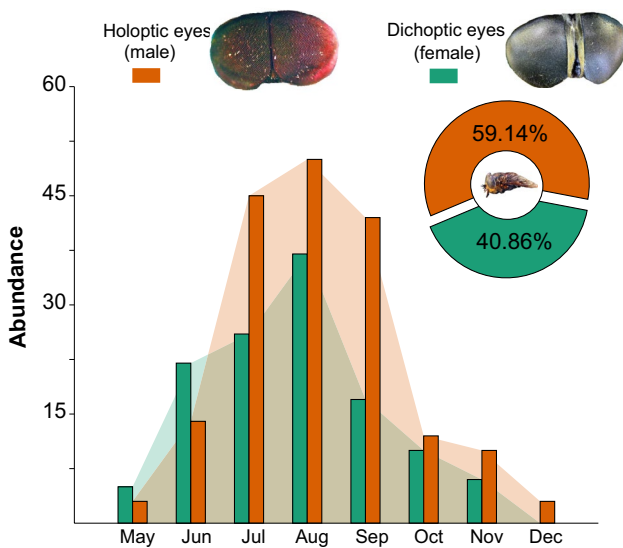
normality of the data using the Levene and Shapiro–Wilk tests, respectively. We then compared the two samples of non-parametric data using the Kruskal–Wallis test or the parametric ANOVA test with Welch correction, both with a reference significance value of  $\alpha=0.05$ . Finally, we related the total monthly abundances of females and males using a GLM to reveal possible population behavior patterns.

### Results

The continuous collection, which spanned 39 months over 8 years across the seven locations studied, comprises only 4.3% of the male tabanids in the total collection of 11,227 individuals. Normality analysis of female density yielded a Shapiro–Wilk (SW) value of 0.85 with a  $p$  value of 0.15. For male density, the SW value was 0.62 with a  $p$  value of 0.0005. In addition, Levene’s test for homogeneity of variance of means yielded a significant value of  $p=0.0007$ . Based on these results, we decided to employ

non-parametric Kruskal–Wallis test to compare medians. The result was  $H(\chi^2)=7.5$  with a  $p$ -value of 0.006, indicating significant differences in collection density medians between females and males across the seven analyzed locations. This means that more females than males were caught by the Malaise traps. This trend continued across all locations, except for Tiquibuzo, where the collection percentage of male horseflies was 59.14% (Fig. 2). In Tiquibuzo exhibited a higher collection density of males over females, representing a distinct pattern (Table 1). Additionally, males’ presences were observed in nine out of the ten species over the eight-month collection period, exhibiting a greater abundance from July to November compared to females (Table 2). In December, the collection was limited to an individual of a single species, indicating decrease during the rainy season, which spans the period from December to April. Among the species collected, a noteworthy pattern emerged wherein male individuals exhibited percentage dominance in half of the species, which is also atypical in this type of collections. However, no statistically significant differences were observed in the total monthly collections of all species combined in Tiquibuzo, according to the Kruskal–Wallis test for equal medians  $H(\chi^2)=0.2585$ ,  $p=0.60$ . Nevertheless, three of the ten species found showed sex differentiation and were statistically significant: *Dasybasis schineri* (Krober, 1931) Welch test  $F=6.263$ ,  $df=8.521$ ,  $p=0.03509$ , *Eristalotabanus violaceus* (Krober, 1931),  $KW:H(\chi^2)=3.938$ ,  $p=0.04$ , and *Di cladocera macula* (Macquart 1846)  $KW:H(\chi^2)=3.692$ ,  $p=0.045$ .

Finally, we generated GLMs of total monthly abundances of females and males. However, due to short sampling periods and the absolute scarcity of males at some locations, only the Tiquibuzo and Cerro Prosperina sites were evaluated. For Tiquibuzo, a generalized linear model with normal distribution and identity link function was applied. A phi dispersion of 119.19 was estimated. The model coefficients were as follows: for the slope (a), 1.3649 (standard error = 0.331), and for the intercept (b), 1.3892 (standard error = 6.3873). The log-likelihood was -3. The goodness-of-fit statistic (G) was 17.005, with a  $p$ -value for the slope equal to  $3.7285 \times 10^{-5}$ . This strong correlation could indicate a balance between the sexes in the horsefly populations (Fig. 3).



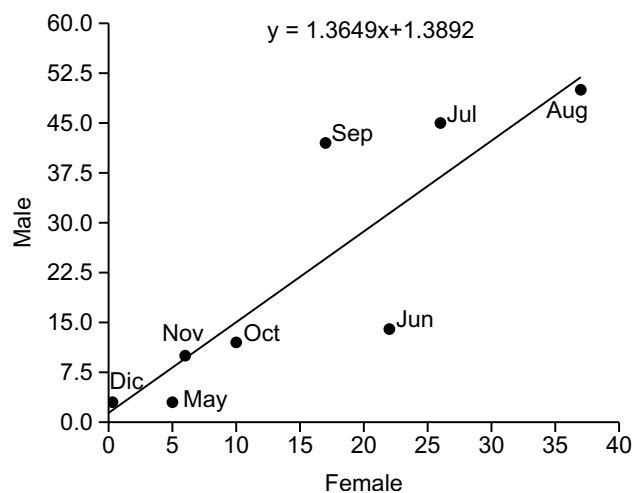
**Fig. 2** Monthly distribution of Tabanidae, showing an atypical pattern in the capture of males, both in the monthly frequency distribution and in the overall relative abundance of the collection

**Table 1** Abundance of tabanid assemblages and collection proportions in seven localities of Ecuador

Locality	Female	Male	F%	M%	Density F	Density M	Months	Year
Galán Arriba	810	0	100	0	162	0	5	2013
Tinajillas	2429	3	99.87	0.12	809.7	1	3	2013
Soroche	488	3	99.38	0.61	122	0.8	4	2012
Prosperina	4996	58	98.85	1.14	217	2.5	23	2011–2012
Plan de Santiago	217	1	99.54	2.18	43.4	0.2	5	2018
Maylas	2081	255	89.08	10.91	693.7	85	3	2008
Tiquibuzo	123	178	<b>40.86</b>	<b>59.14</b>	17.6	25.4	7	2011

**Table 2** Abundance by sex of the ten tabanid species collected during the eight months of sampling in Tiquibuzo (Ecuador)

Species	MAY		JUN		JUL		AUG		SEP		OCT		NOV		DEC		Total	F%	M%
	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M			
<i>Dasybasis schineri</i> (Krober, 1931)	2	3	1	8	2	14	2	11	2	3	4	7	3	66	24.2	75.8			
<i>Esenbeckia testaceiventris</i> (Macquart, 1848)	3		20	11	10	15	2	4						65	60.0	40.0			
<i>Di cladocera tribonophora</i> Fairehild, 1958				6	12	20	5	6	1					62	38.7	61.3			
<i>Eristalotabanus violaceus</i> Krober, 1931				4	2	6	1	18	3	7	1	1		43	16.3	83.7			
<i>Di cladocera clara</i> (Schider, 1868)				2	7	6	1	1						16	43.8	56.3			
<i>Di cladocera macula</i> (Macquart, 1845)			2	2	3	1	2	3	2	1	1			16	75.0	25.0			
<i>Tabanus</i> sp.				2	1	1	3	3	1	1				14	28.6	71.4			
<i>Catachlorops</i> sp.				1	1	3	2	1	1	1				10	50	50			
<i>Scione</i> sp.				2	7									9	100	0			
<i>Spilotabanus multiguttatus</i> (Krober, 1930)	5	3	22	14	26	45	37	50	17	42	10	12	6	1	0	100			



**Fig. 3** GLM of total monthly abundances between females and males in Tiquibuzo

As for the Prosperina site, a phi dispersion of 7.4023 was estimated. The model coefficients were as follows: for the slope (a), 0.0091 (standard error = 0.0049), and for the intercept (b), 1.4608 (standard error = 4.3355). The log-likelihood was -3. The goodness-of-fit statistic (G) was 3.417, with a *p*-value for the slope equal of 0.06.

### Discussion

As previously indicated, male horseflies are captured infrequently, particularly when employing Malaise traps (Krolov et al. 2012). Consequently, it is paradoxical to observe a higher representation of 59.14% and male dominance over a span of seven months in half of the encountered species in Tiquibuzo. We understand that despite the Tiquibuzo data regarding monthly collections not being statistically significant, nonetheless the mere fact of representing almost 60% of the total collections in Tiquibuzo is puzzling considering the extensive dataset spanning nearly eight years of our studies and collections across different months in Ecuador. Undoubtedly, the results indicate, a distinct deviation from the patterns documented in the scientific literature with malaise trap. However, it has been reported that the capture rate of males tends to increase significantly with other mechanisms, such as light trapping in the forest canopy, resulting in representation levels of up to 63% (Krolov et al. 2010). Studies in salt marshes using emergence traps have also consistently shown comparable proportions of male and female individuals (Cookson 1967; Rockel and Hansens 1970). These traps exhibit notable parity in the proportion of females and males collected. This suggests that certain populations have a comparable sex ratio, and collection using interception traps indicates that sex ratios

vary among species. We observed this phenomenon in our field collections in Tiquibuzo, where overall monthly abundances showed no significant variation, except in three instances where male prevalence exceeded that of females. This observation hints at a potential sex-related dynamic in the population structure. Similarly, our analysis using Generalized Linear Models (GLMs) revealed a direct correlation between male and female monthly abundances, as illustrated in Fig. 3. Hence, the primary inquiry should revolve around the reasons behind the elevated male capture rates observed in Tiquibuzo using Malaise traps, as well as the underlying factors contributing to the generally low capture rates of males with these traps. To tackle these inquiries, there are several hypotheses to consider, such as the males horseflies are dominant in the initial emergence, but they become a minority toward the end of the emergence period (Cookson 1967), although this pattern was not evidenced in Tiquibuzo. There are also cases where males have been observed to have a shorter lifespan than females (Karandinos and Axtell 1967; Lane et al. 1983; Matsumura 1995). Hence, if males do indeed exhibit shorter lifespans, the likelihood of encountering and capturing them would correspondingly decrease.

The *hilltopping behavior hypothesis* refers to the behavior of certain insect species that select hill or mountain tops as sites for aggregation and reproduction (Skevington 2008). While this phenomenon has been documented in some insect families, including Tabanidae (Cookson 1967; Smith et al. 1994; Braga da Rosa 2006), the available evidence for this behavior in Tabanidae is limited compared to other groups such as lepidopterans. Other reports also suggest the presence of preferred areas on hilltops, where males were captured more frequently using entomological nets, even during mating season (Leprince et al. 1983). The Tiquibuzo study area is located in a valley an altitude of 2300 m in the foothills. Therefore, the hypothesis of hilltopping behavior (Braga da Rosa 2006; Yuval 2006; Skevington 2008) would not be suitable to explain the observed disturbance. In other locations, such as the Fernando de Noronha Archipelago in Brazil, a significant number of male *Tabanus occidentalis* were captured using Malaise traps. Apparently, the collections at this specific site were near the summit of the island and represented one of the best-preserved areas (Rafael et al. 2021), in contrast to Tiquibuzo, which showed vegetative patches and anthropogenic activity.

Another hypothesis we consider is the hypothesis of *different foraging behavior* of females and males, which could explain the low collection rate of males in Malaise traps. This hypothesis partly explains how the search for host and resources can affect the capture frequency in Malaise traps. The feeding and foraging behavior of horseflies exhibits substantial differences between females and males. Female horseflies are typically facultative and may opportunistically consume blood, nectar and pollen to fulfill their

energy requirements for flight, reproduction and oviposition (Leprince et al. 1983; Karolyi et al. 2014; Mullens 2019). Some of their host, including mammals, reptiles and birds, exhibit evasion and defense behaviors to avoid horsefly bites (Limeira de Oliveira et al. 2002; Barros and Foil 2007; Caro et al. 2014; Altunsoy 2015). This suggest that the foraging behavior of female horseflies can be energetically demanding, therefore, the blood intake provides them with advantages such as increased escape speed (Horváth et al. 2020a, b). This energetic investment in foraging would enhance the likelihood of encountering host due to an increase in flight frequency; however, it would also raise the probability of being captured in Malaise traps. In contrast to females, male horseflies display specialized feeding behavior, exclusively relying on pollen and nectar consumption. However, the energetic costs associated with foraging and reproductive activity, particularly during hovering flight, can be substantial for males (Smith et al. 1994; Smith 2013) and our understanding of male horseflies' energy expenditure and specific feeding patterns remains limited (Allan et al. 1987).

Certain male horseflies are frequently observed in close proximity to water bodies or wet areas on the banks of rivers or lagoons, as many species rely on such environments for reproduction, which is why a portion of the literature focuses on their behavior in these habitats (Cookson 1967; Mullens and Freeman 2017). These areas serve as critical aggregation sites for mating. However, in Tiquibuzo, the absence of significant bodies of water—only small rivulets—limits this behavior, eliminating a reference area for males to orient through positive polarotaxis generated by water reflections, which is crucial for male–female aggregation and courtship (Horváth et al. 2008; Herczeg et al. 2014). Among the genera present in Tiquibuzo, this behavior has been documented within the genus *Tabanus* (Mullens and Freeman 2017). However, available information is more limited for the genera *Esenbeckia* and *Di cladocera*. Regarding *Eristalotabanus violaceus* and *Scione*, field observations in the locality of Maylas revealed the occurrence of reproductive hovering behavior in proximity to water bodies within the páramo. In this particular case, two species of the genus *Scione* were recorded: one morphologically similar to *S. flavohirta* and another identified and typified as *Scione sp.13* according to Buestán et al. (2007). Both species exhibited a high capture frequency compared to other localities (Online resource 1). In forests, certain horsefly species appears to exhibit a preference for flying higher in the canopy (Krolow et al. 2010). Therefore, collecting samples in the undergrowth would reduce the likelihood of intercepting them with Malaise traps.

The hypothesis that emerges as the most plausible is that of an *optimal aggregation zone*, suggesting that in certain areas of Tiquibuzo provides favorable conditions for development and feeding. Therefore, a higher density of



male and female horseflies would increase the probability of catching them with the Malaise traps, despite their inefficiency for this purpose. This suggests that these optimal aggregation zones exist despite the absence of water bodies or hilltopping effects.

Finally, the effect of *habitat reduction and forest fragmentation* must not be ignored. Species behavior tends to change when their habitat is fragmented, as has been observed in forest patches (Debinski and Holt 2000; Harris and Johnson 2004; Baldacchino et al. 2014). A decrease in available habitat creates pressure for optimal reproductive spaces, compelling many species to modify their behavior and coexist with domestic fauna, benefiting from feeding on livestock (Barros and Foil 2007; Baldacchino et al. 2017). In this context, females would acquire resources from nearby livestock and the flora and fauna in the more densely vegetated interior of the forest, where they would collect pollen and nectar, similar to male horseflies (Barros and Foil 2007); subsequently, they would reassemble in this optimal zone. This behavior is possible because studies using marking and weighing techniques have demonstrated that male horseflies exhibit site fidelity, and return to their breeding sites after feeding activities (Smith 2013). Therefore, it is suggested that the reduction of forests and the presence of patches could alter the behavioral ecology of reproduction and foraging in horseflies.

## Conclusions

Horseflies seem to have optimal zones where they are most abundant. Placing the Malaise traps closer to these focal points, which serve as *optimal aggregation zones*, would increase the likelihood of capturing them and thus reduce the disparity in capturing males and females. However, such optimal zones are probably rare, otherwise we would not observe so few males in Malaise traps, current collections and museum collections.

While Malaise traps are essential for capturing local biodiversity, including horseflies, they have inherent biases that limit their effectiveness in capturing the male population of this family. Therefore, it is advisable to complement them with additional trapping mechanisms, such as light traps, polarized refraction traps, and emergence traps to increase the probability of capturing males.

The particular case in the locality of Tiquibuzo represents a fascinating record as it serves as an ideal convergence point for both male and female horseflies, as shown by the presence of males in almost all species, without hilltopping or water bodies being the only direct cause of this disturbance in the observed pattern.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s11756-024-01819-x>.

**Acknowledgements** We would like to thank Mr. Carlos for allowing us to conduct the trapping phase on his property. We also extend our gratitude to the National Institute of Hygiene and Tropical Medicine Leopoldo Izquieta Pérez (now INSPI) for their invaluable logistical support and mobilization. Our special thanks go to Elizabeth Mendoza for her significant contribution to the collection and processing of the samples, as well as to Manuel Mejía for his assistance in the field at the Maylas locality. Lastly, we wish to thank the National Institute of Biodiversity (INABIO), along with Diego Inclán, Alex Pazmiño, and the collaborators from the entomology section, for their receipt and processing of part of the material, and to two anonymous reviewers who provided critical comments that greatly improved this research.

**Author contributions** JB conceptualized the original idea for this article, collected, processed, and identified the study material. GABV contributed to several sampling campaigns, conducted data analysis, and authored the manuscript. Both authors approved the final version of the manuscript.

**Funding** No funding was provided for the conduct of this study.

**Data availability** The data supporting the findings of this study are available as supplementary material accompanying this manuscript. Additional datasets or specific analyses not included in the supplementary material are available from the corresponding author upon reasonable request.

## Declarations

**Conflict of interest** The authors have no conflict of interest.

## References

- Allan SA, Day JF, Edman JD (1987) Visual ecology of biting flies. *Annu Rev Entomol* 32:297–314. <https://doi.org/10.1146/annurev.ento.32.1.297>
- Altunsoy F (2015) Host and feeding side preferences of the horse flies (Diptera: Tabanidae). *J Entomol Res Soc* 17:107–115
- Altunsoy F, Kılıç A (2012) Seasonal abundance of horse fly (Diptera: Tabanidae) in western Anatolia. *J Entomol Res Soc* 14:95–105
- Baldacchino F, Porciani A, Bernard C, Jay-Robert P (2014) Spatial and temporal distribution of Tabanidae in the Pyrenees Mountains: The influence of altitude and landscape structure. *Bull Entomol Res* 104:1–11. <https://doi.org/10.1017/S0007485313000254>
- Baldacchino F, Krčmar S, Bernard C, Manon S, Jay-Robert P (2017) The impact of land use and climate on tabanid assemblages in Europe. *Agric Ecosyst Environ* 239:112–118. <https://doi.org/10.1016/j.agee.2017.01.003>
- Barros A, Foil L (2007) The influence of distance on movement of tabanids (Diptera: Tabanidae) between horses. *Vet Parasitol* 144:380–384. <https://doi.org/10.1016/j.vetpar.2006.09.041>
- Blaho M, Egri A, Bahidszki L, Kriska G, Hegedus R, Akesson S, Horvath G (2012) Spottier targets are less attractive to tabanid flies: on the tabanid-repellency of spotty fur patterns. *PLoS ONE* 7:e41138. <https://doi.org/10.1371/journal.pone.0041138>
- Braga Da Rosa GA (2006) Predation of hilltopping horse-flies (Tabanidae) by birds in Brazil. *Ornitol Neotrop* 17:619–622
- Buestán J, Navarrete R, Mejia M (2007) Lista actualizada de tábanos (Diptera: Tabanidae) del Ecuador. *Rev Ecuat Hig Med Trop* 44:23–62

- Buestán J, Pazmiño A, Brito G (2024) Richness, endemism and seasonality of horseflies (Diptera: Tabanidae) in forests of the Equatorial Pacific Region of Ecuador. *Neotrop Entomol* 53:1–9. <https://doi.org/10.1007/s13744-024-01194-x>
- Caro T, Izzo A, Reiner RC, Walker H, Stankowich T (2014) The function of zebra stripes. *Nat Commun* 5:3535. <https://doi.org/10.1038/ncomms4535>
- Cookson D (1967) Some habits of male horse-flies in Rhodesia (Diptera: Tabanidae). *Ann Natal Mus* 18:647–654
- Debinski DM, Holt RD (2000) A survey and overview of habitat fragmentation experiments. *Conserv Biol* 14:342–355. <https://doi.org/10.1046/j.1523-1739.2000.98081.x>
- do Carmo D, Sampranha S, Santos C, Ribeiro G (2022) Cretaceous horse flies and their phylogenetic significance (Diptera: Tabanidae). *Arthropod Syst Phylogeny* 80:295–307. <https://doi.org/10.3897/asp.80.e86673>
- Harris LF, Johnson SD (2004) The consequences of habitat fragmentation for plant-pollinator mutualisms. *Int J Trop Insect Sci* 24:29–43. <https://doi.org/10.1079/IJT20049>
- Herczeg T, Bláhó M, Száz D, Kriska G, Gyurkovszky M, Farkas R, Horváth G (2014) Seasonality and daily activity of male and female tabanid flies monitored in a Hungarian hill-country pasture by new polarization traps and traditional canopy traps. *Parasitol Res* 113:4251–4260. <https://doi.org/10.1007/s00436-014-4103-6>
- Herczeg T, Száz D, Bláhó M, Barta A, Gyurkovszky M, Farkas R, Horváth G (2018) The effect of weather variables on the flight activity of horseflies (Diptera: Tabanidae) in the continental climate of Hungary. *Parasitol Res* 114:1087–1097. <https://doi.org/10.1007/s00436-014-4280-3>
- Horváth G, Majer J, Horváth L, Szivák I, Kriska G (2008) Ventral polarization vision in tabanids: Horseflies and deerflies (Diptera: Tabanidae) are attracted to horizontally polarized light. *Naturwissenschaften* 95:1093–1100. <https://doi.org/10.1007/s00114-008-0425-5>
- Horváth G, Pereszlényi Á, Egri Á, Fritz B, Guttmann M, Lemmer U, Gomard G, Kriska G (2020a) Horsefly reactions to black surfaces: attractiveness to male and female tabanids versus surface tilt angle and temperature. *Parasitol Res* 119:2399–2409. <https://doi.org/10.1007/s00436-020-06702-7>
- Horváth G, Pereszlényi Á, Egri Á, Tóth T, Jánosi IM (2020b) Why do biting horseflies prefer warmer hosts? Tabanids can escape easier from warmer targets. *PLoS ONE* 15:e0233038. <https://doi.org/10.1371/journal.pone.0233038>
- Karandinos MG, Axtell RC (1967) Effect of temperature on the longevity, fecundity, and activity of adult *Hippelates pusio*, *H. bishoppi*, and *H. pallipes* (Diptera: Chloropidae) I. *Ann Entomol Soc Am* 60:1252–1255. <https://doi.org/10.1093/aesa/60.6.1252>
- Károlyi F, Colville JF, Handschuh S, Metscher BD, Krenn HW (2014) One proboscis, two tasks: Adaptations to blood-feeding and nectar-extracting in long-proboscid horse flies (Tabanidae, *Philolichia*). *Arthropod Struct Dev* 43:403–413. <https://doi.org/10.1016/j.asd.2014.07.003>
- Krčmar S (2013) Comparison of the efficiency of the olfactory and visual traps in the collection of horse flies (Diptera: Tabanidae). *Entomol Gen* 34:261–267. <https://doi.org/10.1127/entom.gen/34/2013/261>
- Krolow TK, Henriques LA, Rafael AJ (2010) Tabanidae (Diptera) no dossel da floresta amazônica atraídos por luz e descrição de machos de três espécies. *Acta Amaz* 40:605–612. <https://doi.org/10.1590/S0044-59672010000300022>
- Krolow TK, Bayless KM, Henriques AL (2012) Newly discovered males and new records of the uncommon Neotropical genera *Eutabanus* Kröber and *Myiotabanus* Lutz (Diptera: Tabanidae). *Zootaxa* 3389:25–33. <https://doi.org/10.11646/zootaxa.3389.1.3>
- Krolow TK, Henriques AL, Pollet M (2017) The Tabanidae of the Mitaraka expedition, with an updated check list of French Guiana (Diptera). *ZooKeys* 684:85–118. <https://doi.org/10.3897/zookeys.684.13197>
- Lane RS, Anderson JR, Philip CB (1983) Biology of autogenous horse flies native to coastal California: *Apatolestes acties* (Diptera: Tabanidae). *Ann Entomol Soc Am* 76:559–571. <https://doi.org/10.1093/aesa/76.4.559>
- Leprince DJ, Lewis DJ, Parent J (1983) Biology of male tabanids (Diptera) aggregated on a mountain summit in southwestern Quebec. *J Med Entomol* 20:608–613. <https://doi.org/10.1093/jmedent/20.6.608>
- Limeira de Oliveira F, Rafael JA, Henriques AL (2002) *Phorcotabanus cinereus* (Wiedemann, 1821) (Diptera, Tabanidae), an ornithophilic species of tabanid in Central Amazon, Brazil. *Mem Inst Oswaldo Cruz* 97:839–842. <https://doi.org/10.1590/S0074-02762002000600015>
- Matsumura T (1995) Development of *Tabanus nipponicus* (Diptera, Tabanidae) confirmed by laboratory-rearing. *Appl Entomol Zool* 30:57–65. <https://doi.org/10.1303/aez.30.57>
- Mihok S (2002) The development of a multipurpose trap (the Nzi) for tsetse and other biting flies. *Bull Entomol Res* 92:385–403. <https://doi.org/10.1079/ber2002186>
- Mullens BA (2019) Horse flies and deer flies (Tabanidae). In: Mullen G, Durden L (eds) *Medical and Veterinary Entomology*, 3rd edn. Academic Press, New York, pp 327–343. <https://doi.org/10.1016/B978-0-12-814043-7.00016-9>
- Mullens BA, Freeman JV (2017) Hovering and swarming behavior of male *Tabanus calens* (Diptera: Tabanidae) in Tennessee and New Jersey, USA. *J Med Entomol* 54:1410–1414. <https://doi.org/10.1093/jme/tjx070>
- Oliveira L, Henriques A, Krolow T (2023) New records, descriptions, and redescrptions of male horse flies (Diptera: Tabanidae) in Brazil. *EntomoBrasilis* 16:1–7. <https://doi.org/10.12741/ebrazil.v16.e1033>
- Rafael JA, Marques DW, Silva-Neto AM, Limeira de Oliveira F (2021) Insect (Hexapoda) diversity in the oceanic archipelago of Fernando de Noronha, Brazil: Seasonality and populational density of tabanidae (diptera). *Biota Neotrop* 21:1–8. <https://doi.org/10.1590/1676-0611-BN-2021-1211>
- Rockel EG, Hansens EJ (1970) Emergence and flight activity of salt-marsh horse flies and deer flies. *Ann Entomol Soc Am* 63:27–31. <https://doi.org/10.1093/aesa/63.1.27>
- Skevington JH (2008) Hilltopping. In: Capinera JL (ed) *Encyclopedia of Entomology*. Springer, Dordrecht, pp 1799–1807. [https://doi.org/10.1007/978-1-4020-6359-6\\_1342](https://doi.org/10.1007/978-1-4020-6359-6_1342)
- Smith SM, Turnbull DA, Taylor PD (1994) Assembly, mating, and energetics of *Hybomitra arpadii* (Diptera: Tabanidae) at Churchill, Manitoba. *J Insect Behav* 7:355–383. <https://doi.org/10.1007/BF01989741>
- Smith S (2013) Survivorship, site fidelity and weight dynamics of male *Hybomitra aurilimba* (Diptera: Tabanidae) at a hilltop mating arena. *Figshare*. <https://doi.org/10.6084/m9.figshare.787744.v2>
- Yuval B (2006) Mating systems of blood-feeding flies. *Annu Rev Entomol* 51:413–440. <https://doi.org/10.1146/annurev.ento.51.110104.151058>

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.