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RESEARCH ARTICLE

Effects of past and current temperatures on the flight performance of invasive pest fruit flies (Diptera: Tephritidae): Climate change may facilitate movements of tropical species to higher latitudes

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Abstract

1. Little is known about how past and current thermal environment interact to determine dispersal in novel environments, and thus invasion potential of major agricultural pests. In this study, we tested experimentally how adult thermal history affects flight-related traits under diverse thermal conditions in three major agricultural pests of invasion concern: *Bactrocera dorsalis*, *Bactrocera zonata* and *Ceratitis capitata*.
2. Across all species, the main factor affecting flight performance was body mass, with heavier individuals performing best. Both current and, to a lesser extent, past thermal environments affected flight performance and periodicity (flight interruptions), although their interaction was rarely significant. Furthermore, we show that 20°C acclimation can have deleterious effects regardless of thermal conditions during flight, particularly in *Bactrocera* females, which had decreased flight performance and increased flight periodicity when acclimated at this temperature.
3. The thermal environment during flight affected both flight periodicity and performance mainly in females of *C. capitata* and *B. dorsalis*, while only flight performance was affected in *B. zonata* males. When compared to warmer temperatures, flight at 20°C tended to reduce flight performance, but flight periodicity increased at 30°C compared to 20°C. Overall, the flight performance of *B. dorsalis* was greater than that of *C. capitata* or *B. zonata*, regardless of the past and present thermal environment, but flight periodicity was lower in *C. capitata*.
4. In all three species investigated, optimal flight performance occurs around 25°C, and flies will therefore cover more distance around this temperature. The lack of

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interaction between past and current thermal environments in these three species indicates that flight-related traits may have low thermal plasticity. Finally, our results suggest that a reduction in thermal variability and average temperatures increasing temperate areas by a few degrees with climate change may facilitate movements of tropical tephritid pests in new areas at higher latitudes.

KEYWORDS
flight performance, phenotypic plasticity, Tephritidae, thermal history

1 | INTRODUCTION

Not only are temperatures rising with climate change, but temperature fluctuations are also changing. Although the rise in temperature is more pronounced further from the equator, diurnal and interannual temperature fluctuations and extremes are predicted to become higher and more frequent in tropical areas and to decrease poleward (Davy et al., 2017; Kotz et al., 2021; Olonscheck et al., 2021). Ectotherms, including many insect species, are directly affected by temperature, and novel thermal conditions resulting from climate change are expected to affect both the abundance, biodiversity and geographical distribution of insect species (Harvey et al., 2023; Rubenstein et al., 2023). For some species, rising temperatures will limit their geographic distribution as well as movements due to relatively invariant upper thermal tolerance, but for others, it may extend the suitable period for population growth and also promote dispersal (Harvey et al., 2023; Terblanche et al., 2024). Because tropical areas experience less variation in diurnal temperature and lower frequency of extreme temperatures, the thermal tolerance range of insects from these areas is expected to be narrower (Deutsch et al., 2008; Shah et al., 2017; Sunday et al., 2011). Reduction in the seasonal diurnal temperature fluctuation in temperate regions with climate warming may facilitate poleward movements for tropical species. Most importantly, invasion events and outbreaks of insect pests are expected to increase with climate warming, which may severely impact food security, socio-economic well-being and human health (Harvey et al., 2023).

While current temperatures affect the expression of various traits in insects, temperatures experienced in the past (i.e., thermal history) can also, positively or negatively, modulate future expression of fitness-related traits via phenotypic plasticity (Kellermann et al., 2017; Sgrò et al., 2016; Terblanche et al., 2024). Thermal plasticity can be induced by acclimation, typically achieved by experimentally modifying an organism's thermal history at the developmental or adult stage (Bowler & Terblanche, 2008). Several hypotheses have suggested a background to predict the outcome of thermal acclimation on functional traits. The beneficial acclimation hypothesis predicts that acclimation to a given temperature will provide performance benefits when later exposed to the same thermal environment (Wilson & Franklin, 2002). The ‘colder is better’ and ‘hotter is better’ hypotheses propose that only acclimation to either cold or hot temperatures will provide performance benefits, in any thermal environment at a later stage (Frazier et al., 2006, 2008). More recently, it has been proposed that intermediate temperature will improve performance (optimal acclimation) and that acclimation to lower or higher temperatures may induce damage (deleterious acclimation) (Terblanche & Kleynhans, 2009). Each hypothesis has received some support from laboratory observations (reviewed in Chown & Terblanche, 2006; Huey et al., 1999), yet only a handful of studies have investigated the effect of thermal treatment on field performance (Boersma et al., 2019; Chidawanyika & Terblanche, 2011; Fay & Meats, 1987a, 1987b; Kristensen et al., 2008; Loeschcke & Hoffmann, 2007; Malod et al., 2024; Steyn et al., 2022; Thomson et al., 2001). However, the effects of acclimation on the phenotype observed in the laboratory do not always match the outcomes of field observations (Boersma et al., 2019; Kristensen et al., 2008; Steyn et al., 2022), and depending on the species, the effects of the thermal treatment do not always readily match the predictions of one of the acclimation hypotheses. This may be explained by differences in the timing and duration of the thermal treatment across studies, which would make direct comparisons between species difficult. The outcome of acclimation can differ depending on the life stage as well as adult age and duration of exposure (Bowler & Terblanche, 2008; Sørensen et al., 2024; Zhang et al., 2015). Finally, this could also be an artefact of phylogeny (e.g., some genotypic constraint) or the environment in which a given species evolved. For example, *Bactrocera dorsalis* (Hendel), a tropical species, has a lower thermal plasticity in lower and upper thermal limits when compared to *Ceratitis* species, which have spread to temperate areas (Pieterse et al., 2017).

Understanding how past and current temperatures affect flight performance is crucial for management of pest insects and species' potential movement with climate change. Such knowledge can, for example, be used to predict dispersal, the risk of invasion or delimiting the size of quarantine areas (Chailleux et al., 2021; Froerer et al., 2010; Hendrichs et al., 2021; Sinclair et al., 2022). Among the most destructive horticultural pests worldwide, fruit flies (Diptera: Tephritidae) require costly management programmes to mitigate damage caused, and information related to their movements is key to understanding how they spread and invade new areas (Papadopoulos, Meyer, et al., 2024). In Africa and Europe, three fruit fly species are of particular concern to food security and plant protection: *B. dorsalis*, *Bactrocera zonata* (Saunders) and *Ceratitis capitata* (Wiedemann), with both *Bactrocera* species being on the quarantine organisms list for the European Union (EFSA Panel on Plant Health et al., 2020).

Bactrocera species originate from Asia and have evolved in tropical regions in association with rainforests (Clarke et al., 2019; Starkie et al., 2024). However, in comparison with *C. capitata*, which originates from Afrotropical regions but became established in temperate regions more than a century ago, the spread of *Bactrocera* species is more recent (König et al., 2022; Malacrida et al., 1998). With climate change, predictive models suggest that the distribution of these species will expand and reach higher latitudes and altitudes (De Meyer et al., 2010; Gilioli et al., 2022; Gutierrez et al., 2021; Hill & Terblanche, 2014; Rao et al., 2024; Zingore et al., 2020). This spread to new areas will also affect community structures, as competitive displacement often occurs in the new environment after the establishment of an invasive fruit fly species (Duyck et al., 2004, Moquet et al., 2021). Despite that, few studies have investigated the link between thermal environment and flight performance in these species (but see Esterhuizen et al., 2014; Makumbe et al., 2020; Malod et al., 2023; Steyn et al., 2022). However, none have assessed under controlled laboratory conditions how recent thermal history affects flight performance in a similar or new thermal environment to assess the link between past and current environmental temperatures on dispersal-related phenotypes.

The aim of this study was to test the different thermal acclimation hypotheses and improve knowledge on how climate change affects the dispersal potential of three tephritid species from different geographical origins. We explored whether (1) cold or warm acclimation in adults that might reflect transient 'cold snaps' or 'warm spells' is beneficial or deleterious to flight-related traits in diverse thermal environments, and (2) if the observed patterns are shared between species that evolved in different geographical areas. Previously, it was shown that acclimation at cooler temperature (i.e., 20°C) decreases flight performance in these species when tested at 25°C (Malod et al., 2023). Furthermore, the optimal thermal window for flight distance in *B. dorsalis* lies between 20 and 24°C, with a substantial decline at temperatures above 32°C (Makumbe et al., 2020), whereas the ability to initiate flight gradually increases in *C. capitata* between 20 and 30°C (Esterhuizen et al., 2014). Considering the overall number of studies supporting the beneficial acclimation hypothesis, we predict that acclimation at a given temperature will benefit flight-related traits in that same thermal environment, and a reduction in performance under other conditions. Furthermore, because *Bactrocera* species have evolved in tropical environments with low seasonal temperature variation, we predict that their thermal flight performance will be less plastic than that of *C. capitata*, which occupies a wider geographic range in areas with high seasonality and greater temperature variation.

2 | MATERIALS AND METHODS

2.1 | Fly husbandry

Cultures of *B. dorsalis*, *B. zonata* and *C. capitata* were maintained at 25°C in climate rooms under laboratory-controlled conditions (Supporting Information).

2.2 | Acclimation

For each species, acclimation at either 20, 25 or 30°C for 48 h took place in incubators. Flies were only acclimated after reaching sexual maturity (i.e., thermal treatment around 14–16 days for *B. dorsalis*, 12–50 days for *B. zonata* and 9–11 days for *C. capitata*) as this age also corresponds to peak flight performance in *Bactrocera* species (Sharp et al., 1975).

2.3 | Tethered flight procedure

The flight mill assays were conducted in a temperature-controlled room at either 20, 25 or 30°C (see Supporting Information for details). We used calibrated, standardized flight mills connected to a multichannel flight mill data acquisition (DAQ) system controlled from a laptop computer. We tested up to nine flies per session. The body mass of each fly was determined before being placed on the flight mill. At least two flies from each temperature group were tested per session. Each session lasted exactly 2 h and started when the last fly was attached to the flight mill. We replicated the experiment to test a minimum of 15 flying individuals of each sex and temperature group. Individuals completing less than one revolution (two data points) were considered non-flying. The data for the groups tested at a flight temperature of 25°C are the same as those presented in Malod et al. (2023).

2.4 | Statistical analyses

All statistical analyses were performed in the R software (v 4.2.0, The R Foundation for Statistical Computing) (see Supporting Information for detailed procedure).

2.4.1 | Variable reduction and selection

A principal components analysis (PCA) was performed to determine how flight-related traits were correlated with each other and to reduce the number of response variables. This was done because an inspection of the data for distance, average and maximum speed, number of flight events and total flight duration showed that they responded similarly to the treatments (Figures S1–S3).

We decided that the principal components (PC) to be retained would explain at least 75% of the variance. The scores for each retained PC were then used as independent response variables in subsequent analyses.

2.4.2 | Intraspecific comparisons of flight performance and body mass

Data were analysed using generalized mixed effects models (see Supporting Information for details). Sexes were analysed separately to focus on the effect of past and current thermal environments and avoid complex third-order interactions. Acclimation temperature, flight temperature and their interaction were entered as fixed effects, with body mass as a continuous covariate. Flight mill channel was added as a random effect if it improved the fit of the model based on the lowest Akaike information criterion (AIC). The model for body mass did not include body mass as a covariate or channel as a random effect (results presented in Figure S4). For models with a random effect, model reduction was performed by removing the interaction term if it was not significant, and models (full and reduced) were compared using AIC. For models without a random effect, stepwise selection was used to determine the minimum adequate model based on the lowest AIC. If a significant main effect or interaction was detected, post hoc pairwise comparison tests were performed.

2.4.3 | Interspecific comparisons of flight performance and body mass

Performance across species was compared for each trait separately using the models from the intraspecific comparisons with the addition of species as a fixed factor. Comparing body mass across species was not the focus of this study (but is available in the Supporting Information) as it was already done in Malod et al. (2023), and because body mass was measured before flight there was no reason to compare the body mass of the species at different flight temperatures. If a significant main effect or interaction was detected, post hoc pairwise comparison tests were performed to identify statistically heterogenous groups.

3 | RESULTS

3.1 | Variable reduction and selection

The PCA showed that principal component 1 (PC1) alone explained 56.5% of the variation, while principal components 2 (PC2) and 3 (PC3) explained 20.7% and 19%, respectively (Figure 1a). The variables distance, average and maximum speed, as well as total flight duration were strongly correlated with PC1 (Figure 1b). Variation in the number of flight events was mainly explained by PC2, while PC3 was moderately correlated with the number of flight events and total flight duration (Figure 1b). We decided to retain PC1 and PC2 for the subsequent analyses, as together they explained 77.2% of the variation and all variables were strongly represented by these two dimensions. The variables correlated with PC3 were already well-represented by PC1 and PC2. The biplot of PC1 and PC2 shows that the number of flight events is negatively correlated with flight duration and distance (Figure 2). Moreover, the clusters for each species are overlapping, but *B. dorsalis* has higher principal component scores on PC1 (Figure 2). In the following sections, we refer to PC1 as 'flight performance' and PC2 as 'flight periodicity'.

3.2 | Intraspecific comparisons

3.2.1 | Flight performance (PC1)

Flight performance of *C. capitata* females was affected by body mass (estimate = 0.20, $p = 0.021$) and flight temperature (Table 1). There was a reduction in flight performance when *C. capitata* females were tested at 20°C in comparison with 25°C (estimate = −0.47, $p = 0.043$), and there was no difference between the other flight temperatures (Figure 3a). Similarly, flight performance of *B. dorsalis* females was affected by body mass (estimate = 0.22, $p < 0.001$) and flight temperature (Table 1). Flight performance was reduced when *B. dorsalis* females were tested at 20°C in comparison with 30°C (estimate = −1.12, $p = 0.018$) (Figure 3a), and there was no difference between the other flight temperatures. For *B. zonata* females, flight performance was only affected by acclimation (Table 1). In this species, acclimation at 20°C reduced flight performance when compared to acclimation at 30°C (estimate = −0.66, $p = 0.018$), and there was no difference between the other acclimation treatments (Figure 3a).

Flight performance in *C. capitata* (estimate = 0.20, $p = 0.049$) and *B. dorsalis* (estimate = 0.33, $p < 0.001$) males was only affected by body mass (Table 1). For *B. zonata* males, flight performance was affected by body mass (estimate = 0.17, $p < 0.001$) and an interaction between acclimation and flight temperature (Table 1). When acclimated at 25°C, a flight temperature of 20°C reduced flight performance when compared to 25°C (estimate = −0.77, $p = 0.026$) (Figure 4a). There was no difference between the other combinations of acclimation and flight temperatures in *B. zonata* males.

3.2.2 | Flight periodicity (PC2)

In *C. capitata* females, flight periodicity was only affected by flight temperature (Table 1). In females of this species, flight was less interrupted when tested at 20°C (estimate = −0.59, $p < 0.001$) or 25°C (estimate = −0.39, $p = 0.001$) in comparison with 30°C, and there was no difference between 20 and 25°C (Figure 3b). Flight periodicity in *B. dorsalis* females was affected by acclimation, flight temperature and the interaction between them (Table 1). For *B. dorsalis* females tested at 20°C, acclimation at 20°C increased flight periodicity in comparison with acclimation at 25°C (estimate = 1.01, $p = 0.003$), and there was no difference between the other acclimation treatments. For females tested at 25°C, acclimation at 20°C increased flight periodicity in comparison with acclimation at 30°C (estimate = 0.73, $p = 0.022$), and there was no difference between the other acclimation treatments. When tested at 30°C, flight periodicity increased in *B. dorsalis* females when acclimated at 20°C in comparison with 25°C (estimate = 0.95, $p = 0.003$), and no other differences between acclimation treatments were detected (Figure 3b). In this species, flight periodicity was reduced in females tested at 30°C (20°C vs. 30°C: estimate = −0.76, $p < 0.001$; 25°C vs. 30°C: estimate = −0.55, $p = 0.002$; 20°C vs. 25°C: estimate = −0.21, $p = 0.407$) regardless of

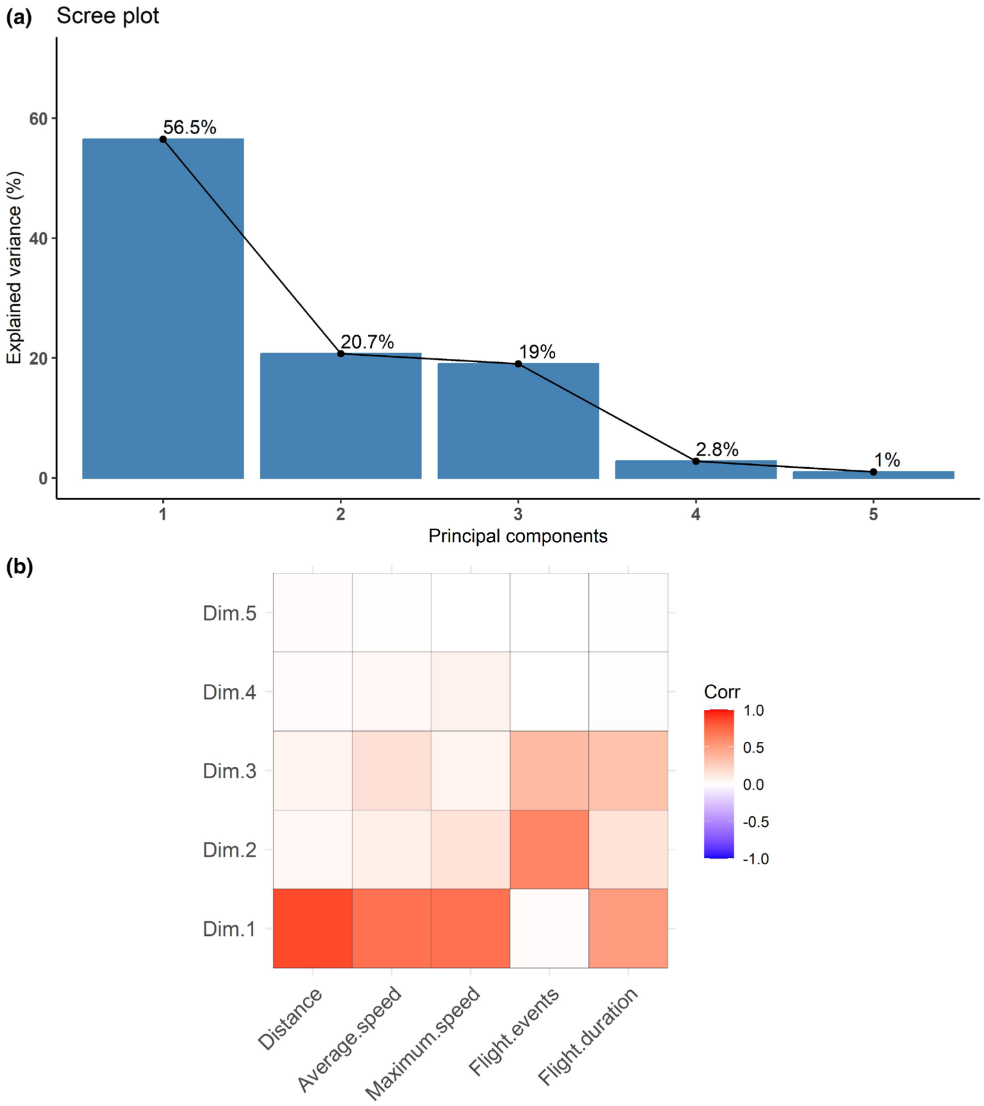

FIGURE 1 Scree plot (a) and correlation plot (b) from a principal component analysis on flight-related traits in three tephritid species. The scree plot indicates how much variance is explained by each principal component. The correlation plot indicates how each trait of interest is correlated with each dimension (principal component). The darkest of red indicates a strong positive correlation, and the darkest shade of purple indicates a strong negative correlation. A white square indicates an absence of correlation between a given trait and principal component.

the acclimation treatment. Regardless of the flight temperature, there was more flight interruption in *B. dorsalis* females acclimated at 20°C (20°C vs. 25°C: estimate $= 0.72$, $p < 0.001$; 20°C vs. 30°C: estimate $= 0.54$, $p = 0.002$; 25°C vs. 30°C: estimate $= -0.17$, $p = 0.538$). Only the acclimation treatment affected the flight periodicity in *B. zonata* females (Table 1). Acclimation at 20°C reduced flight periodicity in comparison with acclimation at 30°C (estimate $= -0.21$, $p = 0.022$), and there was no difference between the other acclimation temperatures (Figure 3b).

Flight periodicity in *C. capitata* males was only affected by flight temperature (Table 1). There were fewer flight interruptions when males were tested at 20°C (estimate $= -0.49$, $p < 0.001$) or 25°C (estimate $= -0.41$, $p = 0.001$) in comparison with 30°C, and there was no difference between 20 and 25°C (Figure 4b). Similarly, only flight temperature had an effect on flight periodicity in *B. dorsalis* males (Table 1). There was only a difference between flight temperatures of 20 and 30°C, with fewer interruptions when tested at 20°C (estimate $= -0.66$, $p < 0.001$) (Figure 4b). For *B. zonata* males, only body mass (estimate $= -0.05$, $p = 0.019$) affected flight periodicity.

3.3 | Interspecific comparisons

3.3.1 | Flight performance (PC1)

Flight performance in females was affected by acclimation and species (Table 2). *Ceratitis capitata* had a lower flight performance than *B. dorsalis* (estimate $= -0.49$, $p < 0.001$), and the latter performed

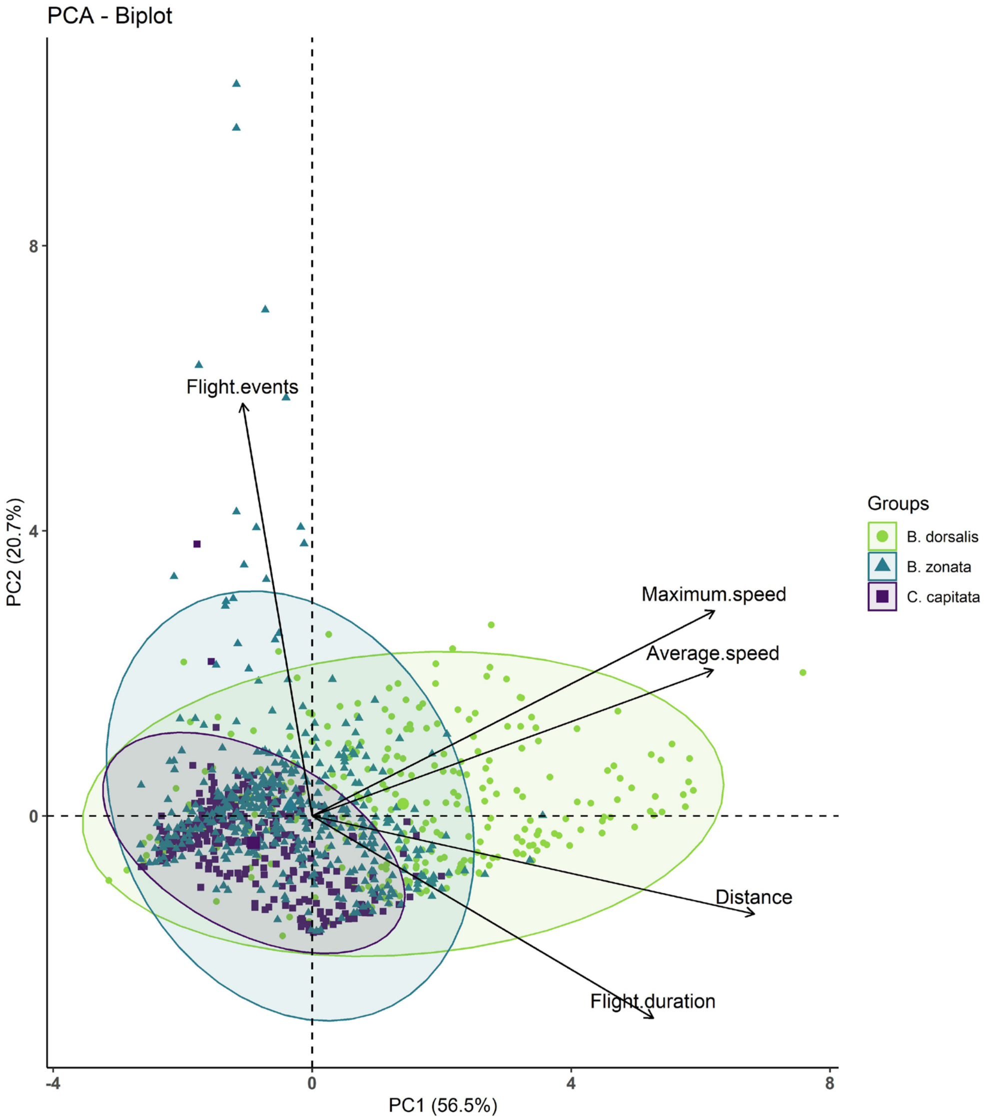

FIGURE 2 Principal component analysis biplot of the correlation between flight-related traits and the first two principal components in three tephritid species. The length and direction of the arrows indicate the strength of the correlation between a given trait and the principal component. The ellipses represent the cluster for each species.

better than *B. zonata* (estimate = 0.42, $p < 0.001$) (Figure 3a). There was no difference between *C. capitata* and *B. zonata* females. Overall, flight performance was reduced in females acclimated at 20°C in comparison with those acclimated at 25°C (estimate = −0.12, $p = 0.041$), and there was no difference between the other acclimation temperatures.

In males, flight performance was affected by species and the interaction between flight temperature and species (Table 2). Regardless of the flight temperature, the performance of *C. capitata* males was lower compared to *B. dorsalis* (estimate = −2.37, $p < 0.001$) and *B. zonata* (estimate = −0.75, $p < 0.001$), and flight performance was greater in *B. dorsalis* compared to *B. zonata* (estimate −1.62, $p < 0.001$) (Figure 4a). At a flight temperature of 30°C only, there was no difference between *C. capitata* and *B. zonata* males, while the overall pattern (*B. dorsalis* > *B. zonata* > *C. capitata*) between species applied to all other test temperatures.

3.3.2 | Flight periodicity (PC2)

In females, flight periodicity was affected by species, flight temperature and the interaction between species and acclimation (Table 2). At 20°C acclimation, flight was less interrupted in *C. capitata* females than in *B. dorsalis* (estimate = −0.39, $p < 0.001$), *B. dorsalis* stopped more often than *B. zonata* (estimate = 0.26, $p < 0.001$), and there was no difference between *C. capitata* and *B. zonata* (Figure 3b). When females were acclimated at 25°C, the only difference was between *C. capitata* and *B. dorsalis*, with less flight interruptions in the former (estimate = −0.34, $p = 0.005$). When acclimated at 30°C, *C. capitata* females stopped less often than *B. dorsalis* (estimate = −0.29, $p = 0.007$) and *B. zonata* (estimate = −0.33, $p = 0.002$), and there was no difference between *Bactrocera* species. Regardless of the species, flight was less interrupted when females were tested at 20°C in comparison with

TABLE 1 Within species effects of acclimation temperature (20, 25 and 30°C) on the flight performance and periodicity at either 20, 25 or 30°C in three tephritid species.

		χ^2	df	*p*	RESI [CI]
Females					
Flight performance (PC1)					
C. capitata	Acclimation	3.94	2	0.139	0.08 [0, 0.31]
	Temperature	**6.07**	**2**	**0.048**	**0.16 [0, 0.37]**
	Body mass	**5.42**	**0**	**0.019**	**0.16 [0, 0.32]**
B. dorsalis	Temperature	**7.56**	**2**	**0.023**	**0.19 [0, 0.39]**
	Body mass	**15.78**	**1**	**<0.001**	**0.35 [0.18, 0.55]**
B. zonata	Acclimation	**10.35**	**2**	**0.005**	**0.20 [0.03, 0.77]**
	Temperature	3.65	2	0.161	0.19 [0.01, 0.55]
	Body mass	2.23	1	0.135	0.07 [0, 0.23]
	Acclimation × temperature	9.01	4	0.061	0.19 [0.04, 0.49]
Flight periodicity (PC2)					
C. capitata	Acclimation	4.14	2	0.126	0.12 [0, 0.33]
	Temperature	**30.78**	**2**	**<0.001**	**0.44 [0.26, 0.70]**
B. dorsalis	Acclimation	**11.49**	**2**	**0.003**	**0.35 [0.18, 0.69]**
	Temperature	**7.43**	**2**	**0.024**	**0.45 [0.29, 0.69]**
	Body mass	3.48	1	0.062	0.12 [0, 0.31]
	Acclimation × temperature	**10.63**	**4**	**0.031**	**0.21 [0, 0.47]**
B. zonata	Acclimation	**7.49**	**2**	**0.023**	**0.19 [0, 0.45]**
	Temperature	4.86	2	0.088	0.20 [0, 0.41]
Males					
Flight performance (PC1)					
C. capitata	Acclimation	3.04	2	0.218	0 [0, 0.25]
	Temperature	1.69	2	0.429	0.22 [0, 0.49]
	Body mass	**3.91**	**1**	**0.048**	**0.14 [0, 0.32]**
	Acclimation × temperature	9.05	4	0.059	0.15 [0, 0.41]
B. dorsalis	Temperature	4.66	2	0.097	0.12 [0, 0.36]
	Body mass	**36.91**	**1**	**<0.001**	**0.47 [0.27, 0.68]**
B. zonata	Acclimation	4.83	2	0.089	0.11 [0, 0.33]
	Temperature	4.94	2	0.084	0 [0, 0.28]
	Body mass	**16.49**	**1**	**<0.001**	**0.25 [0.11, 0.41]**
	Acclimation × temperature	**10.56**	**4**	**0.032**	**0.16 [0, 0.41]**
Flight periodicity (PC2)					
C. capitata	Acclimation	4.04	2	0.132	0.11 [0, 0.32]
	Temperature	**21.21**	**2**	**<0.001**	**0.36 [0.20, 0.57]**
B. dorsalis	Temperature	**15.69**	**2**	**<0.001**	**0.34 [0.17, 0.56]**
	Body mass	2.06	1	0.151	0.10 [0, 0.29]
B. zonata	Body mass	**5.71**	**1**	**0.017**	**0.20 [0, 0.43]**

Note: Significant *p* values are indicated in bold and Robust Effect Size Indexes (RESI) are reported with 95% confidence intervals.

30°C (estimate = −0.15, $p = 0.009$), and there was no difference between the other flight temperatures.

Flight periodicity in males was affected by species and flight temperature (Table 2). Flight in *C. capitata* males was less interrupted than in *B. dorsalis* (estimate = −0.22, $p = 0.004$) and *B. zonata* (estimate = −0.25, $p < 0.001$), and there was no difference between *Bactrocera* males (Figure 4b). Regardless of the species, there were fewer flight interruptions when males were tested at 20°C in comparison with 30°C (estimate = −0.26, $p < 0.001$), and there was no difference between the other flight temperatures.

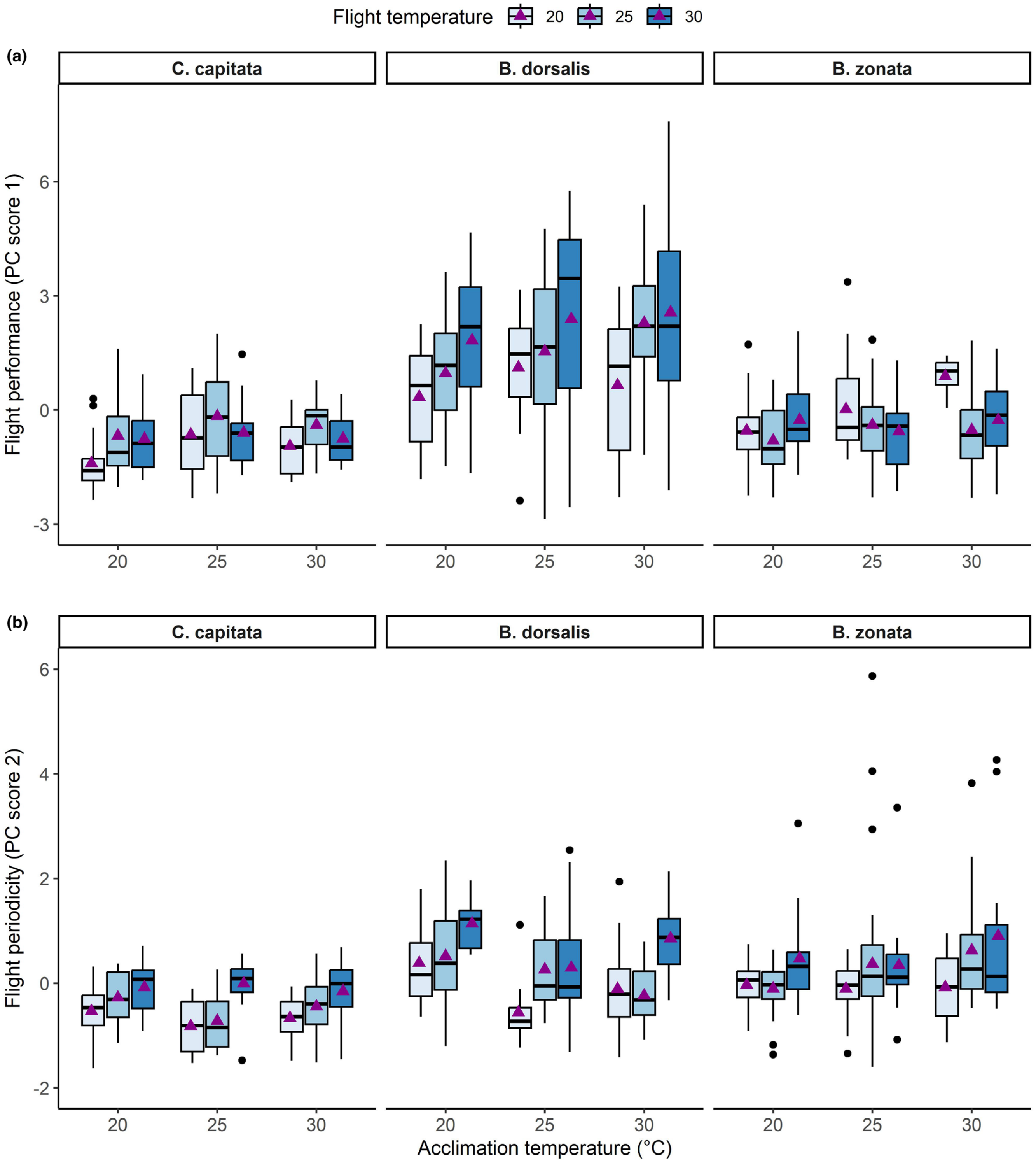

FIGURE 3 Flight performance (a) and periodicity (b) traits in females from three tephritid species acclimated at either 20, 25 or 30°C and tested at either 20, 25 or 30°C. The plotted values are the principal component scores. Each purple triangle represents the mean for each species (*C. capitata*: *n* = 15–17; *B. dorsalis*: *n* = 12–18; *B. zonata*: *n* = 4–43).

4 | DISCUSSION

We investigated whether the effects of adult acclimation at temperatures of 20, 25 or 30°C depend on the thermal environment that flies encounter when tested for flight performance and periodicity in three agricultural pest tephritid species of invasion concern. As found in a previous study, the main factor affecting flight-related traits was body mass (Malod et al., 2023), with *B. dorsalis* being the heaviest species and outperforming the others regardless of the past and current thermal environments. Overall, we observed some deleterious

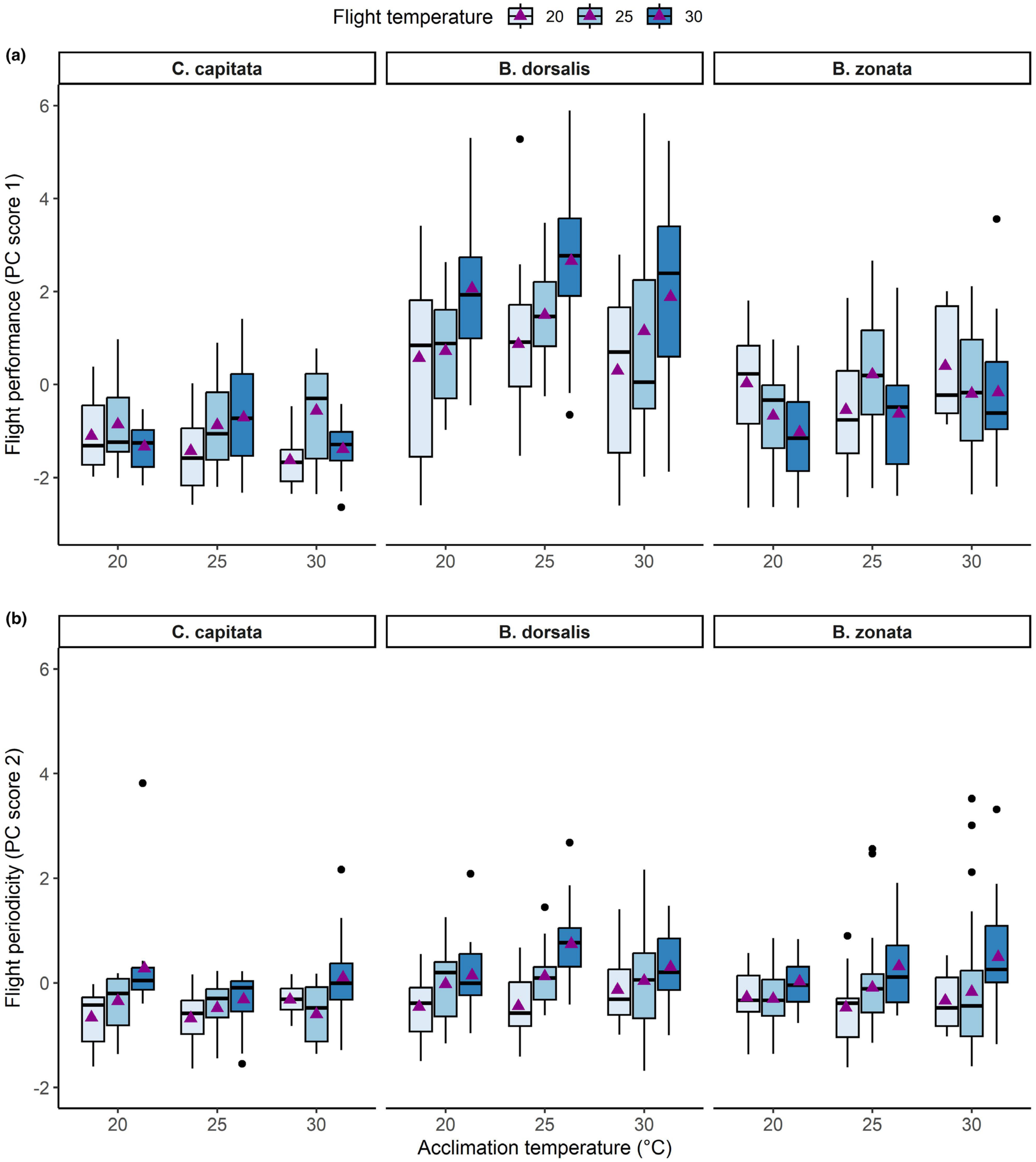

FIGURE 4 Flight performance (a) and periodicity (b) traits in males from three tephritid species acclimated at either 20, 25 or 30°C and tested at either 20, 25 or 30°C. The plotted values are the principal component scores. Each purple triangle represents the mean for each species (*C. capitata*: $n = 15–16$; *B. dorsalis*: $n = 14–17$; *B. zonata*: $n = 5–44$).

effects of low thermal acclimation, and current flight temperature explained flight performance and periodicity more often than thermal history. Furthermore, past and current temperatures rarely interacted with each other on the traits investigated. Although this study does not focus on the sexual dimorphism of thermal plasticity, we note that the effects of acclimation were often trait- and sex-specific, with the effects of thermal history only detected in *Bactrocera* females. Sex differences in thermal plasticity are often observed, without being necessarily biased towards one sex or the other (discussed in Hangartner et al., 2022; Pottier et al., 2021).

TABLE 2 Interspecific comparisons of the effects of acclimation temperature (20, 25 and 30°C) on the flight performance and periodicity at either 20, 25, or 30°C.

		χ^2	df	p	RESI [CI]
Flight performance (PC1)					
Females	Species	**124.68**	**2**	**<0.001**	**0.82 [0.64, 1.05]**
	Acclimation	**6.01**	**2**	**0.049**	**0.14 [0, 0.31]**
	Temperature	5.18	2	0.075	0.12 [0, 0.32]
Males	Species	**50.39**	**2**	**<0.001**	**0.62 [0.52, 0.75]**
	Acclimation	1.64	2	0.439	0.10 [0, 0.21]
	Temperature	0.52	2	0.769	0.11 [0, 0.23]
	Species × temperature	**34.97**	**4**	**<0.001**	**0.19 [0.11, 0.32]**
	Acclimation × temperature	9.31	4	0.054	0.11 [0, 0.24]
Flight periodicity (PC2)					
Females	Species	**30.35**	**2**	**<0.001**	**0.56 [0.43, 0.78]**
	Acclimation	0.03	2	0.982	0 [0, 0.20]
	Temperature	**8.91**	**2**	**0.011**	**0.18 [0.04, 0.32]**
	Species × temperature	**9.85**	**4**	**0.042**	**0.14 [0, 0.33]**
Males	Species	**14.72**	**0**	**<0.001**	**0.31 [0.12, 0.61]**
	Temperature	**15.59**	**2**	**<0.001**	**0.32 [0.18, 0.48]**

Note: Significant *p* values are indicated in bold, and Robust Effect Size Indexes (RESI) are reported with 95% confidence intervals.

Measuring flight performance in controlled laboratory conditions allowed us to test the different acclimation hypotheses in three species around the same physiological age (i.e., sexually maturity). Our observations do not strongly support any of the acclimation hypotheses. Acclimation at intermediate temperatures usually allowed the best performance in any environment, which aligns with the optimal acclimation hypothesis, but we also observed deleterious acclimation effects, mainly in *B. dorsalis*, as acclimation at a colder temperature lowered performance. Our observations, with mainly no effect or deleterious effects of cold or warm acclimation, contrast with field studies where both beneficial and deleterious effects of thermal acclimation were found under specific conditions (Bali et al., 2025; Boersma et al., 2019; Chidawanyika & Terblanche, 2011; Fay & Meats, 1987a, 1987b; Kristensen et al., 2008; Steyn et al., 2022). However, dispersal performance in field studies is typically estimated through the number of insects recaptured relative to the number of insects released. Due to fluctuating environmental conditions in field studies, it remains difficult to assess whether fewer insects are recaptured due to flight performance being directly reduced or if other traits, such as thermal or desiccation stress tolerance, reduce survival. Nevertheless, deleterious effects of thermal acclimation were also observed for the field performance of *B. dorsalis* (Malod et al., 2024). Furthermore, our results align with previous laboratory observations in the same three species, where certain traits associated with flight performance were negatively affected by cold acclimation when tested at 25°C (Malod et al., 2023). Here, we confirm these findings and add that the deleterious effects of cold acclimation mainly exist in *B. dorsalis*, regardless of the thermal environment currently experienced for a temperature range between 20 and 30°C. Together, these results may suggest a lack of beneficial thermal plasticity for this species, or at least in this specific population in the adult stage, as was also found for thermal limits of activity and survival (Pieterse et al., 2017). Nevertheless, in non-acclimated *B. dorsalis*, a severe decline in flight performance occurs below 20°C and above 32°C (Makumbe et al., 2020), and it may be that more pronounced effects of thermal acclimation could be observed in more extreme flight conditions outside of the temperature range used in our study. Although this remains to be tested for *B. zonata*, the lower thermal plasticity of *B. dorsalis* compared to *C. capitata* could be due to the subtropical origins of the population used. Thermal plasticity is known to vary across populations of different geographical origins for the same species of fruit fly, but this effect remains minor (Papadopoulos, Koskinioti, et al., 2024; Weldon et al., 2018). Because plasticity has a cost and depends on the predictability of the environment (Hoffmann & Bridle, 2022; Sgrò et al., 2016), in a relatively stable environment (such as tropical areas), it may be preferable to rely on basal thermal tolerance rather than maintaining the ability to respond to the thermal environment, especially if the change in phenotype is irreversible. In other ectothermic organisms such as copepods, basal thermal tolerance is higher at lower latitudes and is also negatively correlated with thermal plasticity (Bogan et al., 2024). However, the plasticity of upper thermal limits appears to be weakly correlated with latitude and environmental heterogeneity in *Drosophila* species (Sørensen et al., 2016), but similar comparisons between tephritid species have yet to be undertaken.

Flight performance and periodicity were more often affected by the current thermal environment than by the flies' thermal history. We note that flight performance was usually reduced at 20°C in all species, and flight periodicity increased at 30°C in *C. capitata* of both sexes while reducing it in *B. dorsalis* females. The results on flight performance (PC1 strongly correlated with flight distance) align with findings in *B. dorsalis*, where the distance covered was similar between 20 and 32°C (Makumbe et al., 2020). The difference in suitable temperature range between *C. capitata* and *B. dorsalis* for flight periodicity is surprising, given the geographical distribution of *C. capitata* in temperate areas, and might be linked to morphological differences. Compared to *C. capitata*, the wing morphology of *Bactrocera* species appears better suited to fly long distances (Malod et al., 2023), thus potentially reducing energetic demand when engaging in long flights, and therefore the number of breaks required to cover the same distance. Furthermore, as energy expenditure during long flights increases with higher temperatures (Parlin et al., 2023), it might be that the warm temperature exacerbated the morphological disadvantages of *C. capitata*. Higher temperatures can increase the risk of desiccation and overheating when engaging in flight activities in insects (Glass et al., 2024; Terblanche et al., 2024). As flies may also have experienced higher energy expenditure at 30°C, this may explain why *C. capitata* individuals took more breaks. Future studies should consider the link between flight-related traits in different thermal environments with water balance and metabolic rate (Grula et al., 2021; Sinclair et al., 2024).

In conclusion, we showed that mainly the current thermal environment and, to a lesser extent, thermal history can affect the flight performance and periodicity of broadly distributed pest tephritid species. However, we found that within species, past and current adult thermal environment rarely interacted with each other to affect flight-related traits (the only interactions being in *Bactrocera* species), at least in the range of temperatures and at the adult stages investigated here. This pattern shared across species may indicate that flight performance and periodicity have relatively low thermal plasticity. Overall, our observations do not strongly support any of the major acclimation hypotheses proposed. Nevertheless, some observations align with the optimal acclimation hypothesis, where the intermediate acclimation temperature (25°C) was overall the best, regardless of the thermal environment during flight. Furthermore, although *B. dorsalis* was the species most negatively affected by acclimation at the coldest temperature, this species outperformed the two others at any flight temperatures. We also found that body mass was the most important predictor of flight performance within and across species, and this might relate to differences in energy expenditure. Our results suggest that with climate change, rising average temperatures and decreases in the diurnal temperature amplitude in temperate areas will promote movement and spread of invasive tephritid species to higher latitudes. Our observations are also informative for pest management, such as determining the size of quarantine areas or ensuring field performance of sterile insects in SIT programmes. Here, we showed that flight performance, and therefore distance, is optimal if the thermal environment is around 25°C. Our results also suggest that population monitoring via trap captures will be biased by environmental temperatures, and that this effect is species dependent. Further studies on the flight performance of these species should investigate the impact of developmental acclimation, acclimation to daily fluctuating temperatures, as well as potential physiological costs, such as elevated energy requirements and water loss.

AUTHOR CONTRIBUTIONS

John S. Terblanche, Hélène Delatte, Christopher W. Weldon, Minette Karsten and Nikos T. Papadopoulos conceived the ideas and designed the methodology. Kevin Malod, Eleftheria-Maria D. Bali, Vassilis Rodovitis, Laura Moquet, Corentin Gledel, Emma Dieudonné and Evmorfia Bataka collected the data. John S. Terblanche, Hélène Delatte and Nikos T. Papadopoulos were involved in supervision. Anandi Bierman was involved in administration. Kevin Malod analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available on Figshare repository at https://doi.org/10.6084/m9.figshare.29673269.v1 (Malod et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Supplementary methods and results for Malod et al., 2025: Effects of past and current temperatures.

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