

## ORIGINAL ARTICLE

# Evidence for transient deleterious thermal acclimation in field recapture rates of an invasive tropical species, *Bactrocera dorsalis* (Diptera: Tephritidae)

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**Abstract** Knowing how environmental conditions affect performance traits in pest insects is important to improve pest management strategies. It can be informative for monitoring, but also for control programs where insects are mass-reared, and field-released. Here, we investigated how adult thermal acclimation in sterile *Bactrocera dorsalis* affects dispersal and recapture rates in the field using a mark-release-recapture method. We also considered how current abiotic factors may affect recapture rates and interact with thermal history. We found that acclimation at 20 or 30 °C for 4 d prior to release reduced the number of recaptures in comparison with the 25 °C control group, but with no differences between groups in the willingness to disperse upon release. However, the deleterious effects of acclimation were only detectable in the first week following release, whereafter only the recent abiotic conditions explained recapture rates. In addition, we found that recent field conditions contributed more than thermal history to explain patterns of recaptures. The two most important variables affecting the number of recaptures were the maximum temperature and the average relative humidity experienced in the 24 h preceding trapping. Our results add to the handful of studies that have considered the effect of thermal acclimation on insect field performance, but notably lend support to the deleterious acclimation hypothesis among the various hypotheses that have been proposed. Finally, this study shows that there are specific abiotic conditions (cold/hot and dry) in which recaptures will be reduced, which may therefore bias estimates of wild population size.

**Key words** dispersal; mark-release-recapture; sterile insects; thermal acclimation; Tephritidae

## Introduction

As ectotherms, insects rely on ambient temperature to regulate body temperature and maintain physiological functions. Therefore, insect life-history and performance traits are strongly influenced by the thermal environment.

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Different thermal environments modulate expression of traits such as development time, adult lifespan, age of sexual maturity, fecundity and fertility, stress resistance, and locomotor performance (Berger *et al.*, 2008; Kingsolver *et al.*, 2011; Telles-Romero *et al.*, 2011; Kotzé *et al.*, 2015; Marinho *et al.*, 2016; Boersma *et al.*, 2018; Weldon *et al.*, 2018; Makumbe *et al.*, 2020; Shinner *et al.*, 2020; Parratt *et al.*, 2021; Willot *et al.*, 2021). Furthermore, life-history and performance traits of insects are not only affected by current ambient temperature but also by the temperatures experienced in the past (i.e.,

thermal history). Thermal history may induce phenotypic plasticity; as such, a past thermal environment may be beneficial or detrimental to fitness (Sgrò *et al.*, 2016; Kellermann *et al.*, 2017; Mutamiswa *et al.*, 2023). Among the changes in the thermal environment associated with phenotypic plasticity, acclimation usually refers to either, a treatment via modification of an environmental factor in controlled laboratory conditions, or to the response to this treatment that results in a change (negative, neutral or positive) in a given trait (Bowler & Terblanche, 2008).

The outcome of thermal acclimation is not always predictable and various acclimation hypotheses have tried to provide a background to predict it. The beneficial acclimation hypothesis predicts that acclimation to a given environment increases performance in the same environment (e.g., acclimation to cold environment only improves performance when tested in a cold environment) (Wilson & Franklin, 2002). Alternative hypotheses to the beneficial acclimation suggest that acclimation to cold or hot temperatures will be beneficial under any thermal environment (Frazier *et al.*, 2006; Frazier *et al.*, 2008). Finally, some authors have hypothesized that intermediate environments improve performance (optimal acclimation hypothesis), or that damage may occur after acclimation to lower or higher temperatures (deleterious acclimation hypothesis) (Terblanche & Kleynhans, 2009). The effects of thermal acclimation have been well studied under laboratory conditions providing some support to each hypothesis while not necessarily excluding any of them (Huey *et al.*, 1999; Chown & Terblanche, 2006). In springtails, acclimation in the laboratory at constant or fluctuating temperatures (equal mean) have similar effects and it was suggested that, for those species, observations from the laboratory may be transferable to the field (Hoskins *et al.*, 2020). However, it is not always that simple, and often the effects of thermal acclimation on the phenotype observed in the laboratory differ when tested in the field (Kristensen *et al.*, 2008; Boersma *et al.*, 2019; Steyn *et al.*, 2022). Despite this, only a handful of studies have considered the effect of thermal treatment (acclimation or hardening) on field performance (Thomson *et al.*, 2001; Loeschcke & Hoffmann, 2007; Kristensen *et al.*, 2008; Chidawanyika & Terblanche, 2011; Boersma *et al.*, 2019; Steyn *et al.*, 2022). Several decades ago, there was interest in thermal treatments to increase fitness in *Bactrocera tryoni* mass-reared and released for control purposes (Fay & Meats, 1987a; Fay & Meats, 1987b). Those studies found beneficial effects of cold or heat treatments, but only under certain thermal environments, sometimes associated with species-specific costs of the thermal treatment (Table 1). Therefore, increasing the range of species

investigated may contribute to unraveling the effects of thermal history on phenotypic traits associated with field performance, in particular dispersal. This information can be crucial, whether it is to predict movements of pest insects under various thermal conditions, or to improve field performance of mass-reared insects for biological control programs (e.g., sterile insect technique, pollinator or parasitoid augmentation) (Sinclair *et al.*, 2022).

The oriental fruit fly, *Bactrocera dorsalis* (Hendel), is among the most destructive horticultural pests (Malacrida *et al.*, 2007; Ekesi *et al.*, 2016; EFSA Panel on Plant Health (PLH) *et al.*, 2020). The species spread outside of its native subtropical/tropical range in Asia to large parts of continental Africa, some Indian Ocean islands and Hawaii (Mutamiswa *et al.*, 2021). Modeling approaches predicted wider geographical distribution of the pest under climate change (De Meyer *et al.*, 2010; Hill & Terblanche, 2014; Gutierrez *et al.*, 2021). Although we know in the laboratory that flight performance is affected by thermal history (Malod *et al.*, 2023), current ambient temperature (Makumbe *et al.*, 2020) and physiological status (Manoukis & Carvalho, 2020), studies on the field dispersal of this species have been scarce. Field studies have only reported on how far *B. dorsalis* can disperse (Froerer *et al.*, 2010; Shelly & Edu, 2010; Shelly & Nishimoto, 2011). Thus, empirical evidence for how field dispersal of *B. dorsalis* is affected by thermal history is crucial information to complement modeling approaches. Furthermore, the sterile insect technique (SIT) is used or under consideration to be used against *B. dorsalis* in some countries (Sutantawong *et al.*, 2002; Orankanok *et al.*, 2007; Hou *et al.*, 2020; Fezza *et al.*, 2021; Diouf *et al.*, 2022), and this knowledge will be critical in optimizing its implementation. SIT programs release sterile insects *en masse* (for some fruit flies species only males are released) to mate with the wild population, cause reproductive failure and suppress population growth (Lance & McInnis, 2005). The success of the SIT method relies on the performance of the sterile flies (e.g., survival, dispersal, stress resistance, mating, postcopulatory sperm competition) in the field. Due to laboratory adaptation, the fitness of mass-reared insects can be lower than in their wild counterparts (Fezza & Shelly, 2021), especially in challenging environments (Weldon *et al.*, 2013; Mudavanhu *et al.*, 2014; Marec & Vreysen, 2019). Improving the field performance of sterile insects could reduce the number of insects that need to be released and thus the cost of SIT operations.

In this study, we aimed to gain knowledge on how thermal acclimation may benefit or hinder sterile *B. dorsalis* released in the field, but also to better understand movement of the species as a function of

**Table 1** Chronological list of studies investigating field performance in insects after warm or cold thermal treatment.

Species	Treatment	Effects	References
<i>Bactrocera tryoni</i>	Warm/cold acclimation (adults)	Increased field survival in cold acclimated flies, but negative effect in warm acclimated ones under cold conditions.	Fay & Meats (1987a); Fay & Meats (1987b)
<i>Trichogramma carverae</i>	Heat hardening (adults)	Field performance (parasitism) increased in hot conditions when heat hardened. No cost of hardening in normal conditions.	Thomson <i>et al.</i> (2001)
<i>Drosophila melanogaster</i>	Heat hardening (adults)	Beneficial effect of heat hardening under very hot field conditions. Detrimental if conditions are warm or mild.	Loeschke & Hoffmann (2007)
<i>Drosophila melanogaster</i>	Cold acclimation (adults)	Beneficial effect of cold acclimation under cool conditions. Major detrimental effect under warm conditions.	Kristensen <i>et al.</i> (2008)
<i>Cydia pomonella</i>	Warm/cold acclimation (larvae)	Cold acclimated moths recaptured more often in cold conditions. Warm acclimated moths recaptured more often under warm conditions.	Chidawanyika & Terblanche (2011)
<i>Thaumatotibia leucothreta</i>	Cold acclimation (adults)	Beneficial effect of cold acclimation under cool conditions. Detrimental or no effect under mild and warm conditions.	Boersma <i>et al.</i> (2019)
<i>Ceratitis capitata</i>	Warm/cold acclimation (adults)	Beneficial effect of cold acclimation under mild and hot conditions. Detrimental effect of warm acclimation under all conditions.	Steyn <i>et al.</i> (2022)

environmental conditions in an agricultural landscape. Using a mark-release-recapture approach typically used to study tephritid movement (Weldon *et al.*, 2014), we tested how cold and warm acclimation in adults affect recapture rates as a proxy for field performance (i.e., dispersal and survival). Based on field studies in other species (Table 1), and because it was found that acclimation at 20 °C decreases flight performance in *B. dorsalis* in the laboratory when tested at 25 °C (Malod *et al.*, 2023), we predicted that acclimation at 20 °C would be beneficial under cool field conditions, but neutral or detrimental under other conditions. Although no detrimental effects of an acclimation at 30 °C were observed in the laboratory for *B. dorsalis*, we anticipated negative effects of such acclimation in the field based on what was observed in *B. tryoni* and *Ceratitidis capitata* (Table 1).

## Materials and methods

### Fly husbandry

Cultures of *B. dorsalis* were established from wild pupae provided by Citrus Research International (Nelspruit, South Africa) from which the males were mated with laboratory adapted females (less than 15 generations). Pupae (ca. 400) were placed in insect cages (32.5 × 32.5 × 32.5 cm, BugDorm43-030, MegaView Science, Taichung, Taiwan) with unrestricted access to food (hydrolyzed yeast and sugar in separate dishes) and water (water-soaked cotton wool). The cultures were maintained at ~25 °C in a climate room (University of Pretoria, Pretoria, South Africa) with a 14 : 10 light : dark photoperiod. To create optimal mating conditions, the first and last hour of the light phase simulated dawn and dusk with 8 W fluorescent tubes (T4, Eurolux, Sandton, South Africa) that were placed obliquely to the fly culture and turned on before, and turned off after, the main room lights. The remaining room lights, comprising a combination of 20 W (G5, Eurolux, Sandton, South Africa) and 58 W (58W/840, Osram, Germany) fluorescent tubes were also turned on for the remainder of the light period. Each new generation was obtained by allowing females of 20–40 d of age to lay eggs into a 125 mL plastic container (Plastilon, South Africa) covered with a layer of laboratory film (Parafilm M, Bemis, USA) pierced several times with a pin. Tissue paper soaked with 3 mL of guava juice concentrate (Hall's, Tiger Consumer Brands Limited, Bryanston, South Africa) and a slice of guava fruit were placed in the plastic container to provide volatile cues that encouraged females to oviposit through the film. Eggs were then washed out of the artificial

oviposition substrate with water and placed on 125 mL of a carrot-based larval rearing medium in a plastic container at an approximate density of 2.5 eggs/mL of medium. The container of larval rearing medium was then placed in a 2 L plastic box with a layer of sand and a ventilated lid. After 15 d, during the pupal phase, the sand was sifted and the collected pupae were placed in a Petri dish (ø 65 mm) in an insect cage (32.5 × 32.5 × 32.5 cm) to develop to the brown eye stage (48 h before adult emergence; Resilva & Pereira, 2014). They were then transported by road to the National Institute for Communicable Diseases (Johannesburg, South Africa), where they were placed in a rigid container and received a gamma radiation dose of 100 Gy in normoxia from a cobalt-60 source (see Table S1 for dose rates). This procedure reproductively sterilized both females and males (Yusof *et al.*, 2019), and was required due to *B. dorsalis* being an invasive pest under official control in South Africa. After irradiation, the pupae were immediately returned to the University of Pretoria where they were marked with 2 g/L of fluorescent pigment (Lazer red 3, Blaze 5, Comet blue 60, Lunar Yellow 27; all supplied from Swada, UK) and transferred (in equal numbers, ca. 400–2000 per container depending on replicates) to three (one for each treatment) 38.5 L transparent plastic containers (Plastilon, South Africa) for adult emergence. All containers were fitted with nets in their walls to allow ventilation, and emerged adults had unrestricted access to food and water. The containers remained in the same climate room at 25 °C until adults reached 6 d of age. Experimental flies were produced as above, 4–15 generations after crossing laboratory males with the wild females provided by Citrus Research International.

### Acclimation

Acclimation treatments started when flies were 6 d old, because insect flight muscles undergo maturation during the adult stage (Klowden, 2013), and ultrastructure of those muscles allows peak flight performance around 2 weeks of age in *B. dorsalis* females reared at 25 °C (Chen *et al.*, 2015). Flies were acclimated in climate rooms for 4 d by placing the 38.5 L containers at either 20, 25, or 30 °C. Other studies have shown an effect of acclimation treatment after fewer than 4 d (Nyamakondiwa *et al.*, 2010; Malod *et al.*, 2023). We extended the acclimation treatment to 4 d because the flies were to be monitored for 21 d after field release, and an extended treatment duration can in some cases slow the reversal of the effects of thermal acclimation (Hoffmann & Bridle, 2022).

### Mark release recapture

When 10 d old, sterile females and males were released in an agricultural environment at the Innovation Africa campus of the University of Pretoria, South Africa. This environment includes commercial orchards such as citrus (Navel oranges, Eureka lemons), avocados (Fuerte, Hass), pecan nuts (Wichita, Choctaw), deciduous fruits (peaches, plums, apricots, nectarines, pears and apples in a mixed orchard), nuts (almonds), as well as wild host plants such as the marula (*Sclerocarya birrea*). Wild *B. dorsalis* have been previously observed in this environment, and other tephritid species (*Ceratitis quilicii*, and *Dacus* species) were also trapped during the experiment. Release at an age of 10 d was done to align with the onset of sexual maturity and responsiveness of male *B. dorsalis* to one of the lures used in traps (Shelly *et al.*, 2008). On the day of release, all acclimation treatment groups were released at the same time by removing the lid of the plastic containers, which were kept open for 1 h. After release, lids were closed and plastic containers were returned to the laboratory. The number of flies that did not leave the container was counted. Then a 10 mL volume subsample of pupae was sorted to estimate the number of flies that did not emerge. With these numbers we calculated the number of flies that were released in the field for each replicate and temperature group as well as the proportion released (percentage of flies leaving the container) (Table S2).

For the mark-release-recapture approach, we used a grid array (Fig. S1) as recommended by Weldon *et al.* (2014) to investigate tephritid fly movement as a function of abiotic factors. As records of tephritid movement in mark-release-recapture studies are usually under 1 km, we did not focus on maximum distance and the furthest trap was located at 1 km from the release point. A total of 28 yellow bucket traps were deployed. Each trap contained a block of insecticide (Vapona dichlorvos, Acorn group, South Africa) and a lure. Traps were baited with either methyl eugenol ( $n = 6$ ) (Chempac, South Africa), BioLure ( $n = 16$ ) (Chempac, South Africa) or a combination of both for traps off the grid ( $> 500$  m from the release point,  $n = 6$ ). Two lures were used to recapture both females and males, with methyl eugenol being a strong male attractant and BioLure able to attract both sexes (Manoukis *et al.*, 2018; Chailleux *et al.*, 2021). Depending on the available vegetation, traps were hung between 1.2 and 2 m in height. To measure the temperature and the relative humidity at a 10 min interval over the entire duration of each replicate, nine data loggers (iButton, Maxim Integrated, USA) were deployed over three locations. The sensors were placed at the release point as well as at the most southern and northern traps on the

trapping grid. Each location had three sensors, each protected by a 3 D-printed white Stevenson screen (3 pieces of polyactic acid with the sensor placed under the middle one, designed obtained from thingiverse.com), with one placed close to the ground, one placed at about 1.5 m and one at 2.5 m from the ground. The weather variables extracted from the data loggers were: daily average temperature, daily average maximum temperature, daily maximum temperature, daily average minimum temperature, daily minimum temperature, daily average relative humidity (RH), daily average maximum RH, daily maximum RH, daily average minimum RH, and daily minimum RH. The nonaverage maxima and minima correspond to the lowest or highest values recorded in the last 24 h across all data loggers. For the other parameters, the daily average was calculated from all the data loggers. Traps were inspected every day during the first week, starting from the first day after release. After 7 d, traps were inspected every second day until day 21 (one replicate = 3 weeks). Trapped flies were taken back to the laboratory, and for each fly, the sex and pigment color was determined. Pigment color was identified using a UV lamp under a stereomicroscope (Olympus, Japan) in a completely dark room. Flies for which the treatment group could not be identified were not included in the counts. A total of seven releases were completed between 2020 and 2022 (summary of the weather variables 24 h after release and for the entire duration of the experiment are in Tables S3 and S4), not earlier than September and not later than April to avoid low temperatures during the South African winter which would limit flights (Makumbe *et al.*, 2020).

### Statistical analyses

All statistical analyses were performed in R software (v 4.2.1, The R Foundation for Statistical Computing). Because very few females were recaptured, we pooled both sexes together.

To detect whether flies acclimated at different temperatures are differently motivated to disperse we used a generalized linear model. Replicate was not added as a random effect because there were only three data points (one for each acclimation treatment) per replicate (Bolker *et al.*, 2009). To model the response variable we used the function `cbind()` to add to the same vector the number of flies that left the container and the number of flies that did not as recommended by Crawley (2013) for this type of data analysis. The acclimation treatment was added to the model as a fixed effect and to correct for overdispersion a quasibinomial family was used.

Due to a large number of traps that recaptured no flies, as is usually the case in dispersal studies (Lemke *et al.*, 2019; Francis *et al.*, 2023), we used hurdle models to account for the zero recaptures (Feng, 2021). To correct for overdispersion the hurdle models were built with a negative binomial distribution. Hurdle models have two components, one that tests the factors that may affect the count data (count component), and one component that may identify the factors driving the presence or absence of flies in the traps (Hurdle component). In other words, the first component focuses on how many flies were recaptured, taking only the positive observations into account, and the second component focuses on the probability to have zero recaptures in a trap.

We first analyzed the various factors on the entire period of trapping (21 d). We tested in a first model the effects of thermal acclimation, distance (distance of the trap from the release point) and day (day of capture after release), as well as their interactions. As a large majority of the recaptures were in the methyl eugenol baited traps (Table S5), lure type was not included in the models. We added to the model the number of flies recaptured as the response variable, and to account for the difference in number of flies released, the number of flies released for each temperature group per release was added as a covariate (without interactions). The weather variables (no interaction added) were tested in a second separate model, and once again the number of flies released per temperature group in each release was accounted for. In a third model, the effects of thermal acclimation and weather variables (detected in the second model) that had a significant effect on the count of recaptured flies as well as their interaction with the acclimation treatment were tested. The number of flies released per temperature group and per release was once again added as a covariate. A generalized linear model with a negative binomial distribution was used in this case. In each model, the 25 °C acclimation group was set as the reference level.

As most of the recaptures happened during the first week of trapping, we also analyzed the effects of the various factors on the first 7 d, as above. Since no weather variable significantly explained the variation in the recapture counts for the first 7 d, we did not run a third model.

## Results

### *Proportion released*

There was no effect of the acclimation treatment ( $\chi^2 = 0.19$ ,  $df = 2$ ,  $P = 0.908$ ) on fly motivation to leave the release container. For each thermal acclimation group,

**Table 2** Estimates from the hurdle model for the effects of acclimation treatment, day of recapture and distance on the number of flies recaptured over a period of 21 d. The 20 and 30 °C acclimation groups are compared to the 25 °C control group. For each replicate, the number of flies released per acclimation treatment was added to the hurdle model as a covariate. Bold values are the significant estimates.

	20 °C	30 °C
<i>Hurdle component</i>		
Day	−0.0001	−0.0002
Distance	−0.0001	−0.0002
Number released		0.0006
Distance × Day	0.0001	0.0001
<i>Count component</i>		
Day	0.0028	−0.1017
Distance	<b>−0.0067</b>	<b>−0.0059</b>
Number released		0.0001
Distance × Day	<b>0.0006</b>	0.0007

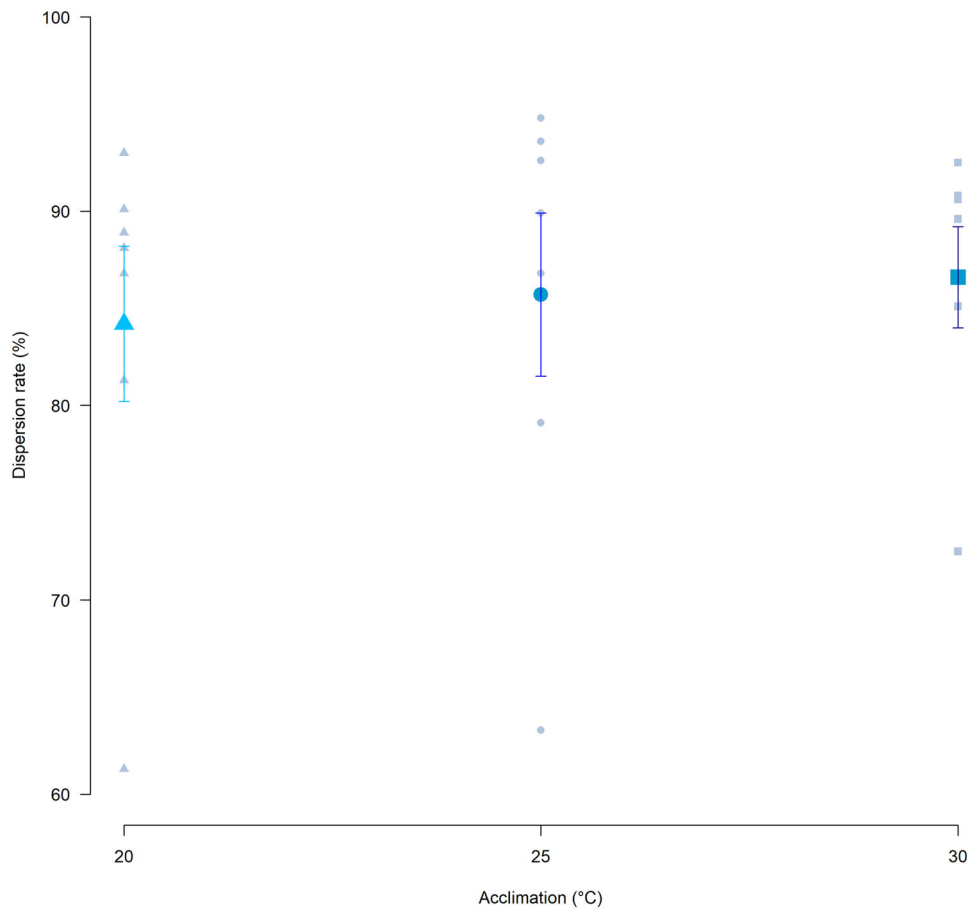
the same proportion of flies (ca. 85%) left the container within the 1-h window after opening the lid (Fig. 1).

### *Trapping over 21 d*

There was a significant interaction between acclimation temperature and distance of recapture. Fewer flies from the 20 and 30 °C groups were recaptured close to the release point (Table 2) when compared with the 25 °C control group (Fig. 2). There was also a significant interaction between day of recapture and distance when comparing the 20 °C to the control group. This is because in the first 3 d, more flies from the control group were recaptured close to the release point in comparison with the 20 °C group (Fig. S2). No factors considered in our models explained the absence of recaptures.

Only two weather variables significantly affected the number of flies recaptured (Table 3). The count model indicated that the number of flies that were recaptured decreased when daily maximum temperature and average RH increased (Table 3). The hurdle model showed that the chance of recapturing more than zero flies in a trap increased as average maximum temperature, daily maximum RH, average minimum RH and the number of flies released increased.

No effect of thermal acclimation was detected when the two significant weather variables were added to the model (Table 4). Furthermore, there was a significant positive interaction between daily maximum temperature and average RH indicating that there were specific weather



**Fig. 1** Percentage of flies released from containers within 1 h after acclimation at either 20, 25, or 30 °C. The large triangle (20 °C), circle (25 °C), and square (30 °C) represent the mean across the seven releases and the error bars represent the standard error to the mean. Each light gray triangle, circle, or square represents one release for each temperature group.

conditions favorable for an improved number of recaptures (see purple areas in Fig. 3).

#### Trapping over 7 d

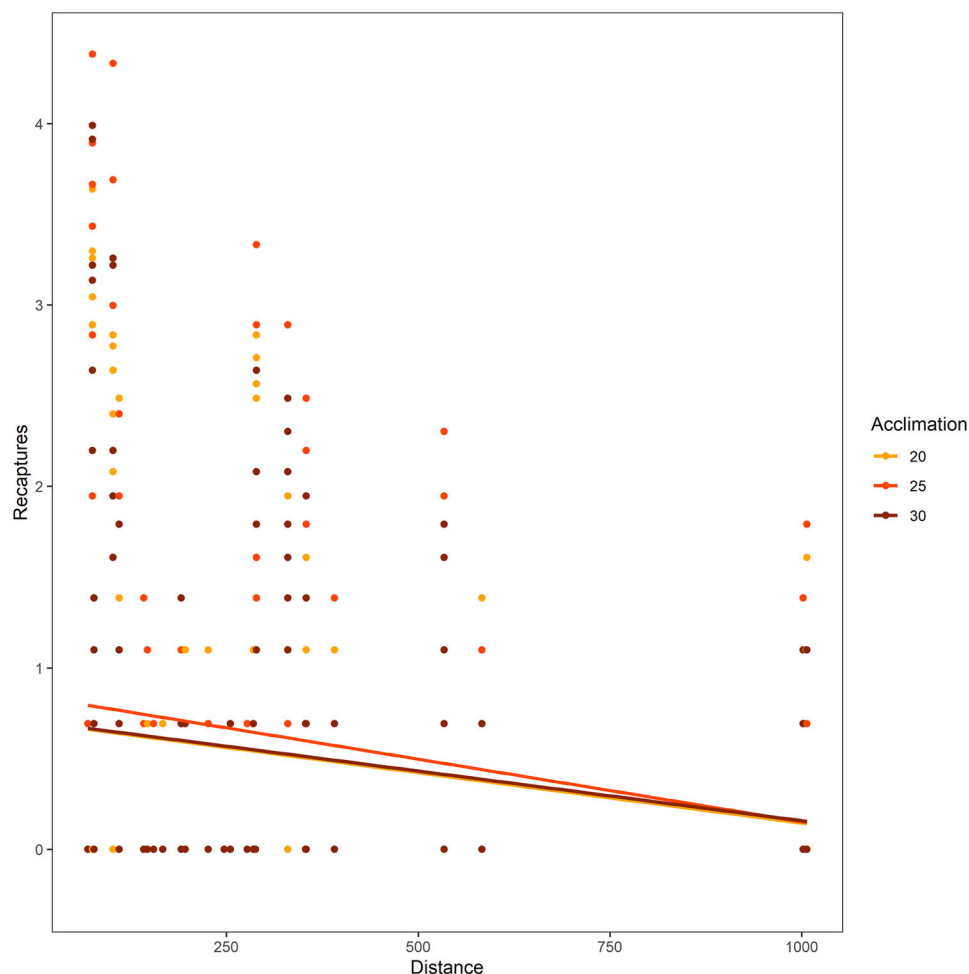
As observed previously over a 21-d period, fewer flies from the 20 and 30 °C groups were recaptured in comparison with the 25 °C group in the vicinity of the release point when focusing on the 7-d period after release (Table 5). During this period, slightly more flies were recaptured as the number of flies released per acclimation treatment increased. The probability of recapture (hurdle component) was only positively affected by the number of flies released (Table 5).

None of the weather variables affected the number of flies recaptured when only the first 7 d were considered (Table 6). However, the probability of recapture was

higher as the highest RH recorded for the last 24 h increased but was lower as daily average maximum RH increased (Table 6).

#### Discussion

Here we investigated how adult thermal history affects field performance of sterile *B. dorsalis* released in an agricultural environment. In partial alignment with our predictions, we found that acclimation at 30 °C, and particularly at 20 °C, can have negative effects, as fewer flies were recaptured close to the release point in comparison with the control group, but no beneficial effects were found. Nevertheless, there was no detectable difference between acclimation treatments in the motivation to leave the release container and disperse. Furthermore, we found that the negative effects of low or high acclimation



**Fig. 2** Distance (m) of recapture ( $\log n + 1$ ) over a 21-d period of flies acclimated at either 20, 25, or 30 °C. Each temperature group has 7 replicates plotted.

temperatures only affected recaptures in the first week of sampling. Over a 3-week period, the weather variables, and in particular maximum temperature and average relative humidity, were more important to explain the absence or the number of flies recaptured.

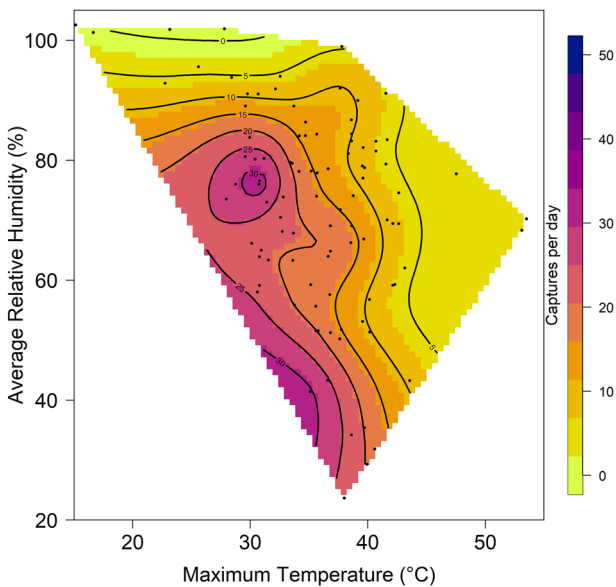
Our results support the deleterious and optimal acclimation hypotheses predicting that acclimation temperatures below and above optimal temperature for the insect could result in negative effects on recapture rates. This aligns with findings in other insect species (Table 1) where deleterious effects of low or high acclimation temperatures were observed under specific conditions in the field (Fay & Meats, 1987a; Fay & Meats, 1987b; Loeschcke & Hoffmann, 2007; Kristensen *et al.*, 2008; Boersma *et al.*, 2019; Steyn *et al.*, 2022). However, in these same studies and others (including two tephritid fruit fly species; Table 1), there was always a combination

of acclimation temperature and environmental temperature leading to beneficial effects of low or high acclimation temperatures, which in contrast to our findings supports the beneficial acclimation hypothesis. Thus, our study is the first one to report detrimental, albeit transient, effects of thermal acclimation in field conditions. This could be due to a lower thermal plasticity of *B. dorsalis* in comparison with close relative species (Pieterse *et al.*, 2017), but also to the timing of the acclimation treatment. In our study adult acclimation and field release took place in older flies than in the other species tested, and future effects of the thermal environment can differ depending on the life stage but also adult age of exposure (Bowler & Terblanche, 2008; Zhang *et al.*, 2015). Nevertheless, our field observations could also differ from the other studies due to the environmental conditions that *B. dorsalis* encountered in the field. In our study,



**Table 3** Estimates of the hurdle model for the effects of weather variables on the number of flies recaptured over a period of 21 d. For each replicate, the number of flies released per acclimation treatment was added to the hurdle model as a covariate. Bold values are the significant estimates.

	Hurdle	Count
Average temperature	0.0802	0.1589
Average maximum temperature	<b>0.1804</b>	0.0103
Maximum temperature	<b>-0.0892</b>	<b>-0.0965</b>
Average minimum temperature	-0.1245	-0.0025
Minimum temperature	0.0574	-0.1102
Average RH	<b>-0.0421</b>	<b>-0.0672</b>
Average maximum RH	-0.0104	0.0012
Maximum RH	<b>0.0372</b>	0.0301
Average minimum RH	<b>0.0559</b>	0.0489
Minimum RH	-0.0177	0.0066
Number released	<b>0.0008</b>	-0.0001



**Fig. 3** The effects of daily average relative humidity and daily maximum temperature on the number of flies recaptured per day over a period of 21 d. The color gradient indicates low (yellow) or high (purple) number of flies recaptured. The black dots represent the recapture observations for a given temperature and RH.

the average daily temperatures encountered by the flies across the seven releases were mainly mild to cold (Table S4). Although flies faced high temperatures during the day in some releases, there was for example no release that was characterized by consistently warm weather. It might be that when facing a heat wave, one of the thermal

acclimation treatments could have been beneficial as was the case for other species (Table 1). For example, in field released *D. melanogaster*, the benefits of warm thermal acclimation were only observed in extremely hot conditions but not in mild ones, and negative effects were also noted in cool weather (Loeschke & Hoffmann, 2007). The detrimental effect of thermal acclimation may reflect a cost of the physiological mechanisms involved in the plastic response, and perhaps a trade-off between dispersal performance and thermal tolerance.

The negative consequences of thermal acclimation in *B. dorsalis* were only detectable in the first week following release. This could be an artifact of an overall lower number of recaptures after the first week, which could have masked the differences between groups. However, it could also reflect a reversibility of the phenotype with time (Hoffmann & Bridle, 2022). Furthermore, Hoffmann & Bridle (2022) also suggest that adult acclimation, which was used in the current study, is more reversible than developmental acclimation. It might be that the beneficial effects of thermal acclimation, usually observed in other species, are rapidly lost in *B. dorsalis*. Within 1 d, rapid reversal of thermal acclimation on thermal tolerance was also observed in other tephritid species, *C. capitata* and *C. rosa* (Weldon *et al.*, 2011), as well as *B. tryoni* (Meats, 1973). Furthermore, it was also shown in the two *Ceratitis* species that the phenotype following thermal acclimation may be modified depending on the new thermal conditions encountered shortly after acclimation (Nyamukondiwa & Terblanche, 2010). Thus, the sterile *B. dorsalis* tested in our study may have encountered field conditions upon release that modified the effect of thermal acclimation.

Considering the results of the current study, thermal acclimation above or below the standard constant temperature for rearing does not prepare sterile males for field conditions within the few days following release. The lower number of recaptures in acclimated flies does not seem to correlate with willingness to move as we found no differences between groups in the proportion of flies leaving the release container. Therefore, differences in recaptures could be explained by decreased survival or dispersal as well as a combination of both. Previous observations in the laboratory support the idea of reduced dispersal, with flight performance of thermally acclimated (20 and 30 °C) *B. dorsalis* decreasing when tested at 25 °C (Malod *et al.*, 2023). If dispersal is reduced, sterile males may be less effective at finding and mating with wild females, which would decrease the effectiveness of SIT programs. However, for *B. dorsalis* sterile males are usually released in the field close to sexual maturity, and if acclimation takes place earlier during the adult stage,

**Table 4** Effects of acclimation treatment, daily maximum temperature, and daily average relative humidity on the number of flies recaptured over a period of 21 d. For each replicate, the number of flies released per acclimation treatment was added to the model as a covariate.

	$\chi^2$	df	P
Acclimation	2.62	2	0.269
Maximum temperature	<b>28.28</b>	<b>1</b>	<b>&lt; 0.001</b>
Average RH	<b>28.16</b>	<b>1</b>	<b>&lt; 0.001</b>
Number released	<b>38.06</b>	<b>1</b>	<b>&lt; 0.001</b>
Acclimation $\times$ Maximum temperature	2.47	2	0.291
Acclimation $\times$ Average RH	1.97	2	0.373
Maximum temperature $\times$ Average RH	<b>23.94</b>	<b>1</b>	<b>&lt; 0.001</b>
Acclimation $\times$ Maximum temperature $\times$ Average RH	1.82	2	0.401

Bold values are the significant p values ( $p < 0.05$ )

**Table 5** Estimates of the hurdle model for the effects of acclimation treatment and distance on the number of flies recaptured over a period of 7 d. The 20 and 30 °C acclimation groups are compared to the 25 °C control group. For each replicate, the number of flies released per acclimation treatment was added to the hurdle model as a covariate. Bold values are the significant estimates.

	20 °C	30 °C
<i>Hurdle component</i>		
Acclimation $\times$ Distance	-0.0005	-0.0001
Number released	<b>0.0006</b>	
<i>Count component</i>		
Acclimation $\times$ Distance	<b>-0.0054</b>	<b>-0.0042</b>
Number released	<b>0.0004</b>	

**Table 6** Estimates from the hurdle model for the effects of weather variables on the number of flies recaptured over a period of 7 d. For each replicate, the number of flies released per acclimation treatment was added to the hurdle model as a covariate. Bold values are the significant estimates.

	Hurdle	Count
Average temperature	0.1417	0.3675
Average maximum temperature	0.0203	-0.1977
Maximum temperature	-0.0301	0.0416
Average minimum temperature	-0.1296	0.0877
Minimum temperature	0.0723	-0.2875
Average RH	-0.0201	-0.4954
Average maximum RH	<b>-0.0243</b>	0.0032
Maximum RH	<b>0.0365</b>	0.0089
Average minimum RH	0.0233	0.0176
Minimum RH	-0.0107	0.0441
Number released	<b>0.0008</b>	0.0003

the deleterious effects of the acclimation treatment may not be problematic for field performance if there is reversal within a week. But, if other traits benefit from the acclimation treatment, it could balance out the negative effects of thermal acclimation on dispersal and increase overall fitness. Guo *et al.* (2023) found that cold acclimation improves cold tolerance in *B. dorsalis*. In addition, studies in other insect (Terblanche & Chown, 2006; Chidawanyika & Terblanche, 2011; Boersma *et al.*, 2018) and tephritid species (Fay & Meats, 1987a; Fay & Meats, 1987b; Weldon *et al.*, 2011; Ben-Yosef *et al.*, 2021) indicate that thermal acclimation can improve traits such as starvation resistance, thermal tolerance, survival and desiccation resistance. Better performance in those traits via thermal acclimation could improve field performance of sterile males, but this remains to be tested in *B. dorsalis*.

For the overall period of trapping, we found that abiotic factors experienced in the field were stronger predictors than acclimation treatment to explain recapture numbers and the probability of recapture. The maximum temperature and average relative humidity were the two main variables explaining the number of recaptures. Recaptures decreased with higher average humidity and maximum temperature experienced in the prior 24 h. Furthermore, we observed that there were specific combinations of relative humidity and peak temperature where recaptures were higher. More flies were recaptured following a day with a maximum temperature around 30 °C and an average relative humidity around either 40% or 75%. Our models also indicated that there is a higher probability of recapturing flies on warm and humid days, with cold and warm dry days having the lowest probabilities. On the one hand, this could be due to the optimal flight temperature for *B. dorsalis*, with short flights being possible in the 12–36 °C range, but long distance flight

optimized between 20 and 24 °C (Makumbe *et al.*, 2020). On the other hand, Inskip *et al.* (2021) have shown in another tephritid species *B. tryoni*, that flies adjust their location in the canopy as a function of environmental conditions, probably to avoid thermal and hydric stress. A similar behavior might explain our recapture patterns, with flies avoiding changing location under stressful conditions. Having evolved in a tropical climate, *B. dorsalis* is probably more challenged by high and low temperatures in dry conditions than other fruit fly species that adapted to subtropical climates. In addition, Pieterse *et al.* (2017) suggest that thermal plasticity of *B. dorsalis* is lower than for species in the genus *Ceratitidis*. Other studies on the seasonality of trapping in wild *B. dorsalis* have also reported higher number of recaptures following warm and humid days, most likely because populations of this species grow during the rainy season (Vayssières *et al.*, 2009; Adzim *et al.*, 2016; Theron *et al.*, 2017). With very precise recording of temperature and humidity, as well as a known size of the population, our study confirms the importance of relative humidity and temperature on trapping and movement patterns in *B. dorsalis*. Our observations also indicate that there are specific environmental conditions that should be preferred when releasing mass-reared *B. dorsalis* to optimize dispersal. In particular, hot and dry as well as cold and humid field conditions may reduce movements of the released insects. Further abiotic factors, such as wind direction, which can affect recaptures of sterile males (Chailleux *et al.*, 2021), should be investigated to better understand *B. dorsalis* movement and improve monitoring.

In conclusion, we showed that low and high temperatures experienced in the past can have a negative effect on flight and dispersal of *B. dorsalis*, but that this can be transient. These observations support the deleterious acclimation hypothesis, with optimal intermediate temperature being more suitable for adults. Considering the current observations, we suggest that adult thermal acclimation at constant temperature below or above standard rearing temperatures may not be effective to prepare sterile males for field conditions in this species, as it seems to hinder its dispersal. However, further studies should also investigate the effect of thermal acclimation with sterilization under hypoxic conditions to reduce irradiation-induced damage (López-Martínez & Hahn, 2014). Our results also suggest that freshly experienced field conditions, in particular maximum temperature and average relative humidity, explain better the patterns of recapture in this species than past thermal environment. These results provide important baseline information in the determination of spread of *B. dorsalis* in a new area. Our observations suggest that a couple of successive

days with cold or hot average temperatures could lead to a decrease in the number of catches and therefore be misrepresentative of the actual size of the wild population. Likewise, population size might be underestimated when current field conditions are dry with cold or hot temperatures (or overestimated in optimal weather conditions), and methods such as the male annihilation technique may become less effective if fewer wild males travel to the attractants used with this control method. Furthermore, releasing sterile males in those environmental conditions may reduce their movements and their ability to find wild females.

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## Disclosure

The authors declare no conflicts of interest.

## Data availability statement

Data are available on Figshare repository at <https://doi.org/10.6084/m9.figshare.26132212.v1>.

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## Supporting Information

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

**Fig. S1** Grid array with the location of the methyl eugenol (red triangles) and BioLure (yellow triangles) baited traps.

**Fig. S2** Distance of recapture ( $\log n + 1$ ) at different time intervals in flies acclimated at either 20, 25, or 30 °C.

**Table S1** Irradiation dose rates for each replicate calculated on the irradiation time needed to reach a 100 Gy dose.

**Table S2** The number of flies released into the field and the proportion released (percentage of flies leaving the container) for each replicate and acclimation treatment.

**Table S3** Temperature (°C) and relative humidity (%) summary of the weather conditions experienced by the flies in the first 24 h following release.

**Table S4** Temperature (°C) and relative humidity (%) summary of the weather conditions experienced by the flies over the 21 d release period.

**Table S5** Total number of flies captured in each replicate as a function of the type of trap.