1 DO THERMAL TOLERANCES AND RAPID THERMAL RESPONSES CONTRIBUTE TO
2 THE INVASION POTENTIAL OF *BACTROCERA DORSALIS* (DIPTERA: TEPHRITIDAE)?

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ABSTRACT

Bactrocera dorsalis (Hendel) (Diptera: Tephritidae) has shown remarkable range expansion over the past 10 years and invaded several new continents including Africa. Here we report results of a detailed assessment of acute high and low temperature survival ability and the plasticity thereof, to test the hypothesis that traits of the thermal niche have contributed to the species' invasion ability. We also assess life-stage-related variation of thermal tolerances to determine potential stage-related environmental sensitivity. The temperatures at which c. 20% of the population survived of *B. dorsalis* were determined to be -6.5°C and 42.7°C, respectively, when using 2 h exposures. Further, four life stages of *B. dorsalis* (egg, 3rd instar larvae, pupae and adults) were exposed to high and low discriminating temperatures to compare their thermal survival rates. The egg stage was found to be the most resistant life stage to both high and low temperatures, since 44±2.3% survived the low and 60±4.2% survived the high discriminating temperature treatments respectively. Finally, the potential for adult hardening responses to mediate tolerance of extremes was also considered using a diverse range of acute conditions (using 2 h exposures to 15°C, 10°C and 5°C and 30°C, 35°C, 37°C and 39°C as hardening temperatures, and some treatments with and without recovery periods between hardening and discriminating temperature treatment). These showed that although some significant hardening responses could be detected in certain treatments (e.g. after exposure to 37°C and 39°C), the magnitude of this plasticity was generally low compared to two other wide-spread and more geographically-range-restricted con-familial species, *Ceratitis capitata* and *C. rosa*. In other words, *Bactrocera dorsalis* adults were unable to rapidly heat- or cold-harden to the same extent as the other *Ceratitis* species examined to date. These results suggest a narrower thermal niche in *B. dorsalis* compared to these *Ceratitis* species - in both basal and plastic terms - and suggests that its geographic distribution might be more restricted in consequence.

Keywords: Environmental stress resistance; niche breadth; adaptation; range limits

1. Introduction

The true fruit flies (Tephritidae) are destructive pests of many fruits and vegetables and are of quarantine importance for the export market (Ekesi *et al.* 2007). The invasive oriental fruit fly *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) is of Asian origin and was first detected in Kenya in 2003 (Lux *et al.* 2003). It has showed a remarkably rapid invasion of the African continent (Drew *et al.* 2005) raising questions surrounding its environmental niche breadth (De Villiers *et al.* 2015) and possible climate change responses (Hill *et al.* 2016). First described as *B. invadens* when it arrived on the African continent in 2005 (Drew *et al.* 2005), it was subsequently synonymized with *B. dorsalis* (Hendel) (Schutze *et al.* 2015a) and re-described by Schutze *et al.* (2015b).

Currently *Bactrocera dorsalis* occurs in the northern and eastern parts of South Africa, with the Western Cape Province still free of *B. dorsalis* (Manrakhan *et al.* 2015) and therefore poses a significant risk to this large, productive deciduous fruit growing region. The presence of *B. dorsalis* in this province will have a serious impact on the export of fruit, as well as hamper fruit fly management strategies.

Extreme temperatures can be detrimental to insects (and other ectotherm) populations either through indirect effects such as activity constraints, or through direct effects including, for example temperature-induced sterility and cellular or tissue injury, resulting in functional limits or mortality (discussed in e.g. Sinclair *et al.* 2012, Andrew and Terblanche 2013). For insects, extreme temperatures can be a significant factor determining population dynamics (reviewed in Terblanche *et al.* 2011; 2015) but understanding when and where such constraints might exist requires foregoing knowledge of a species' thermal tolerances, with due consideration of life-stage-related variation (Bowler and Terblanche 2008). Given that insect populations may cope with thermal extremes using a diverse array of mechanisms and strategies (Andrew and Terblanche 2013), it is also critical that some understanding of phenotypic plasticity of these acute tolerances is obtained (Sgro *et al.* 2016).

The temperature tolerances for *B. dorsalis* adults and immature stages have been explored previously (e.g. Vargas *et al.* 1996; 1997, Ekesi *et al.* 2006, Chen *et al.* 2006, Rwomushana *et al.* 2008, Ye and Liu 2005). Survival, reproduction and longevity under different temperature regimes are important factors to consider when fruit flies are accidentally introduced into new areas and likely form a critical part of the invasion process (i.e. overcoming a key population establishment barrier). For example, extreme high temperatures (minimum temperature of 24°C and maximum temperature of 35°C) reduced the population growth of *C. capitata*, *B. dorsalis* and *B. cucurbitae* and was more limiting for establishment than lower temperatures (Vargas *et al.* 2000). The ability to rapidly alter tolerance and survival through phenotypic plasticity (physiological adjustments) may also improve the survival capacity of a species introduced to a novel environment, as illustrated for Tephritidae by Nyamukondiwa *et al.* (2010) with *C. capitata* relative to *C. rosa*. The ability to survive low temperatures was markedly improved after pre-treating *C. capitata* and *C. rosa* for 2 h at 5°C and 10°C. The survival of *C. capitata* increased after pre-treatment at 0°C and 35°C, but a full (100% survival) hardening response was not achieved (Nyamukondiwa *et al.* 2010). There was a marked difference in the speed and duration of the low temperature plastic responses of these two species which could manifest as an improvement in population survival upon exposure to fluctuating low temperatures in which the opportunities to harden occur intermittently. However, the importance of plastic hardening responses across a wider range of Tephritidae has generally been poorly examined (Nyamukondiwa *et al.* 2010). Hu *et al.* (2014) showed that *B. dorsalis* possess a heat hardening response at 35°C, 37°C, 39°C and 41°C; and has a wider distribution range as well as a higher thermal plasticity than *B. correcta*. However, *B. dorsalis*' thermal responses relative to other economically-important Tephritidae in South Africa has been

poorly explored to date and is essential to understand the relative risks of establishment and population persistence if accidentally introduced in this growing region.

Various niche or distribution models (Stephens *et al.* 2007, Hill and Terblanche 2014, De Villiers *et al.* 2015) predict the spread of *B. dorsalis* to areas further south within South Africa. This region (specifically, the Western Cape Province of South Africa) has a warm, temperate climate, with cool, wet winters and hot, dry summers. According to De Meyer *et al.* (2010), *B. dorsalis* prefers hot and humid environments, but can survive dry seasons. *Bactrocera dorsalis* was observed in areas of West Africa, the Sudan and Zambia where the climate has longer dry periods and hot conditions prevail during part of the year (De Meyer *et al.* 2010). Physiological traits and genetic adaptation to new host plants might also influence the ability of *B. dorsalis* to establish in areas predicted to be suitable and thus alter its fundamental niche during invasion (Hill and Terblanche 2014). Climate change might not increase the possibility of *B. dorsalis* to establish in the Western Cape (Hill *et al.* 2016), but the adaptive capacity of traits of the flies' thermal performance and survival will likely influence its ability to invade a new environment (Sinclair *et al.* 2012, Sgro *et al.* 2016).

The aims of this study were therefore to determine acute temperature survival rates for several key life-stages of *B. dorsalis*, and to determine whether *B. dorsalis* have acute plasticity (i.e. can rapidly cold- or heat-harden (RCH or RHH, respectively)) that might aid their survival and population establishment in this geographic region, which is generally considered less favorable (De Meyer *et al.* 2010, De Villiers *et al.* 2015). The colony of flies we used for our experiments came from the recently invaded sub-tropical Limpopo Province in South Africa and the experiments were conducted after 11 months in the laboratory. Limpopo Province was first invaded during 2008, and then declared fully established in 2015 (Manrakhan *et al.* 2015). Most other experiments on the thermal survival rates of *B. dorsalis* were conducted using flies that originated from the tropics (Vargas *et al.* 1996, 1997, Ekesi *et al.* 2006, Rwomushana *et al.* 2008) and being maintained for extended time periods in laboratory colonies. We were also interested in determining which life stage(s) are most resistant to thermal extremes to gain a better understanding of the species invasion ability to aid pest management or eradication efforts. To further understand the relative invasion risk we make use of comparisons with similar data presently available on con-familial species that possess both broader and narrower geographic distributions, but can be readily found in the region.

2. Materials and methods

2.1 Laboratory culture and rearing conditions

Bactrocera dorsalis was reared in the Insect Quarantine Facility of the Agricultural Research Council in Stellenbosch. The culture was started from infested guavas collected near Thohoyandou in Limpopo Province during March 2014 and wild flies from the same area were added once a year. They were reared at 27°C ($\pm 1^\circ\text{C}$) and 70% ($\pm 5\%$) humidity in PerspexTM cages (30 x 30 x 40 cm, 36 l) with a fabric sleeve under natural light conditions and provided with perforated apples for oviposition, as well as water and a mixture of sugar and yeast as food (Barnes *et al.* 2007). After removing the perforated apple halves from the adult cages, they were placed in plastic fast food bowls with artificial larval rearing medium (Barnes *et al.* 2007) with the addition of 100g carrot powder per kg of mix. The fast food bowls were placed in a plastic box with vermiculite in the bottom and incubated at 27°C ($\pm 1^\circ\text{C}$). Third instar larvae jumped from the bowls with rearing medium into the vermiculite on the bottom of the plastic box for pupation. Seven days after placing the apple on the rearing medium, the vermiculite was sifted daily to remove the pupae. Pupae were placed in honey jars marked with the day of collection and the flies that emerged were placed into new cages, marked with the day of emergence. The flies used in the experiments were 14 (± 1

day) days old. The age of eggs and pupae used in the experiments were 12 h $\pm$ 1h. Third instar larvae were used to gain insight into the larval stage.

2.2 Thermal plasticity

Upper and lower lethal temperatures (ULT and LLT, respectively) that cause 80 – 100% mortality using 2 h exposures (termed the ‘discriminating temperature’) were determined in preliminary trials and based on foregoing information for other Tephritidae (e.g. Nyamukondiwa *et al.* 2010 and Terblanche *et al.* 2010). For all hardening assays, six replicate 60 ml vials of 10 insects (adults) each were placed in a growth chamber at benign rearing conditions (27°C) for 30 min, after which flies were exposed to a range of acute temperatures in programmable incubators, growth chambers and liquid baths for 2 h before plunging vials containing flies directly into a refrigerated circulating liquid bath (filled with 95% EtOH for sub-zero operation) (Grant GP200-R2, Grant Instruments, UK) set at the discriminating temperature (-6.5°C or 42.7°C). Flies were returned to 27°C for 24 h before scoring survival. Survival was defined as a coordinated response to mild stimulation (e.g. prodding) or normal activities (e.g. mating, walking and flying). Six vials with ten flies in each were used as controls, not subjected to any treatment and kept at 27°C during the treatment and recovery time. They were handled in the same way as the treatment flies to control for handling effects that may induce heat shock proteins and could alter conclusions about mortality rates. All flies had access to food and water during the recovery time of the experiments. The cold hardening response of *B. dorsalis* was tested using exposure to 5°C, 10°C and 15°C while heat hardening was assessed using 30°C, 35°C, 37°C and 39°C as hardening temperatures. Gap treatments where flies were kept at 0°C and 5°C and 30°C, 35°C, 37°C and 39°C for two hours and then placed at 27°C for 1 h exposure to the discriminating temperatures at -6.5°C or 42.7°C were also included. Gap treatments for high and low temperature hardening responses were included to provide time for the development of proteins or cryoprotective sugars and polyhydric alcohols (e.g. proline, glycerol or sorbitol for low temperature responses (Misener *et al.* 2001) and various heat shock proteins that can take 20 minutes or longer to develop (Hoffmann *et al.* 2003, Sørensen and Loeschcke 2001), assuming that similar mechanisms underlie potential responses in *B. dorsalis* (Fig. 1).

[Figure. 1]

2.3 Life stage comparison

Six replicate 60 ml vials of either 10 third instar larvae, 10 pupae, 10 adults or 50 eggs each were placed in a growth chamber at 27°C for 30 min, after which the vials containing the eggs, larvae and pupae were plunged directly into a refrigerated circulating liquid bath (filled with 95% EtOH for sub-zero operation) set at lethal (discriminating) temperatures (42.7°C for high temperature responses, -6.5°C for low temperature responses) for two hours. All life stages were returned to 27°C for 24 h before scoring survival.

2.4 Species comparison

For the species comparisons, the most comparable data for *C. capitata* and *C. rosa* were taken from Nyamukondiwa *et al.* (2010). The cold hardening response of *B. dorsalis* was tested using exposure to either 15°C, 10°C or 5°C, and heat hardening was tested at 35°C following plunge protocols described by Nyamukondiwa *et al.* (2010).

2.5 Statistical analyses

To determine the upper and lower discriminating temperatures (expecting c. 20% survival rate based on the pilot data from adult flies) a probit model (and its 95% confidence intervals) was fitted to the replicated survival data against temperature using SAS software (PROC PROBIT, v. 9.4 SAS Institute, Cary, NC, USA). The probit model assumes that survival is a binary probability (an individual is either ‘alive’ or ‘dead’). To determine the

effects of heat and cold hardening a Generalized Linear Model analysis corrected for overdispersion were fitted to the mean percentage survival data using a binomial distribution and the logit link function in SAS (v. 9.0, SAS Institute, Cary, NC, USA). Graphs of the effects were drawn using Statistica 7.0 (Statsoft, Tulsa, USA).

3. Results

3.1 Thermal plasticity

A brief (2 h) cold exposure at a mild (non-lethal) temperature resulted in significant increased survival compared to the control group at the two lower temperatures (5°C and 10°C) at the discriminating temperature of -6.5°C (DF 4, Wald's $\chi^2 = 37.24$, $p < 0.0001$) (Fig. 2a). Exposing *B. dorsalis* to 0°C and 5°C with a gap treatment of 1 h (Fig. 2b) did not improve subsequent survival rates when exposed to the discriminating temperature (-6.5°C). The same percentage of flies as in the control (5% $\pm 3.4\%$) survived the gap treatment at 0°C. At the 5°C gap treatment, 1.7% ($\pm 1.7\%$) flies survived compared to 3.3% ($\pm 2.1\%$) survival in the control group.

[Figure. 2]

The survival of *B. dorsalis* was improved by heat hardening at the two higher temperatures (37°C and 39°C) compared to the control group (DF 5, Wald's $\chi^2 = 120.97$, $p < 0.0001$) (Fig. 2c) when exposed to the high lethal temperature of 42.7°C. Exposing *B. dorsalis* to 30°C and 35°C as hardening temperatures with a gap treatment of 1 h (Fig. 2d) did not improve the ability of the fly to survive the high lethal temperature (42.7°C). Only one fly survived in each treatment group and in the 30°C control group, with no survivors in the 35°C control group.

3.2 Life stage

There is a highly significant (DF 3, Wald's $\chi^2 = 491.62$, $p < 0.0001$) difference in the survival rates the life stages. No larvae or pupae survived the low discriminating temperature (-6.5°C) exposure for 2 h, but 60% ($\pm 4.2\%$) of the eggs and 5% ($\pm 3.4\%$) of the adults survived (Fig. 3). The eggs (44% $\pm 2.3\%$), pupae (56% $\pm 4.9\%$) and some adults (7% $\pm 6.6\%$) survived the high discriminating temperature (42.7°C), with no larval survivors. The eggs (60% $\pm 4.2\%$) and adults (5% $\pm 3.4\%$) were the only life stages able to survive the low discriminating temperature (-6.5°C). The third instar larval stage was the most vulnerable to extreme temperatures in this experiment. The pupae were the most heat resistant life stage and the eggs were able to withstand both the high and low discriminating temperatures.

[Figure 3]

3.3 Species comparison

There was a significant difference in the rapid cold hardening effect at the $p < 0.05$ level for the three temperatures and three species tested. The interaction between temperature and species was highly significant (DF 5, Wald's $\chi^2 = 796.12$, $p < 0.0001$) (Fig. 4a). Both *C. capitata* and *C. rosa* showed a significant cold hardening response after exposure to 5°C and 10°C for 2 h, but *B. dorsalis* did not.

[Figure 4]

There was a statistically significant difference in the rapid heat hardening responses of the three species at the $p < 0.05$ level at 35°C (DF 2, Wald's $\chi^2 = 16.19$, $p < 0.001$) (Fig. 4b) when compared to the control at 35°C. *Ceratitis capitata* was able to heat harden significantly better than the control treatment while *C. rosa* and *B. dorsalis* were not able to develop a statistically significant heat hardening response within the conditions tested.

4. Discussion

The survival of alien or introduced species in a novel environment can be influenced by both basal stress resistance and also the phenotypic responses of the species to mild or extreme thermal conditions (Chown *et al.* 2007, Nyamukondiwa *et al.* 2010) or rapid adaptation of thermal traits (e.g. Foucaud *et al.* 2013, Gibert *et al.* 2016). The difference between temperature extremes are greater in a Mediterranean climate, such as the Western Cape of South Africa, than in the tropical climates that *B. dorsalis* originates from, which might create conditions that are more conducive to the survival of *B. dorsalis* if plasticity responses can expand the thermal range and respond over the time-course of the variability in a predictable way (Sgro *et al.* 2016). However, a test of this notion for *B. dorsalis* in the context of its invasive ability has not been previously undertaken.

The minimum temperature in the Western Cape fruit growing areas ranges between -2°C and 10°C (CapeFarmMapper v. 2.0.2.5), although it seldom drops below 0°C (see also climatological data in Nyamukondiwa *et al.* 2013). Here we found that *B. dorsalis* showed a small but statistically significant improvement in low temperature survival (-6.5°C for 2 h) after exposures to mild hardening temperatures of 5°C and 10°C for 2 h when compared to the control group. Only 23.3% ($\pm 5.58\%$) of flies survived after exposure to 5°C as a hardening treatment, with 23.3% ($\pm 10.54\%$) surviving after a hardening treatment at 10°C. These survival rates do not greatly exceed the survival rate of $\pm 20\%$ expected for the discriminating temperature determined in a separate set of trials. If a population of *B. dorsalis* establishes in the Western Cape, it would therefore probably die out during the winter and be unable to rely on rapid plastic responses induced over diurnal time-scales. Small insects can raise their body temperature by several degrees above the ambient temperature by “basking” in the sun (Digby 1955, Parry 1951, Willmer and Unwin 1981), which could influence the ability of *B. dorsalis* adults to survive exposure to low temperatures for short times. Since *B. dorsalis* can fly as far as 50 km (Shi *et al.* 2005), re-infestation can also occur during the hotter months from adjacent areas where the winter temperature does not go lower than 10°C, thus perhaps sustaining an overwintering population. Nevertheless, a more extensive set of experiments determining plastic and basal responses of multiple thermal traits, and undertaken across longer seasonal time-scales, would be essential to support this conclusion, especially given that divergent plastic responses have been reported among insect populations for traits of low temperature stress resistance or recovery from chilling (e.g. Kleynhans *et al.* 2014, Fischer *et al.* 2010, Hoffmann *et al.* 2005).

Average summer temperatures in the Western Cape (CapeFarmMapper v. 2.0.2.5) seldom exceed 36°C, but maximum daily temperatures can be as high as 41°C in the fruit production areas at certain times of the year (and see discussion in Nyamukondiwa *et al.* 2013). We found that *B. dorsalis* adults were capable of generating a rapid high temperature survival improvement (i.e. heat-hardened at 37°C and 39°C for two hours), so extreme heat might not be immediately lethal to the adult population, but might increase pupal and larval mortality (Rwomushana *et al.* 2008) although further work would be necessary to fully test different life-stages and their respective ability to mount plastic responses to diverse environmental stress.

The third instar larvae of *C. capitata* were apparently more heat resistant than eggs (Gazit *et al.* 2004), but we found here that the eggs of *B. dorsalis* were more heat resistant than the larvae. Gazit *et al.* (2004) however, used shorter exposure times of between 0.17 min at 52°C and 20 min at 46°C. This suggests that stress responses and plasticity of tolerances might be sensitive to the precise methods used (Terblanche *et al.* 2011), and therefore that further work could expand the range of conditions and durations assayed to assess the generality of the responses we documented. According to Ye and Liu (2005), the larvae of *B. dorsalis* die at temperatures lower than 15°C. Female Tephritidae deposit their eggs in a

chamber below the skin of the fruit. The larvae emerge and feed on the fruit pulp tunneling deeper into the fruit (Blomefield *et al.* 2015). This protects the eggs and larvae against temperature extremes, thus improving their chances of survival. However, further work determining their respective microclimates, operative temperatures and relative behavioral reliance on avoiding extremes is necessary (Woods *et al.* 2015).

Ceratitis capitata adults displayed a significantly greater ability to heat harden after exposure to 35°C for two hours than *C. rosa*, which did not develop a statistically significant hardening response under the same conditions. By contrast, *B. dorsalis* did not develop any hardening response compared to the control at this temperature. *Bactrocera dorsalis* is regarded as an aggressive invader, able to out-compete *Ceratitis* species in tropical Africa (Duyck *et al.* 2006, Mwatawala *et al.* 2006, Ekesi *et al.* 2009). *B. dorsalis* only developed a heat-hardening response at higher temperatures (37°C and 39°C). From several lines of evidence presented in this study, the abilities of *C. rosa* and *C. capitata* to survive high temperature exposures better and develop a rapid heat hardening response across a wider range of conditions (e.g. at the lower temperature of 35°C) and to a greater degree, suggests that *B. dorsalis* might not be able to out-compete *C. rosa* and *C. capitata* in the Mediterranean climate of the Western Cape of South Africa based on the thermal niche requirements alone. These results have significant implications for understanding the relative invasion risk of *B. dorsalis* in the region, but also suggest that the thermal niche has likely not contributed significantly to their invasion success into Africa as they appear relatively sensitive to acute extreme temperatures. A wider range of traits and conditions should be tested to assess the generality of this conclusion.

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Figure 1. A graphical representation of the experimental treatments used to test the effect of (a) pre-treatment at 5°C, 10°C and 15°C for 2 h on the ability of *Bactrocera dorsalis* to survive the low discriminating temperature (-6.5°C for 2 h); (b) pre-treatment at 0°C and 5°C with a 1 h gap recovery time at 27°C before exposure to the discriminating temperature (-6.5°C for 2 h); (c) pre-treatment at 30°C, 35°C, 37°C or 39°C for 2 h on the ability of *Bactrocera dorsalis* to survive the high discriminating temperature (42.7°C for 2 h); and (d) pre-treatment at 30°C and 35°C with a 1 h gap recovery time (27°C for 1h) on the ability of *Bactrocera dorsalis* to survive the high discriminating temperature (42.7°C for 2 h). Arrows indicate the survival assessment timepoint.

Two column width

Figure 2. (a) The effect of pre-treatment at 5°C, 10°C and 15°C for 2 h on the ability of *Bactrocera dorsalis* to survive the low discriminating temperature (-6.5°C for 2 h). (b) Survival rates of *B. dorsalis* investigating the effect of pre-treatment at 0°C and 5°C with a 1 h gap recovery time at 27°C before exposure to the discriminating temperature (-6.5°C for 2 h). (c) Comparison of the effect of heat hardening at 30°C, 35°C, 37°C and 39°C for 2 h on the ability of *Bactrocera dorsalis* to survive the high discriminating temperature (42.7°C for 2 h). (d) The effect of heat hardening at 30°C and 35°C with a 1 h gap recovery time (27°C for 1h) on the ability of *Bactrocera dorsalis* to survive the high discriminating temperature (42.7°C for 2 h). Vertical bars denote $\pm$ standard errors. Note that each panel's y-axis scale differs for clarity among groups.

Two column width

Figure 3. Ability of the different life stages (eggs, larvae, pupae and adults) of *Bactrocera dorsalis* to survive the high (42.7°C) and low (-6.5°C) discriminating temperatures for 2 h exposures. Vertical bars denote $\pm$ standard errors.

One column width

Figure 4. (a) Comparison of the effect of cold hardening at 5°C, 10°C and 15°C for 2 h on the ability of *Bactrocera dorsalis*, *Ceratitis capitata* and *Ceratitis rosa* to survive the low discriminating temperature (-6.5°C). (b) Comparison of the effect of heat hardening at 35°C for 2 h on the ability of *Bactrocera dorsalis*, *Ceratitis capitata* and *Ceratitis rosa* to survive the high discriminating temperature (42.7°C). Data used for the hardening responses of *C. capitata* and *C. rosa* are taken from Nyamukondiwa *et al.* (2010). Vertical bars denote $\pm$ standard errors.

Two column width

graphical abstract

- Both *C. capitata* and *C. rosa* cold hardened, *B. dorsalis* did not
- *Ceratitis capitata* heat hardened greatly compared to *C. rosa* and *B. dorsalis*
- *B. dorsalis* has a smaller thermal niche than other invasive Tephritidae