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Synergistic effects of temperature and plant quality, on development time, size and lipid in *Eccritotarsus eichhorniae*

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Abstract

Body size is an important biotic factor in evolutionary ecology, since it affects all aspects of insect physiology, life history, and consequently, fitness in ectothermic insects and how species adapt with their environment. It has been linked to temperature, with lower temperatures resulting in larger size. In this study, we tested the combined impact of temperature and plant quality on the body size, and development time from egg to adult of *Eccritotarsus eichhorniae* (Hemiptera: Miridae), an herbivorous insect used as a biological control agent against the invasive aquatic weed, water hyacinth *Eichhornia crassipes* (Pontederiaceae). We quantified insect size in individuals exposed to three temperatures (20°, 25° and 30°C) combined with three qualities of host plant (high, medium and low) by calculating development time and measuring four traits: tibia length, forewing length, dry body mass and lipid content, and we also determined the wing loading index. The development time, dry body mass and lipid content decreased linearly with increasing temperature and decreasing plant quality. The decrease in size was the greatest when high temperature interacted with low plant quality. Smaller individuals had proportionately less lipid content. Wing loading decreased significantly with lower quality of host plant, resulting in individuals likely to have theoretically higher flight ability. The results support the temperature-size rule (TSR) and that plant quality could influence the relationship between development time and the TSR. Results also provide novel evidence for a possible food quality-size rule for both sexes.

Key words: absolute energy demand, dispersal, interaction, mirid, size

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INTRODUCTION

The capacity of ectothermic insects to establish in specific environments depends on their abundance and distribution, and this is to some extent governed by the abiotic and biotic factors of the environment, and to a large extent by phenotypic plasticity with respect to life history traits and fitness of the insect individuals (Gaston & Lawton, 1988; Chown & Terblanche, 2006; Beukeboom, 2018). The fitness of an insect is a function of individual survivorship and fecundity in the environment in which it lives (Mitchell, 1981). Fitness traits have been positively linked to the size of individuals under normal, non-stressful conditions, implying that bigger individuals have higher reproductive outputs (Stearns, 1992; Chown & Gaston, 2010). Examples of this relationship have been demonstrated in insect parasitoids for both females (Ellers et al., 1998) and males (Lacoume et al., 2006). Body size affects all aspects of physiology and biological processes (Stearns, 1992; Honek, 1993; Kingsolver & Huey, 2008), thus it is a key consideration in ecology and evolutionary theories (Kraushaar & Blanckenhorn, 2002; Angilletta et al., 2004). Larger body size is known to be associated with greater protein and lipid reserves (Roff, 1992; Visser, 1994; Rivero & West, 2002). In insects, lipids are necessary to sustain all biological functions (Arrese & Soulages, 2010) including reproductive processes (Blanckenhorn et al., 2007; Ismail et al., 2010) and flight activities (Haunerland, 1997), therefore lipid availability is a major factor affecting insect viability.

Temperature is considered as the most important abiotic factor affecting growth, development and nutritional content of hosts and thus determining body size in ectothermic insects (Stamp, 1993; Kingsolver et al., 2004; Stillwell et al., 2007; Mega, 2014). Temperature is also known to affect the relationship between lipid and insect size, thus affecting fitness (de Kogel et al., 1999; Ismail et al., 2012). The relationship between body size and temperature leads to an important premise in insect biology, referred to as the temperature-size rule (TSR). Individuals reared at lower temperature present longer development time and larger body size at maturity

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(Atkinson, 1994; Atkinson & Sibly, 1997; Blanckenhorn, 1999; Angilletta & Dunham, 2003). In addition, temperature may have a significant effect on the overall wing loading (the pressure exerted by the wings on the surrounding air) of individuals (Marden & Chai, 1991; Gilchrist & Huey, 2004). This index is important because wing loading has been shown to be correlated to flight capacity in some insect species (Moiroux et al., 2010; Gilchrist & Huey, 2004).

However, in the environment, several factors interact together to affect the development of organisms (Sulmon et al., 2015). For example the availability, as well as the quality, of food are considered to be determinant for several biological parameters of insects (Nylin & Gotthard, 1998; Awmack & Leather, 2002; Ismail et al., 2017), including adult body size (Blanckenhorn, 1998; Bownes et al., 2013). Bownes et al. (2013) showed by measuring body mass that body size of the grasshopper *Cornops aquaticum* (Orthoptera: Acrididae) was bigger when fed on *Eichhornia crassipes* (Pontederiaceae) plants of higher quality, but did not investigate the effect of temperature. Plant quality is dependent on the levels of available nitrogen (Hogendorp *et al.*, 2006; Burke *et al*., 2014), but this can also be modified by the temperature of the environment (Bauerfeind & Fischer, 2013). The interaction between temperature and plant quality has previously been considered in the attempt to understand the impact of plant quality on modulating the relationship between temperature and body size in ectothermic insects and other organisms. For instance, Mascalux et al. (2009) demonstrated the significant effects of temperature and food quality on the clutch size and growth rate of two freshwater cladocerans, *Daphnia magna* and *Simocephalus vetulus* (Cladocera: Daphniidae). Lee et al. (2015) found that the reaction norm between temperature and body size of *Spodoptera litura* (Lepidoptera: Noctuidae) was altered because of changes in food nutrients.

However, most of the studies on the effect of plant quality on TSR have been conducted using different species of plants rather than by varying the quality of the same plant. For instance, Diamond and Kingsolver (2010) evaluated the impact of plant quality on the TSR using the

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insect *Manduca sexta* (Lepidoptera: Sphingidae) on tobacco and devil's claw. In their study, the two proposed plants might not have had the same relative suitability as resources for the particular herbivore insect, despite being of similar quality (Musundire et al., 2012). To our knowledge, no previous study investigated using differing qualities of the same plant species.

In this study, we used the leaf sap-sucking mirid insect *Eccritotarsus eichhorniae* (Hemiptera: Miridae) as a research model. This insect is native to Peru and was previously named *Eccritotarsus catarinensis* (Hill *et al.*, 2000), as it was originally considered to be one of two populations (the other originating from Brazil) of the species *E. catarinensis* (Hill *et al.*, 1999), due to their almost undistinguishable morphologies. However, Paterson et al. (2016) confirmed that they are cryptic species and more recently, Henry (2017) described the Peruvian population as *E. eichhorniae*. The two species were released in South Africa to control the invasive aquatic weed, *E. crassipes*, commonly known as the water hyacinth (Hill *et al.*, 1999, 2000). Adults and nymphs of *Eccritotarsus* feed gregariously on the leaves of water hyacinth, but Paterson *et al.* (2019) demonstrated that *E. eichhorniae* can inflict greater damage on plants than *E. catarinensis*, by removing more chlorophyll. Ismail and Brooks (2016) had earlier demonstrated that *E. eichhorniae* (referred to as the Peruvian strain of *E. catarinensis*) was able to reproduce at higher temperature compared to the Brazilian species *E. catarinensis*. The two species have the same upper thermal thresholds, but the lower thermal thresholds are lower for *E. catarinensis* than for *E. eichhorniae* (Paterson *et al.*, 2019).

The objective in the present study was to evaluate the impact of temperature and plant quality, and their interaction, on morphological and physiological traits of *E. eichhorniae*. In order to understand what impact plant quality would have on the relationship between temperature and size, plant quality was manipulated to provide high, medium and low nutritional status. We predicted that: 1) According to the TSR, individuals exposed to low temperature should present a larger body size at maturity and would have greater lipid content than those raised at high

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temperatures. 2) Individuals raised on high quality food would be bigger, accumulate more lipids and have higher wing loading compared to those reared on low quality plants. 3) The insect size would decrease linearly with increasing temperature and reduced plant quality. 4) The combination of increased temperature with reduced plant quality would be more detrimental and negative effects would be synergetic, lipid content would be lower and insect body size would be smaller than when exposed to one of these factors alone. 5) Changes in relative size would subsequently affect the overall wing loading.

MATERIALS AND METHODS

Eccritotarsus eichhorniae used in this study were from a stock culture originally collected from a tropical area in the upper Amazonian basin of the Yarapa River, near Iquitos in Peru (Hill *et al.*, 2000). The insects were reared and maintained at Waainek Mass Rearing Facility (around 1.2 km from the Department of Zoology and Entomology at Rhodes University). In August 2013 around 200 nymphs and adults of *E. eichhorniae* were taken from a stock population and a new colony established at the department. In the present study insects were reared in net cages with 40 cm x 60 cm clear plastic tubs containing 50L of water, with high quality water hyacinth plants, and incubated in a growth chamber at 25°C. Damaged plants were replaced regularly with fresh healthy plants. Two morphological and two physiological traits and one index were determined for the insects studied.

Plant production

Water hyacinth plants were procured in August 2013 from stock cultures maintained at high levels of nitrogen in Waainek Mass Rearing Facility and a new culture was established at the Department of Zoology and Entomology. To provide plants of 3 different nutrient qualities, mother plants were grown in 40 cm x 60 cm plastic tubs filled with 50L of tap water adjusted to three nitrogen concentration levels, as described in Ismail et al. (2017). There were 6 tubs of

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oligotrophic (low quality, tap water only), mesotrophic (medium quality: 1.5 mg l^{-1}), and eutrophic (high quality: 6.25 mg l^{-1}) waters, based on nitrogen concentrations (Reddy et al., 1989). A water-soluble commercial fertilizer (Multifeed Classic Fertilizer, 19N: 8P: 16K) was used in combination with a commercial iron chelate (33 mg l^{-1}) to prevent chlorosis. The selected concentrations are the averages of nitrogen levels reflecting the range present in South African water bodies (Coetzee & Hill, 2012). Water in the tubs with high, medium and low nutrient levels was replaced every two weeks. Plants grown under high nutrient levels had large green leaves of good quality and were judged to be eutrophic. Plants that were grown under medium nutrient levels had smaller leaves just starting to yellow, and were considered to be mesotrophic. Oligotrophic conditions produced plants of poor quality with small, yellow leaves (Figure 1) (Ismail et al., 2017).

Experimental design

For the experiments, nymphs at the last stage were taken randomly from the insect culture and placed individually in small plastic Petri dishes (20 mm) with moist filter paper and a fresh water hyacinth leaf (replaced if necessary) until the adult stage.

The insects were exposed to 9 treatments, varying temperature against plant quality. Insects were kept at 3 different temperatures (20°, 25° and 30°C) and were fed on 3 qualities of plants (high, medium and low) produced from mother plants. 30°C was considered a stressful temperature since fitness traits were decreased significantly compared to 25 and 20°C (Ismail & Brooks, 2016).

One-day-old adult male and female *E. eichhorniae* were placed in pairs for two days at 25°C in small plastic Petri dishes (20 mm) with moist filter paper and a small fresh water hyacinth leaf from each of the three water nutrient levels from the tub cultures, in order to become reproductively mature. Sexual male and female pairs (the parental generation) were then

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transferred to individual clear plastic bottles (1L) each containing a young, 5 leaved water hyacinth plant, with replicates for each of the three different qualities. Bottles were placed in 3 incubators at the 3 different temperatures (Binder GmbH, KBW 240 (E5.1), Tuttlingen, Germany) with a thermal precision of ± 1°C, under a photoperiod of 14L: 10D, and humidity 75 ± 10%. There were 9 replicates for each treatment, totaling 81 altogether. Fresh plants of the respective plant quality were provided regularly to the nymphs resulting from these adult pairings until they reached the adult stage.

Development time and Body indices

The development time of the progeny was calculated from the day the eggs were laid until the individuals became adults.

In this study two morphological traits representing body size, tibia length and wing length, were measured. Tibia length is the most common indicator of body size in insect parasitoids (Godfray, 1994) and the forewing length is the most commonly used measure of body size in Lepidoptera (Miller, 1977), damselfly (Hassall et al., 2008), mosquitoes (Siegel et al., 1994) and *Drosophila* species (Liefting et al., 2009). A previous study of *E. eichhorniae* (then referred to as *E. catarinensis*) showed that tibia length was similar in females and males, while in females the wings were longer than in males (Ismail & Brooks, 2018).

Measurements for body indices were from 10 individuals (five males and five females) taken randomly from the bottles at each replicate of the 9 combinations (temperature * food quality), totaling 45 individuals of each sex for each combination. Body size was measured using the numeric image analysis software Olympus Stream Motion 1.9 (Olympus Soft Imaging Systems) under a binocular microscope (Olympus SZX-16) linked to a video camera (Olympus DP 72), as follows: the length of the hind tibia (from the femur-tibia joint to the tibia-tarsus

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joint) and the length of the forewing (from base to the apex). The wing loading index was calculated as the ratio of total body fresh mass to squared wing length (Gilchrist & Huey, 2004).

The physiological traits (dry body mass and lipid content)

A total of 135 females and 135 males aged < 04 hours (15 female and 15 male individuals from each of the nine treatments) were killed using liquid nitrogen, in order to immediately halt all metabolic processes. Individuals were then frozen at −20 °C until all replicates were processed. Lipid content was determined based on the method explained in Visser and Ellers, (2012) and Visser et al., (2010). Fresh mass of each mirid was recorded, after which they were freeze-dried for 2 days (VirTis Benchtop 2 K freeze drier: SP Industries, USA) before measuring dry body mass (DBM) of each mirid. Freeze-dried mirids were then placed individually in glass tubes containing 5 ml of ether. After one day the ether was removed, individuals were washed with a fresh batch of ether and freeze-dried for 2 days, after which final dry weight (lean dry mass LDM) was recorded. Body fat mass (FM) was derived by subtracting LDM from DBM, and lipid content (LC) was calculated as a proportion (LC=FM/LDM). All mass measurements were taken using a micro-electrobalance (Sartorius MC 598648-003-48, sensitivity 0.001 mg; Goettingen, Germany) located in an isolated balance room.

Statistical analysis

Statistical analyses were conducted using the statistical software R version 4.0.2 (2020-06-22) (R Core Team, 2020). Development times for males and females were analysed using generalised linear model (GLM) with temperature and plant quality as fixed factors (Gamma distribution with time data). GLM with temperature and plant quality as fixed factors, was also used to analyse the other parameters: hind and wing length for females and males (Gamma distribution), wing loading of males (quasibinomial distribution), wing loading of females,

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DBM for females and males (Gaussian distribution). We used ANCOVA to test the differences in LC in males and females (data were square root transformed), with temperature and food quality as the main factors and incorporating DBM as a covariate. Finally, the previous parameters were further analysed to test the differences between females and males using GLM with sex as a fixed factor. Significant results at $p < 0.05$ were followed by the use of Tukey's honest significant difference test for multiple comparison using the multcomp package and glht function (Hothorn *et al.*, 2008).

RESULTS

Development time

The development time from egg to the adult stage increased significantly with the combination of low plant quality and high temperatures at 25° and 30°C, compared to the combination of medium and high qualities of plant for both sexes (Table 1, Figure 2). Development time decreased significantly with increasing temperature (Table 1) and with high plant quality for both sexes (Table 1). Development time did not vary between females and males (Table 2).

Hind tibia length

A significant interaction was found between temperature and plant quality for both females and males (Table 1). Individuals reared on low quality food under 30°C had the smallest tibia length (Figure 3 A, B). Individuals grew significantly larger as judged by tibia length at low temperature than at high temperature for both sexes (Table 1). Individuals of both sexes were significantly bigger when reared on high quality plants than on low quality plants (Table 1). Females and males had almost the same length of tibia (Table 2).

Wing length

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A significant interaction was found between temperature and plant quality on wing length especially for females only (Table 1). Female individuals fed on low quality plants under 30°C presented the smallest wings and those fed on high quality plants at 20°C had the longest wing (Figure 3 C). Wing length decreased significantly in response to high temperature and to low plant quality for both females and males (Table 1, Figure 3 C, D). Females had significantly longer wings than males (Table 2).

Wing loading

A significant interaction was found between the two factors for females, but not for males (Table 1). While females had greater wing loading when feeding on high quality plants at 30°C, they had lower wing loading when feeding on low quality plants at the same temperature (Figure 4). Temperature had no significant effect on wing loading of *E. eichhorniae* for both sexes (Table 1). Plant quality had a significant impact on wing loading for females and males (Table 1), with greater wing loading when feeding on high quality food compared to low quality food (Figure 4). No significant difference was found between females and males (Table 2).

Dry body mass

No significant interaction was found between temperature and plant quality in females (Table 1), whereas a significant interaction was found between the two factors in males (Table 1). Male individuals feeding on high quality plants at 20°C had larger DBM (Figure 5 B). Dry body mass of individuals decreased significantly with increasing temperature for both sexes (Table 1, Figure 5 A, B). Greater DBM was recorded in individuals fed on good quality food compared to those with poor food quality for both females and males (Table 1, Figure 5 A, B). Dry body mass of females was significantly higher than that of males (Table 2).

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Lipids

There was no interaction between temperature and plant quality on LC in females or males (Table 3). A positive correlation was detected between DBM and LC in females, but not in males (Table 3). Individuals of both sexes presented significantly greater LC at low temperature compared to high temperature (Table 3, Figure 5 C, D). Females tended to contain significantly more LC when fed on high quality plants than on plants of poor quality, but this was not the case for males (Figure 5 C, D). No difference in LC was observed between males and females (Table 2).

DISCUSSION

In this study, individuals of *E. eichhorniae* were exposed to contrasting abiotic and biotic factors: different temperatures and plant qualities. Development time was affected by temperature and plant quality. Tibia and wing length, dry body mass and lipid content decreased significantly with increasing temperature and reduced food quality in both sexes. Wing loading, in contrast, decreased significantly with low plant quality, and this response was more marked in females than in male individuals. In addition, the combined factors presented two types of synergistic effects on the same traits. When optimal factors were combined (*ie.* high plant quality and low temperature), positive synergistic effects were demonstrated on development time and tibia length of both females and males, wing length of females as well as dry body mass of males. On the other hand, when the stressor factors were combined (*ie.* low plant quality and high temperature), negative synergistic effects operated on the aforementioned traits.

Consistent with the typical pattern in ectothermic animals, the results, which follow prediction 1, support the TSR (Atkinson, 1994; Atkinson & Sibly, 1997; Angilletta & Dunham, 2003). The smaller size at high temperature in our study might be related to the greater consumption of plant material (Niesenbaum & Kluger, 2006), resulting in decreased efficiency

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of conversion of food into body matter, because of higher metabolic losses (Kingsolver & Woods, 1998). It can be argued that small size might be an adaptive attribute to cope with the effect of high temperatures, reducing the surface area of the insect, and hence the rate of evaporation from the body. In addition, the reduction of evaporation from individual bodies is considered to be a consequence of decreased cell size (Partridge et al., 1994; Partridge & French, 1996). These arguments are also consistent with the absolute energy demand hypothesis, which predicts that smaller individuals are at an advantage under stressful conditions (Blanckenhorn et al., 1995; Ismail et al., 2012). Smaller individuals may be able to withstand environmental stress because they require less energy to sustain their biological functions. Weldon et al. (2019) showed that smaller individuals of the marula fruit fly *Ceratitis cosyra* (Diptera: Tephritidae) had higher desiccation and starvation resistance than bigger ones.

As foreseen in prediction 2, we found that individuals feeding on high quality plants developed faster and matured at larger size than those feeding on low quality plants. Body size for both sexes followed a linear pattern according to the quality of the plant at each tested temperature, confirming prediction 3. Thus, it appears that food of high quality is a major factor as a prerequisite for larger individuals, operating in a similar way to insect response to temperature in TSR. According to these results, we propose that further study may justify a food-size rule (FSR) equivalent to the TSR. A similar response of faster development time was found when nymphs of the Brazilian species *E. catarinensis* fed on high nutrient leaves comparing with those fed on low nutrient leaves (Burke *et al.*, 2014). Mukarugwiro *et al.*, (2018) demonstrated that larvae of *Neochetina eichhorniae* (Coleoptera: Curculionidae) have larger body size and shorter larval developmental time when feeding on high quality plants of water hyacinth.

It is known that plant nutritional quality for insects is determined by the amino acid concentration and composition of the phloem sap, as well as the ratio of total sugars (Abisgold

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et al., 1994; Simpson et al., 1995; Albittar et al., 2019). Both amino acids and sugars are linked to nitrogen content in plants. Plant quality, however, varies during growth and development because of many abiotic and biotic factors. For instance, nutritional quality of plants decreased with increasing temperature (Bauerfeind & Fischer, 2013) and depends on the levels of nutrients in the environment in which they grow (Galloway et al., 2003). Thus, any change in the nutritional quality of plants can influence the efficiency of converting ingested food into body matter in insects. It has been shown that the efficiency of converting ingested food decreased with decreasing quality of diet (Timmins *et al.*, 1988). Previous studies showed that nitrogen content of water hyacinth leaves increased with fertilizer treatments (Reddy *et al.*, 1989; Center & Dray, 2010; Burke *et al.*, 2014; Hill, 2014). It was also demonstrated that plant quality of water hyacinth increased with increasing nitrogen content and decreasing the carbon/nitrogen ratio (Burke *et al.*, 2014; Hill, 2014), justifying our assumption that nitrogen content, and consequently plant quality, of experimental plants increased with fertilizer treatments (Figure 1).

In this study, we present evidence that the combination of two stressor effects, high temperature and low plant quality, had greater synergistic negative effects, confirming prediction 4. Individuals reared at 30°C and fed on plants of differing quality, exhibited the smallest size on poor quality plants. A consequence of smaller body size of adults for successive generations continuing to feed on plants of lower quality, particularly at high temperature, would be the reduction in fitness traits of the individuals. Indeed, individuals of *E. eichhorniae* (then referred to as *E. catarinensis*) presented the lowest reproduction and survival rate of immature individuals when exposed to the combined effect of high temperature and low plant quality (Ismail et al., 2017). This also confirms findings that a combination of multiple environmental factors had a greater negative impact on fitness traits of individuals as well as

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populations, than one factor alone (Scherber et al., 2013; Sulmon et al., 2015; Feehan et al., 2018).

Furthermore, reduced plant quality may affect the TSR. The protracted development time of immature mirid individuals in our study in response to low quality plant when combined with higher temperature might be due to the requirement for greater quantities of food when it is of poor quality. This would necessitate more time spent on feeding, yet still yield a smaller size. Importantly, extended time taken to reach the adult stage may be necessary in order to maximize the rate of nutrient uptake from low quality plants (Taylor, 1988), due to decreased conversion efficiency of digestive enzymes (Lindroth et al., 1991). Diamond and Kingsolver (2010) found that a stressful combination of high temperature and low dietary quality could reverse the temperature-size rule. They found that the pupal mass of the moth *M. sexta* was higher when feeding on devil's claw than feeding on tobacco at 30°C. Our study is the first to make these comparisons by using different qualities of the same plant at three temperatures.

The slight increase in wing loading with higher temperature results in the need to increase wing beat frequency, and this may serve as an adaptation to a warmer environment, as it has the additional effect of reducing the impact of higher temperature by cooling the body (Mani, 1968; Morin et al., 1999). On the other hand, the individuals responded to lower quality plant by having lower wing loading, which is associated with superior flying ability (Marden & Chai, 1991; Gilchrist & Huey, 2004; Moiroux et al., 2010), conforming to prediction 5. Having a low wing load would enable an insect to fly further. Ability to disperse over greater distances would enable individuals to migrate further in search of higher quality plant, which could have fitness consequences for themselves and their offspring. Our results indicate that both sexes of *E. eichhorniae* would respond to lower food quality with a theoretical increase in their flight capacity. This response has already been shown among aphids, where starvation due to low plant quality is a significant factor affecting flight initiation (Walters & Dixon, 1982;

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Parry, 2013). In contrast, Center & Dray (2010) demonstrated that flight ability of two weevil species *N. eichhorniae* and *N. bruchi* was at the expense of reproduction when feeding on high quality of water hyacinth.

Smaller body size was directly linked with reduced lipid content for both sexes. While lipid content decreased with increasing temperature for both sexes, the response varied among females and males according to food quality. Females tended to accumulate significantly more lipids during immature stages when feeding on higher quality food rather than on poor quality food. Plant quality is an essential factor for accumulation of lipids in females, whereas for males, increased food quality does not necessarily result in increased lipid content. This may be related to the fact that females need more energy than males, to sustain biological activities such as egg production and maturation (Bonduriansky, 2001; Ismail et al., 2012). Insect body fat plays an essential role in energy storage and utilization, as well as in multiple metabolic activities (Law & Wells, 1989; Arrese & Soulages, 2010). Therefore, low quality leaves may not provide sufficient nutrition to allow females to accumulate the quantity of lipids required to sustain all of their metabolic and energetic functions, including successful reproduction.

In conclusion, individuals attained greater size at maturity by feeding on plants of high quality and this relationship was linear at each tested temperature. However further investigations including other insect species would be essential to justify a food-size rule. These results demonstrate that plant quality could influence the relationship between development time and the TSR, particularly at increased temperatures. Plant quality interacting with temperature had positive or negative synergetic effects on the insects depending on whether the combination was optimal or stressful, respectively. Based on our results, the potential dispersal of individuals may depend on plant quality rather than temperature. Larger individuals of *E. eichhorniae* emerged when feeding on high quality plants at low temperature. However, since

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water hyacinth presents the biggest problem in eutrophic temperate areas, this may not necessarily mean successful biological control. Small individuals feeding on high quality plants at higher temperature may be more likely to stay, whereas smaller individuals emerging when feeding on low quality plants at higher temperature, may have greater flying capability, enabling them to disperse and thus limiting the population in the area of concern. In any of these circumstances, re-release of larger individuals with greater reproductive efficiency due to stored energy reserves may be advisable, as this would make the population more sustainable, and so help to assure the success of biological control.

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CONFLICT OF INTEREST: The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTION

MI conceived research, conducted the experiments and analysed data. MI, MB, JB and LA wrote and approved the manuscript

DATA AVAILABILITY STATEMENT

The data that support the finding of this study is available on Mendeley:

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Table legends

Table 1. Results of GLM for the effects of temperature and plant quality and their interaction on the measured parameters of the herbivore *Eccritotarsus eichhorniae*. Significant effects are in bold.

		Females			Males		
Parameter	Factor	df	F	P	df	F	P
Development time (Days)	Temperature	2	1865.77	**< 0.001**	2	1774.022	**< 0.001**
	Plant quality	2	39.11	**< 0.001**	2	35.78	**< 0.001**
	Interaction	4	19.10	**< 0.001**	4	20.43	**0.001**
	Residuals	169			169		
Tibia length (mm)	Temperature	2	75.42	**< 0.001**	2	155.47	**< 0.001**
	Plant quality	2	62.66	**< 0.001**	2	27.14	**< 0.001**
	Interaction	4	5.77	**< 0.001**	4	4.74	**< 0.001**
	Residuals	396			396		
Wing length (mm)	Temperature	2	141.71	**< 0.001**	2	148.45	**< 0.001**
	Plant quality	2	51.97	**0.001**	2	20.03	**0.001**
	Interaction	4	2.66	**0.03**	4	1.36	0.24
	Residuals	326			300		
Wing loading	Temperature	2	0.37	0.68	2	0.97	0.38
	Plant quality	2	9.21	**< 0.001**	2	7.76	**< 0.001**
	Interaction	4	2.62	**0.03**	4	1.51	0.20
	Residuals	126			126		

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DBM (mg)	Temperature	2	39.41	**< 0.001**	2	47.65	**< 0.001**
	Plant quality	2	41.4	**< 0.001**	2	73.25	**< 0.001**
	Interaction	4	1.07	0.37	4	2.62	**0.03**
	Residuals	126			126		

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Table 2.

Results of GLM for the effect of sex on the measured parameters of the herbivore *Eccritotarsus eichhorniae*. Significant effects are in bold.

	df	F	P
Development time (Days)	1, 354	0	**< 0.001**
Tibia length (mm)	1, 808	0.54	0.46
Wing length (mm)	1, 643	39.66	**< 0.001**
Wing loading	1, 268	3.47	0.06
DBM (mg)	1, 268	22.57	**< 0.001**
LC	1, 268	0.03	0.86

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Table 3. ANCOVA with the effects of temperature and plant quality and their interaction (temperature x plant quality) and with dry body mass as a covariate, on lipid content of the herbivore *Eccritotarsus eichhorniae*. Significant effects are in bold.

		Females			Males		
Parameter	Factor	df	F	P	df	F	P
LC	Temperature	2	11.06	**< 0.001**	2	13.39	**< 0.001**
	Plant quality	2	8.19	**< 0.001**	2	1.60	0.20
	Interaction	4	0.11	0.97	4	1.04	0.38
	DBM	1	13.42	**< 0.001**	1	0.63	0.42
	Residuals	125			125		

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Figure legends

Figure 1

Three plants of water hyacinth that were grown under high (a), medium (b) and low (c) nutrient levels..

Figure 2

Development time in days for females and males of *Eccritotarsus eichhorniae* reared at three temperatures (20, 25 and 30°C), and fed on three qualities of plant (high, medium and low). Small letters indicate the significant interaction between temperature and plant quality for both sexes.

Figure 3

Tibia length (A, B) and wing length (C, D) for both females and males of *Eccritotarsus eichhorniae*, reared at three temperatures and fed on three qualities of plant (high, medium and low). In figures (A, B and C) small letters indicate the significant interaction between the two factors and represent the differences among the treatments for both sexes. In Figure (D) small letters indicate the significant differences among the different qualities of plant. Capital letters indicate the significant difference among different temperatures.

Figure 4

Wing loading for both females and males of *Eccritotarsus eichhorniae* reared at three temperatures (20, 25 and 30°C), and fed on three qualities of plant (high, medium and low). For males, small letters indicate the significant difference among the different qualities of plant. For females, small letters indicate the significant interaction between temperature and plant quality and represent the differences among the treatments.

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Figure 5

Dry body mass (A and B) and lipid content (C and D) of females and males of *Eccritotarsus eichhorniae* reared at three temperatures and fed on three qualities of plant (high, medium and low). In figures (A, C and D) small letters indicate the significant differences among the different qualities of plant. Capital letters indicate the significant difference among different temperatures. In Figure (B) small letters indicate the significant interaction between temperature and plant quality and represent the differences among the treatments.

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Figure 1

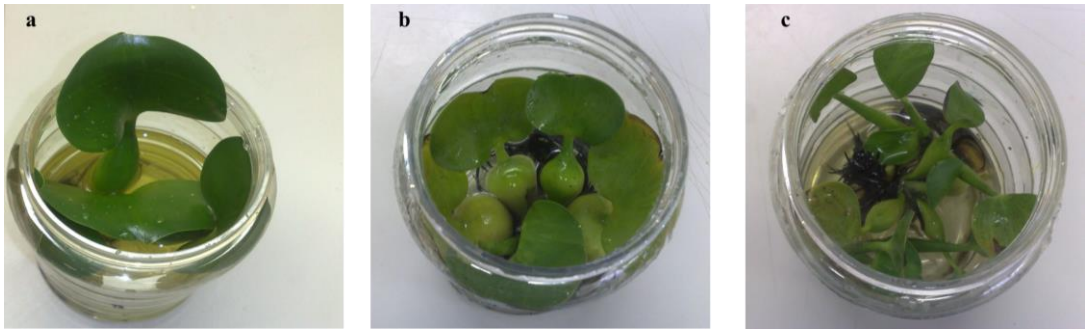

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Figure 2

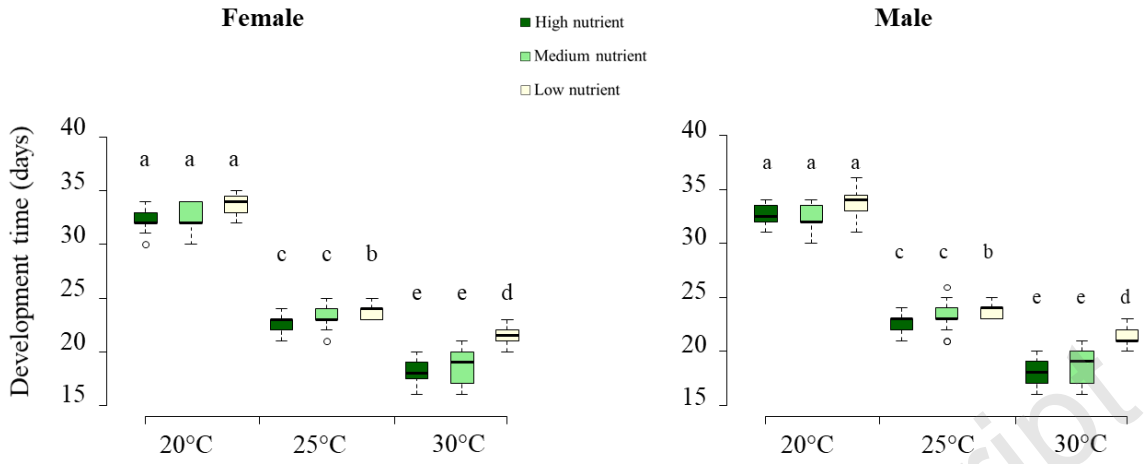

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Figure 3

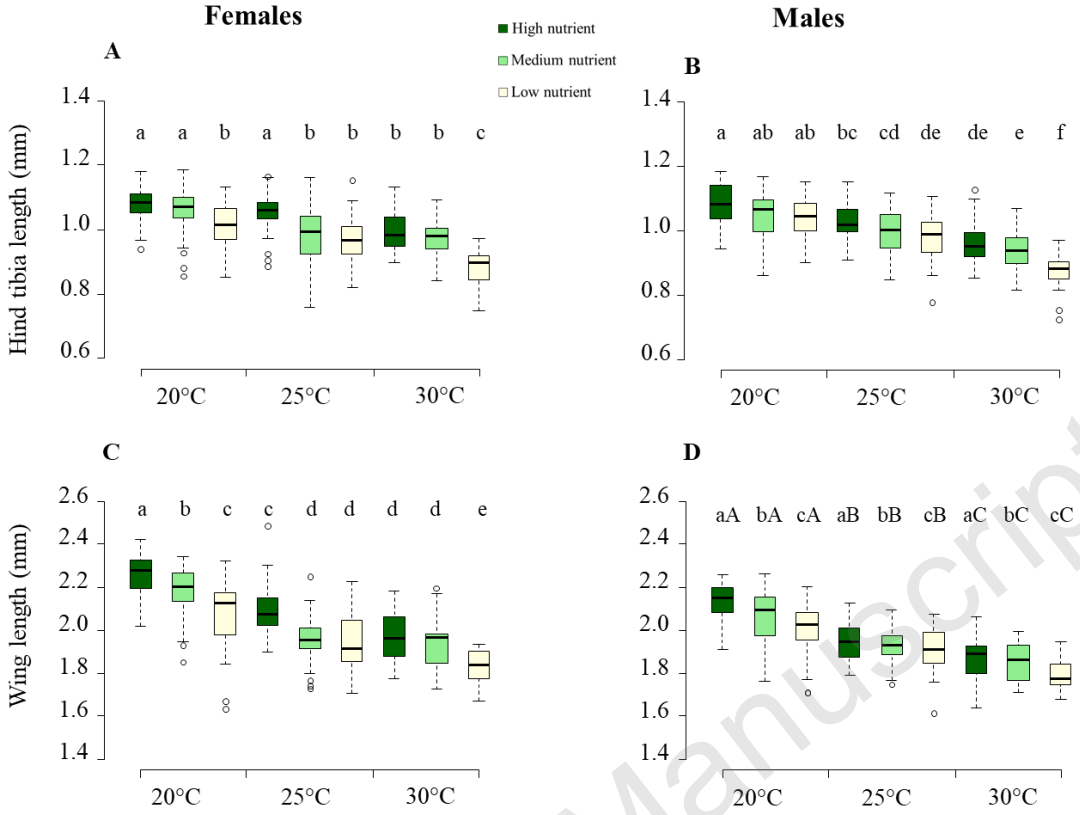

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Figure 4

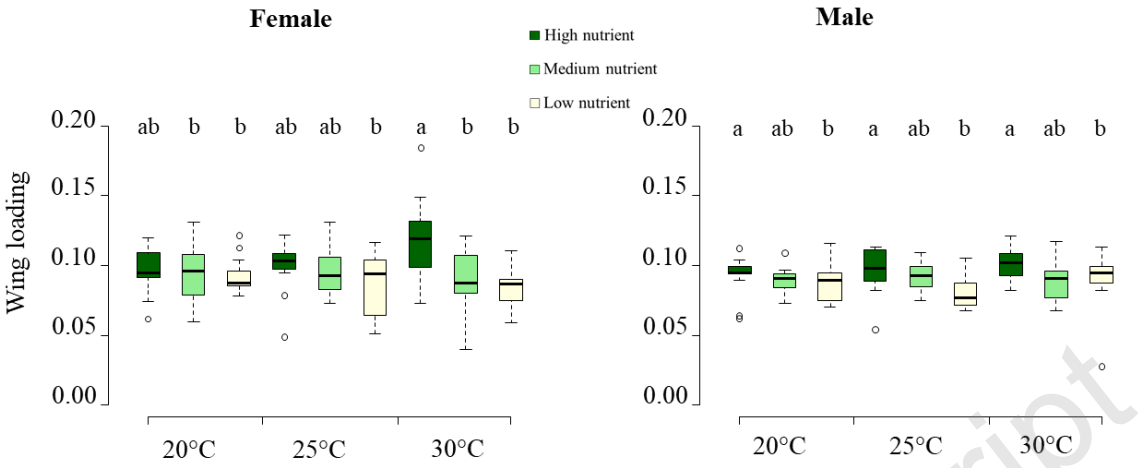

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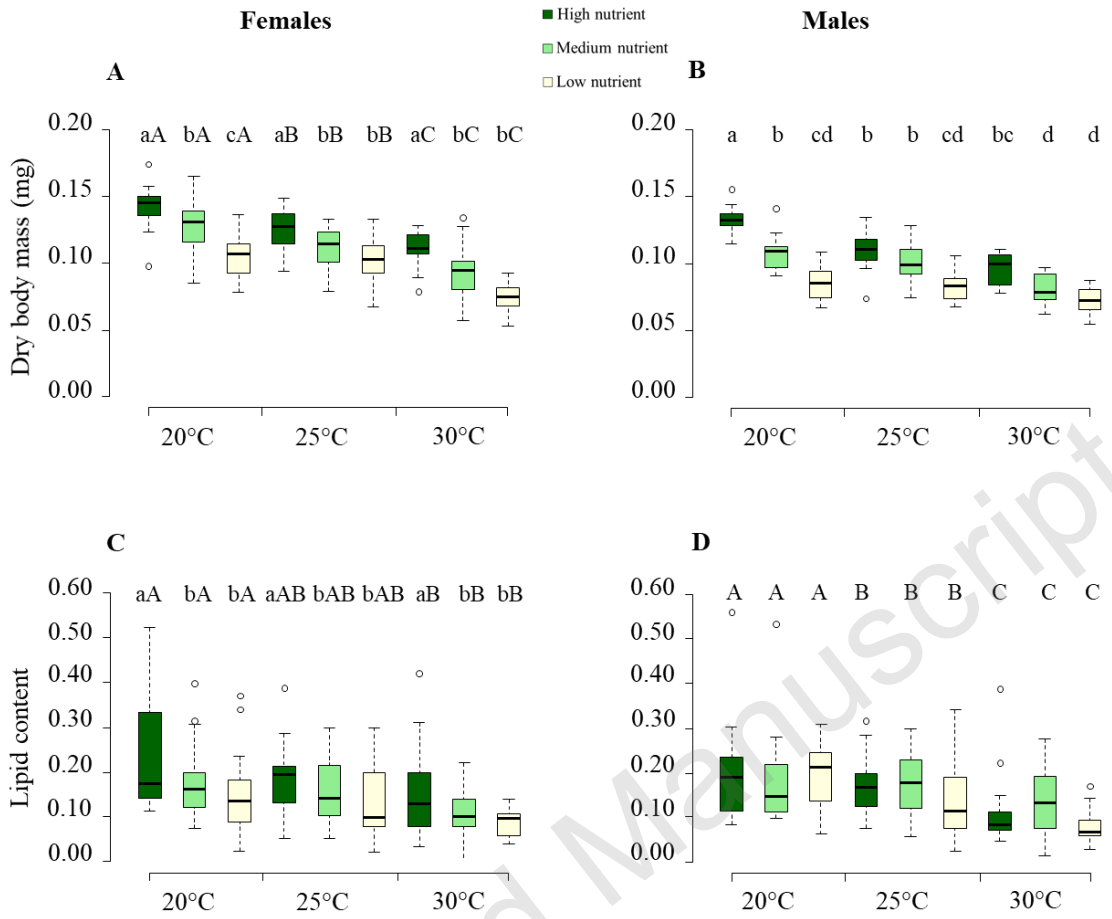
Figure 5



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