



**HAL**  
open science

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

Mohannad Ismail, Margot B Brooks, Joan van Baaren, Loulou Albittar

► **To cite this version:**

Mohannad Ismail, Margot B Brooks, Joan van Baaren, Loulou Albittar. Synergistic effects of temperature and plant quality, on development time, size and lipid in *Eccritotarsus eichhorniae*. *Journal of Applied Entomology*, 2021, 145 (3), pp.239-249. 10.1111/jen.12841 . hal-03095738

**HAL Id: hal-03095738**

**<https://hal.science/hal-03095738>**

Submitted on 2 Feb 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3

4 Mohannad Ismail <sup>1,2\*</sup>, Margot Brooks <sup>3</sup>, Joan van Baaren <sup>4</sup>, Loulou Albittar <sup>2</sup>

5

6 1 Department of Zoology and Entomology, Rhodes University, Grahamstown, South Africa.

7 2 Department of Biochemistry and Microbiology, Rhodes University, Grahamstown, South  
8 Africa.

9 3 UMR-CNRS 6553 EcoBio, Université de Rennes 1, France.

10 4 Earth and Life Institute, Biodiversity Research Centre, UCLouvain, Louvain-la-Neuve 1348,  
11 Belgium.

12

13 \* Corresponding author

14 Earth and Life Institute, Biodiversity Research Centre, UCLouvain, Louvain la neuve 1348,  
15 Belgium

16 E-mail: [mohannad.ismail1@gmail.com](mailto:mohannad.ismail1@gmail.com)

17

18 **Abstract**

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

37

38

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

40

## 41 INTRODUCTION

42 The capacity of ectothermic insects to establish in specific environments depends on their  
43 abundance and distribution, and this is to some extent governed by the abiotic and biotic factors  
44 of the environment, and to a large extent by phenotypic plasticity with respect to life history  
45 traits and fitness of the insect individuals (Gaston & Lawton, 1988; Chown & Terblanche, 2006;  
46 Beukeboom, 2018). The fitness of an insect is a function of individual survivorship and  
47 fecundity in the environment in which it lives (Mitchell, 1981). Fitness traits have been  
48 positively linked to the size of individuals under normal, non-stressful conditions, implying that  
49 bigger individuals have higher reproductive outputs (Stearns, 1992; Chown & Gaston, 2010).  
50 Examples of this relationship have been demonstrated in insect parasitoids for both females  
51 (Ellers et al., 1998) and males (Lacoume et al., 2006). Body size affects all aspects of  
52 physiology and biological processes (Stearns, 1992; Honek, 1993; Kingsolver & Huey, 2008),  
53 thus it is a key consideration in ecology and evolutionary theories (Kraushaar & Blanckenhorn,  
54 2002; Angilletta et al., 2004). Larger body size is known to be associated with greater protein  
55 and lipid reserves (Roff, 1992; Visser, 1994; Rivero & West, 2002). In insects, lipids are  
56 necessary to sustain all biological functions (Arrese & Soulages, 2010) including reproductive  
57 processes (Blanckenhorn et al., 2007; Ismail et al., 2010) and flight activities (Hauerland,  
58 1997), therefore lipid availability is a major factor affecting insect viability.

59 Temperature is considered as the most important abiotic factor affecting growth, development  
60 and nutritional content of hosts and thus determining body size in ectothermic insects (Stamp,  
61 1993; Kingsolver et al., 2004; Stillwell et al., 2007; Mega, 2014). Temperature is also known  
62 to affect the relationship between lipid and insect size, thus affecting fitness (de Kogel et al.,  
63 1999; Ismail et al., 2012). The relationship between body size and temperature leads to an  
64 important premise in insect biology, referred to as the temperature-size rule (TSR). Individuals  
65 reared at lower temperature present longer development time and larger body size at maturity

66 (Atkinson, 1994; Atkinson & Sibly, 1997; Blanckenhorn, 1999; Angilletta & Dunham, 2003).  
67 In addition, temperature may have a significant effect on the overall wing loading (the pressure  
68 exerted by the wings on the surrounding air) of individuals (Marden & Chai, 1991; Gilchrist &  
69 Huey, 2004). This index is important because wing loading has been shown to be correlated to  
70 flight capacity in some insect species (Moiroux et al., 2010; Gilchrist & Huey, 2004).  
71 However, in the environment, several factors interact together to affect the development of  
72 organisms (Sulmon et al., 2015). For example the availability, as well as the quality, of food  
73 are considered to be determinant for several biological parameters of insects (Nylin & Gotthard,  
74 1998; Awmack & Leather, 2002; Ismail et al., 2017), including adult body size (Blanckenhorn,  
75 1998; Bownes et al., 2013). Bownes et al. (2013) showed by measuring body mass that body  
76 size of the grasshopper *Cornops aquaticum* (Orthoptera: Acrididae) was bigger when fed on  
77 *Eichhornia crassipes* (Pontederiaceae) plants of higher quality, but did not investigate the effect  
78 of temperature. Plant quality is dependent on the levels of available nitrogen (Hogendorp *et al.*,  
79 2006; Burke *et al.*, 2014), but this can also be modified by the temperature of the environment  
80 (Bauerfeind & Fischer, 2013). The interaction between temperature and plant quality has  
81 previously been considered in the attempt to understand the impact of plant quality on  
82 modulating the relationship between temperature and body size in ectothermic insects and other  
83 organisms. For instance, Mascalux et al. (2009) demonstrated the significant effects of  
84 temperature and food quality on the clutch size and growth rate of two freshwater cladocerans,  
85 *Daphnia magna* and *Simocephalus vetulus* (Cladocera: Daphniidae). Lee et al. (2015) found  
86 that the reaction norm between temperature and body size of *Spodoptera litura* (Lepidoptera:  
87 Noctuidae) was altered because of changes in food nutrients.  
88 However, most of the studies on the effect of plant quality on TSR have been conducted using  
89 different species of plants rather than by varying the quality of the same plant. For instance,  
90 Diamond and Kingsolver (2010) evaluated the impact of plant quality on the TSR using the

91 insect *Manduca sexta* (Lepidoptera: Sphingidae) on tobacco and devil's claw. In their study,  
92 the two proposed plants might not have had the same relative suitability as resources for the  
93 particular herbivore insect, despite being of similar quality (Musundire et al., 2012). To our  
94 knowledge, no previous study investigated using differing qualities of the same plant species.  
95 In this study, we used the leaf sap-sucking mirid insect *Eccritotarsus eichhorniae* (Hemiptera:  
96 Miridae) as a research model. This insect is native to Peru and was previously named  
97 *Eccritotarsus catarinensis* (Hill et al., 2000), as it was originally considered to be one of two  
98 populations (the other originating from Brazil) of the species *E. catarinensis* (Hill et al., 1999),  
99 due to their almost undistinguishable morphologies. However, Paterson et al. (2016) confirmed  
100 that they are cryptic species and more recently, Henry (2017) described the Peruvian population  
101 as *E. eichhorniae*. The two species were released in South Africa to control the invasive aquatic  
102 weed, *E. crassipes*, commonly known as the water hyacinth (Hill et al., 1999, 2000). Adults  
103 and nymphs of *Eccritotarsus* feed gregariously on the leaves of water hyacinth, but Paterson et  
104 al. (2019) demonstrated that *E. eichhorniae* can inflict greater damage on plants than *E.*  
105 *catarinensis*, by removing more chlorophyll. Ismail and Brooks (2016) had earlier  
106 demonstrated that *E. eichhorniae* (referred to as the Peruvian strain of *E. catarinensis*) was able  
107 to reproduce at higher temperature compared to the Brazilian species *E. catarinensis*. The two  
108 species have the same upper thermal thresholds, but the lower thermal thresholds are lower  
109 for *E. catarinensis* than for *E. eichhorniae* (Paterson et al., 2019).

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

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

123

## 124 MATERIALS AND METHODS

125 *Eccritotarsus eichhorniae* used in this study were from a stock culture originally collected from  
126 a tropical area in the upper Amazonian basin of the Yarapa River, near Iquitos in Peru (Hill *et*  
127 *al.*, 2000). The insects were reared and maintained at Waainek Mass Rearing Facility (around  
128 1.2 km from the Department of Zoology and Entomology at Rhodes University). In August  
129 2013 around 200 nymphs and adults of *E. eichhorniae* were taken from a stock population and  
130 a new colony established at the department. In the present study insects were reared in net cages  
131 with 40 cm x 60 cm clear plastic tubs containing 50L of water, with high quality water hyacinth  
132 plants, and incubated in a growth chamber at 25°C. Damaged plants were replaced regularly  
133 with fresh healthy plants. Two morphological and two physiological traits and one index were  
134 determined for the insects studied.

### 135 *Plant production*

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

141 oligotrophic (low quality, tap water only), mesotrophic (medium quality: 1.5 mg l<sup>-1</sup>), and  
142 eutrophic (high quality: 6.25 mg l<sup>-1</sup>) waters, based on nitrogen concentrations (Reddy et al.,  
143 1989). A water-soluble commercial fertilizer (Multifeed Classic Fertilizer, 19N: 8P: 16K) was  
144 used in combination with a commercial iron chelate (33 mg l<sup>-1</sup>) to prevent chlorosis. The  
145 selected concentrations are the averages of nitrogen levels reflecting the range present in South  
146 African water bodies (Coetzee & Hill, 2012). Water in the tubs with high, medium and low  
147 nutrient levels was replaced every two weeks. Plants grown under high nutrient levels had large  
148 green leaves of good quality and were judged to be eutrophic. Plants that were grown under  
149 medium nutrient levels had smaller leaves just starting to yellow, and were considered to be  
150 mesotrophic. Oligotrophic conditions produced plants of poor quality with small, yellow leaves  
151 (Figure 1) (Ismail et al., 2017).

152

### 153 *Experimental design*

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

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

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



166 transferred to individual clear plastic bottles (1L) each containing a young, 5 leaved water  
167 hyacinth plant, with replicates for each of the three different qualities. Bottles were placed in 3  
168 incubators at the 3 different temperatures (Binder GmbH, KBW 240 (E5.1), Tuttlingen,  
169 Germany) with a thermal precision of  $\pm 1^{\circ}\text{C}$ , under a photoperiod of 14L: 10D, and humidity  
170  $75 \pm 10\%$ . There were 9 replicates for each treatment, totaling 81 altogether. Fresh plants of the  
171 respective plant quality were provided regularly to the nymphs resulting from these adult  
172 pairings until they reached the adult stage.

173

#### 174 *Development time and Body indices*

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

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

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

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

192

### 193 *The physiological traits (dry body mass and lipid content)*

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

207

### 208 *Statistical analysis*

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

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

222

## 223 **RESULTS**

### 224 *Development time*

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

230

### 231 *Hind tibia length*

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

238

### 239 *Wing length*

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

246

#### 247 *Wing loading*

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

255

#### 256 *Dry body mass*

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

264

265 *Lipids*

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

273

## 274 **DISCUSSION**

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

286 Consistent with the typical pattern in ectothermic animals, the results, which follow  
287 prediction 1, support the TSR (Atkinson, 1994; Atkinson & Sibly, 1997; Angilletta & Dunham,  
288 2003). The smaller size at high temperature in our study might be related to the greater  
289 consumption of plant material (Niesenbaum & Kluger, 2006), resulting in decreased efficiency

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

301 As foreseen in prediction 2, we found that individuals feeding on high quality plants  
302 developed faster and matured at larger size than those feeding on low quality plants. Body size  
303 for both sexes followed a linear pattern according to the quality of the plant at each tested  
304 temperature, confirming prediction 3. Thus, it appears that food of high quality is a major factor  
305 as a prerequisite for larger individuals, operating in a similar way to insect response to  
306 temperature in TSR. According to these results, we propose that further study may justify a  
307 food-size rule (FSR) equivalent to the TSR. A similar response of faster development time was  
308 found when nymphs of the Brazilian species *E. catarinensis* fed on high nutrient leaves  
309 comparing with those fed on low nutrient leaves (Burke *et al.*, 2014). Mukarugwiro *et al.*,  
310 (2018) demonstrated that larvae of *Neochetina eichhorniae* (Coleoptera: Curculionidae) have  
311 larger body size and shorter larval developmental time when feeding on high quality plants of  
312 water hyacinth.

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

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

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

339 populations, than one factor alone (Scherber et al., 2013; Sulmon et al., 2015; Feehan et al.,  
340 2018).

341 Furthermore, reduced plant quality may affect the TSR. The protracted development  
342 time of immature mirid individuals in our study in response to low quality plant when combined  
343 with higher temperature might be due to the requirement for greater quantities of food when it  
344 is of poor quality. This would necessitate more time spent on feeding, yet still yield a smaller  
345 size. Importantly, extended time taken to reach the adult stage may be necessary in order to  
346 maximize the rate of nutrient uptake from low quality plants (Taylor, 1988), due to decreased  
347 conversion efficiency of digestive enzymes (Lindroth et al., 1991). Diamond and Kingsolver  
348 (2010) found that a stressful combination of high temperature and low dietary quality could  
349 reverse the temperature-size rule. They found that the pupal mass of the moth *M. sexta* was  
350 higher when feeding on devil's claw than feeding on tobacco at 30°C. Our study is the first to  
351 make these comparisons by using different qualities of the same plant at three temperatures.

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



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

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

379  
380 In conclusion, individuals attained greater size at maturity by feeding on plants of high  
381 quality and this relationship was linear at each tested temperature. However further  
382 investigations including other insect species would be essential to justify a food-size rule. These  
383 results demonstrate that plant quality could influence the relationship between development  
384 time and the TSR, particularly at increased temperatures. Plant quality interacting with  
385 temperature had positive or negative synergetic effects on the insects depending on whether the  
386 combination was optimal or stressful, respectively. Based on our results, the potential dispersal  
387 of individuals may depend on plant quality rather than temperature. Larger individuals of *E.*  
388 *eichhorniae* emerged when feeding on high quality plants at low temperature. However, since

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

397

398

399

Accepted Manuscript

400 **ACKNOWLEDGMENTS**

401 This study was supported by funding from Rhodes University, as well as from the South African  
402 Research Chairs Initiative of the Department of Science and Technology, and the National  
403 Research Foundation of South Africa. We thank Shirley Pinchuck and Marvin Randall for  
404 facilitating work at the Electron Microscope Unit.

405

Accepted Manuscript

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

407

408 **AUTHOR CONTRIBUTION**

409 MI conceived research, conducted the experiments and analysed data. MI, MB, JB and LA

410 wrote and approved the manuscript

411

412 **DATA AVAILABILITY STATEMENT**

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

414 (<http://dx.doi.org/10.17632/pnj7247t7n.1#file-742dd7fe-e22b-49fc-98b4-1f3ecc4db0c8>)

415

416

Accepted Manuscript

417 **REFERENCES**

- 418 Abisgold, J.D., Simpson, S.J. & Douglas, A.E. (1994) Nutrient regulation in the pea aphid  
419 *Acyrtosiphon pisum*: application of a novel geometric framework to sugar and amino acid  
420 consumption. *Physiological Entomology*, **19**, 95–102.
- 421 Albittar, L., Ismail, M., Lohaus, G., Ameline, A., Visser, B., Bragard, C., *et al.* (2019) Bottom-  
422 up regulation of a tritrophic system by *Beet yellows virus* infection: consequences for aphid-  
423 parasitoid foraging behaviour and development. *Oecologia*, **191**, 113–125.
- 424 Angilletta, M.J. & Dunham, A.E. (2003) The temperature-size rule in ectotherms: Simple  
425 evolutionary explanations may not be general. *American Naturalist*, **162**, 332–342.
- 426 Angilletta, M.J., Steury, T.D. & Sears, M.W. (2004) Temperature, growth rate, and body size  
427 in ectotherms: Fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, **44**,  
428 498–509.
- 429 Arrese, E.L. & Soulages, J.L. (2010) Insect fat body: energy, metabolism, and regulation.  
430 *Annual Review of Entomology*, **55**, 207–225.
- 431 Atkinson, D. (1994) Temperature and organism size - a biological law for ectotherms. In  
432 *Advances in Ecological Research, Vol 25*, Advances in Ecological Research. pp. 1–58.
- 433 Atkinson, D. & Sibly, R.M. (1997) Why are organisms usually bigger in colder environments?  
434 Making sense of a life history puzzle. *Trends in Ecology & Evolution*, **12**, 235–239.
- 435 Awmack, C.S. & Leather, S.R. (2002) Host plant quality and fecundity in herbivorous insects.  
436 *Annual Review of Entomology*, **47**, 817–844.
- 437 Bauerfeind, S.S. & Fischer, K. (2013) Increased temperature reduces herbivore host-plant  
438 quality. *Global Change Biology*, **19**, 3272–3282.
- 439 Beukeboom, L.W. (2018) Size matters in insects – an introduction. *Entomologia*  
440 *Experimentalis et Applicata*, **166**, 2–3.

441 Blanckenhorn, W.U. (1998) Adaptive phenotypic plasticity in growth, development, and body  
442 size in the yellow dung fly. *Evolution*, **52**, 1394–1407.

443 Blanckenhorn, W.U. (1999) Different growth responses to temperature and resource limitation  
444 in three fly species with similar life histories. *Evolutionary Ecology*, **13**, 395–409.

445 Blanckenhorn, W.U., Fanti, J. & Reim, C. (2007) Size-dependent energy reserves, energy  
446 utilization and longevity in the yellow dung fly. *Physiological Entomology*, **32**, 372–381.

447 Blanckenhorn, W.U., Preziosi, R.F. & Fairbairn, D.J. (1995) Time and energy constraints and  
448 the evolution of sexual size dimorphism - to eat or to mate. *Evolutionary Ecology*, **9**, 369–381.

449 Bonduriansky, R. (2001) The evolution of male mate choice in insects: a synthesis of ideas and  
450 evidence. *Biological Reviews*, **76**, 305–339.

451 Bownes, A., Hill, M.P. & Byrne, M.J. (2013) Nutrient-mediated effects on *Cornops aquaticum*  
452 Bruner (Orthoptera: Acrididae), a potential biological control agent of water hyacinth,  
453 *Eichhornia crassipes* (Mart.) Solms (Pontederiaceae). *Biological Control*, **67**, 548–554.

454 Burke, A.M., Coetzee, J.A. & Hill, M.P. (2014) Effect of nutrient quality and leaf age of water  
455 hyacinth, *Eichhornia crassipes* *Eichhornia crassipes*, on the development of its co-evolved  
456 herbivore, *Eccritotarsus catarinensis* (Hemiptera: Miridae). *African Entomology*, **22**, 896–899.

457 Center, T.D. & Dray, A. (2010) Effects of host quality on flight muscle development in  
458 *Neochetina eichhorniae* and *N. bruchi* (Coleoptera: Curculionidae). *Florida Entomologist*, **93**.

459 Chown, S.L. & Gaston, K.J. (2010) Body size variation in insects: a macroecological  
460 perspective. *Biological Reviews*, **85**, 139–169.

461 Chown, S.L. & Terblanche, J.S. (2006) Physiological Diversity in Insects: Ecological and  
462 Evolutionary Contexts. *Advances in insect physiology*, **33**, 50–152.

463 Coetzee, J.A. & Hill, M.P. (2012) The role of eutrophication in the biological control of water  
464 hyacinth, *Eichhornia crassipes* *Eichhornia crassipes*, in South Africa. *Biocontrol*, **57**, 247–261.

465 Diamond, S.E. & Kingsolver, J.G. (2010) Environmental Dependence of Thermal Reaction  
466 Norms: Host Plant Quality Can Reverse the Temperature-Size Rule. *American Naturalist*, **175**,  
467 1–10.

468 Ellers, J., Alphen, J.J.M. van & Sevenster, J.G. (1998) A field study of size-fitness relationships  
469 in the parasitoid *Asobara tabida*. *Journal of Animal Ecology*, **67**, 318–324.

470 Feehan, C.J., Ludwig, Z., Yu, S. & Adams, D.K. (2018) Synergistic negative effects of thermal  
471 stress and altered food resources on echinoid larvae. *Scientific Reports*, **8**, 12229.

472 Galloway, J.N., Aber, J.D., Erisman, J.W., Seitzinger, S.P., Howarth, R.W., Cowling, E.B., *et*  
473 *al.* (2003) The nitrogen cascade. *Bioscience*, **53**, 341–356.

474 Gaston, K.J. & Lawton, J.H. (1988) Patterns in the distribution and abundance of insect  
475 populations. *Nature*, **331**, 709.

476 Gilchrist, G.W. & Huey, R.B. (2004) Plastic and genetic variation in wing loading as a function  
477 of temperature within and among parallel clines in *Drosophila subobscura*. *Integrative and*  
478 *Comparative Biology*, **44**, 461–470.

479 Godfray, H.C.J. (1994) *Parasitoids: behavioral and evolutionary ecology*. Princeton University  
480 Press, Princeton.

481 Hassall, C., Thompson, D.J. & Harvey, I.F. (2008) Latitudinal variation in morphology in two  
482 sympatric damselfly species with contrasting range dynamics (Odonata: Coenagrionidae).  
483 *European Journal of Entomology*, **105**, 939–944.

484 Haunerland, N.H. (1997) Transport and utilization in insect flight muscles. *Comparative*  
485 *Biochemistry and Physiology B-Biochemistry & Molecular Biology*, **117**, 475–482.

486 Hill, J.M. (2014) Investigations of growth metrics and  $\delta^{15}\text{N}$  values of water hyacinth  
487 (*Eichhornia crassipes* Eichhornia crassipes, (Mart.) Solms-Laub) in relation to biological  
488 control. *Aquatic Botany*, **114**, 12–20.

489 Hill, M.P., Center, T.D., Stanley, J., Cordo, H.A., Coetzee, J.A. & Byrne, M.J. (2000) The  
490 performance of the water hyacinth mirid, *Eccritotarsus catarinensis*, on water hyacinth and  
491 pickerel weed: a comparison of laboratory and field results. In *The Xth International Symposium*  
492 *on the Biological Control of Weeds 4-14 July, 1999* (ed. by Spencer, N.R.). Montana State  
493 University, pp. 357–366.

494 Hill, M.P., Cilliers, C.J. & Nesar, S. (1999) Life history and laboratory host range of  
495 *Eccritotarsus catarinensis* (Carvalho) (Heteroptera : Miridae), a new natural enemy released on  
496 water hyacinth (*Eichhornia crassipes* (Mart.) Solms-Laub.) (Pontederiaceae) in South Africa.  
497 *Biological Control*, **14**, 127–133. Henry T. J. (2017).  
498 Description of a cryptic new species of the plant bug genus *Eccritotarsus* (Heteroptera: Miridae:  
499 Bryocorinae) from Peru, a new biocontrol agent of water hyacinth, *Eichhornia crassipes*  
500 (Pontederiaceae). *Proceedings of the Entomological Society of Washington*, *119*, 398–407.  
501 <http://doi.org/10.4289/0013-8797.119.3.398>

502 Hogendorp, B.K., Cloyd, R.A. & Swiader, J.M. (2006) Effect of nitrogen fertility on  
503 reproduction and development of citrus mealybug, *Planococcus citri* Risso (Homoptera :  
504 Pseudococcidae), feeding on two colors of coleus, *Solenostemon scutellarioides* L. Codd.  
505 *Environmental Entomology*, **35**, 201–211.

506 Honek, A. (1993) Intraspecific variation in body size and fecundity in insects - a general  
507 relationship. *Oikos*, **66**, 483–492.

508 Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous Inference in General Parametric  
509 Models. *Biometrical Journal*, **50**, 346–363.

510 Ismail, M. & Brooks, M. (2016) The impact of geographical origin of two strains of the  
511 herbivore, *Eccritotarsus catarinensis*, on several fitness traits in response to temperature.  
512 *Journal of Thermal Biology*, **60**, 222–230.



513 Ismail, M. & Brooks, M. (2018) Male mating preference of two cryptic species of the  
514 herbivorous insect *Eccritotarsus catarinensis*. *Biocontrol Science and Technology*, 529–543.

515 Ismail, M., Compton, S.G. & Brooks, M. (2017) Interaction between temperature and water  
516 nutrient levels on the fitness of *Eccritotarsus catarinensis* (Hemiptera: Miridae), a biological  
517 control agent of water hyacinth. *Biological Control*, **106**, 83–88.

518 Ismail, M., Vernon, P., Hance, T. & Baaren, J. van. (2010) Physiological costs of cold exposure  
519 on the parasitoid *Aphidius ervi*, without selection pressure and under constant or fluctuating  
520 temperatures. *Biocontrol*, **55**, 729–740.

521 Ismail, M., Vernon, P., Hance, T., Pierre, J.S. & Baaren, J. van. (2012) What are the possible  
522 benefits of small size for energy-constrained ectotherms in cold stress conditions? *Oikos*, **121**,  
523 2072–2080.

524 Kingsolver, J.G. & Huey, R.B. (2008) Size, temperature, and fitness: three rules. *Evolutionary*  
525 *Ecology Research*, **10**, 251–268.

526 Kingsolver, J.G., Izem, R. & Ragland, G.J. (2004) Plasticity of size and growth in fluctuating  
527 thermal environments: Comparing reaction norms and performance curves. *Integrative and*  
528 *Comparative Biology*, **44**, 450–460.

529 Kingsolver, J.G. & Woods, H.A. (1998) Interactions of temperature and dietary protein  
530 concentration in growth and feeding of *Manduca sexta* caterpillars. *Physiological Entomology*,  
531 **23**, 354–359.

532 Kogel, W.J. de, Bosco, D., Hoek, M. van der & Mollema, C. (1999) Effect of host plant on  
533 body size of *Frankliniella occidentalis* (Thysanoptera: Thripidae) and its correlation with  
534 reproductive capacity. *European Journal of Entomology*, **96**, 365–368.

535 Kraushaar, U. & Blanckenhorn, W.U. (2002) Population variation in sexual selection and its  
536 effect on size allometry in two dung fly species with contrasting sexual size dimorphism.  
537 *Evolution*, **56**, 307–321.

538 Lacoume, S., Bressac, C. & Chevrier, C. (2006) Effect of host size on male fitness in the  
539 parasitoid wasp *Dinarmus basalis*. *Journal of Insect Physiology*, **52**, 249–254.

540 Law, J.H. & Wells, M.A. (1989) Insects as biochemical models. *Journal of Biological*  
541 *Chemistry*, **264**, 16335–16338.

542 Lee, K.P., Jang, T., Ravzanaadii, N. & Rho, M.S. (2015) Macronutrient balance modulates the  
543 temperature-size rule in an ectotherm. *American Naturalist*, **186**, 212–222.

544 Lieferting, M., Hoffmann, A.A. & Ellers, J. (2009) Plasticity versus environmental canalization:  
545 population differences in thermal responses along a latitudinal gradient in *Drosophila serrata*.  
546 *Evolution*, **63**, 1954–1963.

547 Lindroth, R.L., Barman, M.A. & Weisbrod, A.V. (1991) Nutrient deficiencies and the gypsy  
548 moth, *Lymantria dispar*: effects on larval performance and detoxification enzyme activities.  
549 *Journal of Insect Physiology*, **37**, 45–52.

550 Mani, M.S. (1968) *Ecology and Biogeography of High Altitude Insects*. Junk Publishers, The  
551 Hague.

552 Marden, J.H. & Chai, P. (1991) Aerial predation and butterfly design: how palatability, mimicry  
553 and the need for evasive flight constrain mass allocation. *American Naturalist*, **138**, 15–36.

554 Masclaux, Hé., Bec, A., Kainz, M.J., Desvillettes, C., Jouve, L. & Bourdier, G. (2009)  
555 Combined effects of food quality and temperature on somatic growth and reproduction of two  
556 freshwater cladocerans. *Limnology and Oceanography*, **54**, 1323–1332.

557 Mega, N.O. (2014) The adult body size variation of *Dryas iulia* (Lepidoptera, Nymphalidae,  
558 Heliconiinae) in different populations is more influenced by temperature variation than by host-  
559 plant availability during the seasons. *Entomological Science*, **17**, 376–387.

560 Miller, W.E. (1977) Wing measure as a size index in lepidoptera - family Olethreutidae. *Annals*  
561 *of the Entomological Society of America*, **70**, 253–256.

562 Mitchell, R. (1981) Insect Behavior, Resource Exploitation, and Fitness. *Annual Review of*  
563 *Entomology*, **26**, 373–396.

564 Moiroux, J., Le Lann, C., Seyahooei, M.A., Vernon, P., Pierre, J.-S., Van Baaren, J., *et al.*  
565 (2010) Local adaptations of life-history traits of a *Drosophila parasitoid*, *Leptopilina boulardi*:  
566 does climate drive evolution? *Ecological Entomology*, **35**, 727–736.

567 Morin, J.P., Moreteau, B., Petavy, G. & David, J.R. (1999) Divergence of reaction norms of  
568 size characters between tropical and temperate populations of *Drosophila melanogaster* and *D*  
569 *simulans*. *Journal of Evolutionary Biology*, **12**, 329–339.

570 Mukarugwiro, J. d’Arc, Newete, S., Hauptfleisch, K. & Byrne, M. (2018) The effect of water  
571 nutrients on the feeding intensity and development of larvae of *Neochetina eichhorniae*  
572 (Warner) (Coleoptera: Curculionidae), a biocontrol agent of the invasive water hyacinth.  
573 *African Entomology*, **26**, 63–72 . <http://doi.org/10.4001/003.026.0063>.

574 Musundire, R., Chabi-Olaye, A. & Krueger, K. (2012) Host plant effects on morphometric  
575 characteristics of *Liriomyza huidobrensis*, *L. sativae* and *L. trifolii* (Diptera: Agromyzidae).  
576 *Journal of Applied Entomology*, **136**, 97–108.

577 Niesenbaum, R.A. & Kluger, E.C. (2006) When studying the effects of light on herbivory,  
578 should one consider temperature? The case of *Epimecis hortaria* F. (Lepidoptera: Geometridae)  
579 feeding on *Lindera benzoin* L. (Lauraceae). *Environmental Entomology*, **35**, 600–606.

580 Nylin, S. & Gotthard, K. (1998) Plasticity in life-history traits. *Annual Review of Entomology*,  
581 **43**, 63–83.

582 Parry, H.R. (2013) Cereal aphid movement: general principles and simulation modelling.  
583 *Movement ecology*, **1**, 14–14.

584 Partridge, L., Barrie, B., Fowler, K. & French, V. (1994) Evolution and development of body  
585 size and cell size in *Drosophila melanogaster* in response to temperature. *Evolution*, **48**, 1269–  
586 1276.

587 Partridge, L. & French, V. (1996) Thermal evolution of ectotherm body size: why get big in the  
588 cold? In *Animals and temperature: phenotypic and evolutionary adaptation* (ed. by Johnston,  
589 I.A. & Bennett, A.F.). Cambridge University Press, Cambridge, pp. 265–292.

590 Paterson, I.D., Coetzee, J.A., Weyl, P., Griffith, T.C., Voogt, N. & Hill, M.P. (2019) Cryptic  
591 species of a water hyacinth biological control agent revealed in South Africa: host specificity,  
592 impact, and thermal tolerance. *Entomologia Experimentalis et Applicata*, **167**, 682–691.

593 Paterson, I.D., Mangan, R., Downie, D.A., Coetzee, J.A., Hill, M.P., Burke, A.M., *et al.* (2016)  
594 Two in one: cryptic species discovered in biological control agent populations using molecular  
595 data and crossbreeding experiments. *Ecology and Evolution*, **6**, 6139–6150.

596 R. Core Team. (2020) *R: A language and environment for statistical computing*. R Foundation  
597 for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0, URL [http://www.R-](http://www.R-project.org/)  
598 [project.org/](http://www.R-project.org/).

599 Reddy, K.R., Agami, M. & Tucker, J.C. (1989) Influence of nitrogen supply rates on growth  
600 and nutrient storage by water hyacinth (*Eichhornia crassipes*) plants. *Aquatic Botany*, **36**, 33–  
601 43.

602 Rivero, A. & West, S.A. (2002) The physiological costs of being small in a parasitic wasp.  
603 *Evolutionary Ecology Research*, **4**, 407–420.

604 Roff, D.A. (1992) *The evolution of life histories: theory and analysis*. Chapman and Hall,  
605 London.

606 Scherber, C., Gladbach, D.J., Stevnbak, K., Karsten, R.J., Schmidt, I.K., Michelsen, A., *et al.*  
607 (2013) Multi-factor climate change effects on insect herbivore performance. *Ecology and*  
608 *Evolution*, **3**, 1449–1460.

609 Siegel, J.P., Novak, R.J. & Ruesink, W.G. (1994) Relationship between wing length and dry  
610 weight of mosquitoes. *Journal of the American Mosquito Control Association*, **10**, 186–196.

611 Simpson, S.J., Abisgold, J.D. & Douglas, A.E. (1995) Response of the pea aphid  
612 (*Acyrtosiphon pisum*) to variation in dietary levels of sugar and amino acids: the significance  
613 of amino acid quality. *Journal of Insect Physiology*, **41**, 71–75.

614 Stamp, N.E. (1993) A temperate region view of the interaction of temperature, food quality,  
615 and predators on caterpillar foraging. In *Caterpillars: ecological and evolutionary constraints*  
616 *on foraging* (ed. by Stamp, N.E. & Casey, T.M.). Chapman & Hall, New York, pp. 478–508.

617 Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.

618 Stillwell, R.C., Wallin, W.G., Hitchcock, L.J. & Fox, C.W. (2007) Phenotypic plasticity in a  
619 complex world: interactive effects of food and temperature on fitness components of a seed  
620 beetle. *Oecologia*, **153**, 309–321.

621 Sulmon, C., Baaren, J. van, Cabello-Hurtado, F., Gouesbet, G., Hennion, F., Mony, C., *et al.*  
622 (2015) Abiotic stressors and stress responses: What commonalities appear between species  
623 across biological organization levels? *Environmental Pollution*, **202**, 66–77.

624 Taylor, M.F.J. (1988) Field measurement of the dependence of life history on plant nitrogen  
625 and temperature for a herbivorous moth. *Journal of Animal Ecology*, **57**, 873–891.

626 Timmins, W.A., Bellward, K., Stamp, A.J. & Reynolds, S.E. (1988) Food intake, conversion  
627 efficiency, and feeding behaviour of tobacco hornworm caterpillars given artificial diet of  
628 varying nutrient and water content. *Physiological Entomology*, **13**, 303–314.

629 Visser, B. & Ellers, J. (2012) Effects of a lipid-rich diet on adult parasitoid income resources  
630 and survival. *Biological Control*, **60**, 119–122.

631 Visser, B., Le Lann, C., Blanken, F.J. den, Harvey, J.A., Alphen, J.J.M. van & Ellers, J. (2010)  
632 Loss of lipid synthesis as an evolutionary consequence of a parasitic lifestyle. *Proceedings of*  
633 *the National Academy of Sciences of the United States of America*, **107**, 8677–8682.

634 Visser, M.E. (1994) The importance of being large - the relationship between size and fitness  
635 in females of the parasitoid *Aphaereta minuta* (Hymenoptera, Braconidae). *Journal of Animal*  
636 *Ecology*, **63**, 963–978.

637 Walters, K.F.A. & Dixon, A.F.G. (1982) The effect of host quality and crowding on the settling  
638 and take-off of cereal aphids. *Annals of Applied Biology*, **101**, 211–218.

639 Weldon, C.W., Mnguni, S., Démares, F., Rand, E.E. du, Malod, K., Manrakhan, A., *et al.* (2019)  
640 Adult diet does not compensate for impact of a poor larval diet on stress resistance in a tephritid  
641 fruit fly. *The Journal of Experimental Biology*, **222**, jeb192534.

642

Accepted Manuscript

643

## Table legends

644 Table 1. Results of GLM for the effects of temperature and plant quality and their interaction

645 on the measured parameters of the herbivore *Eccritotarsus eichhorniae*. Significant effects are

646 in bold.

Parameter	Factor	Females			Males		
		df	F	P	df	F	P
Development time (Days)	Temperature	2	1865.77	< <b>0.001</b>	2	1774.022	< <b>0.001</b>
	Plant quality	2	39.11	< <b>0.001</b>	2	35.78	< <b>0.001</b>
	Interaction	4	19.10	< <b>0.001</b>	4	20.43	<b>0.001</b>
	Residuals	169			169		
Tibia length (mm)	Temperature	2	75.42	< <b>0.001</b>	2	155.47	< <b>0.001</b>
	Plant quality	2	62.66	< <b>0.001</b>	2	27.14	< <b>0.001</b>
	Interaction	4	5.77	< <b>0.001</b>	4	4.74	< <b>0.001</b>
	Residuals	396			396		
Wing length (mm)	Temperature	2	141.71	< <b>0.001</b>	2	148.45	< <b>0.001</b>
	Plant quality	2	51.97	<b>0.001</b>	2	20.03	<b>0.001</b>
	Interaction	4	2.66	<b>0.03</b>	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	< <b>0.001</b>	2	7.76	< <b>0.001</b>
	Interaction	4	2.62	<b>0.03</b>	4	1.51	0.20
	Residuals	126			126		

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

647

648

Accepted Manuscript



649 Table 2.

650 Results of GLM for the effect of sex on the measured parameters of the herbivore *Eccritotarsus*

651 *eichhorniae*. Significant effects are in bold.

652

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

653

654

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

658

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

659

660

661

662

## Figure legends

663 Figure 1

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

666

667 Figure 2

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

672

673 Figure 3

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

680

681 Figure 4

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

687 Figure 5

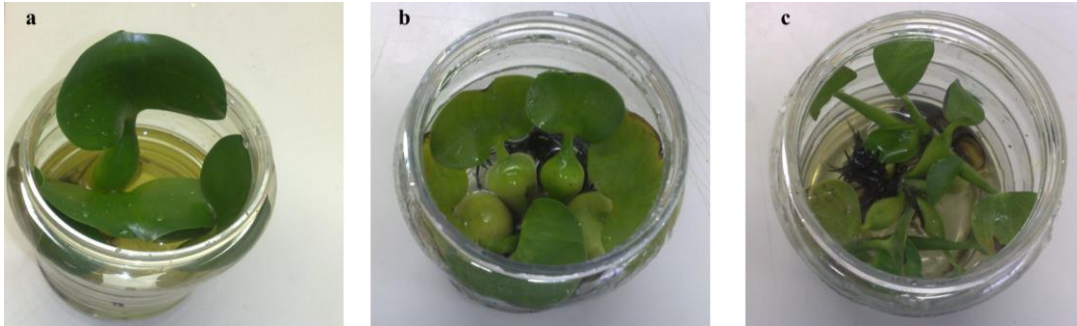
688 Dry body mass (A and B) and lipid content (C and D) of females and males of *Eccritotarsus*  
689 *eichhorniae* reared at three temperatures and fed on three qualities of plant (high, medium and  
690 low). In figures (A, C and D) small letters indicate the significant differences among the  
691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

694

Accepted Manuscript

695 Figure 1

696

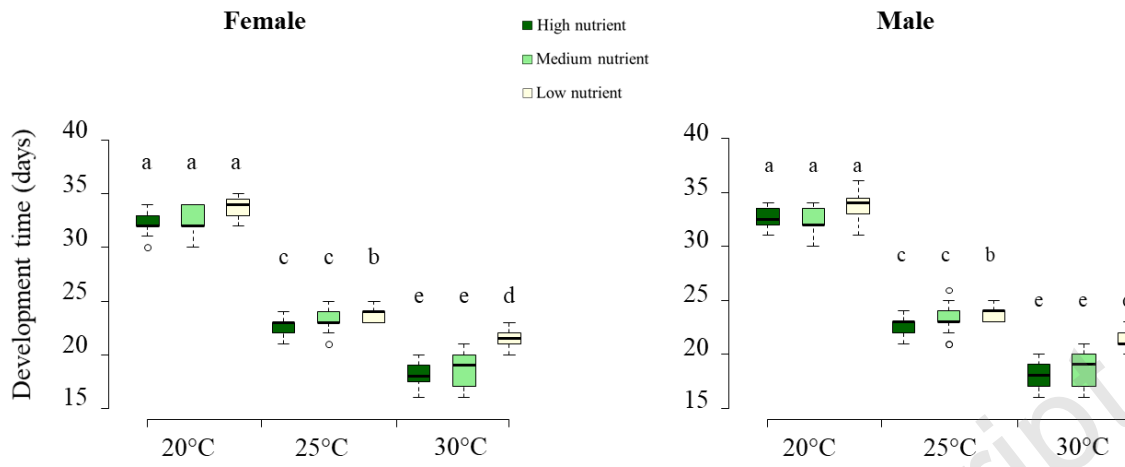


697

Accepted Manuscript

698 Figure 2

699



700

701

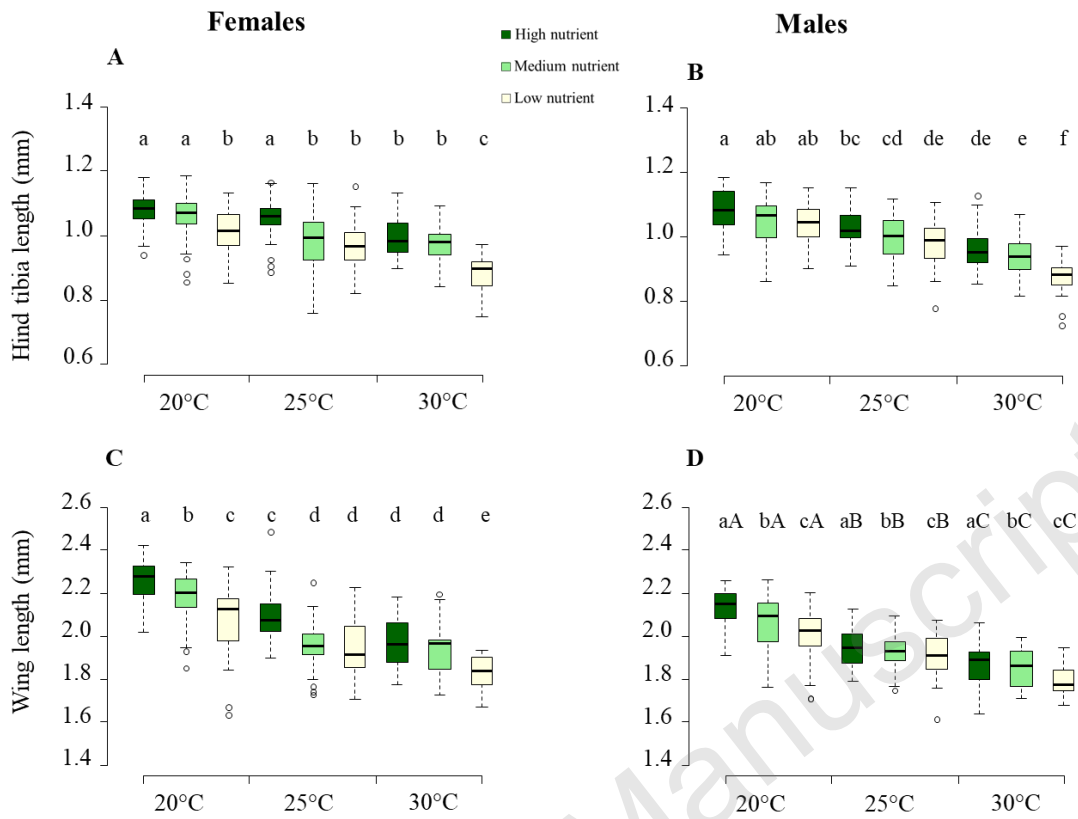
702

703

704

Accepted Manuscript

705 Figure 3



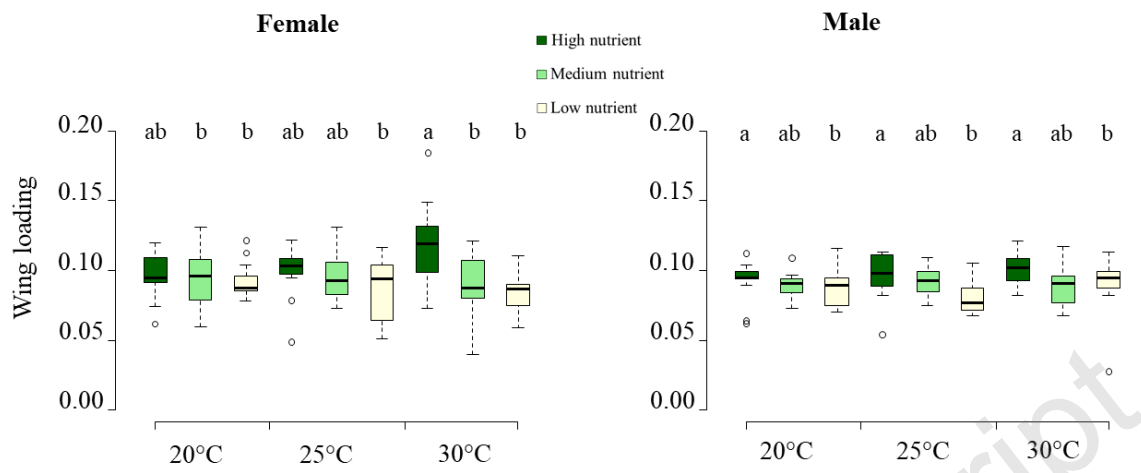
706

707

708

709 Figure 4

710



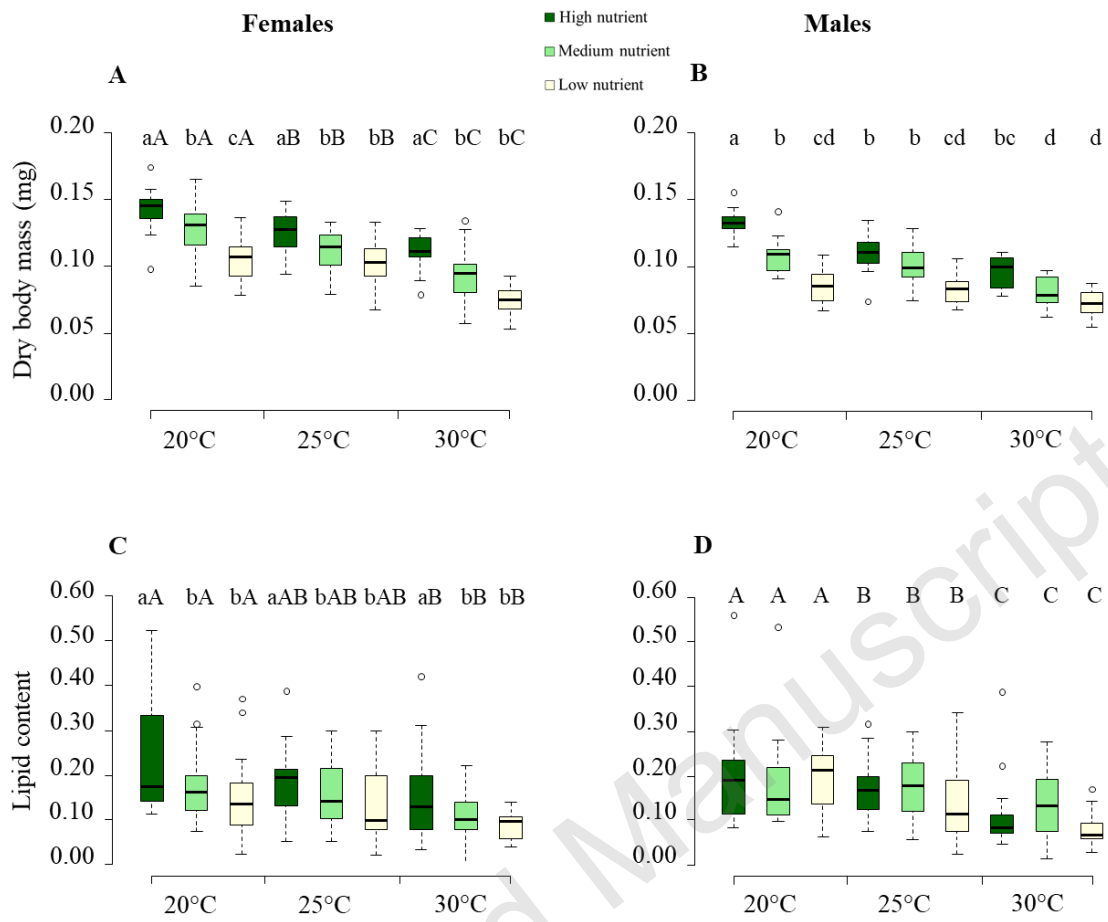
711

712

713



714 Figure 5



715  
716