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► **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-03095738v1>

Submitted on 2 Feb 2021

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HAL Authorization

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

3

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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⁻¹), and
142 eutrophic (high quality: 6.25 mg l⁻¹) 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⁻¹) 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°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.

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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

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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>)

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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	< 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		

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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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	< 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

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	< 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		

659

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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

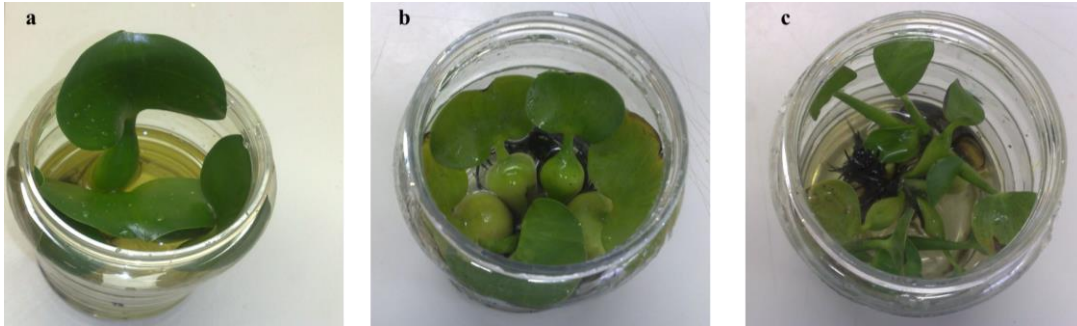
688 Dry body mass (A and B) and lipid content (C and D) of females and males of *Eccritotarsus*
689 *eichhorniae* reared at three temperatures and fed on three qualities of plant (high, medium and
690 low). In figures (A, C and D) small letters indicate the significant differences among the
691 different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

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695 Figure 1

696

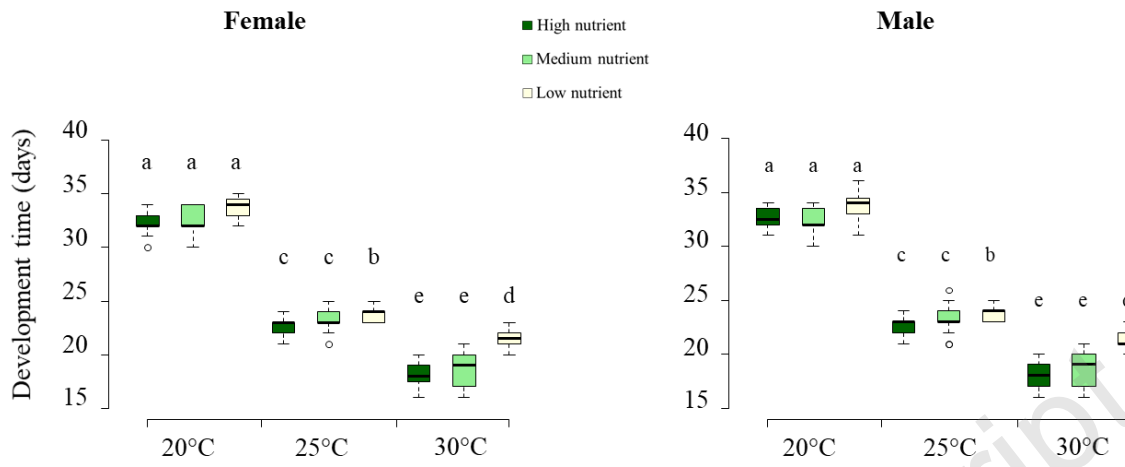


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698 Figure 2

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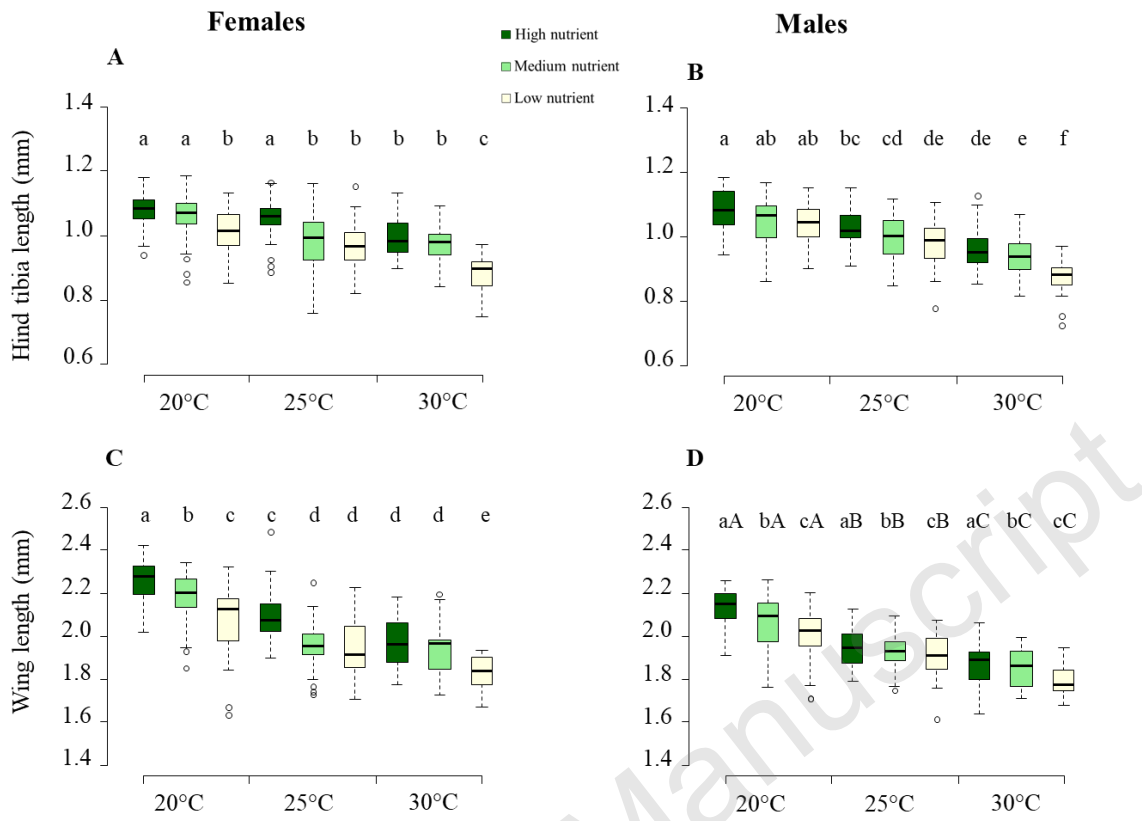
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705 Figure 3



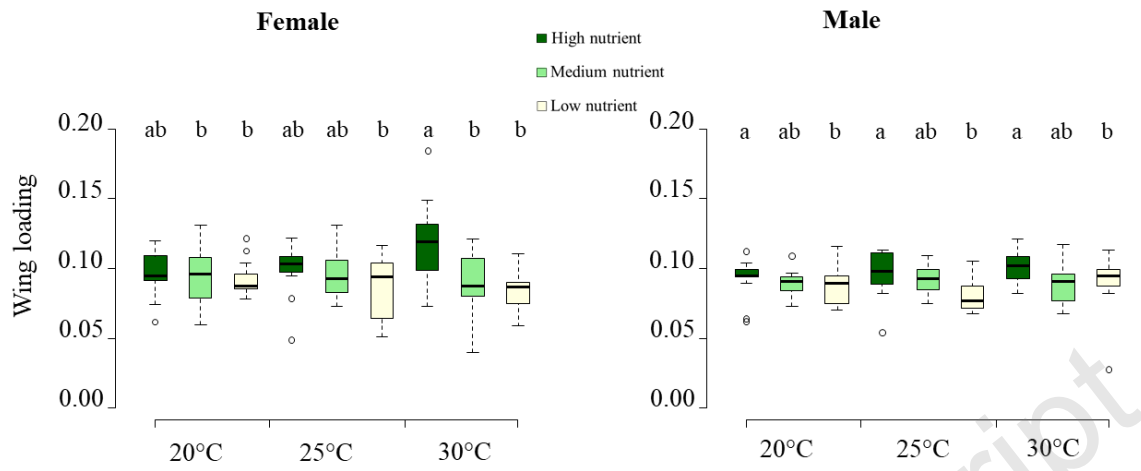
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709 Figure 4

710

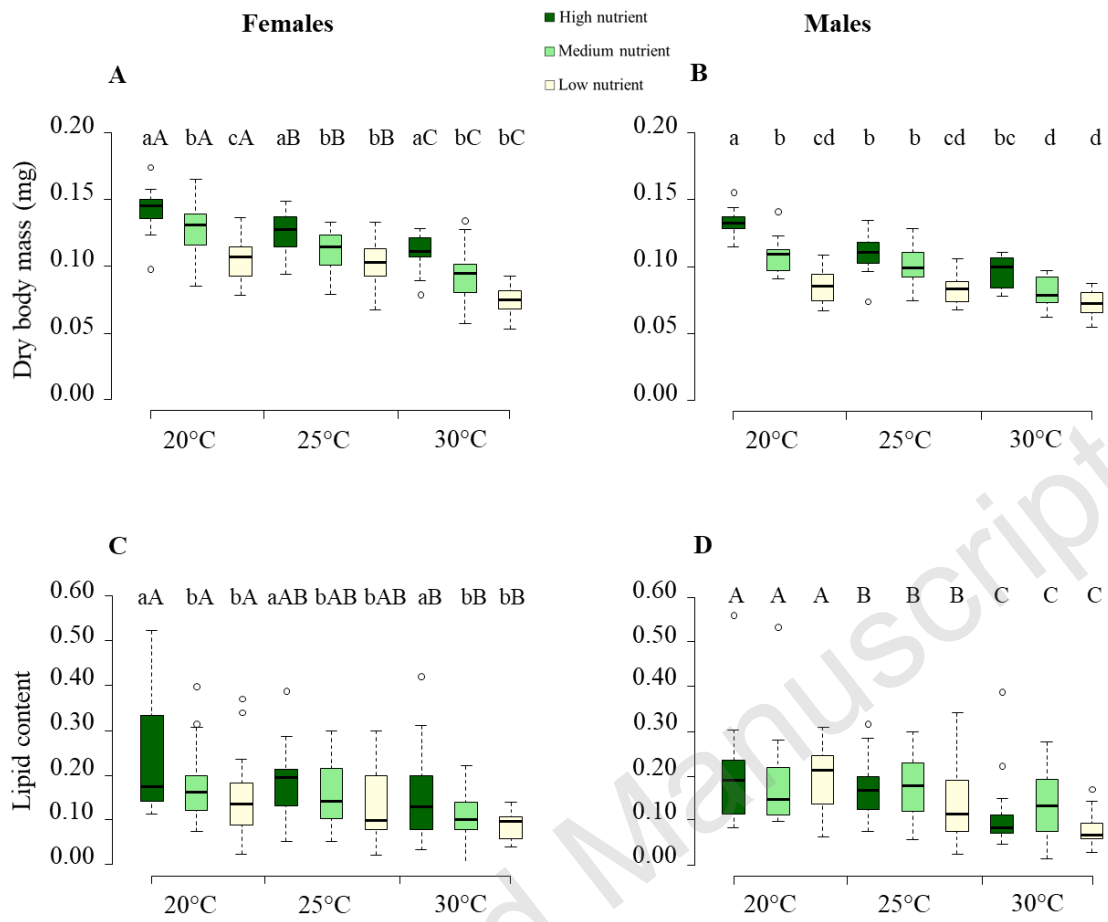


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714 Figure 5



715
716