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Post-Embryonic Growth Models of Four Grasshopper Species From The South Cameroon Rainforests: *Taphronota Ferruginea* (Fabricius, 1781), *Pyrgomorpha Vignaudii* (Guérin-Méneville 1849), *Atractomorpha Acutipennis* (Guerin-Meneville, 1844) (*Caelifera*, *Pyrgomorphidae*) And *Eyprepocnemis Plorans Ibandana* (Giglio-Tos, 1907) (*Caelifera, Acrididae*)

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ABSTRACT
Introduction: grasshoppers' growth models remain unclear and are particularly important in developing efficient pest management programs. In this study, we investigated on the morphometric relationships existing between the different nymphal instars (where instars are converted to ages or times) of four grasshopper species with relevant pest status in the laboratory (*Atractomorpha acutipennis, Epreypocnemis plorans ibandana, Taphronota ferruginea and Pyrgomorpha vignaudii*).
Methods: one thousand four hundred and fifty-eight (1458) individuals at different stages of development (266 *P. vignaudii*, 366 *A. acutipennis*, 390 *T. feruginea* and 536 *E. p. ibandana*) were collected from natural vegetation in Yaoundé, Mfou and Mbalmayo, monitored and measured in the laboratory from March 2012 to March 2017. The growth model, the growth ratio and the allometric growth model of each species were determined.
Results: we found that the growth models of nymphal instars varied among the four species, sex and organs. The growth model of the 4 grasshopper species was compared between 8 models that is: exponential, gompertz, hyperbole, linear, logarithm, logistic, power law and quadratic models. The power law was the best growth model. Growth ratio of each organ from one instar to the next varied among stages, sexes and species. Hypoallometry was the main allometric growth pattern in these grasshoppers.
Conclusion: these findings improve knowledge of the characteristics of acridians inhabiting forest agroecosystems.
Keywords: Acridians; Nymphal Development; Growth, Allometry; Pest.

Introduction

The increase in body length, as growth, is key characteristic of all living organisms (Hirst and Forster 2013). Understanding growth is fundamental to many areas of biology, as well as being crucial for livestock and agriculture-based industries (Lee *et al.* 2020). Modelling such a size change is fundamental, as body size determines many life-history traits (Whitman 2008), such as fecundity (Honek 1993; Kiørboe and Hirst 2008; Hirst and Forster 2013), mortality (La Barbera 1989) and population growth rates (Fenchel 1974). However, there is still much debate as to the best way for modelling growth that is based on the data collected from developmental stages (ontogeny) (Day and Taylor 1997; West *et al.* 2001; Ricklefs 2003; Tammaru and Esperk 2007). Being able to quantitatively describe such growth curves, and to determine whether taxa share a single universal response or indeed differ in that respect, are critical to the ability to formulate mechanistic approaches to their metabolism and life history. Such models also add to our ability to make predictions of rates and their pattern in nature (Hirst and Forster 2013).

Recently, the West Brown Enquist (WBE) equation, formulated as part of the metabolic theory of ecology, has been proposed as a universal growth model (West *et al.* 2001). This equation has the advantage that it has a biological basis, but its ability to describe invertebrate growth patterns has not been well tested in comparison to more simple models (Hirst and Forster, 2013). The majority of the data on allometric scaling of growth rate comes from vertebrates and plants (Enquist *et al.* 1999; Tammaru and Esperk 2007). In contrast, attempts to physiologically characterize

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insect growth using allometry are rather scarce. This is a clear gap of information because insects are much used models in life-history research, including various studies on the evolution of body size (Tammaru *et al.* 2002; Gotthard 2004). Based on this research tradition, it is often supposed or at least implicitly assumed that larvae grow exponentially (Abrams *et al.* 1996; Berger *et al.* 2006).

Body size and the relative dimensions of body parts are the most characteristic attributes of species (Nijhout and Callier 2015). Indeed, size and shape are the primary characteristics by which species are defined. The developmental mechanisms that control size and shape remain poorly understood in all organisms except insects (Nijhout and Callier 2015). Insects have several developmental characteristics that make them suitable for investigating intraspecific allometry and interactions between growth and development (Blossman-Myer and Burggren 2010). Most significant are their typically discrete stages of development, characterized by highly distinctive morphological markers and behaviours (ecdysis) (Blossman-Myer and Burggren 2010). Insects are characterized by their small size, large numbers, impressive reproductive output and rapid growth. However, their growth is not simply rapid; rather, they follow a qualitatively distinct pattern from many other animals (Meino and Kearney 2015). This study investigates the growth patterns of 4 grasshopper species, *A. acutipennis*, *E. p. ibandana*, *P. vignaudii* and *T. ferruginea* in the laboratory. More specifically, its aim is to determine (1) the growth equations of those 4 species, (2) in each species, the growth ratio, from one stage to the next, of the organs' length, and (3) the allometric scaling of organs in each species. In this study, we want to test the hypothesis that in grasshopper: (1) growth patterns follow the exponential types; (2) growth ratio is constant and (3) the isoallometric model is more frequent.

Materials and Methods

Origin of the Specimens

One thousand four hundred and fifty-eight (1458) individuals of *Atractomorpha acutipennis*, *Eyprepocnemis plorans ibandana*, *Pyrgomorpha vignaudii* and *Taphronota ferruginea* used were collected in the natural vegetation of Yaounde, Mfou and Mbalmayo (south Cameroon rainforests) and reared in the laboratory from March 2012 to March 2017. These four grasshopper species are amongst the most frequent crop pests in the study area. The study area is located in semi-deciduous forest and the vegetation is much degraded because of the anthropic activity (Gockowski *et al.* 2004). The climate is of Guinean equatorial type with four seasons: a small rainy season (from mid-March to June); a long rainy season (from September to mid-November); a long dry season (from mid-November to mid-March) and a short dry season (from July to August). The rainfall is about 1600 mm annually and the temperatures are between 19° C and 33° C (Suchel 1987).

Study of Growth Model in Laboratory

The 1458 captured grashoppers at various developmental stages (Table 1) were reared in the laboratory and identified as described by Kekeunou

Table 1. Number of individuals measured in each studied species per instar .

<table>
<tr><th rowspan="2">Species</th><th rowspan="2">Sex</th><th colspan="7">Nymphs</th><th rowspan="2">Adults</th><th rowspan="2">Total</th><th rowspan="2">References</th></tr>
<tr><th>Instar 1</th><th>Instar 2</th><th>Instar 3</th><th>Instar 4</th><th>Instar 5</th><th>Instar 6</th><th>Instar 7</th></tr>
<tr><td rowspan="3">A. accutipennis</td><td>Male</td><td>25</td><td>32</td><td>29</td><td>24</td><td>23</td><td>/</td><td>/</td><td>31</td><td>164</td><td rowspan="3">Kekeunou et al. 2020</td></tr>
<tr><td>Female</td><td>30</td><td>29</td><td>30</td><td>28</td><td>25</td><td>30</td><td>/</td><td>30</td><td>202</td></tr>
<tr><td>Total</td><td>55</td><td>61</td><td>59</td><td>52</td><td>48</td><td>30</td><td>/</td><td>61</td><td>366</td></tr>
<tr><td rowspan="3">P. vignaudii</td><td>Male</td><td>20</td><td>18</td><td>20</td><td>12</td><td>12</td><td>18</td><td>/</td><td>21</td><td>121</td><td rowspan="3">Kekeunou et al. 2015</td></tr>
<tr><td>Female</td><td>21</td><td>24</td><td>20</td><td>18</td><td>17</td><td>12</td><td>/</td><td>33</td><td>145</td></tr>
<tr><td>Total</td><td>41</td><td>42</td><td>40</td><td>30</td><td>29</td><td>30</td><td>/</td><td>54</td><td>266</td></tr>
<tr><td rowspan="3">T. ferruginae</td><td>Male</td><td>18</td><td>27</td><td>30</td><td>24</td><td>30</td><td>31</td><td>/</td><td>32</td><td>192</td><td rowspan="3">Kekeunou et al. 2018</td></tr>
<tr><td>Female</td><td>15</td><td>25</td><td>27</td><td>32</td><td>30</td><td>34</td><td>/</td><td>35</td><td>198</td></tr>
<tr><td>Total</td><td>33</td><td>52</td><td>57</td><td>56</td><td>60</td><td>65</td><td>/</td><td>67</td><td>390</td></tr>
<tr><td rowspan="4">E. p. ibandana</td><td>Male</td><td>32</td><td>30</td><td>30</td><td>30</td><td>33</td><td>36</td><td>/</td><td>25</td><td>216</td><td rowspan="4">Djomang Nkwala et al. 2019</td></tr>
<tr><td>Female 6</td><td rowspan="2">30</td><td rowspan="2">30</td><td rowspan="2">30</td><td rowspan="2">31</td><td>23</td><td>30</td><td>/</td><td>36</td><td>210</td></tr>
<tr><td>Female 7</td><td>20</td><td>32</td><td>38</td><td>20</td><td>110</td></tr>
<tr><td>Total</td><td>62</td><td>60</td><td>60</td><td>61</td><td>76</td><td>98</td><td>38</td><td>81</td><td>536</td></tr>
</table>

Legend: Female 6: female with six nymphal instars, Female 7: female with seven nymphal instars.

et al. (2020) for *A. acutipennis*, Djomang Nkwala et al. (2019) for *E. p. ibandana*, Kekeunou *et al.* (2018) for *T. ferruginea* and Kekeunou *et al.* (2015) for *P. vignaudii*. All species length and size were measured with an electronic caliper.

Morphological parameters were measured, according to the comparative study of De Gregorio (1987) and Defaut (2012). They included: total body length (Lt), length (Lcc) and width (lcc) of cephalic capsule, length of thorax (Lth), abdomen (Labd), pronotum (Lpr), antenna (La), elytra (Lel), hind wing (Lai), anterior (Lcu1), median (Lcu2) and posterior (Lcu3) femur, anterior (Lti1), median (Lti2) and posterior (Lti3) tibia.

Plotting of the Growth Models

The function Y= f(X) translating the relationship between each measured character and the development time of each instar, was adjusted to numerous models from the exponential model ($Y = ae^x$), logarithm model (Y=loga + (log *b*)X) (Meino and Kearney 2015), the linear model ($Y = a_0 + an_1X$) (Yang & Joern 1994), the polynomial model ($Y = a_0 + a_1X^2 \ldots + a_nX^n$) (Meino and Kearney 2015), power law model ($Y= aX^b$), the hyperbolic model ($Y = \frac{1}{a_0+a_1X}$), the Gompertz model ($Y= ab^{e^x}$) (Stoner 1941) and the logistic model ($Y = \frac{1}{ab^x+g}$) to assess the goodness-of-fit of our data using Excel 2016 and the package "easynls version 5.0" (Arnhold 2017) in R 4.10 software. These models have been chosen because they are the most frequent in the growth model studies. The best-fitted model for each measured parameter was chosen based on the lowest BIC (Bayesian Information Criteria) (Stoica and Selen 2004). The development time of each instar of the studied grasshopper species are indicated in table 2 (Kekeunou *et al.* 2015; Kekeunou *et al.* 2018; Djomang Nkwala *et al.* 2019; Kekeunou *et al.* 2020).

Assessment of the Growth Ratio

The growth ratio of each organ for each grasshopper was determined by calculating the ratio Yn+ 1 / Yn, which represents the ratio of the increase in length of an organ from instar n to instar n+1. Growth ratios were calculated using R.4.1.0 software. For each instar of the studied grasshopper species, the mean and the related standard error were determined. Means were compared by performing the One-Way Analysis of Variance (ANOVA) test and Tukey post hoc test at the level of significance $\alpha = 0.05$.

Study of the Allometric Growth Model

The allometric constant k (allometric coefficient) represents the scaling relationship between X and Y; where X = body length of instar i and Y = length of a given organ of instar i. k> 1: positive allometry (or hyperallometry), k <1: negative allometry (or hypoallometry), k = 1: isometric allometry (isoallometry) (Canard & Poinsot, 2004; Nijhout and Callier, 2015). Allometries are usually modelled using the power function $Y = b.X^k$ (Shingleton *et al.* 2007). Therefore, k was directly calculated by using the R software where the mean and the standard error were expressed. A t-student test was carried to determine whether each k value is significantly different from 1 at the level of significance $\alpha = 0.05$.

Results

Growth Model

The growth patterns of the nymphal instars of the four studied grasshopper species varied per species, sex and organs (Table 3). The growth model was tested among 8 models (power law, gompertz, quadratic, linear, logarithm, logistic, hyperbole and exponential models), and the data were adjusted for only six of them: power law, gompertz, quadratic,

Table 2. Nymphal development time (in days) of *A. acutipennis*, *E. p. ibandana*, *P. vignaudii* and *T. ferruginea* in the laboratory.

Species	Sex	Nymphs							References
		Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Instar 6	Instar 7	
A. acutipennis	Male	17.14±0.62	12.91±0.62	13.45±0.69	13.80±0.68	15.23±0.55	/	/	Kekeunou *et al.* 2020
	Female	16.18±0.54	13.13±0.59	12.49±0.42	13.19±0.58	14.58±0.61	16.57±0.68	/	
P. vignaudii	Male	17.21±1.31	14.19±0.86	13.60±1.49	14.52±1.06	15.81±1.89	15.83±2.20	/	Kekeunou *et al.* 2015
	Female	16.09±1.12	14.94±1.49	12.93±1.25	15.86±1.87	14.36±2.47	16.60±1.65	/	
T. ferruginea	Male	20.00±1.33	20.23±2.07	20.63±0.85	23.02±1.23	26.70±0.92	31	/	Kekeunou *et al.* 2018
	Female	20.21±1.97	19.58±1.59	19.91±1.06	23.53±1.13	26.38±1.29	34	/	
E. p. ibandana	Male	12.22±0.13	11.32±0.17	11.53±0.17	12.64±0.19	13.5±0.20	18±0.28	—	Djomang Nkwala *et al.* 2019
	Female 6	12.78±0.17 12.0±0.27	11.70±0.19 10.81±0.24	12.10±0.22 11.19±0.30	13.72±0.25 12.74±0.40	14.92±0.31	24.72±0.48	—	
	Female 7					13±0.34	14.27±0.42	20.52±0.63	

Notes: Values in table indicate: mean ± standard error. Female 6: female with six nymphal instars. Female 7: female with seven nymphal instars.

linear, logarithm and exponential. Data did not apply to the logistic and the hyperbolic models (Table 3). The best growth model was the power law with the lowest BIC in nearly all species, sex and organs, except for the length of abdomen of male *P. vignaudii* where quadratic function was the best (Table 3). However, the Gompertz model appears as an additional one to the power law model for the elytra in *A. acutipennis*, male *E. p. ibandana*, female with six nymphal instars *E. p. ibandan* and male *P. vignaudii*, as well as for the hind wing in female with six nymphal instars *E. p. ibandan* and male *P. vignaudii* (Table 3).

Growth Ratio

The growth ratio of each organ from one instar to the next varied between stages, sexes and species (Table 4). In all species, the growth ratios of elytra length and hind wing length were high and varied between 2 and 4, except for *E. p. ibandana* F7 where the growth ratios between nymphal instars 6 and 7 were low (between 1 and 1.07). Meanwhile, the growth ratio for the other 13 organs varied between 0.8 and 2.

Table 3. Summary of BIC values for all growth models tested in the organs of *A. acutipennis* (Atrac), *E. p. ibandana* (Eypre), *P. vignaudii* (Pyrgo) and *T. ferruginea* (Taphr).

Species	Sex	Model	Lt	La	Lcc	lcc	Lth	Lpr	Labd	Lel	Lai	Lcu1	Lcu2	Lcu3	Lti1	Lti2	Lti3
Atrac	MF	Exponential	1730	910	963	290	931	833	1254	206	178	655	657	1272	540	547	1190
		Linear	1244	308	392	-77	486	350	920	206	174	78	96	643	0.25	43	563
		Quadratic	1238	292	380	-152	420	241	923	206	140	66	44	587	-36	-5	492
		Power law	**-352**	**-338**	**-384**	**-264**	**-204**	**-244**	**-177**	**19**	**-16**	**-292**	**-371**	**-416**	**-318**	**-295**	**-416**
		Logarithm	1244	308	392	-77	486	350	920	206	174	78	96	643	0.25	43	563
		Gompertz	307	305	228	99	379	434	319	19	56	348	321	321	322	287	304
		Logistic	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Hyperbole	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Eypre	M	Exponential	1004	590	490	383	490	437	834	112	75	330	719	845	320	420	716
		Linear	624	93	7	-22	178	-105	544	112	75	-63	373	341	-88	-0.1	219
		Quadratic	618	72	-3.4	-42	183	-116	532	112	75	-63	377	338	-91	-22	216
		Power law	**-298**	**-278**	**-377**	**-417**	**-252**	**-318**	**-174**	**-112**	**-116**	**-256**	**-76**	**-334**	**-264**	**-212**	**-354**
		Logarithm	624	93	7	-22	178	-105	544	112	75	-63	373	341	-88	-0.1	219
		Gompertz	165	167	65	100	92	198	249	-112	-115	133	305	177	125	166	103
		Logistic	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Hyperbole	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	F6	Exponential	962	619	533	424	515	483	798	184	52	380	414	855	349	456	749
		Linear	675	393	225	98	243	195	548	184	52	135	156	541	30	114	463
		Quadratic	597	287	157	63	205	56	515	184	52	79	88	410	-129	-9	316
		Power law	**-171**	**-87**	**-150**	**-211**	**-152**	**-121**	**-121**	**-18**	**-120**	**-117**	**-111**	**-135**	**-120**	**-117**	**-131**
		Logarithm	675	393	225	98	243	195	548	184	52	135	156	541	30	114	463
		Gompertz	170	176	100	128	142	214	220	-18	-120	158	158	201	146	189	147
		Logistic	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Hyperbole	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	F7	Exponential	1387	930	787	722	822	797	1182	440	414	666	719	1223	617	725	1099
		Linear	980	573	357	393	449	410	782	389	361	289	373	827	209	317	732
		Quadratic	985	561	363	393	455	408	787	151	139	293	378	830	214	322	322
		Power law	**-165**	**-83**	**-200**	**-168**	**-130**	**-92**	**-108**	**136**	**128**	**-98**	**-76**	**-127**	**-123**	**-122**	**-137**
		Logarithm	980	573	357	393	449	410	782	389	361	289	373	827	209	317	732
		Gompertz	308	304	202	258	262	355	362	204	195	302	305	375	280	314	279
		Logistic	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Hyperbole	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Pyrgo	M	Exponential	547	603	270	86	459	203	414	46	46	23	34	347	21	17	337
		Linear	365	449	70	-87	290	-5	273	46	46	-0.4	2	113	7	1	144
		Quadratic	366	329	74	-83	227	-80	-147	46	46	-1.5	0.5	115	7	-5	146
		Power law	**-115**	**-79**	**-89**	**-131**	**-75**	**-98**	**-69**	**-30**	**-22**	**-38**	**-37**	**-144**	**-23**	**-34**	**-112**
		Logarithm	365	449	70	-87	290	-5	273	46	46	-0.4	2	113	7	1	144
		Gompertz	102	64	51	36	89	108	115	-30	-22	3	14	78	9.8	-10	78.5
		Logistic	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Hyperbole	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	F	Exponential	635	334	337	117	424	254	449	40	35	64	68.5	430	53	50	414
		Linear	436	163	86	-45	305	99	342	45	46	31	40.3	195	9	32	209
		Quadratic	418	117	73	-56	286	60.5	330	29	27	21	13	164	-1.6	5	180
		Power law	**-135**	**-74**	**-189**	**-119**	**-83**	**-48**	**-45**	**-26**	**-19**	**-35**	**-31.5**	**-151**	**-39**	**-23**	**-128**
		Logarithm	436	163	86	-45	305	99	342	45	46	31	40.3	195	9	32	209
		Gompertz	139	117	67	56	461	134	137	-0.4	3	25	33.5	113	38	26	113
		Logistic	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Hyperbole	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Taphr	M	Exponential	867	558	425	173	424	398	680	198	178	250	281	599	236	547	596
		Linear	640	386	149	-27	305	169	533	160	174	125	158	346	110	43	380
		Quadratic	628	308	125	-42	286	101	526	127	74	76	113	294	68	-5	339
		Power law	**-202**	**-128**	**-238**	**-197**	**-83**	**-102**	**-109**	**-83**	**-16**	**-147**	**-149**	**-208**	**-131**	**-295**	**-179**
		Logarithm	640	386	149	-27	305	169	533	160	174	125	158	346	110	43	380
		Gompertz	23	49	19	-29	46	117	56	67	56	-24	-29	16	-14.3	-33	33.2
		Logistic	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Hyperbole	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
	F	Exponential	917	603	466	194	459	432	733	228	179	287	315	643	269	286	626
		Linear	701	449	225	23	290	276	573	200	192	184	169	417	190	181	409
		Quadratic	630	329	192	-62	227	157	540	162	122	101	96	332	104	98	328
		Power law	**-140**	**-79**	**-181**	**-156**	**-75**	**-31**	**-74**	**-42**	**-21**	**-110**	**-158**	**-155**	**-80**	**-113**	**-147**
		Logarithm	701	449	225	23	290	276	573	200	192	184	169	417	190	181	409
		Gompertz	44	64	20	-34	57	112	82	60	44	-12	-14	31	-10.3	-17	39
		Logistic	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
		Hyperbole	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Legend: M: male, F: female, F6: female with six nymphal instars, F7: female with seven nymphal instars, body length (Lt), length (Lcc) and width (lcc) of cephalic capsule, length of thorax (Lth), abdomen (Labd), pronotum (Lpr), antenna (La), elytra (Lel), hind wing (Lai), anterior (Lcu1), median (Lcu2) and posterior (Lcu3) femur, anterior (Lti1), median (Lti2) and posterior (Lti3) tibia. NA: not applicable.

Table 4. Growth ratio (Yn+ 1 / Yn) of each organ of *A. acutipennis* (Atrmph), *E. p. ibandana* (E.p.i), *P. vignaudii* (Pygmph) and *T. ferruginea* (Tphrn) in the laboratory.

Organs	Stages	Species/Sexes							
		Atrmph	E.p.i-M	E.p.i-F6	E.p.i-F7	Pygmph-M	Pygmph-F	Tphrn-M	Tphrn-F
Lt	L2/L1	1.62±0.04a	1.53±0.06a	1.54±0.06a	1.54±0.06a	1.57±0.1a	1.87±0.07a	1.3±0.05a	1.3±0.06ab
	L3/L2	1.25±0.03b	1.44±0.03a	1.36±0.02b	1.36±0.02b	1.4±0.1a	1.37±0.06b	1.2±0.03ab	1.2±0.04b
	L4/L3	1.3±0.03b	1.11±0.02b	1.16±0.03b	1.16±0.03b	1.2±0.07b	1.14±0.06b	1.13±0.02b	1.16±0.03b
	L5/L4	1.08±0.04b	1.23±0.04b	1.47±0.03a	1.37±0.05b	1.25±0.06b	1.3±0.05b	1.22±0.04ab	1.27±0.05ab
	L6/L5	1.6±0.04a	1.2±0.03b	1.45±0.02a	1.62±0.04a	1.3±0.04b	1.4±0.05b	1.26±0.04ab	1.4±0.05a
	L7/L6				1±0.02c				
	A/L6	1±0.02b	1.42±0.02a	1.42±0.03a		1.06±0.04b	1.4±0.07b	1.2±0.04ab	1.45±0.03a
	A/L7				1.4±0.05a				
Lcc	L2/L1	1.45±0.04a	1.16±0.03a	1.2±0.02a	1.2±0.02a	1.2±0.1a	1.32±0.05a	1.2±0.04ab	1.4±0.04a
	L3/L2	1.35±0.03a	1.4±0.02b	1.3±0.02ab	1.3±0.02b	1.54±0.24b	1.32±0.25a	1.3±0.04b	1.13±0.04b
	L4/L3	1.24±0.02b	1.2±0.02a	1.2±0.02a	1.2±0.02a	1.12±0.03a	1.2±0.25ab	1.1±0.03a	1.16±0.03b
	L5/L4	1.11±0.03b	1.16±0.02a	1.4±0.03b	1.27±0.04ab	1.22±0.04a	1.2±0.03ab	1.2±0.02ab	1.17±0.03b
	L6/L5	1.45±0.04a	1.14±0.02a	1.33±0.03ab	1.47±0.03b	1.15±0.02a	1.3±0.05a	1.3±0.03b	1.33±0.02a
	L7/L6				1.03±0.01c				
	A/L6	1±0.02b	1.25±0.03a	1.2±0.02a		1.07±0.02a	1.17±0.03b	1.2±0.03ab	1.32±0.03a
	A/L7				1.16±0.01a				
lcc	L2/L1	1.14±0.01a	1.47±0.03a	1.53±0.05a	1.53±0.05a	1.25±0.07ab	1.36±0.04a	1.25±0.04a	1.3±0.04a
	L3/L2	1.22±0.02a	1.2±0.02b	1.14±0.01b	1.14±0.01b	1.3±0.05b	1.27±0.3ab	1.2±0.03ab	1.1±0.04b
	L4/L3	1.3±0.07ab	1.23±0.02b	1.2±0.03b	1.2±0.03b	1.2±0.04a	1.17±0.03b	1.12±0.01b	1.16±0.03b
	L5/L4	1.17±0.05a	1.15±0.01b	1.47±0.03a	1.24±0.04b	1.17±0.06a	1.25±0.03ab	1.15±0.02b	1.2±0.03ab
	L6/L5	1.43±0.05b	1.16±0.02b	1.27±0.03ab	1.7±0.05a	1.17±0.03a	1.28±0.07ab	1.25±0.04a	1.33±0.03a
	L7/L6				1±0.02b				
	A/L6	1.1±0.02a	1.12±0.01b	1.15±0.02b		1.2±0.03a	1.36±0.07a	1.2±0.03ab	1.3±0.03a
	A/L7				1.1±0.01b				
Lth	L2/L1	1.46±0.04a	1.3±0.04a	1.5±0.1a	1.5±0.1a	2.2±0.12a	1.86±0.2a	1.35±0.08a	1.35±0.04a
	L3/L2	1.34±0.04a	1.45±0.04b	1.35±0.02ab	1.35±0.02ab	1.18±0.05b	1.82±0.2a	1.23±0.04ab	1.15±0.03b
	L4/L3	1.4±0.03a	1.1±0.02c	1.2±0.02b	1.2±0.02b	1.17±0.06b	1.17±0.03b	1.14±0.02b	1.11±0.04b
	L5/L4	1.27±0.04a	1.16±0.03ac	1.28±0.02b	1.34±0.02ab	1.23±0.06b	1.47±0.1ab	1.22±0.04b	1.4±0.07a
	L6/L5	1.75±0.06a	1.27±0.03ac	1.44±0.02a	1.4±0.01a	1.32±0.06a	1.36±0.1ab	1.36±0.04a	1.32±0.05a
	L7/L6				1.03±0.02c				
	A/L6	1.1±0.01b	1.44±0.04b	1.47±0.03a		1.12±0.04b	1.28±0.05b	1.4±0.05a	1.61±0.05a
	A/L7				1.44±0.03a				
Labd	L2/L1	1.63±0.06a	1.91±0.1a	1.75±0.07a	1.75±0.07a	1.5±0.09a	1.6±0.05a	1.42±0.06a	1.42±0.06a
	L3/L2	1.21±0.04b	1.43±0.04b	1.44±0.04a	1.44±0.04a	1.46±0.08a	1.51±0.07a	1.15±0.04b	1.2±0.05b
	L4/L3	1.24±0.04b	1.12±0.03c	1.14±0.04b	1.14±0.04b	1.36±0.08ab	1.21±0.04b	1.2±0.05b	1.21±0.04b
	L5/L4	1.17±0.03b	1.26±0.05c	1.53±0.04a	1.5±0.07a	1.24±0.07b	1.21±0.04b	1.23±0.06b	1.25±0.07b
	L6/L5	1.27±0.05b	1.24±0.05c	1.43±0.04a	1.6±0.04a	1.3±0.05ab	1.6±0.1a	1.24±0.06b	1.46±0.08a
	L7/L6				1.02±0.02b				
	A/L6	1.23±0.04b	1.35±0.04b	1.55±0.05a		1.16±0.04b	1.63±0.15a	1.25±0.06b	1.57±0.05a
	A/L7				1.45±0.07a				

Lpr	L2/L1	1.6±0.07a	1.35±0.03ab	1.42±0.03ab	1.42±0.03a	1.43±0.08a	1.43±0.1a	1.42±0.1a	1.38±0.06a
	L3/L2	1.42±0.04b	1.5±0.02a	1.42±0.03ab	1.42±0.03a	1.47±0.08a	1.56±0.04a	1.36±0.04a	1.17±0.05b
	L4/L3	1.4±0.03b	1.22±0.03b	1.22±0.03b	1.22±0.03b	1.35±0.07a	1.18±0.06b	1.04±0.02b	1.2±0.06b
	L5/L4	1.27±0.06b	1.35±0.03ab	1.7±0.05a	1.33±0.05ab	1.24±0.07ab	1.44±0.06a	1.48±0.05a	1.5±0.05a
	L6/L5	1.64±0.05a	1.25±0.02b	1.45±0.03a	1.92±0.02a	1.3±0.03ab	1.43±0.05a	1.4±0.04a	1.45±0.03a
	L7/L6				1±0.01b				
	A/L6	0.8±0.01c	1.21±0.02b	1.1±0.02b		1.1±0.01b	1.33±0.06ab	1.21±0.06ab	1.36±0.04ab
	A/L7				1.05±0.02b				
La	L2/L1	1.35±0.04a	1.32±0.04a	1.32±0.03ab	1.32±0.03a	1.35±0.05a	1.46±0.1a	1.27±0.05ab	1.27±0.06ab
	L3/L2	1.36±0.03a	1.41±0.02a	1.34±0.02ab	1.34±0.02a	1.33±0.05a	1.36±0.06ab	1.3±0.04b	1.3±0.06ab
	L4/L3	1.4±0.03a	1.24±0.02a	1.25±0.03b	1.25±0.03a	1.32±0.05a	1.21±0.06b	1.06±0.03a	1.12±0.06b
	L5/L4	1.16±0.04b	1.3±0.02a	1.6±0.06a	1.23±0.05a	1.29±0.05a	1.38±0.1ab	1.36±0.04b	1.4±0.06a
	L6/L5	1.35±0.04a	1.26±0.02a	1.47±0.04a	1.82±0.05b	1.32±0.05a	1.44±0.1a	1.4±0.03b	1.44±0.02a
	L7/L6				1.08±0.03a				
	A/L6	1.22±0.03ab	1.62±0.02b	1.22±0.02b		1.33±0.07a	1.3±0.05ab	1.3±0.03b	1.3±0.04ab
	A/L7				1.16±0.03a				
Lel	L2/L1								
	L3/L2								
	L4/L3								
	L5/L4								
	L6/L5	2.32±0.15a	2.58±0.07a	2.9±0.13a		2.1±0.07a	2.27±0.08a	2.24±0.06a	2.2±0.08a
	L7/L6				1.01±0.02a				
	A/L6	2.86±0.05b	3.76±0.13b	3.7±0.2b		3.1±0.1b	2.7±0.1b	3.74±0.14b	4.4±0.12b
	A/L7				3.43±0.1b				
Lai	L2/L1								
	L3/L2								
	L4/L3								
	L5/L4								
	L6/L5	2.41±0.18a	2.12±0.06a	2.29±0.04a		2.28±0.06a	2.61±0.11a	2.45±0.14a	2.47±0.14a
	L7/L6				1.02±0.02a				
	A/L6	2.46±0.17a	3.74±0.08b	3.77±0.07b		2.9±0.1b	2.21±0.08b	4±0.15b	4.5±0.12b
	A/L7				3.6±0.1b				
Lcu1	L2/L1	1.34±0.03a	1.15±0.01a	1.2±0.03a	1.2±0.03a		1.7±0.12a	1.3±0.09a	1.32±0.1a
	L3/L2	1.5±0.04b	1.51±0.02b	1.47±0.03b	1.47±0.03b		1.4±0.11a	1.16±0.02ab	1.15±0.05b
	L4/L3	1.27±0.03a	1.2±0.02a	1.2±0.03a	1.2±0.03a		1.05±0.13b	1.03±0.02b	1.05±0.04b
	L5/L4	1.45±0.11b	1.25±0.04a	1.52±0.03b	1.3±0.04ab	1.13±0.05a	1.3±0.06a	1.27±0.04a	1.27±0.03ab
	L6/L5	2.28±0.15c	1.26±0.04a	1.4±0.04b	1.77±0.04b	1.36±0.05b	1.5±0.1a	1.34±0.04a	1.44±0.04a
	L7/L6				1.07±0.02a				
	A/L6	2.85±0.05d	1.6±0.03b	1.3±0.04ab		1.24±0.04ab	1.3±0.06a	1.24±0.04a	1.4±0.04a
	A/L7				1.3±0.03a				

Lcu2	L2/L1	1.34±0.03a	1.2±0.03a	1.3±0.04a	1.3±0.04a		1.7±0.06a	1.3±0.07a	1.27±0.06ab
	L3/L2	1.41±0.04a	1.47±0.03b	1.4±0.04a	1.4±0.04a		1.4±0.12a	1.11±0.02b	1.18±0.05a
	L4/L3	1.3±0.04a	1.2±0.04a	1.1±0.03b	1.1±0.03b		1.02±0.12b	1.04±0.02b	1.1±0.05a
	L5/L4	1.23±0.05b	1.3±0.03c	1.7±0.05c	1.35±0.05a		1.3±0.08a	1.3±0.04a	1.23±0.04a
	L6/L5	1.5±0.05a	1.3±0.02c	1.35±0.03a	1.73±0.06c	1.4±0.02a	1.53±0.09a	1.34±0.04a	1.43±0.03b
	L7/L6				1.02±0.04b				
	A/L6	1±0.23b	1.54±0.03b	1.35±0.03a		1.24±0.04b	1.33±0.06a	1.2±0.04ab	1.35±0.05b
	A/L7				1.25±0.03a				
Lcu3	L2/L1	1.45±0.02a	1.33±0.01ab	1.41±0.02a	1.41±0.02a	1.32±0.06ab	1.41±0.03a	1.24±0.04a	1.27±0.05ab
	L3/L2	1.4±0.02a	1.4±0.02b	1.35±0.02b	1.35±0.02b	1.4±0.1a	1.46±0.05a	1.29±0.03a	1.2±0.05ab
	L4/L3	1.28±0.03b	1.3±0.03a	1.25±0.04b	1.25±0.04b	1.26±0.06ab	1.16±0.04b	1.04±0.02b	1.15±0.06a
	L5/L4	1.18±0.03b	1.29±0.03a	1.7±0.05a	1.32±0.05b	1.18±0.05b	1.32±0.04a	1.34±0.02a	1.31±0.03b
	L6/L5	1.5±0.04a	1.25±0.02a	1.37±0.02ab	1.77±0.04c	1.23±0.03ab	1.37±0.05a	1.29±0.02a	1.3±0.02b
	L7/L6				1.01±0.01d				
	A/L6	1±0.01c	1.25±0.02a	1.26±0.03b		1.24±0.03ab	1.3±0.05a	1.24±0.03a	1.4±0.03b
	A/L7				1.25±0.03b				
Lti1	L2/L1	1.34±0.02a	1.15±0.02a	1.2±0.02a	1.2±0.02a		1.9±0.14a	1.3±0.09a	1.25±0.1a
	L3/L2	1.4±0.04a	1.45±0.03b	1.4±0.02b	1.4±0.02b		1.3±0.14b	1.2±0.03a	1.2±0.1a
	L4/L3	1.37±0.03a	1.23±0.03b	1.2±0.03a	1.2±0.03a		1.1±0.08c	1±0.02b	1.08±0.04b
	L5/L4	1.13±0.04b	1.26±0.03b	1.56±0.03b	1.3±0.04ab		1.36±0.05b	1.32±0.05a	1.27±0.03a
	L6/L5	1.53±0.05a	1.24±0.03b	1.37±0.02ab	1.7±0.04c	1.37±0.01a	1.43±0.06b	1.33±0.04a	1.48±0.05a
	L7/L6				1±0.01d				
	A/L6	1±0.2b	1.28±0.03b	1.21±0.01a		1.3±0.06a	1.3±0.04b	1.24±0.03a	1.32±0.04a
	A/L7				1.26±0.02a				
Lti2	L2/L1	1.31±0.02a	1.21±0.03a	1.3±0.03a	1.3±0.03a		1.83±0.08a	1.26±0.06a	1.31±0.06ab
	L3/L2	1.34±0.04a	1.45±0.03b	1.4±0.03a	1.4±0.03a		1.34±0.11a	1.16±0.03a	1.11±0.05a
	L4/L3	1.35±0.04a	1.21±0.03a	1.22±0.03a	1.22±0.03a		1.07±0.12b	1±0.03b	1.2±0.05a
	L5/L4	1.3±0.08a	1.4±0.04b	1.71±0.05b	1.34±0.05a		1.41±0.1a	1.31±0.05a	1.24±0.04a
	L6/L5	1.42±0.06a	1.25±0.02a	1.32±0.02a	1.72±0.05b	1.4±0.03a	1.5±0.1a	1.33±0.04a	1.45±0.04b
	L7/L6				1±0.01c				
	A/L6	1±0.02b	1.29±0.02ab	1.3±0.02a		1.21±0.05b	1.4±0.1a	1.3±0.03a	1.36±0.04b
	A/L7				1.26±0.03a				
Lti3	L2/L1	1.45±0.02a	1.28±0.02a	1.33±0.02a	1.33±0.02a	1.31±0.1ab	1.34±0.02a	1.26±0.06a	1.25±0.05ab
	L3/L2	1.36±0.02ab	1.25±0.02a	1.22±0.01a	1.22±0.01a	1.46±0.1a	1.52±0.05a	1.3±0.03a	1.27±0.05a
	L4/L3	1.28±0.03b	1.26±0.02a	1.26±0.03a	1.26±0.03a	1.22±0.04b	1.11±0.05b	1.05±0.02b	1.15±0.06b
	L5/L4	1.23±0.04b	1.26±0.02a	1.6±0.04b	1.26±0.02a	1.2±0.06b	1.34±0.04a	1.31±0.03a	1.3±0.04a
	L6/L5	1.45±0.04a	1.19±0.02a	1.4±0.02ab	1.73±0.04b	1.24±0.04b	1.4±0.06a	1.32±0.03a	1.36±0.02a
	L7/L6				1±0.01c				
	A/L6	1.28±0.02b	1.4±0.02b	1.23±0.02a		1.15±0.08b	1.28±0.05a	1.25±0.03a	1.38±0.04a
	A/L7				1.35±0.02a				

Notes: Each value of the table represents: mean and standard error. Means were compared by performing One-Way ANOVA test and Tukey post hoc test at the α = 0.05 level of significance. Within columns, means with same letters are not significantly different. Legend: La: length of antenna. Labd: length of abdomen. Lai: length of the hind wing.Lcc: length of cephalic capsule. lcc: width of cephalic capsule. Lcu1, Lcu2 and Lcu3: length of femur 1, length of femur 2, length of femur 3. Lel: length of elytra. Lpr: length of pronotum. Lt: length of body. Lti1, Lti2, Lti3: length of tibia 1, length of tibia 2, length of tibia 3. Lth: length of thorax. M: male. F: female. F6: female with six nymphal instars. F7: female with seven nymphal instars. L: nymphal instars. A: adult instars.

Allometric Growth

The allometric growth was not harmonious in the studied grasshopper species (Table 5). For each organ, there is a disproportionate variation of the allometric coefficient from one instar to another. Hypoallometries were the most dominant in all four grasshopper species. However, 7 cases of hyperallometries were noticed namely in the width of cephalic capsule in the adult instar of *E. p. ibandana* M ((k=1.5±1.6, p<0,05); the Pronotum's length in *E. p. ibandana* F7 (in the fifth (k=1.1±0.08, p<0,05) and the seventh (k=1.14±1.16, p<0,05) nymphal instars; the lengths of tibia 1 and 2 in *E. p. ibandana* F6 and *E. p. ibandana* F7, in the sixth nymphal instars (k=1.43±0.4 for tibia 1 and k=4.1±0.36 for tibia 2 (the strongest one), p<0,05) and the seventh nymphal instars

Table 5. Allometric coefficient (k) of each organ of *A. acutipennis* (Atrmph), *E. p. ibandana* (E.p.i), *P. vignaudii* (Pygmph) and *T. ferruginea* (Tphrn) in the laboratory.

Organs	Stages	Species/Sexes							
		Atrmph	E.p.i-M	E.p.i-F6	E.p.i-F7	Pygmph-M	Pygmph-F	Tphrn-M	Tphrn-F
Lcc	L1	-0.6±0.1*	-0.9±0.3*	-1.3±0.4*	-1.3±0.4*	-0.64±0.3*	-0.7±0.2*	-0.9±0.3*	-0.5±0.3*
	L2	-0.8±0.1*	-0.5±0.3*	-0.6±0.1*	-0.6±0.1*	-0.55±0.2*	-0.4±0.4*	-0.65±0.2*	-0.3±0.2*
	L3	-0.5±0.1*	-0.9±0.3*	-1.1±0.3*	-1.1±0.3*	0.14±0.4*	-0.2±0.3*	-0.7±0.2*	-0.7±0.1*
	L4	-0.6±0.2*	-0.4±0.2*	-0.15±0.15*	-0.15±0.15*	0.4±0.3*	-0.3±0.3*	-0.18±0.18*	-0.7±0.1*
	L5	0.1±0.1*	-1.2±0.3*	-0.5±0.1*	0.02±0.07*	-0.7±0.7*	-0.2±0.2*	-0.4±0.2*	-0.3±0.2*
	L6	-0.3±0.2*	-0.5±0.4*	-0.75±0.2*	-0.54±0.6*	-0.7±0.3*	0.4±0.3*	-0.04±0.3*	-0.4±0.4*
	L7				-1.3±0.4*				
	Adult	0.3±0.07*	-0.75±0.1*	-0.6±0.2*	-0.2±0.7*	0.03±0.3*	0.2±0.4*	-0.2±0.2*	-0.8±0.1*
lcc	L1	-0.72±0.7*	-0.5±0.2*	-0.56±0.2*	-0.56±0.2*	-1.15±0.2*	-0.9±0.16*	-0.62±0.2*	-0.6±0.23*
	L2	-0.54±0.27*	-0.5±0.3*	-0.56±0.44*	-0.56±0.44*	0.04±0.36*	-0.7±0.4*	-0.99±0.2*	-02±0.2*
	L3	-1.2±0.1*	-0.96±0.33*	0.45±0.4*	0.45±0.4*	-0.7±0.3*	-1±0.24*	-0.9±0.22*	-0.56±0.1*
	L4	-1.14±0.1*	-0.52±0.1*	-0.36±0.16*	-0.36±0.16*	-0.5±0.3*	-0.85±0.3*	-0.42±0.3*	-0.45±0.18*
	L5	-0.7±0.2*	-0.06±0.5*	0.08±0.1*	0.25±0.1*	-1.3±0.4*	-0.7±0.2*	-0.36±0.16*	-0.24±0.2*
	L6	-0.72±0.2*	-0.6±0.16*	-0.24±0.07*	-0.8±0.02*	-0.95±0.3*	-0.4±0.2*	-0.06±0.16*	-0.4±0.2*
	L7				0.23±0.1*				
	Adult	-0.3±0.07*	1.5±1.6*	-0.36±0.2*	-0.32±0.33*	-1.2±0.2*	-1±0.3*	-0.24±0.2*	-0.9±0.12*
Lth	L1	-0.7±0.07*	-0.5±0.1*	-0.55±0.1*	-0.55±0.1*	-0.75±0.2*	-0.76±0.07*	-0.55±0.1*	-0.53±014*
	L2	-0.65±0.07*	-0.4±0.1*	-0.62±0.16*	-0.62±0.16*	-0.33±0.14*	-0.64±0.12*	-0.62±0.1*	-0.4±0.1*
	L3	-0.84±0.1*	-0.3±0.1*	-0.41±0.1*	-0.41±0.1*	0.02±0.24*	-0.11±0.12*	-0.62±0.12*	-0.7±0.1*
	L4	-0.4±0.1*	-0.27±0.1*	-0.2±0.1*	-0.2±0.1*	-0.04±0.4*	-0.56±0.2*	-0.9±0.1*	-0.72±0.1*
	L5	-0.5±0.1*	-0.2±0.1*	-0.3±0.16*	-0.54±0.05*	-0.61±0.2*	-0.8±0.07*	-0.5±0.1*	-0.6±0.2*
	L6	-0.4±0.1*	-0.5±0.16*	-0.07±0.06*	-0.5±0.06*	-0.61±0.2*	-0.35±0.24*	-0.5±0.13*	-0.7±0.16*
	L7				0.14±0.1*				
	Adult	-0.3±0.06*	-0.86±0.1*	-0.25±0.1*	-0.21±0.2*	-0.23±0.23*	-0.6±0.25*	-0.42±0.12*	-0.84±0.07*
Labd	L1	-0.55±0.08*	*0.42±0.13*	-0.6±0.1*	-0.6±0.1*	-0.7±0.13*	-0.75±0.08*	-0.36±0.12*	-0.52±0.08*
	L2	-0.5±0.05*	-0.36±0.1*	-0.4±0.1*	-0.4±0.1*	-0.1±0.1*	-0.5±0.1*	-0.34±0.08*	-0.4±0.12*
	L3	-0.34±0.05*	-0.3±0.06*	-0.3±0.06*	-0.3±0.06*	-0.3±0.1*	-0.34±0.1*	-0.44±0.07	-0.54±0.12*
	L4	-0.42±0.04*	-0.4±0.07*	-0.07±0.07*	-0.07±0.07*	-0.31±0.12*	-0.4±0.1*	-0.62±0.1*	-0.5±0.05*
	L5	-0.4±0.1*	-0.35±0.03*	-0.46±0.15*	-0.1±0.01*	-0.55±0.16	-0.8±0.2*	-0.6±0.08*	-0.5±0.05*
	L6	-0.5±0.07*	-0.4±0.03*	-0.75±0.1*	-0.3±0.08*	-0.5±0.1*	-0.3±0.1*	-0.45±0.07*	-0.52±0.08*
	L7				-0.2±0.02*				
	Adult	-0.24±0.03*	-0.6±0.2*	-0.44±0.05*	-0.43±0.1*	-0.74±0.11*	-0.4±0.03*	-0.36±0.06*	-0.6±0.05*

Lpr	L1	-0.64±0.08*	-0.25±0.37*	-1.4±0.6*	-1.4±0.6*	-0.9±0.16*	-1.1±0.08*	-0.75±0.12*	-0.66±0.14*
	L2	-1.2±0.1*	-0.3±0.2*	-0.7±0.2*	-0.7±0.2*	-0.11±0.2*	-0.9±0.33*	-0.73±0.17*	-0.6±0.14*
	L3	-0.55±0.13*	-0.3±0.3*	-0.1±0.5*	-0.1±0.5*	-0.25±0.26*	-0.44±0.3*	-1.03±0.17*	-0.7±0.1*
	L4	-0.52±0.12*	-0.42±0.12*	-0.4±0.1*	-0.4±0.1*	-0.3±0.3*	-0.7±0.2*	-0.93±0.3*	-0.82±0.1*
	L5	-0.2±0.06*	0.24±0.7*	-0.12±0.24*	1.1±0.08*	-1.05±0.5*	-0.46±0.16*	-0.5±0.2*	-0.9±0.14*
	L6	-0.5±0.3*	-0.6±0.22*	-0.13±0.13*	-0.4±0.08*	-0.6±0.25*	-0.43±0.25*	-0.25±0.22*	-0.41±0.22*
	L7				1.14±0.16*				
	Adult	-0.2±0.05*	-0.7±0.16*	-0.42±0.15*	0.11±0.25*	-0.51±0.3*	-0.43±0.4*	-0.63±0.1*	-0.81±0.1*
La	L1	-0.7±0.1*	-0.62±0.15*	0.07±0.23*	0.07±0.23*	-1.07±0.14*	-0.64±0.13*	-0.61±0.2*	-0.65±0.23*
	L2	-0.6±0.2*	-0.5±0.33*	-0.92±0.23*	-0.92±0.23*	-0.06±0.36*	-0.24±0.2*	-0.36±0.2*	-0.3±0.2*
	L3	-0.9±0.07*	-1.3±0.44	-0.53±0.35*	-0.53±0.35*	-0.28±0.27*	-0.61±0.22*	-1.02±0.14*	-0.7±0.1*
	L4	-0.6±0.14*	-0.08±0.16*	-0.4±0.13	-0.4±0.13	-0.44±0.34*	-0.77±0.2*	-0.76±0.21*	-0.75±0.1*
	L5	-0.32±0.18*	-0.8±0.34*	-0.9±0.11*	-0.5±0.12*	-0.64±0.4*	-0.63±0.2*	-0.91±0.25*	-0.7±0.23*
	L6	-0.23±0.16*	-0.6±0.2*	-0.5±0.1*	-0.9±0.03*	-0.8±0.23*	-0.65±0.22*	-0.66±0.23*	-0.5±0.22
	L7				-0.3±0.07*				
	Adult	-0.76±0.3*	-1.83±4.9*	-0.72±0.2*	-0.06±0.4*	-0.6±0.2*	-0.35±0.3*	-0.52±0.32*	-0.84±0.1*
Lel	L1								
	L2								
	L3								
	L4								
	L5	-0.73±0.08*	-0.52±0.31*	-0.8±0.11*	-1.34±0.05	-0.81±0.35*	-1.1±0.22*	-0.98±0.1*	-0.8±0.08*
	L6	-0.7±0.22*	-0.7±0.1*	-0.91±0.06*	-0.4±0.13*	-0.83±0.12*	-0.5±0.35*	-0.84±0.17*	-0.53±0.1*
	L7				-0.41±0.1*				
	Adult	-0.05±0.05*	-1.03±0.02*	-0.51±0.17*	-0.01±0.18*	-0.85±0.17*	-0.84±0.3*	-0.43±0.1*	-0.92±0.06*
Lai	L1								
	L2								
	L3								
	L4								
	L5	-0.8±0.08	-0.63±0.2*	-0.5±0.11*	/	-0.91±0.3*	-0.99±0.27*	-1.05±0.07*	-0.79±0.08*
	L6	-0.6±0.2*	-0.65±0.12*	0.21±0.07*	-0.8±0.02*	-1±0.08*	-1.3±0.37*	-0.8±0.11*	-0.72±0.14*
	L7				0.01±0.09*				
	Adult	0.04±0.07*	-1.03±0.02*	-0.6±0.14*	-0.15±0.16*	-0.8±0.17	-1.15±0.25*	-0.42±0.1*	-0.93±0.06*
Lcu1	L1	-0.72±0.08*	-1.73±0.55*	-0.96±0.7*	-0.96±0.7*	±	±	-0.66±0.14*	-0.67±0.15*
	L2	-0.92±0.11*	-0.99±0.4*	-1.05±0.22*	-1.05±0.22*	±	-0.82±0.35*	-0.85±0.25*	-0.01±0.19*
	L3	-0.78±0.12*	-0.51±0.24*	-1.17±0.21*	-1.17±0.21*	±	-0.25±0.04*	-0.64±0.21*	-0.72±0.1*
	L4	-0.73±0.22*	-0.41±0.21*	-0.32±0.18*	-0.32±0.18*	±	-0.55±0.2*	-0.65±0.17*	-0.62±0.14*
	L5	-0.14±0.12*	-0.59±0.11*	-0.3±0.14*	-0.11±0.13*	-0.87±0.37*	-0.55±0.15*	-0.32±0.18*	-0.7±0.24*
	L6	-0.44±0.14*	-0.77±0.22*	-0.93±0.1*±	-1.36±0.11	-0.92±0.2*	-0.85±0.23*	-0.47±0.17*	0.55±0.14*
	L7				-0.5±0.16*				
	Adult	0±0.11*	-0.72±0.16*	-0.55±0.17*	-0.25±0.33*	-0.85±0.3*	-0.88±0.25*	-0.46±0.21*	-0.81±0.08*

Lcu2	L1	-0.88±0.04*	-0.94±0.43*	-1.27±0.5*	-1.27±0.5*	±	-1.8±0.4*	-0.63±0.2*	-0.62±0.27*
	L2	-0.93±0.07*	-1.47±0.27*	-1.02±0.16*	-1.02±0.16*	-0.6±0.2*	-2.3±0.7*	-0.76±0.25*	-0.03±0.25*
	L3	-0.82±0.16*	-0.9±0.13*	-0.98±0.27*	-0.98±0.27*	0.2±1.45*	-0.53±0.18*	-0.96±0.14*	-0.66±0.12*
	L4	-1.05±0.2*	-0.7±0.15*	-0.4±0.12*	-0.4±0.12*	±	-0.56±0.17*	-0.8±0.17*	-0.68±0.11*
	L5	-0.28±0.14*	-0.35±0.28*	-0.68±0.11*	-0.1±0.1*	±	-0.53±0.17*	-0.5±0.17*	-0.26±0.21*
	L6	-0.17±0.22*	-0.7±0.15*	-0.46±0.11*	-0.43±0.02*	-1.03±0.22*	-1.13±0.27*	-0.55±0.18*	-0.46±0.15*
	L7				-0.02±0.05*				
	Adult	0.2±0.1*	-0.67±0.18*	-0.55±0.18*	-0.13±0.26*	-0.65±0.24*	-0.38±0.28*	-0.37±0.2*	-0.83±0.07*
Lcu3	L1	-0.47±0.09*	0±0.7*	0.997±0.7	0.997±0.7	-0.37±0.42*	-0.52±0.29*	-0.4±0.26*	-0.41±0.22*
	L2	-0.94±0.07*	-0.02±0.4*	-0.46±0.3*	-0.46±0.3*	-0.11±0.19*	0.56±0.37*	-0.56±0.22*	-044±0.27*
	L3	-0.44±0.14*	-0.4±0.2*	-0.83±0.35*	-0.83±0.35*	-0.17±0.39*	-0.65±0.3*	-0.85±0.21*	-0.72±0.1*
	L4	-0.4±0.2*	-0.31±0.15*	-0.31±0.12*	-0.31±0.12*	-0.14±0.33*	-0.62±0.21*	-0.64±0.31*	-0.7±0.12*
	L5	-0.46±0.15*	-0.4±0.2*	-0.39±0.13*	0.35±0.18	-0.31±0.7*	-0.08±0.22*	-0.51±0.26*	-0.33±0.36*
	L6	-0.2±0.24*	-0.54±0.2*	-0.01±0.17*	-0.71±0.05*	-0.75±0.36*	-0.04±0.33*	-0.08±0.28*	-0.29±0.28*
	L7				-0.22±0.17*				
	Adult	-0.16±0.07*	-0.23±0.15*	-0.72±0.12*	-0.16±0.23*	-0.33±0.36*	-0.3±0.4*	-0.23±0.22*	-0.77±0.11*
Lti1	L1	-0.61±0.1*	-0.43±0.67*	-0.57±0.73*	-0.57±0.73*	±	±	-0.77±0.14*	-0.72±0.16*
	L2	-0.89±0.13*	-1.2±0.4*	-1.1±0.24*	-1.1±0.24*	±	±	-0.61±0.2*	-0.3±0.15*
	L3	-0.88±0.12*	-0.95±0.15*	-1.22±0.2*	-1.22±0.2*	±	0.11±0.43*	-0.54±0.25*	-0.75±0.1*
	L4	-0.72±0.18*	-0.7±0.17*	-0.35±0.2*	-0.35±0.2*	±	-0.51±0.22*	-0.81±0.15*	-0.78±0.11*
	L5	-0.43±0.05*	-1.15±0.2*	-0.67±0.13*	-0.38±0.27*	-0.94±0.34*	-0.47±0.1*	-0.36±0.0.14*	-0.78±0.23*
	L6	-0.88±0.2*	-0.7±0.17*	1.43±0.4*	-0.51±0.07*	-1.2±0.15*	-0.5±0.37*	-0.7±0.21*	-0.64±0.14*
	L7				1.66±0.53*				
	Adult	0.26±0.1*	-0.7±0.18*	-0.43±0.17*	0.01±0.32	-0.7±0.5*	-1.12±0.29*	-0.6±0.18*	-0.87±0.07*
Lti2	L1	-0.57±0.07*	-1.3±0.21*	-0.27±0.47*	-0.27±0.47*	±	±	-0.71±0.2*	-0.64±0.22*
	L2	-0.97±0.07*	-1.22±0.26*	-1.03±0.2*	-1.03±0.2*	±	-1.25±0.7*	-0.8±0.25*	-0.23±0.27*
	L3	-0.89±0.11*	-0.85±0.18*	-0.7±0.24*	-0.7±0.24*	-0.36±0.65*	-0.42±0.52*	-0.95±0.15*	-0.78±0.1*
	L4	-0.8±0.15*	-0.75±0.17*	-0.4±0.13*	-0.4±0.13*	±	-0.6±0.15*	-0.8±0.12*	-0.73±0.11*
	L5	-0.74±0.12*	-1.4±0.24*	-0.42±0.15*	-0.21±0.2*	-0.38±0.36*	-0.47±0.14*	-0.51±0.14*	-0.18±0.18*
	L6	-0.9±0.2*	-0.41±0.24*	4.1±0.36*	-0.53±0.05*	-1.05±0.2*	-0.31±0.36*	-0.73±0.2*	-0.44±0.17*
	L7				1.65±0.51*				
	Adult	-0.1±0.1*	-0.84±0.32*	-0.62±0.2*	-0.22±0.22*	-0.77±0.18*	-0.45±0.26*	-0.56±0.2*	-0.82±0.08*±
Lti3	L1	-0.63±0.1*	0.43±0.54*	-0.68±0.9*	-0.68±0.9*	-0.31±0.42*	-0.59±0.31*	-0.58±0.19*	-0.41±0.22*
	L2	-0.99±0.2*	-0.03±0.4*	-0.55±0.3*	-0.55±0.3*	-0.19±0.17*	-0.85±0.3*	-0.2±0.2*	-0.4±0.3*
	L3	-0.64±0.15*	-0.61±0.19*	-0.84±0.4*	-0.84±0.4*	0.05±0.3*	-0.56±0.24*	-0.73±0.18*	-0.73±0.09
	L4	-0.75±0.18*	-0.2±0.19*	-0.16±0.16*	-0.16±0.16*	-0.22±0.27*	-0.6±0.2*	-0.26±0.34*	0.73±0.11*
	L5	-0.57±0.17*	-0.46±0.35*	0.08±0.9*	0.29±0.08*	-0.82±0.27*	-0.06±0.19*	-0.7±0.2*	-0.8±0.33*
	L6	-0.44±0.24*	-0.4±0.17*	-0.53±0.24*	-0.8±0.05*	-0.87±0.28*	-0.46±0.33*	-0.64±0.21*	-0.45±0.27*
	L7				0.9±0.2*				
	Adult	-0.06±0.08*	-0.13±0.21*	-0.54±0.24*	-0.2±0.34*	-0.86±0.09*	-0.47±0.41*	-0.11±0.19*	-0.82±0.08*

Notes: Each value of the table represents: mean and standard error. Asterisk (*), means that from the t-student test k is significantly different from 1. Legend: La: length of antenna. Labd: length of abdomen. Lai: length of the hind wing.Lcc: length of cephalic capsule. lcc: width of cephalic capsule. Lcu1, Lcu2 and Lcu3: length of femur 1, length of femur 2, length of femur 3. Lel: length of elytra. Lpr: length of pronotum. Lti1, Lti2, Lti3: length of tibia 1, length of tibia 2, length of tibia 3. Lth: length of thorax. M: male. F: female. F6: female with six nymphal instars. F7: female with seven nymphal instars. L= nymphal instars. A= adult instars.

(k=1.66±0.53 for tibia 1 and k=1.65±0.51 for tibia 2, p<0,05) (Table 5). Only 2 cases of isoallometries were noticed, mainly in the length of femur 3 in first nymphal instars females of *E. p. ibandana* (k=0.99±0.7, p>0,05) (Table 5).

Discussion

This study showed that the growth model of the grasshopper species follows many types namely the power law, the Gompertz, the quadratic, the linear, the logarithm and the exponential models. This heterogeneous characteristic of the growth model is a common phenomenon in insects (Hirst and Forster 2013). However, for some authors, insect growth models are universal (West *et al.* 2001). These controversies could be due to the extreme sensibility of the larval growth ratio of insects to their living environment (temperature and humidity) and to the food quality accessible to them (Ayres and MacLean 1987; Esperk and Tammaru 2004). Thus, each larval instar might respond differently to these factors. These ideas might also explain the fact that the growth ratio of each organ between consecutive instars is not constant in each species and sex.

The power law model presented in this study as the best-fitted model for the studied grasshoppers would be a first observation in Acridomorpha group and might be linked to their feeding behaviour and developmental duration type. These grasshoppers share the same habitats and all are herbivorous and their developmental times are generally high in the first and last instars and low between those two instars. In general, being able to understand which model(s) best describe the growth curves, both empirically and ultimately mechanistically, is a real challenge (Hirst and Forster 2013). Only linear and exponential growth models were noted in Orthopteran populations (Von Bertalanffy 1951). At *Lucilia sericata* (Diptera: Calliphoridae) in South Korea, the logarithmic model was identified as the best fitting regression model (Shin *et al.* 2021). Invertebrate growth has often been modelled using exponential (Hirst and Bunker 2003; Nylin 1992; Hawkins 1986) or power mathematical form as the von Bertalanffy growth equation (von Bertalanffy 1957) and 73% growth of 58 marine invertebrates was best modelled by an exponential function (Hirst and Forster 2013). Additionally, sigmoidal functions, such as the von Bertalanffy growth equation, have been commonly applied to many vertebrates (Von Bertalanffy 1960; Kimura 1980; Zullinger 1984).

The limited amount of detailed information about the growth curves of insect larvae may partly result from technical difficulties (Tammaru and Esperk 2007). In particular, the existence of distinct larval instars makes larval growth curves complex, and any measurements of the instantaneous growth ratio should therefore explicitly consider the exact phase of the moulting cycle (Esperk and Tammaru 2004; Tammaru and Esperk 2007). Another drawback is the extreme sensitivity of larval growth ratios to environmental conditions, temperature and food quality, in particular (Tammaru and Esperk 2007).

The significant variation of growth ratios (growth coefficients) noticed in this study in each organ, between consecutive nymphal instars of each grasshopper species, reflect the positive covariance noticed in most Orthoptera by Whitman (2008) between most cuticular structures and the size of the individual of each species. Similar results were reported in earlier studies on various insects (Klingenberg and Zimmermann 1992). These results show that Dyar's rule does not apply in a strict sense to the growth of the material considered here. According to this law, each cuticular sclerite size increases in linear dimensions by a constant ratio (Dyar's coefficient or growth coefficient) at each moult. These different ratios noticed at the organ level of each species would reflect different growth strategies, and any change in the normal value of the growth coefficient for a species during a particular moult would represent an evolutionary adaptation of the growth pattern to environmental perturbations (Sehnal 1985, Whitman 2008).

The present study also showed that the allometric coefficient varied according to organs, sex, instars and species. The same conclusion has been obtained by Shingleton *et al.* (2007) with *Drosophila melanogaster* in USA and could be explained by the fact that this coefficient depends on environmental and physical conditions associated with increasing size (Whitman 2008).

The fact that hypoallometry model was the most adapted to describe the growth pattern of grasshoppers in this study suggests that in general, each organ of these grasshoppers experiences less relative growth compared to the overall growth of the organism. This result is close to that obtained in the Chinese dobsonfly (between male body size and ectoproct length (a male grasping structure)), in humans (between the skull and the human body) and in honey bees (abdomen, thorax, head, antenna, proboscis, pollen basket, maxillae, hind limb, fore wing and hind wing from the rainforest, Guinea savannah and the derived savannah zones of Nigeria) which exhibit negative allometric growth pattern (Cao *et al.* 2019; Bamidele 2021). This model may be dominant among grasshoppers and could be explained by the fact that the two parameters (size of organ and that of the whole body) are responding independently to what the growing insect is eating (Shingleton *et al.* 2007). Those grasshoppers are polyphytophagous and their organs respond differently to the variation of the characteristics factors of their habitat compared to the whole organism.

The few cases (7 cases) of hyperallometry noticed in the Width of cephalic capsule in the adult instar of *E. p.*

ibandana M; the Pronotum's length in *E. p. ibandana* F7 and the seventh nymphal instars; the lengths of tibia 1 and 2 in *E. p. ibandana* F6 and *E. p. ibandana* F7, in the sixth nymphal instars and the seventh nymphal instars, suggest the relatively faster growth of these organs compared to the overall growth of these grasshoppers. Similar results have been obtained by Cao *et al.* (2019) between male body size and mandible length of Chinese dobsonfly.

Only 2 cases of isoallometries growth were noticed, mainly in the length of femur 3 in first nymphal instars females of *E. p. ibandana*. Such isoallometric growth suggest that relative growth of a part of an organism is identical to the overall growth of that organism and would result in a dramatic mass-specific decrease in strength, because the maximum-force output of muscles scales proportionally to muscle cross-sectional area; but muscle cross-sectional area (and thus force output) increases proportionally less than mass, as size increases (Whitman 2008). However, in insects, there are usually isometric relationships between body size and other body parts (Cao *et al.* 2019).

In general, the nature of the nutrients circulating in the hemolymph affects the growth of insects. Morphology is correlated with the metabolic rate (Hirst *et al.* 2014, Glazier *et al.* 2015) and the type of allometric growth might depend on insect-specific assimilation rate. The specific assimilation varies during ontogenesis in many animals, resulting in greater absorptive capacity achieved by temporarily increasing organ size (Piersma et al. 1997, Hume *et al.* 2002). Increasing specific assimilation implies that organs do not develop isomorphically. Consistent specific assimilation can be expected if organs related to nutrient uptake grow isomorphically with body size (Maino and Kearney 2015). The use of these nutrients is also dependent on circulating hormone peaks (Joly 1968, David *et al.* 1999). For example, the water metabolism of locusts is dependent on diuretic (AVP-like Insect Diuretic hormone, peptidergic in nature) and antidiuretics (Neuroparsine, Chloride Transport Stimulating Hormone, antidiuretic hormone) hormones. Neurosparin is also involved in energy metabolism and phase polymorphism of Locusts (Proux, 1991).

The insulin / IGF (« Insulin-like Growth factor or Somatomedin ») signaling which play a key role in the longevity, diabetes, and the regulation of the size of cells, organs and the whole body could equally have a central role in the regulation of the organism shape (Nijhout et Callier 2015). In *D. melanogaster* nutrition poor in amino acids can be directly detected be dividing cells, causing a reduction of the insulin signalling pathway in these cells and then a reduction of the growth ratio (Neufeld 2003, Oldham *et al.* 2000, Goberdhan and Wilson 2002). Then, the allometric variation could be due to the organ 'specific changes in response to the hormones (Shingleton *et al.* 2007).

Most authors including Shingleton *et al.* (2007) draw their conclusions on the type of allometry (Hyper-, Iso- and Hypoallometries) based only on a simple comparison of the coefficient k to 1 (without statistical test). The application of a statistical test as in this study to make such comparison facilitated the interpretation of this coefficient and help to draw robust conclusions. However, the ease of calculation and interpretation of the allometric coefficient made the model generally useful, but there is some question about the capacity of a power function of the type $y = ax^b$ to describe relative growth (Bervian *et al.* 2006).

Conclusion

The growth models of *A. acutipennis*, *E. p. ibandana*, *P. vignaudii* and *T. ferruginea* are not unique. Under laboratory conditions, those grasshoppers have been represented by six types of growth models: power, gompertz, quadratic, linear, logarithm and exponential. The power law model was the best-fitted one in all the grasshopper species. The growth ratios of elytra length and hind wing length were high and varied between 2 to 4 except for *E. p. ibandana* F7 where the multiplication factors from nymphal instars 6 to 7 were close to 1; meaning that the wings' size lowly changed between the two stages. For each organ, a disproportionate variation in the allometric coefficient from one instar to another was observed. These findings will go a long way to improve the knowledge of the characteristics of acridians inhabiting forest agroecosystems.

Ontogeny is affected by both genetic and environmental factors that operate through complex molecular and physiological mechanisms. Anyway, we are still a long way from understanding the mechanisms that underlie nymphal development scaling patterns of insects.

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