1   Coccinellid host morphology dictates morphological diversity of the parasitoid wasp

2   *Dinocampus coccinellae*

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Abstract

Pararsitoid-host interactions involving host species that are newly introduced into the range of a generalist parasitoid provide systems that can be examined for phenotypic plasticity and evolutionary changes in parasitoid-host dynamics. The solitary Braconid parasitoid wasp, *Dinocampus coccinellae*, has a cosmopolitan distribution and parasitizes approximately 50 species of predatory lady beetles (ladybirds) in the family Coccinellidae. In this study we quantified the effect of six (4 native North American and 2 non-native North American) host species on the morphometrics of *D. coccinellae*. Adult lady beetles were collected from 13 locations in the United States and reared in the laboratory until *D.coccinellae* exited from their adult beetle hosts. Eighty-nine individual *D. coccinellae* females and their associated host were weighed and morphometric measurements were taken. The smallest lady beetle host *Hippodamia parenthesis* produced the smallest adult wasps; the largest host species, *Coccinella septempunctata*, produced the largest female wasps. A directional cline in morphology of wasps and their coccinellid hosts was also observed in a dry-weight regression ($R^2 = 0.4066$, p-value < 0.0001). Two underlying mechanisms may explain the results of our study: (1) morphometric variation in *D. coccinellae* is governed by phenotypic plasticity with the size of the emerging offspring contingent on the size of the coccinellid host, and/or (2) that morphometric variation in *D. coccinellae* is governed by genomic adaptation to coccinellid host populations.

Keywords: Morphology, parasitoid-host interaction, phenotypic plasticity

47   **Introduction**

48   Parasitic Hymenoptera make up at least 280,000 species of all parasitic insects

49   (Pennacchio and Strand 2006). Numerous studies have examined the relationship between hosts

50   and their parasitoids. (Hochberg and Ives 2000, Godfray 1994). Importantly, several studies have

51   shown that the morphological characteristics of adults and fecundity of female parasitoids are

52   affected by host characteristics, for example, host species (Nicol et al., 1999), host life stage

53   (Traynor et al., 2005), host instars (Cloutier et al., 2000), and host size (Harvey et al., 2006;

54   Mackauer et al., 2001). The size and species of hosts have been shown to greatly influence the

55   evolutionary history of morphological characteristics in parasitoids (Brandl et al., 1987; Belshaw

56   et al., 2003; Charnov et al., 1984; Bakker K et al., 1985; Moore et al., 2002; Symonds et al.,

57   2013). It has been hypothesized that host-parasitoid co-evolution could eventually lead to

58   increased fitness of parasitoids allowing them to parasitize multiple species (Charnov et al.,

59   1984; Ellers et al., 2002; Sampaio et al., 2008). This also points to evidence of host-specificity in

60   a majority of parasitoids, in that parasitoids adaptively evolve in response to host characteristics,

61   and eventually may specialize in parasitizing only particular host species. Few studies examine

62   generalist parasitoids that parasitize multiple host species, and correspondingly exhibit

63   quantitative variability in morphology, potentially in response to host characteristics. For

64   example, parasitoid size as a plastic trait has been studied using *Aphidus ervi*

65   *(Hymenoptera:Aphidiidae),* an aphid parasitoid, that attacks multiple host species (Henry et al.,

66   2006). There is little understanding, however, of the biological processes that lead to generalist

67   behavior of parasitoids.

68

69 *Dinocampus coccinellae* (Hymenoptera: Braconidae) is a thelytokous parthenogenic

70 species, in which females are produced from unfertilized eggs (Ceryniger et al 2012). Males have

71 been rarely observed; one laboratory study observed mating to occur, but all offspring were

72 females (Wright 1980). This process results in offspring being maternal clones. *D. coccinellae*

73 are generalist wasps, capable of parasitizing over 50 species of coccinellids across various

74 climates worldwide (Balduf 1926, Ceryniger et al 2012). Within the beetle host, *D. coccinellae*

75 larvae feed on teratocytes derived from the parasitoid egg, thus the adult beetle host typically

76 survives the larval development of *D. coccinellae* (Ceryniger et al 2012). However, most

77 parasitized adult beetles die following the exit of the parasitoid larva, when they become

78 entangled in the pupal coccoon produced by the parasitoid (Ceryniger et al 2012, Dheilly et al

79 2015). Several predatory lady beetle hosts of *D. coccinellae* are natural enemies that are

80 beneficial species for biological control (including the native North American species

81 *Hippodamia convergens*, and two non-native species in North America, *Coccinella*

82 *septempunctata*, and *Harmonia axyridis*). Coupled with low survival rates of parasitized beetles,

83 and the generalist nature of *D. coccinellae*, these wasps are of biological, ecological, and

84 economic interest. Specifically, we are interested in examining the ecological basis of host-

85 specific plastic or adaptive morphological traits, that make *D. coccinellae* amenable to

86 parasitizing coccinellid beetles. In this study we analyze the geometric morphometrics of field-

87 collected, lab-reared *D. coccinellae* and their coccinellid beetle hosts (from six host species),

88 sampled across the United States. Our goals in this study were twofold: (1) to quantify the

89 variability in morphometrics of *D. coccinellae* across its primary range in the United States, (2)

90 to correlate the variability in morphometrics of *D. coccinellae* with morphometrics of their hosts.

91   Broadly, we hypothesize that morphometric diversity of the host species will dictate the

92   morphometrics of the parasitoid wasps parasitizing them.

93

94   **Methods**

95   Ninety-nine parasitoid wasps within their adult hosts (*Harmonia axyridis* (*Har. axyridis*),

96   *Coleomegilla maculata* (*Col. maculata*), *Coccinella septempunctata* (*Cocc. septempunctata*),

97   *Hippodamia convergens* (*H. convergens*), *Cycloneda munda* (*Cyc. munda*), and *Hippodamia*

98   *parenthesis* (*H. parenthesis*)) were field-collected in the states of Kentucky, Ohio, Illinois, New

99   York, Missouri and Kansas (see Fig. 1) The Hippodamia convergens samples from Arizona were

100   field-collected and shipped to the authors. Adult lady beetles were collected from agricultural

101   fields, prairie, and roadside vegetation using sweep nets. Predatory Coccinellidae are commonly

102   found in these habitats when their aphid prey is present. Following field collection, adult beetles

103   were reared in the laboratory (L:D 16:8, 22°C, on pea aphids) until the last larval stage of the

104   wasps' development at which point the parasitoid larva exits the host and pupates within a

105   cocoon, typically woven between the coccinellid beetle hosts' legs. After eclosion of the adult

106   parasitoid, both the beetle host and parasitoid were then stored in 95% ethanol at -20C. Of these

107   samples, 89 were viable for the morphological analyses which needed intact, undamaged

108   samples of both the parasitoid and host. It is of interest to note that of the six host species of

109   coccinellids, *Harmonia axyridis* and *Coccinella septempunctata* are not native to continental

110   United States (derived from Asia, and Europe respectively, (Obrycki and Kring 1988), thus the

111   interaction between these host species and North American *D. coccinellae* may be a recently

112   evolving interaction. Alternately, *D. coccinellae* could also be native to Europe or Asia

113   (Ceryniger et al 2012), and have shifted hosts since their introduction to North America. Dry

114   weights of wasps and host were recorded individually on a Mettler Toledo XS105 DualRange

115   Analytical Balance after 1 minute of air-drying on a Kimtech Kimwipe to allow for evaporation

116   of alcohol. After weighing, each wasp and its respective host were photographed individually in

117   two replicate rounds using an optical microscope with a SPOT Idea camera attachment. Wasps

118   were photographed from a lateral view (see Fig. 3), and their hosts were photographed from

119   lateral, dorsal, and ventral views to include key morphological characteristics and maintain

120   consistency in imaging (see Fig. 2). Images were uploaded into Image-J (version 1.51j8) for

121   morphometric measurement (in mm) of host and wasp morphological characteristics with a scale

122   bar (included in the parasitoid/host mounting stage) to ensure consistent scaling. Wing length of

123   the wasp was not included in further statistical analyses due to many wings being folded, or

124   crushed during storage. Body depth of hosts (measured as the "height" of a beetle from the

125   lateral view) was also excluded due to measurement inconsistency on the styrofoam mounting

126   stage.. All high-resolution images from this study will be deposited with

127   http://www.morphbank.net/ upon acceptance.

128   All statistical analyses of morphometric measurements were carried out for each round

129   separately (except for dry weight which was recorded in one round) using Rstudio (version

130   1.0.143) and the package: ggplot2. Variation in means of recorded morphometrics of wasps and

131   their hosts were visualized using boxplots, and summaries (means, medians, standard deviations)

132   were computed. Due to lack of normality across most morphometric measures, a Wilcoxon

133   signed rank test was performed across wasp morphometric measures (grouped by their respective

134   host species) to test the null hypothesis of non-significant deviation from the mean. Similar

135   Wilcoxon signed rank tests were also performed on coccinellid host morphometrics. We then

136   performed a Kruskal-Wallis non-parametric one way ANOVA, followed by a posthoc Dunn's

137   Test on each morphometric measure in the parasitoid versus its host species, to test for

138   significant morphometric differences by host. Parasitoid dry-weight was also regressed onto host

139   dry-weight, as a proxy of size variation between the two. Additionally, a Principal Components

140   Analysis (PCA) was used to orthogonally transform morphometrics (including dry-weights) of

141   parasitoids and their hosts, and project their variability onto principal components of maximum

142   variance.

143

144   **Results**

145   Summaries of morphometric measurements in coccinellid hosts (Table 1), and parasitoid wasps

146   (Table 2) are shown in Figures 4 and 5. The smallest hosts (Fig. 4 as judged by all

147   measurements), *H. parenthesis* produced the smallest adult wasps (Fig. 5). Similarly, the largest

148   hosts, *Coccinella septempunctata*, produced the largest wasps. This directional cline (Fig. 6) in

149   morphology of wasps and their coccinellid hosts is also reflected in a dry-weight regression (R^2

150    $= 0.4066$, p-value < 0.0001). A non-parametric Kruskal-Wallis one-way analysis of variance

151   (ANOVA) test of host morphometric variation and parasitoid wasp morphometric variation was

152   significant at a p-value threshold of 0.05 on each morphometric measurement, rejecting the null

153   hypothesis that there is no variation in means of measured morphometric variables in parasitoid

154   wasps, among their corresponding host species. Additionally, coccinellid host measurements

155   were significantly variable ($p < 0.001$) among all host species measured, indicating significant

156   variability in sizes of coccinellid hosts. Conservative posthoc Dunn's tests indicated that the

157   variability observed between pronotum width in coccinellid adult hosts had the greatest level of

158   significance. A similar post-hoc Dunn's test in parasitoid wasp measurements indicated that

159   thorax length varied more than other morphometric measurements. A Principal Components

160   Analysis (PCA) showed that the first two PC's account for 70 -75% of variability in both rounds

161   (Fig. 7). Interestingly, morphometric variables in the two introduced beetle species, *Cocc.*

162   *septempunctata* and *Har. axyridis* share no overlapping points with the native species, *Col.*

163   *maculata*, *Cyc. munda*, and *H. parenthesis*, but show close association with the native species *H.*

164   *convergens*.

165

166   **Discussion**

167   The parthenogenic parasitoid *Dinocampus coccinellae* (Schrank) (Hymentoptera:

168   Braconidae), a cosmopolitan species, attacks over 50 species in the subfamily Coccinellinae

169   (Ceryngier et al., 2012). This parasitoid typically attacks adults, but laboratory studies and field

170   collections of pre-imaginal stages have documented that it will attack larval and pupal stages of

171   ladybird beetle hosts (Ware et al 2010; Obrycki et al 1985). A recent study has shown that the

172   replication of an endosymbiotic RNA virus in the parasitoid *D. coccinellae* is correlated with the

173   changes in host behavior following parasitization (Dheilly et al 2015). Results indicate that the

174   manipulation of host behaviors by this parasitoid may be regulated by this endosymbiotic virus.

175   In our current study of the parasitoid-host interactions between *D. coccinellae* and several

176   native North American and introduced species of Coccinellidae, we have quantified the influence

177   of host size on the size of parasitoid females. Our study clearly shows that larger coccinellid

178   hosts that are parasitized by *D. coccinellae* produce larger female parasitoids, an observation that

179   has also been reported by Obrycki (1988, 1989), Belnavis (1988 - except this study indicated that

180   larger host beetles did not always produce larger wasps). It is interesting to note that two of the

181   larger host species examined in this study, *Cocc. septempunctata* and *Har. axyridis* are

182   introduced species, which have established and spread throughout North America during the past

183   four decades (Sethuraman et al 2017). It is not yet known if populations of *D. coccinellae* was

184   introduced with *Cocc. septempunctata* or *Har. axyridis* creating a situation that may indicate that

185   the newly introduced parasitoid populations have adaptively shifted hosts in North America since

186   introduction in the early 20th century. This possibility will be explored in a follow up study by

187   delineating the evolutionary history and genomics of *D. coccinellae*. Nonetheless, our findings

188   could have two potential causes - (1) morphometric variation in *D. coccinellae* is governed by

189   phenotypic plasticity with the size of the emerging offspring contingent on the size of the

190   coccinellid host (Boivin 2010, Benard 2004), and/or (2) morphometric variation in *D.*

191   *coccinellae* is governed by genomic adaptation to its coccinellid host population (Henry et al.,

192   2006).

193   Importantly, morphometric size variation in parasitoid wasps play a causal role in

194   parasitization efficacy across their hosts. Previous studies of *D. coccinellae* parasitization

195   efficacy in the non-native *Har. axyridis* adults have indicated the potential for behavioral

196   adaptations in adult hosts, resulting in greater time to parasitize, when compared to the native

197   North American species, *Col. maculata* (Firlej et al., 2009). It has also been noted that

198   parasitization efficacy by *D. coccinellae* is significantly lower in *Har. axyridis*), when compared

199   to conspecific native species (*Cocc. septempunctata*) in England (Comont et al., 2014), and the

200   native species *Col. maculata* in North America (Hoogendoorn et al., 2002). However, a

201   contradictory study of the two species that compared the parasitization rates of *D. coccinellae* of

202   native versus introduced populations of *Cocc. septempunctata* and *Har. axyridis* in Japan and

203   England indicated no differences based on their geographical origin, but complement the study

204   of Firlej et al. 2009 in showing that *Har. axyridis* are parasitized at a significantly lower rate than

205   *Cocc. septempunctata*. *Har. axyridis* is also known to be a voracious and invasive species across

206   its geographical range in the world, potentially owing to behavioral and morphological

207   adaptations to parasitization, and "enemy release" (Ceryngier et al., 2012). However, a more

208   recent study by Dindo et al., 2016 compared the interactions of *D. coccinellae* with *Har.*

209   *axyridis*, and *Adalia bipunctata* in the field, showing that *D. coccinella*e had more of a negative

210   effect on the fitness of the *Har. axyridis* population, than on that of *A. bipunctata*. These

211   contradicting observations in different populations of the same species indicate that behavioral,

212   morphological, or biochemical adaptations to parasitization potentially have a genomic basis, as

213   previously observed in *D. melanogaster* (Orr and Irving 1997). Studying the population genomic

214   variation across coccinellid species (currently underway in the authors' laboratories) will thus

215   allow us to explore functional genomic variation in *Har. axyridis* and *Cocc. septempunctata*

216   leading to defense against parasitization by *D. coccinellae*. Complementarily, we are also

217   studying the genomics of *D. coccinellae* to study changes in the parasitoid wasp and/or

218   intraspecific variation among populations , that allow for higher rates of successful parasitization

219   of *Har. axyridis* in North America, or alternately, adaptively evolving to parasitize a several new

220   host species in North America.

221   Body size of coccinellid hosts have also been studied to directly affect the rate of

222   parasitization by parasitic wasps during different life history stages (*Cocc. septempunctata*, see

223   Song et al., 2017). Since our study only controlled for the life history stage of the emerging

224   wasp, and not for the life history stage of the coccinellid host, further studies are required to

225   understand the efficacy of parasitization of large versus small parasitoid wasps on larval versus

226   adult coccinellid hosts. Additionally, the sex of the coccinellid host, and prey availability in the

227   field could also influence variability in size of adults (Belnavis 1988), which were not controlled

228   in our study.

229   Our study however brings into question the fecundity of larger adult female *D. coccinellae*

230   (presumably greater than that of smaller adult female *D. coccinellae* possibly due to more eggs

231   and or larger eggs in larger female parasitoids and possibly longer life span of larger females,

232   and thus greater rates of parasitization of larger hosts - see Obrycki 1989). Thus if there is indeed

233   positive fecundity selection for larger females in a population, we would expect an ongoing trend

234   of observing larger *D. coccinellae* in the field, which thus parasitize a larger number of native,

235   and non-native species. Of potential interest then is the differential efficacy of parasitization of

236   small *D. coccinellae* on larger coccinellid hosts, and vice versa. Within our 99 sampled wasps in

237   the current study, one *D. coccinellae* female reared from a field collected *Cyc. munda*

238   successfully parasitized and produced female F1 progeny from *Cocc. septempunctata*, *Har.*

239   *axyridis* and *Col. maculata*, with the former two species being the largest of Coccinellid host

240   species studied in this study work.

241

242   **Acknowledgments**

247

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329   **Disclosure**

330   The authors declare no conflict of interest, financial or other vested interests in the study species,

331   or industrial applications of the species for biological control

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342 **Tables and Figures**

343 Table 1: Summary of Coccinellid host (*H. parenthesis, H. convergens, C. maculata, C.*

344 *septempunctata, H. axyridis, C. munda*) morphometric measurements from the first round of

345 measurements, including abdominal widths, abdominal lengths, pronotum widths, elytron chord

346 lengths, pronotum lengths, body lengths, and body widths, in millimeters. The p-values are

347 derived from Wilcoxon signed-rank tests for significant deviation from mean morphometric

348 measurements within each host species class.

349 Table 2: Summary of parasitoid wasp (*D. coccinellae*) morphometric measurements, including

350 head length, head depth, thorax length, thorax depth, and abdomen length, in millimeters, from

351 the first round of measurements. The p-values are derived from Wilcoxon signed-rank tests for

352 significant deviation from mean morphometric measurements within each host species class.

353 Figure 1: Map of locations from which Coccinellid hosts with their parasitoid wasp were field-

354 collected (except *H. convergens* from Arizona, which was shipped to the authors).

355 Figure 2: Morphometric variables measured from Coccinellid hosts, shown in three perspectives

356 - dorsal, lateral, and venral views. Image courtesy: D. Sustaita.

357 Figure 3: Morphometric variables measured from parasitoid wasps, *D. coccinellae*, shown in a

358 single lateral perspective. Image courtesy: D. sustaita.

359 Figure 4: Box plot summary of Coccinellid host (*H. parenthesis, H. convergens, C. maculata, C.*

360 *septempunctata, H. axyridis, C. munda*) morphometric measurements from the first round of

361 measurements, including abdominal widths, abdominal lengths, pronotum widths, elytron chord

362 lengths, pronotum lengths, body lengths, and body widths, in millimeters. Shown are means, and

363 interquartile ranges within each measurement.

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364   Figure 5: Box plot summary of parasitoid wasp (*D. coccinellae*) morphometric measurements,

365   including head length, head depth, thorax length, thorax depth, and abdomen length, in

366   millimeters, from the first round of measurements, categorized by their respective host species.

367   Shown are means, interquartile ranges within each measurement. These measurements are

368   consistent with observations on *D. coccinellae* in Table 2 of Obrycki 1988.

369   Figure 6: Regression of coccinellid host dry weight versus parasitoid wasp dry weight in

370   milligrams, showing the positive correlation between size of the host and the size of its parasitoid

371   wasp. $R^2 = 0.407$, p-value = 3.09e-11.

372   Figure 7: A Principal Components Analysis (PCA) plot of all variability in morphometric

373   measurements from parasitoid wasps, and their coccinellid hosts from round 1 of measurements.

374   The first two PC's accounted for most of the variability in the data (PC1: 62.1%, PC2: 13.2%),

375   with the PC1 describing variation in the coccinellid host morphometrics, and PC2 describing

376   variation in the parasitoid wasp morphometrics.

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386   *Table 1*

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Coccinellid Host	Host Length						
	Abdominal Width	Abdominal Length	Pronotum Width	Elytron Chord Length	Pronotum Length	Body Length	Body Width
H. parenthesis	2.47 (sd = 0.2, p-value = 2.384e-07, min = 1.92, median = 2.48, max = 2.76,)	3.42 (sd = 0.22, p-value = 2.886e-05, min = 2.82, median = 3.43, max = 3.7,)	1.98 (sd = 0.15, p-value = 2.883e-05, min = 1.64, median = 2.01, max = 2.24,)	3.85 (sd = 0.25, p-value = 2.384e-07, min = 3.21, median = 3.96, max = 4.22,)	1.24 (sd = 0.1, p-value = 2.886e-05, min = 1.05, median = 1.23, max = 1.47,)	4.9 (sd = 0.39, p-value = 2.384e-07, min = 4.26, median = 4.81, max = 5.76,)	2.91 (sd = 0.2, p-value = 2.384e-07, min = 2.4, median = 2.93, max = 3.24,)
H. convergens	3.18 (sd = 0.27, p-value = 0.001656, min = 2.77, median = 3.06, max = 3.7,)	4.41 (sd = 0.42, p-value = 0.0002441, min = 3.84, median = 4.35, max = 5.22,)	2.41 (sd = 0.18, p-value = 0.0002441, min = 2.19, median = 2.35, max = 2.77,)	4.81 (sd = 0.6, p-value = 0.0002441, min = 3.39, median = 4.65, max = 5.68,)	1.54 (sd = 0.11, p-value = 0.0002441, min = 1.38, median = 1.55, max = 1.76,)	5.96 (sd = 0.46, p-value = 0.0002441, min = 5.3, median = 5.9, max = 6.82,)	3.78 (sd = 0.32, p-value = 0.0002441, min = 3.43, median = 3.64, max = 4.52,)
C. maculata	2.6 (sd = 0.19, p-value = 2.328e-10, min = 2, median = 2.6, max = 2.94,)	3.96 (sd = 0.28, p-value = 2.328e-10, min = 3.02, median = 4.01, max = 4.38,)	2.1 (sd = 0.12, p-value = 5.63e-07, min = 1.72, median = 2.1, max = 2.37,)	4.35 (sd = 0.35, p-value = 2.328e-10, min = 3.32, median = 4.31, max = 5.37,)	1.3 (sd = 0.12, p-value = 5.642e-07, min = 1.06, median = 1.31, max = 1.51,)	5.61 (sd = 0.41, p-value = 2.328e-10, min = 4.37, median = 5.72, max = 6.26,)	3.21 (sd = 0.22, p-value = 2.328e-10, min = 2.53, median = 3.22, max = 3.66,)
H. axyridis	4.32 (sd = 0.28, p-value = 0.125, min = 3.97, median = 4.34, max = 4.63,)	5.21 (sd = 0.2, p-value = 0.125, min = 4.96, median = 5.24, max = 5.39,)	3.09 (sd = 0.2, p-value = 0.125, min = 2.85, median = 3.08, max = 3.34,)	5.79 (sd = 0.27, p-value = 0.125, min = 5.57, median = 5.73, max = 6.15,)	1.9 (sd = 0.06, p-value = 0.125, min = 1.85, median = 1.89, max = 1.98,)	6.81 (sd = 0.21, p-value = 0.125, min = 6.59, median = 6.79, max = 7.07,)	5.44 (sd = 0.27, p-value = 0.125, min = 5.05, median = 5.52, max = 5.66,)

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C. munda	2.73 (sd = 0.27, p-value = 0.003906, min = 2.34, median = 2.71, max = 3.12,)	3.36 (sd = 0.38, p-value = 0.003906, min = 2.91, median = 3.17, max = 4.00,)	2.26 (sd = 0.18, p-value = 0.003906, min = 2.05, median = 2.23, max = 2.51,)	4.08 (sd = 0.64, p-value = 0.003906, min = 3.38, median = 3.96, max = 5.5,)	1.34 (sd = 0.07, p-value = 0.003906, min = 1.22, median = 1.37, max = 1.41,)	4.58 (sd = 0.45, p-value = 0.003906, min = 3.98, median = 4.52, max = 5.28,)	3.69 (sd = 0.3, p-value = 0.003906, min = 3.18, median = 3.69, max = 4.14,)
C7	4.08 (sd = 0.41, p-value = 0.02225, min = 3.93, median = 3.74, max = 4.86,)	5.19 (sd = 0.53, p-value = 0.01563, min = 4.72, median = 4.91, max = 6.17,)	3.26 (sd = 0.34, p-value = 0.01563, min = 2.93, median = 3.07, max = 3.78,)	5.57 (sd = 0.92, p-value = 0.01563, min = 4.21, median = 5.8, max = 6.89,)	2.01 (sd = 0.42, p-value = 0.01563, min = 1.13, median = 2.09, max = 2.48,)	6.85 (sd = 0.64, p-value = 0.01563, min = 6.33, median = 6.52, max = 8.1,)	5.4 (sd = 0.44, p-value = 0.01563, min = 4.81, median = 5.54, max = 5.98,)

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403   *Table 2*

|	Wasp Length				
Coccinellid Host					
	Head Length	Head Depth	Thorax Length	Thorax Depth	Abdomen Length
H. parenthesis	0.77 (sd = 0.05, p-value = 2.384e-07, min = 0.65, median = 0.77, max = 0.83,)	0.49 (sd = 0.04, p-value = 2.88e-05, min = 0.43, median = 0.48, max = 0.56,)	1.28 (sd = 0.15, p-value = 2.384e-07, min = 0.94, median = 1.29, max = 1.62,)	0.68 (sd = 0.09, p-value = 2.886e-05, min = 0.5, median = 0.7, max = 0.87,)	2.52 (sd = 0.37, p-value = 2.384e-07, min = 1.85, median = 2.44, max = 3.18,)
H. convergens	0.82 (sd = 0.05, p-value = 0.0002441, min = 0.71, median = 0.83, max = 0.93,)	0.51 (sd = 0.05, p-value = 0.001651, min = 0.42, median = 0.51, max = 0.58,)	1.35 (sd = 0.11, p-value = 0.0002441, min = 1.21, median = 1.33, max = 1.56,)	0.72 (sd = 0.07, p-value = 0.0002441, min = 0.61, median = 0.7, max = 0.84,)	2.52 (sd = 0.37, p-value = 0.0002441, min = 2.00, median = 2.48, max = 3.13,)
C. maculata	0.78 (sd = 0.05, p-value = 5.639e-07, min = 0.67, median = 0.78, max = 0.91,)	0.5 (sd = 0.05, p-value = 5.636e-07, min = 0.37, median = 0.51, max = 0.63,)	1.29 (sd = 0.14, p-value = 5.642e-07, min = 0.92, median = 1.3, max = 1.51,)	0.7 (sd = 0.1, p-value = 5.639e-07, min = 0.5, median = 0.69, max = 0.91,)	2.35 (sd = 0.33, p-value = 2.328e-10, min = 1.68, median = 2.28, max = 3.12,)
H. axyridis	0.86 (sd = 0.03, p-value = 0.09751, min = 0.83, median = 0.85, max = 0.9,)	0.61 (sd = 0.02, p-value = 0.125, min = 0.58, median = 0.62, max = 0.64,)	1.44 (sd = 0.05, p-value = 0.125, min = 1.37, median = 1.45, max = 1.49,)	0.79 (sd = 0.1, p-value = 0.125, min = 0.66, median = 0.81, max = 0.9,)	2.93 (sd = 0.45, p-value = 0.125, min = 2.54, median = 2.83, max = 3.51,)
C. munda	0.76 (sd = 0.05, p-value = 0.003906, min = 0.67, median = 0.77, max = 0.82,)	0.53 (sd = 0.05, p-value = 0.009091, min = 0.46, median = 0.52, max = 0.6,)	1.26 (sd = 0.1, p-value = 0.009091, min = 1.07, median = 1.29, max = 1.44,)	0.69 (sd = 0.03, p-value = 0.003906, min = 0.65, median = 0.69, max = 0.72,)	2.27 (sd = 0.4, p-value = 0.003906, min = 1.85, median = 2.18, max = 3.2,)
C7	0.87 (sd = 0.05, p-value = 0.01563, min = 0.8, median = 0.87, max = 0.96,)	0.52 (sd = 0.06, p-value = 0.01563, min = 0.42, median = 0.52, max = 0.58,)	1.55 (sd = 0.1, p-value = 0.01563, min = 1.37, median = 1.57, max = 1.65,)	0.82 (sd = 0.06, p-value = 0.01563, min = 0.75, median = 0.84, max = 0.88,)	2.89 (sd = 0.37, p-value = 0.01563, min = 2.26, median = 2.88, max = 3.36,)

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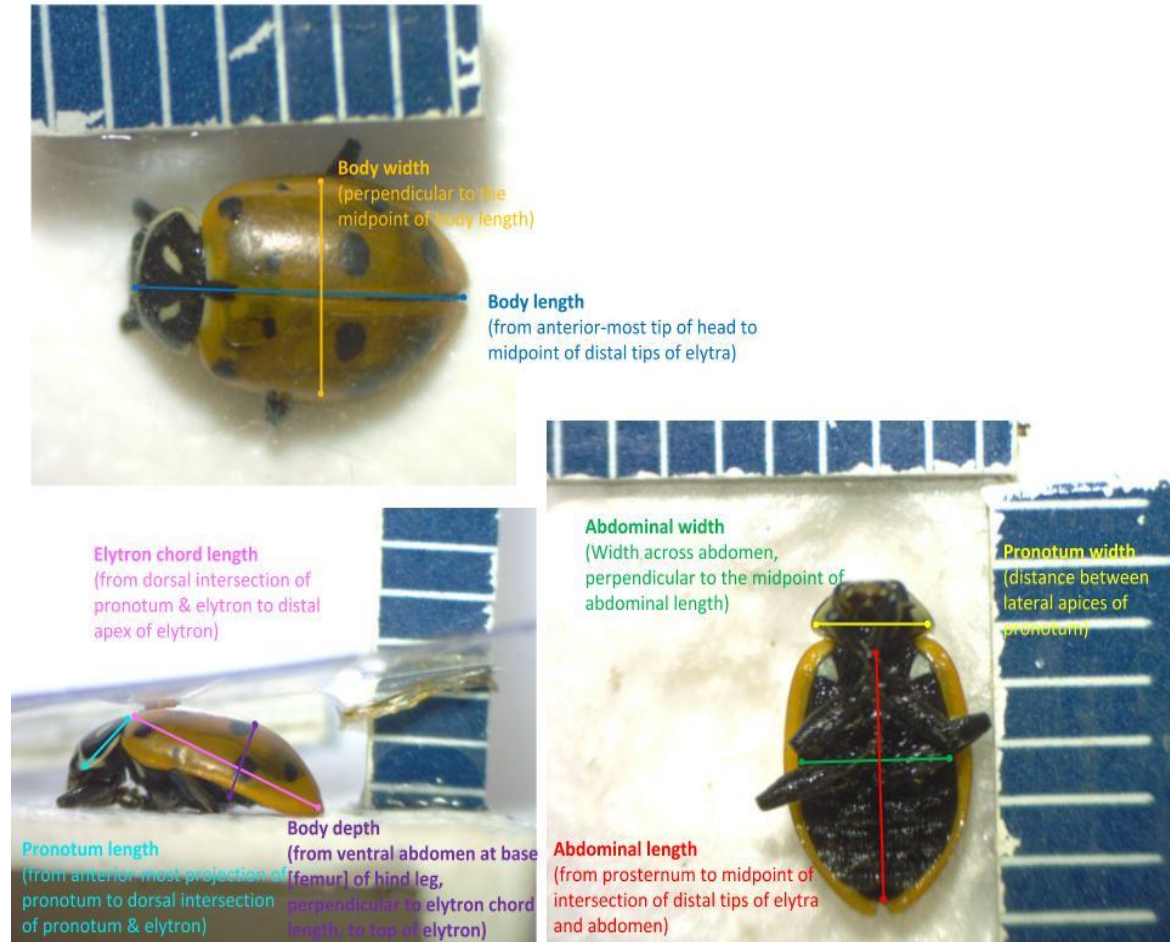

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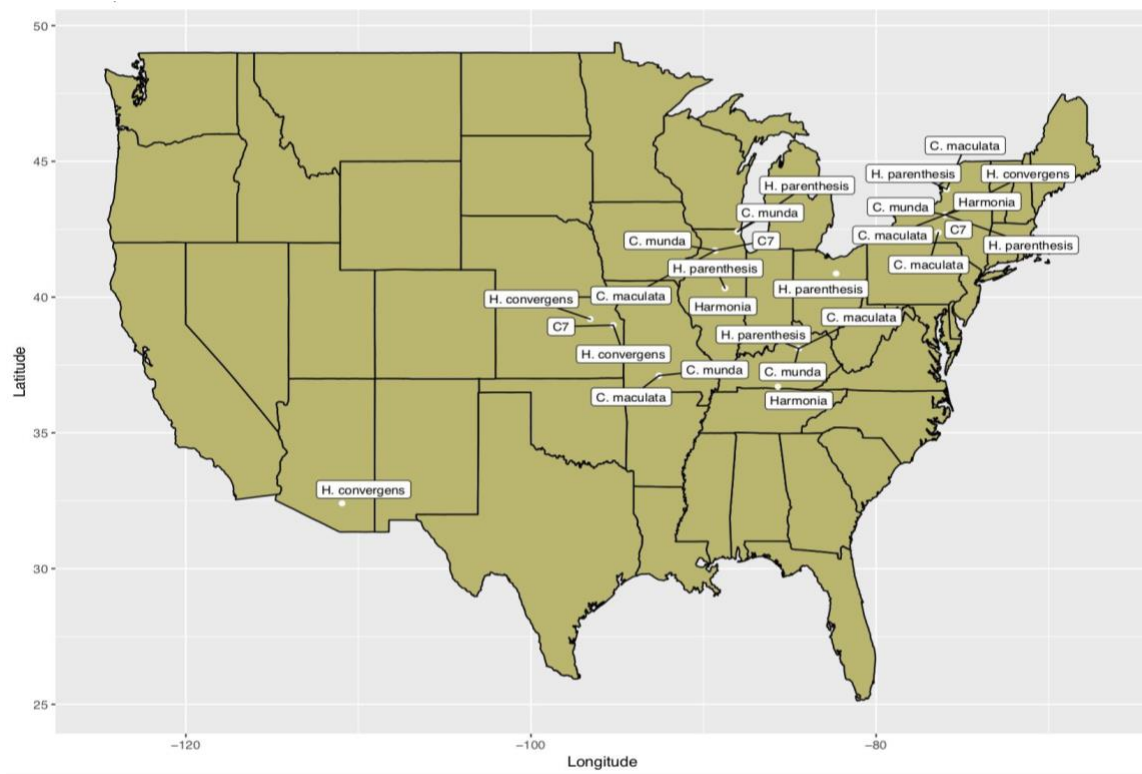
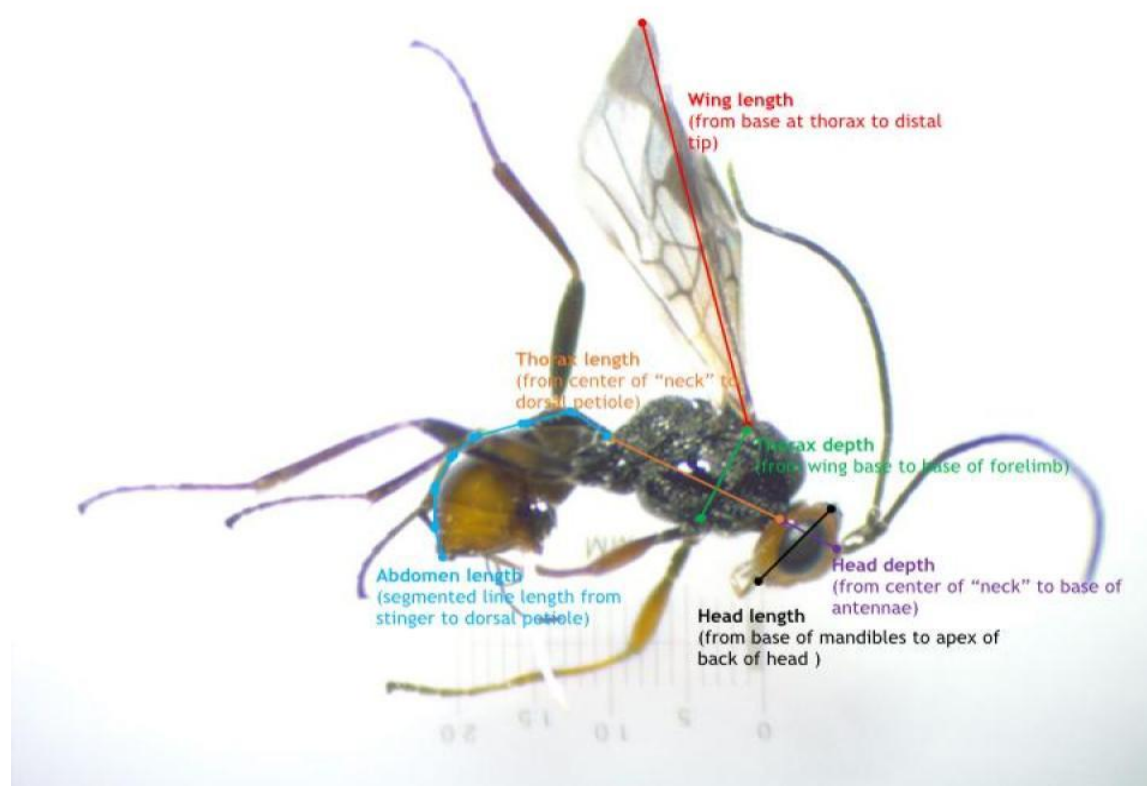*Figure 1*

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418   *Figure 2*

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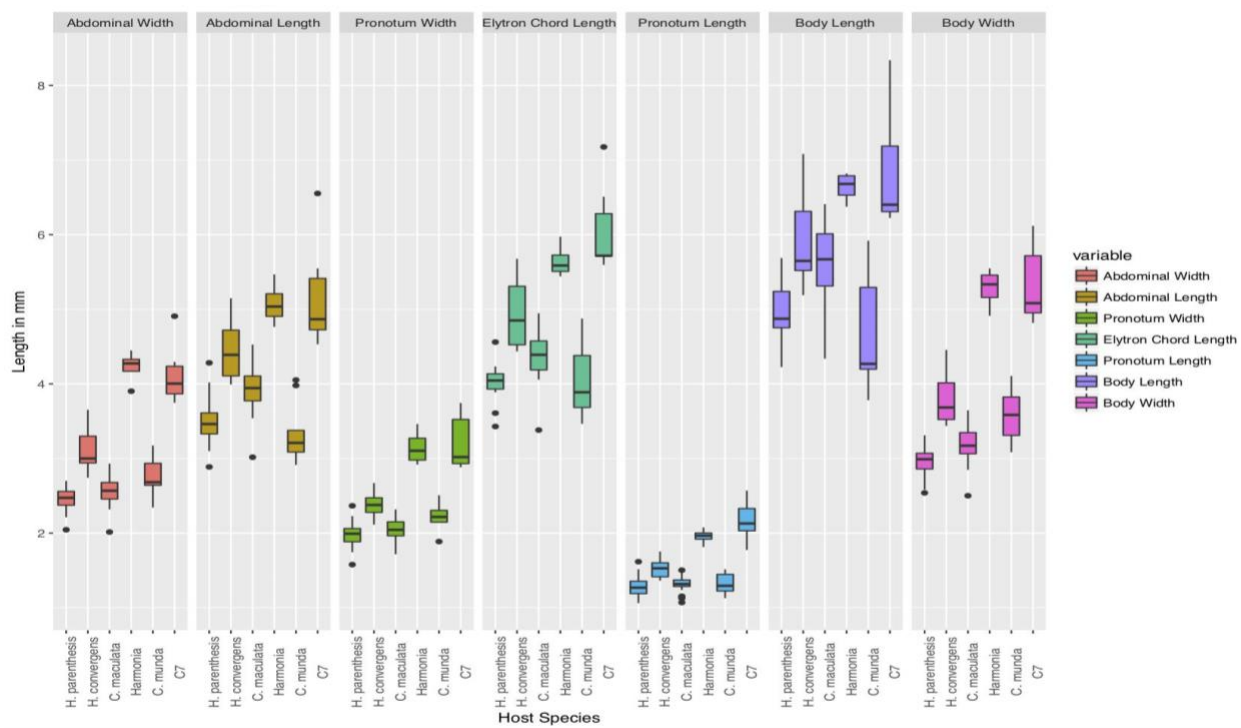
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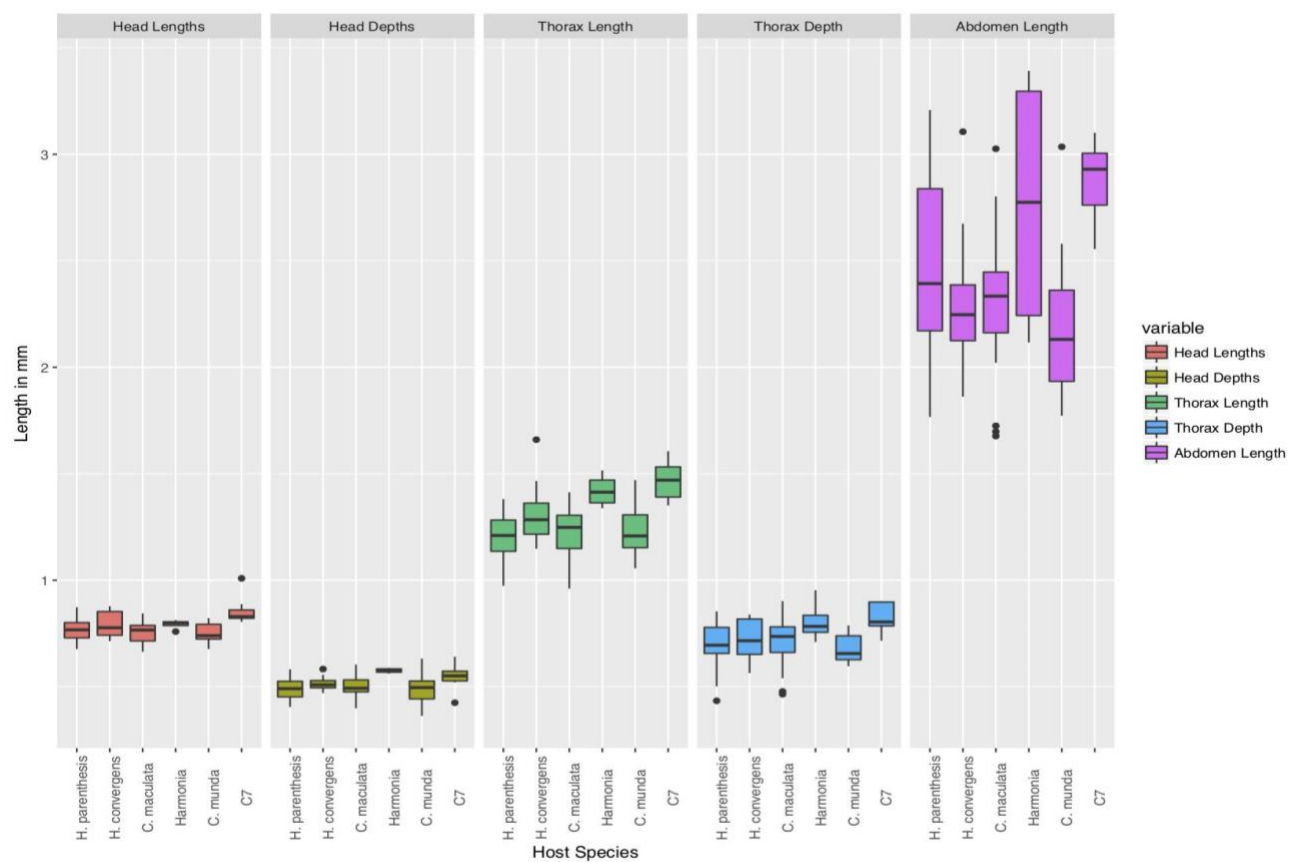
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Figure 5

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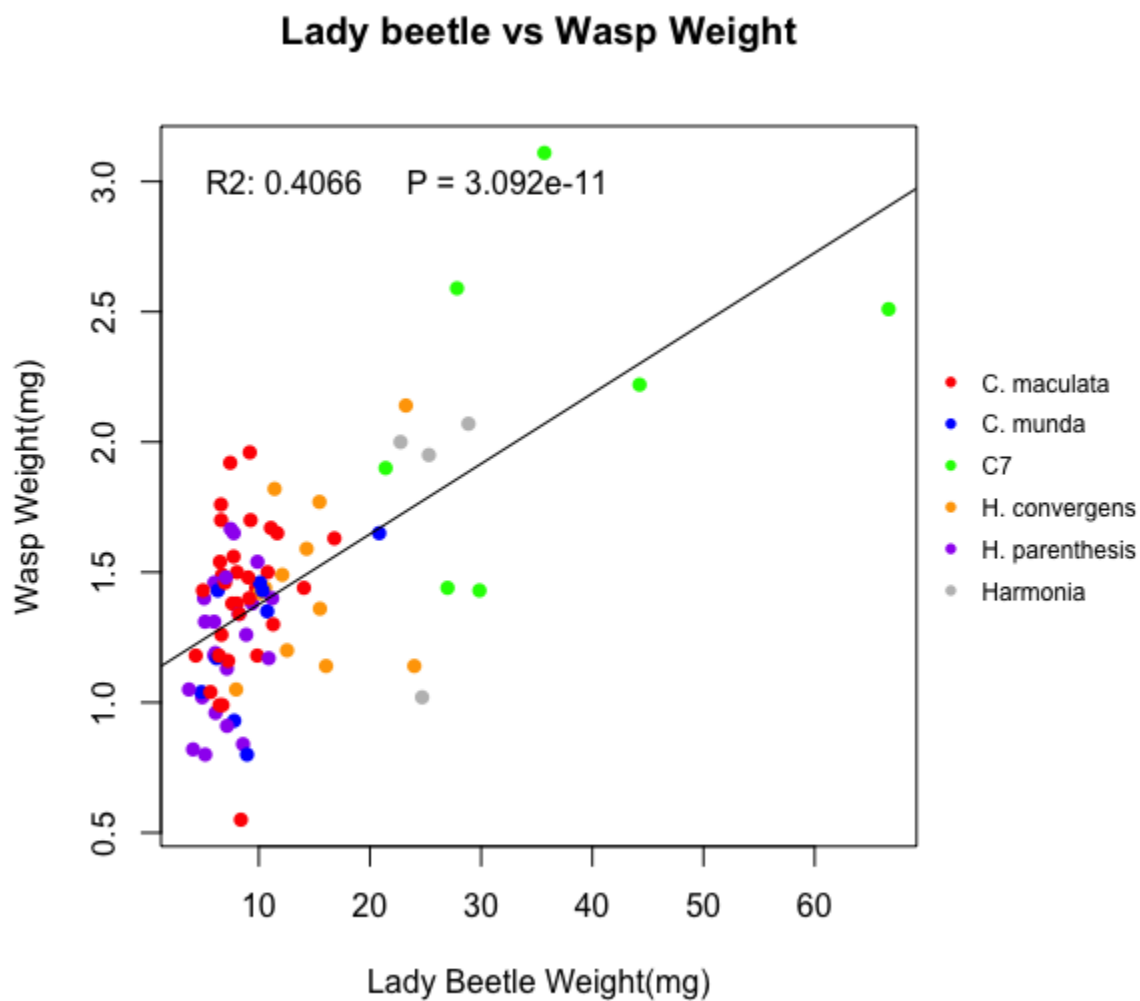
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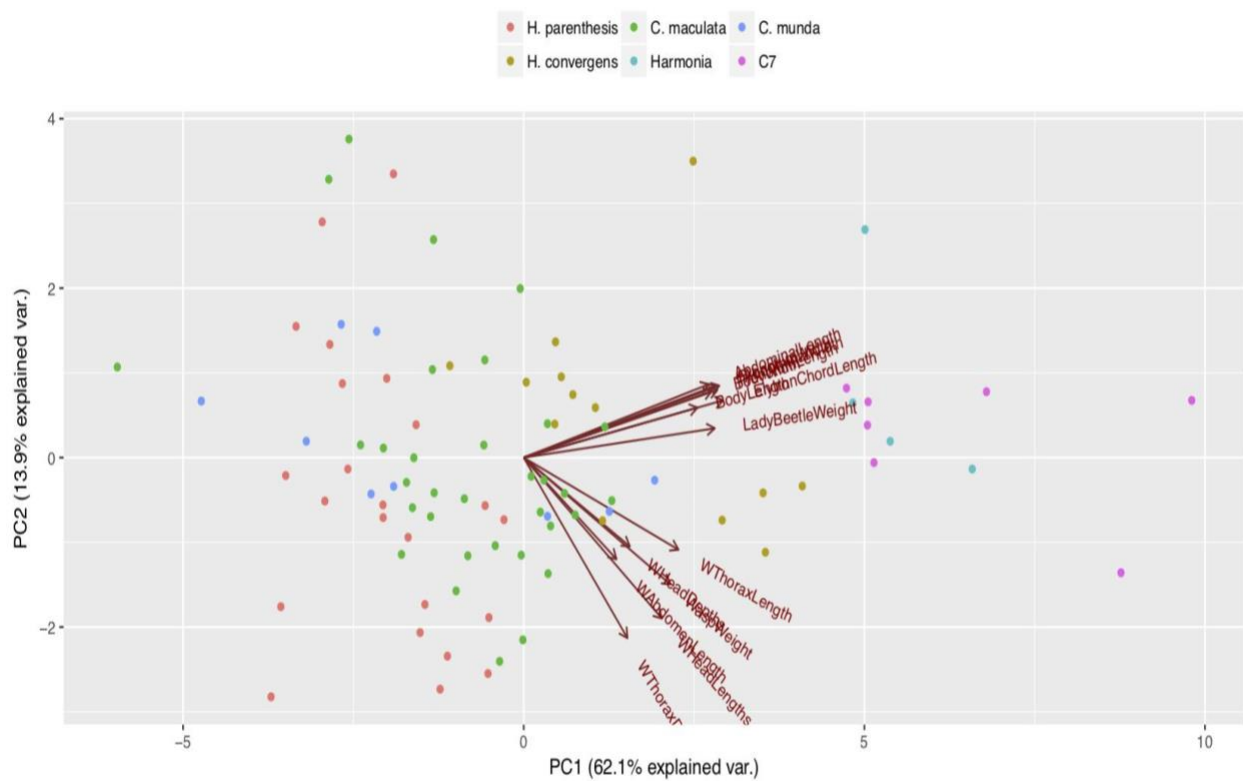441

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446   *Figure 6*

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Figure 7

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