

1 **Original Article**

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3 **Large mothers produce progeny with high survival rates during the immature stage and**
4 **large sizes at adulthood in a parasitoid species**

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6 **Weri Herlin^{1,2}, Hideto Yoshimura^{1,3}, and Yoshihiro Y. Yamada¹**

7

8 ¹ Insect Ecology Laboratory, Graduate School of Bioresources, Mie University

9 Tsu, Mie 514-8507, Japan

10

11 Current address:

12 ² Department of Agroecotechnology, Faculty of Agriculture, University of Sriwijaya.

13 Indralaya 30662, South Sumatra, Indonesia

14 ³ Division of Agro-Environment Research, Tohoku Agricultural Research Center, NARO,

15 Morioka, Iwate 020-0198, Japan

16

17

18 *Correspondence: Yoshihiro Y. Yamada

19 Tel.: +81 59 231 9498, Fax: +81 59 231 9540

20 E-mail: yamada-y@bio.mie-u.ac.jp

21 ORCID: 0000-0002-2192-3256

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25

26 **Abstract**

27

28 Parasitoid researchers have generally thought that the body size of the mother parasitoid
29 does not affect the fitness performance of the progeny during the immature stage, as long as
30 the progeny develop in the same environment. We reveal for the first time that this is not
31 true for the parasitoid *Echthrodelphax fairchildii* (Hymenoptera: Dryinidae), which is
32 parasitic on planthoppers. Large females ensured an increased survival rate for their
33 progeny during the immature stage and a large body size at adult emergence. Maternal
34 body size differentially affected the body sizes and survival rates of male and female
35 progeny. Small females did not produce female progeny, and the survival rate of the female
36 progeny increased more steeply with increasing maternal body size than that of the male
37 progeny. Meanwhile, the body size of male progeny increased more steeply with increasing
38 maternal body size. The influence of maternal body size on progeny survival to adult
39 emergence has never been reported in insects before. In addition, large females were more
40 likely to lay female eggs, suggesting that females control the sex ratio of progeny in response
41 to their own body size.

42

43 Keywords body size · Dryinidae · fitness · parasitoid · planthopper

44

45 **Introduction**

46

47 The body size of animals is closely related to their fitness performance (Peters 1983;
48 Shingleton 2011), with large individuals usually—but not always—exhibiting relatively high
49 fitness within a species (Kingsolver and Pfennig 2004). This is also applicable to parasitoid
50 wasps, many of which are widely used as biological control agents. Larger female
51 parasitoids have a higher lifetime fecundity and/or are better at foraging and ovipositing
52 than smaller female wasps (e.g., Heinz 1991; Visser 1994; West et al. 1996), and
53 consequently, they are likely to find more high-quality hosts over their lifetime. However,

54 there have been no reports of large female parasitoids producing large adult progeny or
55 ensuring high immature survival rates for their progeny. A positive relationship between
56 maternal body size and egg size is often found in insects (Fox and Cresak 2000; Fischer et al.
57 2002). However, the relationship between maternal body size and the fitness performance of
58 progeny during the immature stage is marginal or unclear in insects (Torres-Vila and
59 Rodríguez-Molina 2002; Kojima 2015); the effects of egg size on the fitness performance
60 during part of the immature stage have been often reported (Fox and Cresak 2000), but the
61 reporting of an egg-size effect on the fitness performance during the whole immature stage is
62 quite rare (Fox 2000). Mother size affects progeny adult size in some insects (Kojima 2015;
63 Fox 1994a; Steiger 2013), and the effects are caused by genetic factors (Fox 1994b) or
64 differences in the ability of the mother to care for her offspring (Kojima 2015; Steiger 2013).
65 To the best of our knowledge, the effects of maternal body size on the survival rate to adult
66 emergence have not been reported in insects.

67 Parasitoids have frequently been used to verify predictions of theoretical models of
68 foraging and ovipositing, including host preference, patch use, and sex allocation (Godfray
69 1994; Wajnberg et al. 2008). This is because they are easy to rear in the laboratory and their
70 decision-making about ovipositing is directly related to their fitness since the progeny must
71 live on/in the host selected by the mother. The fitness performance of female parasitoid
72 adults is determined mainly by lifetime fecundity and characteristics related to foraging and
73 oviposition strategies, as mentioned above. If large female adults produce large adult
74 progeny and/or ensure high survival rates during the immature stage for their progeny, the
75 size of female parasitoids has a greater influence on their fitness than researchers
76 previously thought, and this would greatly impact our understanding of the foraging and
77 ovipositing strategies of parasitoids. A typical example is found in the host quality model
78 (Charnov et al. 1981; Charnov 1982) for sex allocation, which has been applied to sex
79 allocation in many parasitoids (Godfray 1994); the model predicts that the female should lay
80 female and male eggs on high- and low-quality hosts, respectively. The precondition for the
81 model is that the increase in adult size differentially affects the fitness of the female and

82 male adults; female adults achieve more fitness gains than male adults as the adult size
83 increases. Many researchers have tried to verify the precondition (e.g., van den Assem et al.
84 1989; Heinz 1991; Kazmer and Luck 1995; Ueno 1998, 1999), but no researchers have
85 addressed the effects of maternal body size on the survival of immatures and the size of
86 emerging adults. If such effects are present, sex differences in size are greater than
87 researchers previously thought, and the precondition appears to be satisfied easily.

88 Here, we investigated the effects of maternal body size on progeny size and survival
89 rate using the parasitoid *Echthrodelphax fairchildii* Perkins (Hymenoptera: Dryinidae).

90

91 **Materials and methods**

92

93 **Insects and rearing**

94

95 *Echthrodelphax fairchildii* is a semisolitary ectoparasitoid of several planthopper species
96 (Homoptera: Delphacidae), including *Laodelphax striatellus* (Fallén); two adults often
97 emerge under superparasitism conditions (Yamada and Ikawa 2005). Male and female
98 adults have different morphologies. This parasitoid uses planthoppers as prey or hosts;
99 third to fifth instars are used as both hosts and prey, whereas first and second instars are
100 used as prey only. Female adults are synovigenic and usually live for 2–4 weeks. The daily
101 fecundity is 15–25 eggs when the female parasitoid is 3–20 days old (Y. Y. Yamada and S.
102 Yamaguchi, unpublished data). The female of *E. fairchildii* lays an egg under the forewing
103 bud of the host. Parasitized hosts continue to feed on host plants, but they do not molt.

104 *Echthrodelphax fairchildii* is therefore classified as a koinobiont (Godfray 1994; Quicke
105 1997), although koinobionts typically allow the host to molt. The immature parasitoids are
106 sedentary at the site of oviposition. Approximately 1 week after oviposition, part of the
107 immature parasitoid, called a larval sac, is visible to the naked eye on the surface of the
108 host. After maturing sufficiently, the immature parasitoid leaves the host and spins a
109 cocoon on a nearby plant.

110 *Echthrodelphax fairchildii* and *L. striatellus* were collected at two locations
111 separated by 10 km in 1992 in Tsu, Mie, Japan, and reared continuously under laboratory
112 conditions. The two parasitoid populations collected at the different sites were maintained
113 separately, while the two host populations were reared in a mixed manner. Field-collected
114 insects were added to the laboratory population every few years after 2005.

115 To obtain parasitoids for use in experiments, parasitoid pupae were gathered from
116 the laboratory populations and kept individually in 5-mL plastic vials. After emergence,
117 females were individually placed into 340-mL plastic cages containing a 50% (by weight)
118 honey solution, water, 20 second-instar hosts, 20 third-instar hosts, 1 fifth-instar host, 2
119 male wasps for mating (the males and female came from populations collected at the
120 different sites) and approximately 20 rice seedlings. The honey solution, water, hosts, and
121 rice seedlings were renewed every day. Individual parasitoids were used only once for one
122 parasitism event. The insects were reared in a room at 24–26°C, with 40–50% relative
123 humidity and a 16-h light/8-h dark photoperiod.

124

125 **Parasitism and rearing of parasitized hosts**

126

127 Mated females aged 4–5 days were allowed to lay an egg on a fourth-instar host that was
128 within 24 h of molting. In an oviposition event, a female in a rearing cage was moved to a
129 clean 4-mL transparent plastic vial containing four second-instar hosts for food immediately
130 after the light was turned on; she was kept there in for 4 h before a healthy fourth-instar
131 host was added. We observed ovipositing behavior under fluorescent lighting using a
132 supersensitive video camera (WAT-902H, Watec, Yamagata, Japan) attached to a binocular
133 microscope. The sex of the egg was identified based on observations of the movement of the
134 genitalia (Yamada and Imai 2000). The parasitized host was removed immediately after the
135 end of oviposition so that it was not superparasitized.

136 Parasitized hosts were reared individually in 30-mL glass vials with five or six rice
137 seedlings. The development of the immature parasitoids was observed daily. The head

138 widths of the mothers and their progeny were measured a few weeks after their death using
139 an ocular micrometer (96× magnification).

140

141 **Data analysis**

142

143 The effects of maternal body size (head width) on the sex ratio and survival rate of the
144 progeny were examined with a logistic regression analysis (LogXact®10, Cytel Software,
145 Cambridge, MA, USA). Significance was tested by calculating the exact probability (Cytel
146 2012). The effects of maternal body size on the body size (head width) and developmental
147 period of the progeny were analyzed using a mixed linear model. Significance was tested
148 using the likelihood-ratio test implemented with the “anova” function in the “lme4” package
149 of the R program (version 3.4.3) (R Core Team 2016). When examining the survival rate,
150 body size, and developmental period of the progeny, the sex and maternal body size were
151 included in the model as fixed factors, and the collection site was included as a random
152 factor. In addition, the strength of the relationship between maternal size and progeny size
153 was assessed separately for males and females by calculating the partial R^2 value using a
154 multiple regression model with the collection site included as a fixed categorical value. This
155 analysis was performed using NCSS (version 11, NCSS Statistical Software, Kaysville, UT,
156 USA). The sample sizes for the survival rate, head width and developmental period were
157 352, 282 and 282 for males and 112, 44 and 44 for females, respectively.

158

159 **Results**

160

161 **Effects of maternal body size on the sex ratio and survival rate of the progeny**

162

163 Large female wasps were more likely to lay female eggs ($P < 0.001$, Fig. 1). The interaction
164 between the sex and maternal body size was significant ($P < 0.001$), and the statistical
165 analysis of the survival rate was performed separately for males and females. The survival

166 rates of both male and female progeny increased with increasing maternal body size (in both
167 males and females, $P < 0.001$; Fig. 2): that of the female progeny increased more steeply
168 than that of the male progeny. When the head width of the mother was < 0.60 mm, most of
169 the female progeny did not emerge. Death occurred mainly after the appearance of the
170 larval sac, particularly between the appearance of the larval sac and cocoon spinning in
171 females (Table 1).

172

173 **Effects of maternal body size on the body size and developmental period of the progeny**

174

175 The interaction between the sex and maternal body size was significant ($X_1^2 = 5.7$, $P = 0.017$),
176 and the statistical analysis of progeny body size was performed separately for males and
177 females. Large female wasps produced large male and female progeny (for males, $X_1^2 = 8.2$,
178 $P = 0.004$; for females, $X_1^2 = 12.9$, $P < 0.001$; Fig. 3). The body size of the male progeny
179 increased more steeply with increasing maternal body size than that of the female progeny.
180 The strength of the relationship between maternal body size and progeny body size was
181 similar between males and females: with partial R^2 values of 0.202 and 0.254, respectively.
182 Moreover, maternal body size did not affect the developmental period of the progeny in
183 either sex (size, $X_1^2 = 2.3$, $P = 0.131$; sex, $X_1^2 = 34.9$, $P < 0.001$; interaction, $X_1^2 = 1.1$, $P =$
184 0.293). The developmental period of the female progeny was a little longer than that of the
185 male progeny: 21.78 ± 0.09 days ($M \pm SE$) for males and 22.86 ± 0.17 days for females.

186

187 **Discussion**

188

189 This is the first study to find that large mother parasitoids produce large progeny and
190 ensure high survival rates of the progeny during the immature stage. A particularly
191 interesting finding was that the effect of maternal body size on the fitness of the progeny
192 was stronger in female progeny than in male progeny. This difference is probably related to
193 sexual dimorphism, but its underlying mechanisms are unknown at present. Small adults

194 did not produce female progeny and refrained from laying female eggs, whereas large female
195 adults were more likely to lay female eggs. This suggests that females changed the sex of
196 their eggs in response to their own body size; female hymenopterans can determine the sex
197 of their eggs by controlling the release of sperm stored in the spermatheca (Godfray 1994;
198 Quicke 1997). Moreover, the female-biased sex ratio for large females is explained well by
199 the host-quality model (Charnov et al. 1981; Charnov 1982). The females used for the
200 experiment encountered many low-quality hosts (third instars) before encountering fourth-
201 instar hosts; consequently, the large parasitoids were likely to lay female eggs on the host.
202 The host-quality model predicts that a female should respond to the relative sizes of the
203 hosts available to her.

204 Some parasitoids, including bethylids, guard their immature progeny to protect them
205 from attack by competing parasitoids, predators, and other host individuals (Quicke 1997;
206 Jervis 2007; Wang et al. 2014). This kind of guarding may ensure high survival rates and
207 produce large adults. However, *E. fairchildii* females do not guard their progeny. A possible
208 alternative mechanism for the mother-size effects in *E. fairchildii* is that large females are
209 more likely to succeed in regulating the host's physiology than small females. To succeed in
210 parasitism, the parasitoid should force the host to continue feeding on the plant after the
211 parasitism attack and prohibit it from molting. Large females might do so more successfully.
212 The physiology of the host could be manipulated by parasitoid mothers injecting some
213 compounds while ovipositing and/or by parasitoid larvae releasing some compounds from
214 their mouths. Large mothers are known to lay large eggs in some parasitoid species (Klomp
215 and Teerink 1967; Visser 1994). Large eggs reportedly ensure a high survival rate for a
216 period of time after hatching in many arthropods (Fox and Cresak 2000). Therefore, the
217 following scenario is plausible: large mothers lay large eggs, and the larvae hatching from
218 the large eggs release a large amount of host-physiology regulating agents, leading to
219 increased success in parasitism. Unfortunately, no studies have been conducted to explore
220 the mechanisms for such host-physiology manipulation in Dryinidae. Whether genetic
221 factors are involved in the mother-size effects in *E. fairchildii* also remains to be elucidated

222 in future studies.

223 While ovipositing, braconid and ichneumonid parasitoids inject some compounds,
224 including venom and polydnaviruses, to suppress the host immune defense (Söller and
225 Lanzrein 1996; Burke and Strand 2012; Strand and Burke 2015). These agents are also
226 considered to be involved in controlling the host physiology. Teratocytes also function to
227 control the immune defense system and physiology of the host in some braconids
228 (Pennacchio and Strand 2007; Burke and Strand 2012). However, teratocytes are released
229 in the host body when the parasitoid eggs hatch, and thus, the ectoparasitoid *E. fairchildii*
230 cannot use them. Larvae of *E. fairchildii* insert only their modified mouth into the host body
231 after hatching (Olmi 1984) and are likely to circumvent the host immune defense. Agents
232 produced by *E. fairchildii* are considered to be involved in regulating the physiological
233 development system rather than suppressing the immune defense of the host. Therefore,
234 the mechanisms for regulation of the host's physiology in *E. fairchildii* are considered to be
235 quite different from those that have been explored in braconid and ichneumonid
236 endoparasitoids. Several researchers have recently reported that some parasitoids
237 manipulate the behavior of the hosts to increase fitness gains (Weinersmith 2019).
238 Symbionts (RNA viruses) injected by adults while ovipositing are responsible for the
239 manipulation of host behavior in the parasitoid *Dinocampus coccinellae* (Dheilly et al. 2015).
240 Such symbionts might be found in *E. fairchildii*.

241 Gao et al. (2016) recently reported no effects of maternal body size on the size of
242 adult progeny, developmental period of immatures, and sex ratio among adult progeny in the
243 gregarious ectoparasitoid *Sclerodermus pupariae* (Hymenoptera: Bethyilidae). This species
244 and *E. fairchildii* belong to the superfamily Chrysidoidea, but the former is an idiobiont,
245 while the latter is a koinobiont. The amount of host sources available for the immature
246 parasitoid is fixed in idiobiont parasitoids when the host is parasitized. Thus, the effects of
247 maternal body size on the fitness performance of immatures are likely to be found in
248 koinobiont parasitoids. It is interesting to elucidate how common mother-size effects are in
249 koinobiont parasitoids, including dryinids.

250

251 **Acknowledgments**

252

253 The authors thank Takahito Kuroda for helping with the preliminary experiment.

254

255 **References**

256

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351
352
353

354 **Figure captions**

355

356 **Fig. 1** Effects of maternal body size (head width) on the proportion of male eggs laid. Values
357 on the bars indicate sample sizes

358

359 **Fig. 2** Effects of maternal body size (head width) on the survival rates of male (open) and
360 female (solid) progeny during the immature stage. Values on the bars indicate sample sizes

361

362 **Fig. 3** Effects of maternal body size (head width) on the body sizes (head widths) of male
363 (open) and female (solid) progeny. The lines are from mixed linear model analyses

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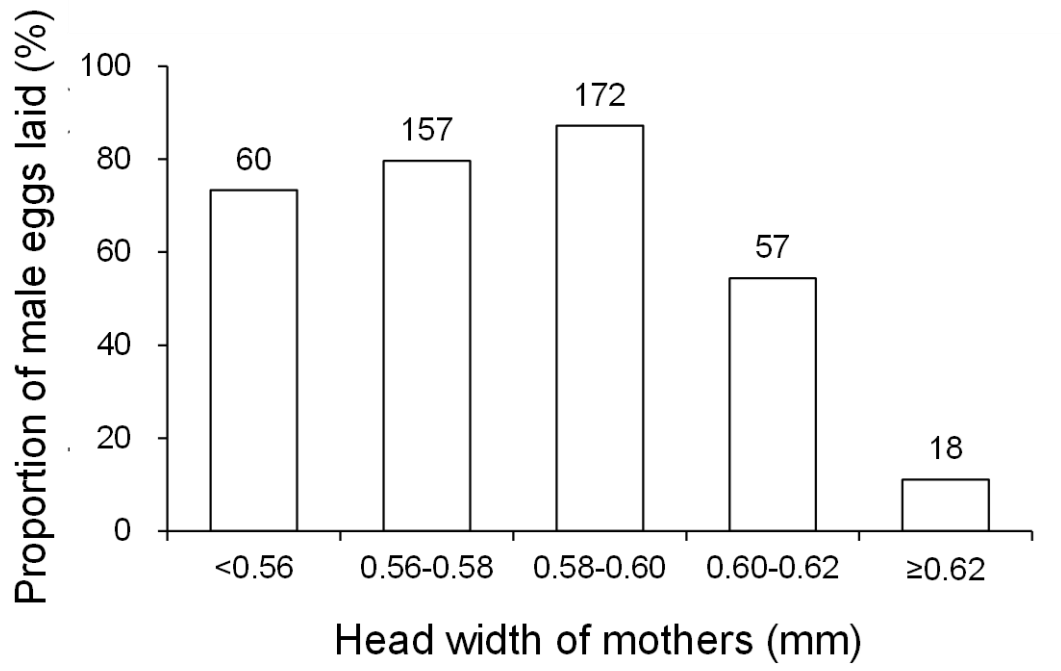
369 **Table 1** Survival rates (%) of immature progeny during the different developmental stages

	Developmental stage			
	Oviposition to larval-sac appearance	Larval-sac appearance to host leaving	Host leaving to cocoon spinning	Cocoon spinning to adult emergence
Sex				
Male	97.4 (<i>N</i> = 352)	88.9 (<i>N</i> = 343)	92.7(<i>N</i> = 305)	86.9 (<i>N</i> = 283)
Female	92.8 (<i>N</i> = 112)	63.4 (<i>N</i> = 104)	54.5 (<i>N</i> = 66)	94.4 (<i>N</i> = 36)

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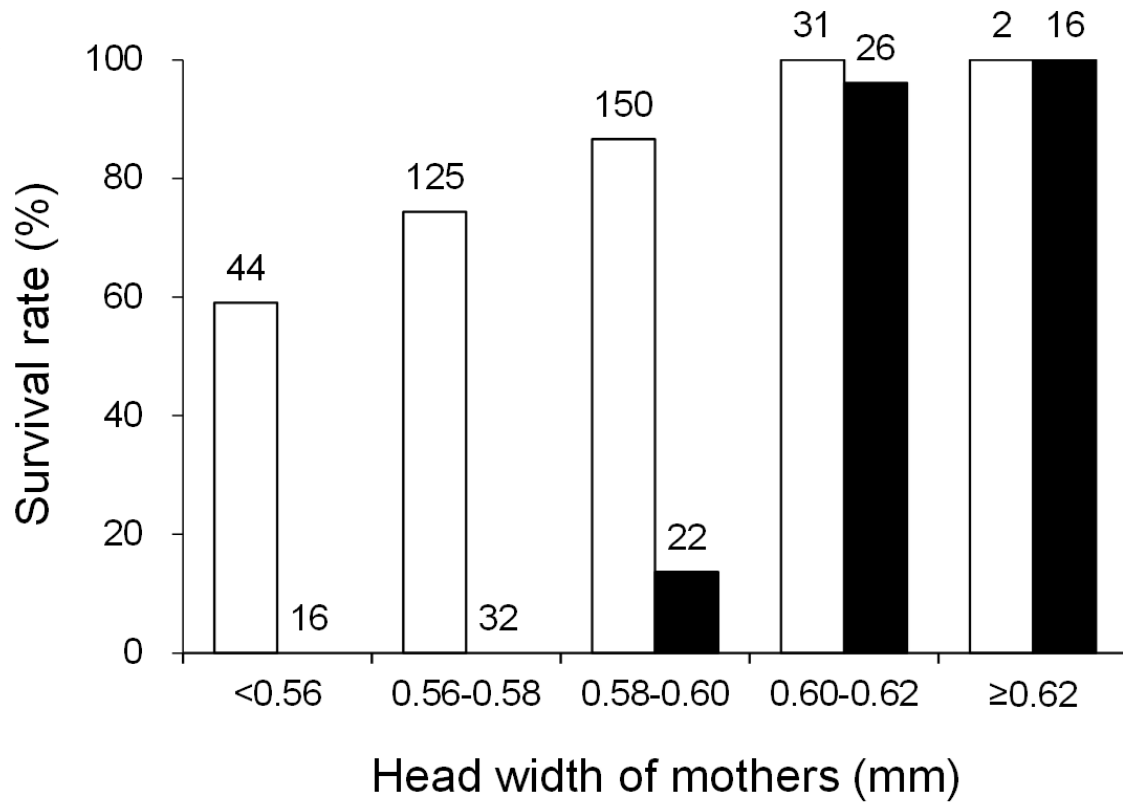
371

Figure 1



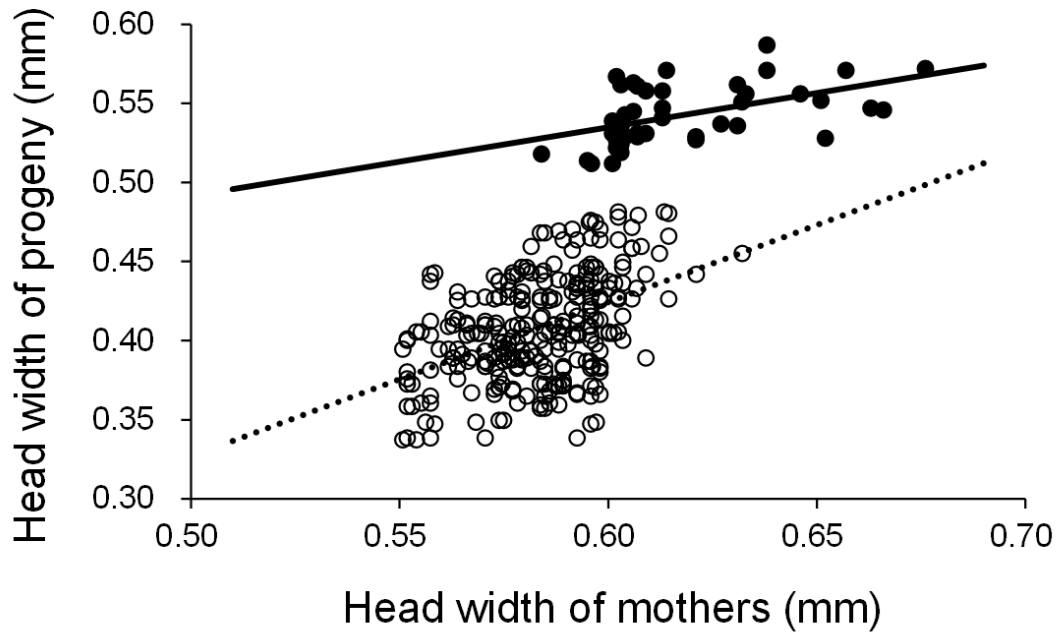
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Figure 2



373

Figure 3



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