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Differing effects of parental and natal hosts on the preference and performance of the stored product pests *Callosobruchus maculatus* and *C. analis*

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ABSTRACT

Bean beetles (Bruchinae) are a taxon of seed predators and several species are economically significant stored product pests. Seed quality may affect adult life history traits, with consequences for their population dynamics. We investigated if variation in host quality (poor quality: lentil; high quality: mung bean) as experienced by the parental (i.e. the individuals ovipositing) generation and the natal (i.e. the study individuals emerging from the host) generation influenced the preference and performance of *Callosobruchus maculatus* and *C. analis.* Both species preferred ovipositing on mung bean regardless of experience. Emergence rate was high for all treatments except for *C. maculatus* reared on mung, whose offspring did poorly when developing in lentil. The sex ratio of emerging offspring was 1:1 except for *C. analis* emerging from lentil, which was female biased if the parents were reared on lentil, but male biased if reared on mung. In *C. analis*, lentil parental host resulted in larger offspring irrespective of natal host, while in *C. maculatus* larger offspring emerged from mung as natal host. Overall, males emerging from lentils obtained more matings, except with *C. maculatus* where females had emerged from mung, where there was no preference. Development time for beetles was increased for those with parents reared on mung and for those with lentil natal hosts. For *C. analis* there was no difference in survival time for those where the parental host was lentil, but when the parental host was mung, then there was a significant reduction in survival time for those whose natal host was also mung, compared to those emerging from lentils. This work shows that predicting the effect of host quality on traits requires more than single-species, single-generation studies, as transgenerational effects can influence the performance and preference of closely related stored product pest species in quite different ways.

1. Introduction

Callosobruchus Pic (Coleoptera: Chrysomelidae) is one of the most important genera of stored product pests, causing serious damage and economic loss to a wide range of legumes and non-leguminous crops (Tuda et al., 2005). There are approximately 20 tropical and subtropical species in this genus (Tuda et al., 2006). Pest species include the cosmopolitan cowpea weevil *C. maculatus* (F.), and *C. analis* (F.), which is widespread across the tropics and subtropics (Beck and Blumer, 2014).

Both species lay eggs on the surface of a bean; after the eggs hatch the larvae bore into the bean where they develop and pupate (Giga and Smith, 1991). Thus, the whole immature development takes place inside an individual bean seed (Giga and Smith, 1991; Tuda et al., 2005). The adult beetles emerge from the host and require no food or water to complete their life cycle (although providing nutrients can influence longevity and fecundity; Moller et al., 1989; Srisakrapikoop et al., unpublished data), so adult traits are influenced by the natal host (Beck and Blumer, 2014). Seed resources are limited, and therefore host species (and hence female choice) affects offspring traits, such as development time, larval mortality, emergence mass, size (e.g. pronotum width or elytral length), rate of adult emergence, adult longevity, and fecundity (Timms, 1998; Paukku and Kotiaho, 2008; Mainali et al., 2015; Hosamani et al., 2018; Messina et al., 2018).

Oviposition choice can be influenced by olfactory (Ajayi et al., 2015) and chemical cues emanating from hosts (volatile and surface chemicals) (Giga and Smith, 1985; Gokhale et al., 1990), the curvature of host seeds (Gokhale et al., 1990), seed size (Cope and Fox, 2003), vibration from larvae already inside the seeds (Guedes and Yack, 2016) and chemical markers deposited by other females (Giga and Smith, 1985; Yamamoto, 1990). Bean beetles are

63   responsive to these cues, affecting host preference (Messina, 2004; Messina et al., 2018). Most

64   studies show that females preferred their natal host when given a choice (Messina and Slade,

65   1997; Boeke et al., 2004; Paukku and Kotiaho, 2008; Rova and Björklund, 2011; Bergeron et al.,

66   2019), suggesting a learned response, but some studies did not find a preference (Mainali et al.,

67   2015; Bergeron et al., 2019). Therefore while many studies have demonstrated the capability of

68   herbivorous insects to learn during oviposition (Jones and Agrawal, 2017), the existence of such

69   a learned response in *Callosobruchus* is uncertain.

70   While studies generally focus on female fitness traits (typically measured as fecundity, as

71   this links directly to pest status), little is known as to how host quality may affect male traits.

72   Most bean beetle species show sexual size dimorphism, with females being larger than males

73   (Guntrip et al., 1997; Savalli and Fox, 1999). In terms of male mate choice, male *C. maculatus*

74   show no preference between females differing in size (Holme, 2019; Kirschke et al., 2019), but

75   when two males compete for mating, larger males have an advantage (Savalli and Fox, 1998).

76   However, it is not clear if natal host, by affecting the traits of emerging adults, also affects mate

77   choice in *Callosobruchus*.

78   Studies have shown the existence of transgenerational effects in some insect taxa. These

79   effects can affect offspring performance (Mbande et al., 2020; Tougeron et al., 2020), change

80   offspring predator avoidance behavior (Keiser and Mondor, 2013), and alter resistance to

81   pathogens and pesticides (Brevik et al., 2018; Schulz et al., 2019). For herbivorous insects

82   transgenerational effects can be induced by variation in host plant quality (Mousseau and Fox,

83   1998). Although transgenerational effects are transmitted from the parental generation, where the

84   environment experienced by the mother can influence offspring life histories, the environment is

85   usually dynamic and the environment for the parental generation can change and consequently

86   differ for the offspring generation. Therefore, the environment directly experienced by the

87   offspring may be more important in determining their fitness.

88   *Callosobruchus maculatus* and *C. analis* both attack a range of legume hosts, and show

89   notable differences in competitive behavior, in particular showing scramble (*C. maculatus*) and

90   contest (*C. analis*) forms of competition (Giga and Smith, 1983), where with the former multiple

91   adults emerge from a bean (but each is smaller) and with the latter form only one adult emerges

92   from a bean (Toquenaga and Fujii, 1991). This difference in behavior may have profound effects

93   on weevil life histories, causing different species to react differently on the same host. They

94   therefore provide useful model systems to explore the effects of different stored products on the

95   fitness of their most economically important insect pests.

96   In this laboratory study we ask: 1) if host preference shows evidence of transgenerational

97   or maternal effects (parental host effects), and if these can be modified by experience (learning;

98   natal host effects); 2) if performance is influenced by parental (transgenerational effects) and/or

99   natal (current environment) hosts; and 3) if these effects are consistent across pest species with

100   differing life histories.

101   **2. Materials and methods**

102   *Callosobruchus maculatus* and *C. analis* were cultured separately on either mung beans

103   or lentils in a culture room at $28 \pm 2°C$ with 40% relative humidity and constant light (termed

104   culture room). This produced four cultures of the beetle; *C. maculatus* reared on mung (CmM),

105   *C. maculatus* reared on lentil (CmL), *C. analis* reared on mung (CaM) and *C. analis* reared on

106   lentil (CaL). CmM, CmL, CaM and CaL have been cultured on their hosts since 2010, 2016,

107   2011 and 2013, respectively. Twenty mated females of each species from each culture were

108   placed together in a 90 mm Petri dish containing a single layer of the same bean from which they

109   had emerged. They were left for two hours to lay eggs in the culture room to produce beans

110   harboring a single egg. Each mung bean and lentil harboring a single egg was then selected and

111   stored in a perforated Eppendorf tube before the beetles hatched. All subsequent experiments

112   used only the beetles emerging from the beans harboring a single egg to exclude the confounding

113   effect of larval competition.

2.1. Oviposition experience experiments

115   After beetles emerged from the seeds, any remaining seeds were discarded. Each beetle

116   was sexed and a single male and female from the same culture were then placed in a 1 ml

117   perforated Eppendorf tube for 48 hours to mate before experiments. All the following

118   experiments were conducted in a controlled environment (CE) room at 28°C with 60% relative

119   humidity.

2.1.1. No choice experiment (first oviposition, naïve)

121   A single mated female was put into a Petri dish containing 50 evenly dispersed seeds of

122   either mung bean or lentil (termed the focal hosts). This was replicated with 32 females from

123   each of the four cultures for both of the focal hosts, producing eight treatments in total. The

124   beetles were left in the dark (mimicking storage conditions) to oviposit eggs for six hours (a time

125   frame found to be suitable through personal observation). The number of eggs laid on each bean

126   was then counted to determine host acceptance rate, and emergence rate was recorded three

127   weeks after oviposition to allow all adults to emerge. This experiment also created an oviposition

128   experience for the females on the given focal host (i.e., same or different to their natal host).

129   Each female was kept individually in a perforated Eppendorf in the CE room before being used

130   in the choice experiment 24 hours later.

131 *2.1.2. Choice experiment (second oviposition, experienced)*

132   Each female used in the no choice experiment was put into individual Petri dishes

133 containing 100 evenly dispersed seeds (50 mung beans and 50 lentils; focal host) and allowed to

134 oviposit for a further six hours in the dark. The number of eggs laid on each bean was then

135 counted. Host acceptance rate and emergence rate were recorded as previously described.

136 *2.1.3. Oviposition preference: quality or quantity?*

137   Previous studies showed that *C. maculatus* oviposits more eggs on larger seeds (Cope and

138 Fox, 2003; Yang et al., 2006; Paukku and Kotiaho, 2008); therefore, we performed a second

139 choice experiment with 30 different mated females from each of the four cultures, under the

140 same conditions as previously described. This time the females were offered fifteen small seed

141 mung beans and fifteen lentils and allowed to oviposit for two hours. The number of eggs laid on

142 each host were counted. Thirty randomly selected seeds of lentil and small seed mung bean were

143 measured under a high-performance stereomicroscope (Leica MZ9.5), and a significant

144 difference in size between lentil [5.18 ± 0.06 mm (n = 30)] and small seed mung bean [4.38 ±

145 0.06 mm (n = 30)] was confirmed (Wilcoxon rank sum test: W = 879.5, n_1 = 30, n_2 = 30, *P* <

146 0.001).

147 *2.2. Development and survival time*

148   Each bean from the no choice experiment harboring a single egg (eight groups [CmLL,

149 CmLM, CmML, CmMM, CaLL, CaLM, CaML and CaMM]. The first two letters represent

150 species where Cm = *C. maculatus* and Ca = *C. analis*. The third and fourth letters represent

151 parental host and natal host, respectively. L = lentil, M = mung bean.) was transferred into a 1 ml

152 perforated Eppendorf tube with a unique code. These beans were kept in the CE room and were

153 checked once a day, starting three weeks after oviposition, to record emergence date from which

154 development time was calculated. The emerged beetles were kept in the 1 ml perforated

155 Eppendorf tubes without resources and moved into a laboratory at room temperature where they

156 were checked every twelve hours until death, to calculate adult survival time.

157 *2.3. Performance*

158 *2.3.1. Size and sex of offspring from no choice experiment*

159 Dead beetles from the survival experiment were sexed and the pronotum width and right

160 elytron length were measured under a high-performance stereomicroscope (Leica MZ9.5).

161 *2.3.2. Male-male competition*

162 Two 24-hour old unmated males of the same species but emerging from different hosts

163 (e.g., CmM vs CmL and CaM vs CaL), were placed in a 1 ml perforated Eppendorf tube at room

164 temperature which contained a single 24-hour old unmated female that emerged from either a

165 mung bean or lentil. Males were marked with a permanent marker to distinguish host origin. The

166 two males were put into the Eppendorf tube at the same time to reduce bias. The beetles were

167 continually observed until a successful mating occurred. The host origin of the successful male

168 was recorded.

169 *2.3.3. Copulation time and male fitness*

170 Twenty-four-hour old bean beetles were used in this experiment. An unmated female

171 from each of the four cultures was mated with an unmated male that had emerged from the same

172 or a different host (8 groups in total) in a perforated Eppendorf tube at room temperature.

173 Copulation time is defined here as the time since the male beetle started palpating the female

174 until the time they separated. After copulation, each female was put in a 90 mm Petri dish

175 containing a single layer of the same host bean that she had emerged from and was allowed to

176 oviposit in the dark CE room at 28°C 60% relative humidity until she died. Forty-five days after

177 the copulation, the Petri dishes were put in a freezer to prevent a new generation of beetles

178 emerging. The number of bean beetles (less one; the original female) in each Petri dish was

179 counted.

180 *2.4. Statistical analysis*

181 *2.4.1. Oviposition experience, development and survival time*

182   All analyses were performed using R 4.0.4 (R Core Team, 2021). Host acceptance rate

183 and mean number of eggs oviposited on each host were calculated for no-choice and choice

184 experiments. Emergence rate obtained from beans in no-choice experiment was calculated as

185 well as sex ratio which was analyzed using *G*-tests with expected 1:1 sex ratio.

186   The number of eggs oviposited in the no-choice experiment for each species was

187 modelled with zero-inflated negative-binomial model (ZINB) using *pscl* package (Zeileis et al.,

188 2008) with natal and focal hosts as independent variables. Models were generated from a global

189 model from dredge function in *MuMIn* package (Barton, 2019). Development and survival time

190 were modelled with accelerated failure time models (AFT) using *survival* package (Therneau,

191 2021) with parental host, natal host and sex as independent variables. Models were selected with

192 stepwise method using *MASS* package (Venables and Ripley, 2002) and validated by deviance

193 residuals analysis (Achilonu et al., 2019). All models were selected based on Akaike's

194 Information Criteria (AIC) (Burnham and Anderson, 2003). Collinearity was not detected as VIF

195 values ranged from 1.00 to 2.28.

196 *2.4.2. Performance*

197   Three-way ANOVA was performed to examine the effect of parental host, natal host and

198 sex on pronotum width and right elytron length of the offspring from each species. Copulation

199 time and offspring number (male fitness) of each species were compared between host origin

200   (from lentil or mung bean) of females and males using two-way ANOVA and the Scheirer-Ray-

201   Hare test (non-parametric two-way ANOVA) from the *rcompanion* package (Mangiafico, 2021),

202   respectively. Mating times for *C. maculatus* and *C. analis* were $\log_{10}$ and square root transformed

203   respectively to meet normality assumptions. Competition between males from different natal

204   hosts was tested using a *G*-test with expected mating success taken as equal. We hypothesized

205   that size may contribute to mating success; therefore, we extracted the size data from the no

206   choice experiment (only individuals that came from the same bean type for both parental and

207   natal hosts (no host switching e.g. CmLL, CmMM, CaLL and CaMM)) and then a *t*-test was

208   performed to quantify the differences in size between males and females of each species from

209   lentil and mung bean in the male-male competition experiment.

210   **3. Results**

211   *3.1. Oviposition experience experiment*

212   In the no choice experiment, both bean beetles species more readily accepted and

213   oviposited more eggs on mung bean regardless of natal host (Table 1). Our results showed that

214   prior oviposition experience (no choice experiment) did not influence subsequent oviposition

215   preference (choice experiment) in both bean beetles species as the percentage of host acceptance

216   and numbers of oviposited eggs were higher on mung bean regardless of experience (Table 2).

217   Both bean beetle species oviposited more eggs on mung bean as focal host [*C. maculatus*: lentil

218   6.73 ± 1.06 (n = 60), mung 22.40 ± 1.10 (n = 54); *C. analis*: lentil 2.78 ± 0.66 (n = 58), mung

219   24.00 ± 1.36 (n = 56)], but bean beetles emerging from lentils laid significantly more eggs than

220   those emerging from mung bean (*C. maculatus*: lentil 17.4 ± 1.45 (n = 60), mung 10.5 ± 1.40 (n

221   = 54); *C. analis*: lentil 17 ± 1.91 (n = 59), mung 9.13 ± 1.39 (n = 55); Table 3). In addition, when

222   the beetles were given a choice between small seed mung bean and lentil, both beetle species still

223   preferred to oviposit on mung bean, suggesting that host species (quality), rather than host size

224   (quantity), mattered (Table 4).

225

Table 1. Percentage and mean ± SE number of eggs oviposited on focal hosts (no choice experiment) grouped by natal host of the bean beetles. Number of ovipositing individuals is given in parentheses and N is the sample size.

Species and natal host	Focal host	N	% Acceptance	Mean ± SE no. egg
C. maculatus (Lentil)	Lentil	31	87.10 (27)	10.89 ± 1.62
	Mung	29	100 (29)	25.90 ± 1.20
C. maculatus (Mung)	Lentil	29	51.72 (15)	7.33 ± 2.00
	Mung	25	100 (25)	18.32 ± 1.58
C. analis (Lentil)	Lentil	30	53.33 (16)	8.50 ± 1.54
	Mung	29	100 (29)	29.90 ± 1.53
C. analis (Mung)	Lentil	28	21.43 (6)	4.17 ± 1.45
	Mung	27	96.30 (26)	18.35 ± 1.46

Table 2. Percentage host acceptance and mean ± SE number of eggs oviposited by females in the choice experiment. Number of individuals that oviposited eggs is given in parentheses and N is the sample size.

Species and natal host	Experience	N	Focal host	% Acceptance	Mean ± SE no. egg
C. maculatus (Lentil)	Lentil	31	Lentil	32.26 (10)	0.45 ± 0.13
			Mung	100 (31)	19.65 ± 1.77
	Mung	29	Lentil	6.90 (2)	0.07 ± 0.05
			Mung	100 (29)	12.24 ± 0.74
C. maculatus (Mung)	Lentil	29	Lentil	10.35 (3)	0.10 ± 0.06
			Mung	100 (29)	22.69 ± 1.54
	Mung	25	Lentil	8.00 (2)	0.12 ± 0.09
			Mung	100 (25)	12.88 ± 0.75
C. analis (Lentil)	Lentil	30	Lentil	3.33 (1)	0.10 ± 0.10
			Mung	100 (30)	32.27 ± 1.32
	Mung	29	Lentil	0 (0)	0
			Mung	100 (29)	16.34 ± 1.12
C. analis (Mung)	Lentil	28	Lentil	7.14 (2)	0.07 ± 0.05
			Mung	100 (28)	23.68 ± 1.77
	Mung	27	Lentil	3.70 (1)	0.04 ± 0.04
			Mung	100 (27)	18.11 ± 1.00

Table 3. Summary of coefficients and model selection based on AIC for models predicting number of eggs oviposited by bean beetles in no choice experiment with zero-inflated negative-binomial model (ZINB). Only models with the lowest AIC are shown.

Species	Dependent variable	Independent variable	Coefficient value $\pm$ SE	*P*-value
C. maculatus	Egg number	Intercept	2.37 ± 0.105	<0.001
		Focal host (Mung)	0.90 ± 0.125	<0.001
		Natal host (Mung)	-0.37 ± 0.125	0.003
C. analis	Egg number	Intercept	2.09 ± 0.111	<0.001
		Focal host (Mung)	1.32 ± 0.125	<0.001
		Natal host (Mung)	-0.52 ± 0.102	<0.001

Table 4. Percentage and mean ± SE of eggs oviposited on focal hosts (between small seed mung bean and lentil) in relation to female natal host. N = 20 for each natal and focal host combination.

Natal host	Focal host	% Acceptance	Mean ± SE no. egg
C. maculatus (Lentil)	Lentil	45	1.25 ± 0.40
	Mung	100	15.60 ± 1.11
C. maculatus (Mung)	Lentil	30	0.55 ± 0.23
	Mung	100	7.95 ± 0.76
C. analis (Lentil)	Lentil	60	1.50 ± 0.39
	Mung	100	12.00 ± 0.93
C. analis (Mung)	Lentil	15	0.15 ± 0.08
	Mung	100	6.60 ± 0.90

277   Emergence rate was high for all treatments (>88% emergence) regardless of parental or

278   natal host, except for CmM (from mung), which performed very poorly on lentil with only 16%

279   successfully emerging (Table 5). The sex ratio did not differ between cultures, except for CaL

280   and CaM on lentil, which showed significant female (67%) and male (66%) bias, respectively

281   (Table 5).

282

Table 5. The total emergence rate and the emergence rate by sex of *C. maculatus* and *C. analis* offspring from parental and natal hosts (no choice experiment). Number of emerged and un-emerged individuals, and emerged individuals by sex is given in parentheses. *G*-test for deviation from 1:1 sex ratio.

Parental host	Natal host	% Total Emerged		Emerged		G value	*P*-value
		Emerged	Un-emerged	% Female	% Male		
C. maculatus (Lentil)	Lentil	92.06 (58)	7.94 (5)	47.37 (27)	52.63 (30)	0.32	0.574
	Mung	90.32 (56)	9.68 (6)	42.86 (24)	57.14 (32)	2.31	0.126
C. maculatus (Mung)	Lentil	15.52 (9)	84.48 (49)	44.44 (4)	55.56 (5)	0.22	0.636
	Mung	100 (60)	0 (0)	41.67 (25)	58.33 (35)	3.38	0.066
C. analis (Lentil)	Lentil	95.31 (61)	4.69 (3)	67.21 (41)	32.79 (20)	15.39	<0.001
	Mung	96.77 (60)	3.23 (2)	43.33 (26)	56.67 (34)	2.15	0.142
C. analis (Mung)	Lentil	93.48 (43)	6.52 (3)	34.15 (14)	65.85 (27)	8.69	0.003
	Mung	88.33 (53)	11.67 (7)	47.17 (25)	52.83 (28)	0.34	0.560

294 *3.2. Performance*

295   Overall the effect of parental host, natal host and sex was significant for both pronotum

296 width and right elytron length of both species (Table 6). Generally, females were larger than

297 males for both species [*C. maculatus* pronotum width: female 1.31 ± 0.01 mm (n = 80), male

298 1.28 ± 0.008 mm (n = 98); *C. maculatus* right elytron length: female 2.09 ± 0.016 mm (n = 78),

299 male 2.02 ± 0.012 mm (n = 99); *C. analis* pronotum width: female 1.32 ± 0.008 mm (n = 104),

300 male 1.22 ± 0.006 mm (n = 109); *C. analis* right elytron length: female 2.12 ± 0.012 mm (n =

301 104), male 1.94 ± 0.011 mm (n = 108)], and the offspring were larger when the parental host was

302 lentil or natal host was mung bean for *C. analis* (Fig. 1). A significant two-way interaction

303 between parental and natal hosts was detected only on *C. maculatus* (Table 6) where the beetles

304 emerging from mung bean natal hosts were larger, but performance was very poor when beetles

305 came from mung bean parental hosts and had lentil as natal host (Fig. 1).

306

307 **Table 6.** The effect of parental host, natal host and sex on pronotum width and right elytron length of *C.*
308 *maculatus* and *C. analis* offspring analyzed using three-way ANOVA. Only significant terms are
309 reported.

|	Source	F	*P*-value
C. maculatus			
Pronotum width	Parental host	$F_{1,170} = 57.53$	<0.001
	Natal host	$F_{1,170} = 35.86$	<0.001
	Sex	$F_{1,170} = 31.34$	<0.001
	Parental host: Natal host	$F_{1,170} = 32.68$	<0.001
Right elytron length	Parental host	$F_{1,168} = 87.75$	<0.001
	Natal host	$F_{1,168} = 67.52$	<0.001
	Sex	$F_{1,168} = 41.97$	<0.001
	Parental host: Natal host	$F_{1,168} = 58.73$	<0.001
C. analis			
Pronotum width	Parental host	$F_{1,202} = 100.85$	<0.001
	Natal host	$F_{1,202} = 9.80$	0.002
	Sex	$F_{1,202} = 157.52$	<0.001
Right elytron length	Parental host	$F_{1,205} = 92.41$	<0.001
	Natal host	$F_{1,205} = 18.16$	<0.001
	Sex	$F_{1,205} = 219.80$	<0.001

327
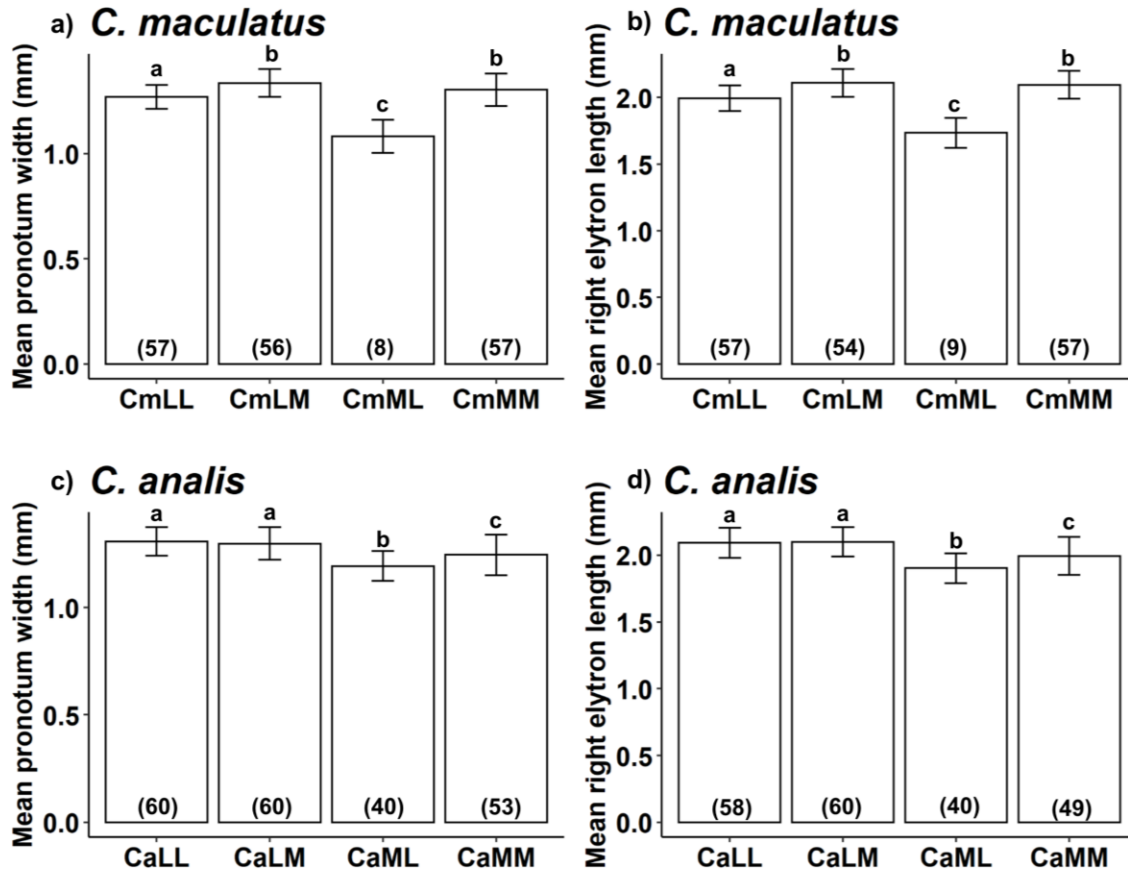
Fig. 1. Mean ± SD of *C. maculatus* a) pronotum width and b) right elytron length. Mean ± SD of *C. analis* c) pronotum width and d) right elytron length. The letters above bar represent significant differences between groups calculated from Tukey's test. The number of individuals in each group is given in parentheses. The first two letters represent species where Cm = *C. maculatus* and Ca = *C. analis*. The third and fourth letters represent parental host and natal host, respectively. L = lentil, M = mung bean.

334

335   Males from lentil were more successful in competition for mates against males from

336   mung bean (Table 7). We hypothesized that size may influence the outcome of mating success

337   where larger males are more likely to outcompete smaller rivals; however, we found a reverse

338   size trend between the two bean beetle species in both sexes. *Callosobruchus maculatus* was

339   larger on mung bean (compared with *C. maculatus* from lentil), whereas *C. analis* was larger on

340   lentil (compared with *C. analis* from mung bean) (Fig. 1; CmLL vs CmMM and CaLL vs

341   CaMM). No significant terms were detected for *C. analis* (lentil: 516.62 ± 18.35 seconds (n =

342   60); mung: 522.61 ± 20.08 seconds (n = 60), Fig. 2). Male *C. maculatus* from lentil had

343   significantly longer mating times than males which emerged from mung bean (lentil: $629.32 \pm$

344   28.78 seconds (n = 60), mung: 522.84 ± 20.86 seconds (n = 60), $F_{1,116} = 10.14$, $P = 0.002$). This

345   was the only significant factor affecting mating time and mating times for lentil reared *C.*

346   *maculatus* were longer than in *C. analis*. Our results also showed that male natal host did not

347   affect male fitness in terms of offspring number in either species (*C. maculatus*: $H_{1,115} = 0.47$, *P*

348    $= 0.495$; *C. analis*: $H_{1,116} = 3.1$, $P = 0.078$), but female natal host (from lentil or mung bean) did

349   significantly affect fecundity (*C. maculatus*: $H_{1,115} = 29.32$, $P < 0.001$; *C. analis*: $H_{1,116} = 21.6$, *P*

350   < 0.001). Females from mung bean had more offspring than females from lentil (*C. maculatus*:

351   lentil: 44.37 ± 4.31 (n = 60), mung: 77.59 ± 2.97 (n = 59), Wilcoxon rank sum test: W = 751.5,

352    $n_1 = 60$, $n_2 = 59$, $P < 0.001$; *C. analis*: lentil: 59.62 ± 4.96 (n = 60), mung: 92.40 ± 1.89 (n = 60),

353   Wilcoxon rank sum test: W = 914.5, $n_1 = 60$, $n_2 = 60$, $P < 0.001$).

354   **Table 7.** Percentage of male bean beetles from different hosts succeeding in mating with female bean
355   beetles from different hosts. The expected mating success is 1:1 and deviation from expected is shown.
356   Number of trials is given in parentheses.

357

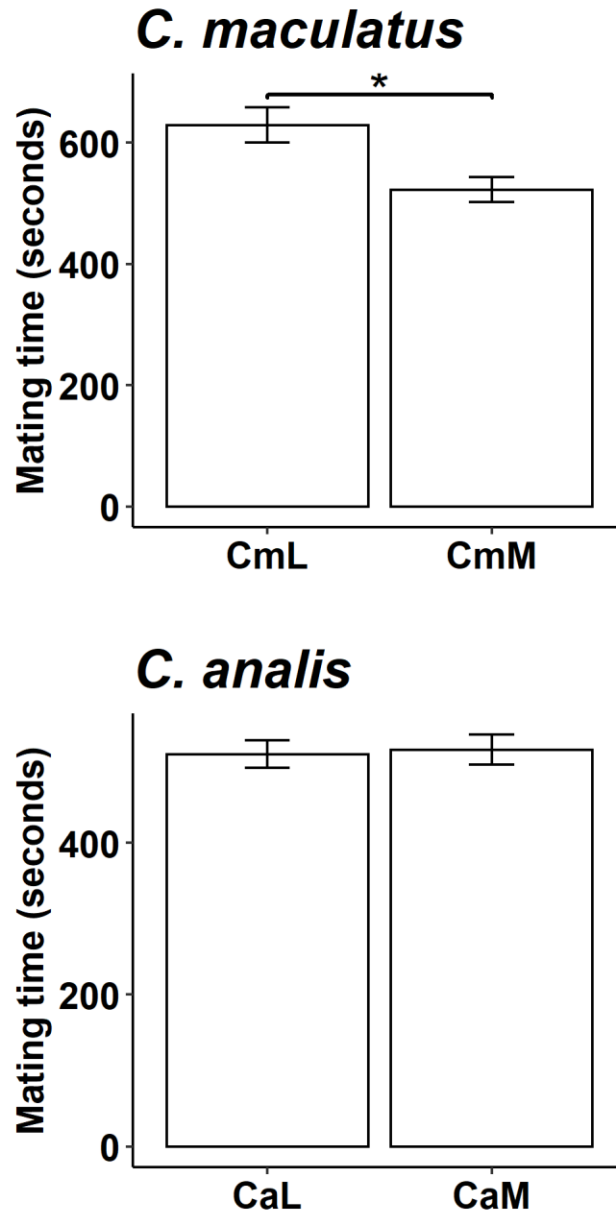| Female and natal host	Percentage of male mating success		G value	P-value
	Males from lentil	Males from mung		
C. maculatus (Lentil)	77.78 (21)	22.22 (6)	19.93	<0.001
C. maculatus (Mung)	48.15 (13)	51.85 (14)	0.074	0.785
C. analis (Lentil)	72.72 (24)	27.28 (9)	15.28	<0.001
C. analis (Mung)	76.67 (23)	23.33 (7)	20.08	<0.001

362

C. maculatus

C. analis

363

Fig. 2. Mean ± SE mating time in seconds of males of *C. maculatus* (above) and *C. analis* (below) that
emerged from the two different hosts (mung and lentil). *Callosobruchus maculatus* reared on mung
(CmM), *C. maculatus* reared on lentil (CmL), *C. analis* reared on mung (CaM) and *C. analis* reared on
lentil (CaL).

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370

371 *3.3. Development and starvation resistance time*

372   *Callosobruchus maculatus* with mung bean parental hosts had a longer development time

373 than beetles with lentil parental hosts, and they showed a greater difference between different

374 natal hosts (Table 8, 9). Beetles from lentil natal hosts had a longer development time, compared

375 with those from mung natal hosts. We found similar results for *C. analis* development time

376 (Table 8, 9), as having mung bean as a parental host caused longer development times, but

377 having mung bean as a natal host decreased development time. Male beetles developed more

378 quickly than females. An interaction between parental and natal host was detected and suggests

379 that *C. analis* with mung bean as parental host and lentil as natal host had the longest

380 development time (Table 9).

381

Table 8. Summary of coefficients and model selection based on AIC for models predicting development and survival time with accelerated failure time models (AFT). Only models with the lowest AIC are shown. The significant terms are designated in bold. PtHost = Parental host, NtHost = Natal host, (M) = Mung bean.

Species	Dependent variable	Independent variable	Coefficient value ± SE	P-value	Model distribution
C. maculatus	Development time	Intercept	3.35 ± 0.008	<0.001	Lognormal distribution
		PtHost(M)	**0.02 ± 0.01**	**0.018**	
		NtHost(M)	**-0.03 ± 0.01**	**0.013**	
		Sex(Male)	-0.01 ± 0.008	0.102	
C. analis	Development time	Intercept	3.35 ± 0.005	<0.001	Loglogistic distribution
		PtHost(M)	**0.05 ± 0.009**	**<0.001**	
		NtHost(M)	**-0.02 ± 0.008**	**0.004**	
		Sex(Male)	**-0.02 ± 0.006**	**<0.001**	
		PtHost(M): NtHost(M)	**-0.06 ± 0.012**	**<0.001**	
C. analis	Survival time	Intercept	45.03 ± 1.20	<0.001	Gaussian distribution
		PtHost(M)	**3.68 ± 1.76**	**0.037**	
		NtHost(M)	0.72 ± 1.83	0.693	
		Sex(Male)	-1.59 ± 1.73	0.359	
		PtHost(M): NtHost(M)	**-7.97 ± 2.35**	**<0.001**	
		NtHost(M): Sex(Male)	**-5.77 ± 2.33**	**0.013**	

388 **Table 9.** Mean ± SE development and survival time of *C. maculatus* and *C. analis* offspring in relation to
389 their parental and natal hosts. The number of individuals is given in parentheses.

390

Parental host	Natal host	Development time (days)	Survival time (days)
C. maculatus (Lentil)	Lentil	28.30 ± 0.201 (56)	37.70 ± 1.170 (56)
	Mung	27.60 ± 0.174 (56)	37.30 ± 1.100 (56)
C. maculatus (Mung)	Lentil	54.70 ± 2.590 (9)	37.80 ± 2.540 (9)
	Mung	29.40 ± 0.439 (58)	39.40 ± 1.310 (58)
C. analis (Lentil)	Lentil	28.40 ± 0.130 (60)	44.50 ± 1.010 (61)
	Mung	27.60 ± 0.153 (58)	41.60 ± 1.170 (60)
C. analis (Mung)	Lentil	29.50 ± 0.196 (31)	47.70 ± 1.110 (41)
	Mung	27.60 ± 0.246 (52)	37.60 ± 1.420 (53)

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395

396   We found no significant terms in the *C. maculatus* survival time model. For *C. analis*,

397   having mung bean as parental host led to a longer lifespan (Table 8, 9). The interaction between

398   parental and natal host was significant (Table 8). Having lentil as the parental host resulted in

399   similar survival times regardless of natal host (Table 9). The interaction between natal host and

400   beetle sex suggests that male *C. analis* with mung bean as both parental and natal host had the

401   shortest lifespans (Table 9, 10).

402   **Table 10.** Mean ± SE survival time of *C. analis* grouped by sex in relation to their natal host. The number
403   of individuals is given in parentheses.

404

Natal host	Sex	Survival time (days)
C. analis (Lentil)	Female	46.00 ± 1.12 (55)
	Male	45.60 ± 1.02 (47)
C. analis (Mung)	Female	43.60 ± 1.39 (51)
	Male	36.50 ± 1.09 (62)

407

4. Discussion

We examined the effects of parental host, natal host and oviposition experience on the fitness parameters of two related, economically significant stored product pests, *C. maculatus* and *C. analis*. Parental and natal host greatly affected life history traits (fecundity, host acceptance, emergence rate, development time, survival time, size, sex ratio, mating competition and mating time), and responses differed between the beetle species.

We found no effects of natal host and oviposition experience on overall ovipostion preference, with both preferring mung bean, but oviposition experience with lentil did increase the chance of acceptance of lentil for future oviposition. Females of both species emerging from lentil laid more eggs when the better host (mung bean) was provided. However, host switching by *C. maculatus* from better (mung bean) to poor (lentil) quality hosts had a negative effect on fitness (emergence rate, development time and size). Females were larger than males, and the effect of parental and natal hosts affected offspring size. In *C. analis*, both parental and natal host influenced observed offspring sex ratios, which were male skewed when the parental host was mung and natal host was lentil, but female skewed when the parental host was lentil and the natal host was lentil. No other combinations deviated from expected. Males from lentil tended to outcompete males from mung bean in mating competition, with the exception of male *C. maculatus* emerging from lentil which spent longer mating than males emerging from mung bean, and female *C. maculatus* emerging from mung bean showed no preference between males emerging from mung or lentil. No effect of natal host was found on male fitness, but was observed in female fecundity instead. Parental and natal host influenced development time and

429   survival time. Generally, having mung bean as parental host resulted in increased development

430   time while mung bean as natal host decreased development time of both beetle species.

431   Previous work has considered ovipositional experience of *C. maculatus*, but the study did

432   not include the effects of natal host (Chiu and Messina, 1994). In no choice and choice

433   experiments both beetle species, regardless of their natal hosts, clearly preferred to oviposit more

434   eggs (in terms of focal host) on mung bean over lentil. Previous studies have suggested that *C.*

435   *maculatus* preferred larger beans within (Cope and Fox, 2003; Yang et al., 2006) and between

436   species (Paukku and Kotiaho, 2008). However, we found that both beetle species preferred

437   ovipositing on smaller sized mung beans compared with lentils (which were larger in size

438   compared to the small seed mung). Seed size is not the only factor determining bean beetle

439   oviposition preference, which is also affected by chemical signals (Pouzat, 1981), smoothness

440   (Sulehrie et al., 2003), curvature of seeds (Gokhale et al., 1990) and the presence of other eggs

441   (Otake and Dobata, 2018). Our results suggest oviposition preference in bean beetles is not

442   transgenerational as host quality comes before host quantity.

443   Lentil is considered to be an inferior host to mung bean (Messina et al., 2009). In terms of

444   natal host, both beetle species emerging from lentil laid more eggs than those emerging from

445   mung bean when a better host (mung bean) was provided. This result is consistent with a

446   previous study showing that *C. maculatus* fecundity was enhanced when reared on lentil

447   (Messina and Jones, 2009). Poor early life nutrition can lead to the thrifty phenotype (Hales and

448   Barker, 2001), the characteristic which helps organisms to perform best under poor resource

449   conditions by promoting fat storage and high glucose blood levels. This may lead to the

450   accumulation of lipid storage in insects (Barrett et al., 2009; Jehrke et al., 2018) which is

451   important in programmed cell death of fat cells contributing to ovary maturation and fecundity

452   (Aguila et al., 2013). This may explain why beetles from lentil had higher fecundity.

453   Responses differed between species when they switched to a poorer natal host (lentil);

454   while *C. maculatus* suffered from switching to the inferior host in terms of emerging adults, *C.*

455   *analis* had no such response. This result is consistent with survival time results in this study, as

456   *C. analis* survived for longer compared with *C. maculatus* with lentil as a natal host. In addition,

457   the performance of *C. maculatus* offspring was also affected when the parental host was mung

458   bean and natal host was lentil (Fig. 1). The poor performance seen in *C. maculatus* resulting

459   from switching to the inferior host (lentil) may be linked to reduced expression of genes which

460   help detoxify plant secondary metabolites (Rêgo et al., 2020).

461   In both beetle species, having lentil as the parental host resulted in larger offspring.

462   Again, mothers already adapted to a poor quality host may invest more in fewer offspring,

463   resulting in offspring more tolerant to poor quality hosts (Amarillo-Suárez and Fox, 2006),

464   improving offspring fitness. In terms of natal host, mung bean is a better-quality host as emerged

465   adults were larger than those from lentil. Overall, females were larger than males, following the

466   general trend in insects (Stillwell et al., 2010; Teder, 2014).

467   In the absence of local mate competition and haplodiploidy, a 1:1 female: male sex ratio

468   is favoured through natural selection (Trivers and Willard, 1973; King, 1987) We found a

469   deviation in sex ratio from 1:1 only in *C. analis* when the natal host was lentil. Differences in

470   parental host yielded different sex biases; where the parental host was lentil, the offspring had a

471   female bias, while where mung bean was the parental host we saw a male bias. There is no

472   evidence that bruchid bean beetles can directly control their offspring sex ratio, but deviations

473 from a 1:1 ratio can occur through intraspecific competition and differential mortality between

474 sexes (Cipollini, 1991; Ishihara and Shimada, 1993; Reece et al., 2005).

475   This study found males that emerged from lentil were generally more successful in

476 gaining matings than those from mung bean regardless of species. Even though larger males tend

477 to achieve more mating success by outcompeting other male competitors during direct conflict

478 (Andersson, 1994), smaller males can gain more mating success through better mobility when

479 acquiring females (Mclachlan and Allen, 1987) or better morphological compatability during

480 mating (Weissman et al., 2008). A similar study system found that larger male S*itophilus oryzae*

481 are preferred by females, demonstrated by reduced pairing time and increased mating time

482 (Holloway and Smith, 1987). Higher mating success in larger male bean beetles can be explained

483 only in the case of *C. analis* where males from lentil were also larger, but not for *C. maculatus*

484 where males from mung bean were larger. Thus, in this study size may not fully explain the

485 outcome of male-male competition. In this study, *C. maculatus* from mung bean seemed to be

486 less active than those from lentil (pers. obs.) which provided an opportunity for the smaller males

487 to mate.

488   Nutritional quality may influence male fitness in terms of number of offspring as shown

489 in studies in other insects (Fricke et al., 2008; Morimoto and Wigby, 2016). In this study we

490 found no difference in the number of offspring sired by the two male bean beetle species which

491 emerged from different hosts. Male size is not likely to be a good proxy for male fitness (Savalli

492 and Fox, 1999). *Callosobruchus maculatus* males that previously mated still provide many more

493 sperm than females need (Eady, 1995). Hence, it seems that host quality could not account for a

494 difference in offspring number among treatments as in this study we used unmated males.

495   Egg size varies both within and among females of *C. maculatus*, and individuals from

496   larger eggs develop faster and emerge as larger adults (Fox, 1994). Developmental times were

497   also found to be influenced by host; where mung bean was a parental host development rate was

498   slower (whereas lentil as a parental host reduced development time) in both species. The effect

499   of maternal rearing host on offspring is still unclear (Amarillo-Suárez and Fox, 2006); therefore,

500   we remain cautious about the interpretation of the interactions between parental host and natal

501   host on development time in this study. In contrast, both *Callosobruchus* species that developed

502   in mung bean as a natal host had reduced development times. Mothers who are pre-adapted to

503   poor food quality may change resource allocation to eggs resulting in offspring better able to

504   tolerate poor quality food (Amarillo-Suárez and Fox, 2006). Thus, when offspring are reared on

505   better quality food, they might in turn perform better. Interestingly, in *C. analis* whose parental

506   host was mung bean and natal host was lentil showed the longest development time compared to

507   other groups. This is similar to the reduction in performance seen in *C. maculatus*'s offspring

508   when switching to the inferior quality host. This was not found in *C. analis*, but their increase

509   change in development time suggests host quality also affects this species.

510   Studying adult lifespan is more complicated than we expected. We found no significant

511   terms in the *C. maculatus* survival time model. While *C. maculatus* development time and

512   emergence rates were affected by switching to lentil, host quality did not affect *C. maculatus*

513   lifespan. In contrast, we found a significant effect of parental host on adult longevity for *C.*

514   *analis*. Fox et al. (2004) also failed to detect the effect of rearing hosts on *C. maculatus* lifespan,

515   which may be due to the use of two closely related hosts (*Vigna radiata* and *V. unguiculata*).

516   Finding an interaction effect of parental and natal hosts on *C. analis* survival time was

517   unexpected. Male *C. analis* with mung bean as both parental and natal hosts had a more reduced

518   lifespan than females and males from other treatments, but why this is so is not known.

519   Overall, our results indicate that differences in larval seed host can greatly influence the

520   fitness and life histories of bean beetles, but responses differ between species, making it difficult

521   to draw generalities (Srisakrapikoop et al., 2021). Bean beetles preferred high quality over poor

522   quality hosts, and this has profound effects both directly (natal host) and indirectly (parental

523   host) on their behavior and fitness. Switching from poor to high quality hosts generally improves

524   offspring performance but when switching from high to poor quality hosts, effects are species

525   dependent. Our study provides insights into how host quality can affect offspring performance.

526   Understanding how these pests may respond and adapt to the introduction of novel hosts

527   provides us with a better understanding of both the fundamental biology of the system, and also

528   how this knowledge can be applied to fundamental challenges in pest management.

529   **CRediT authorship contribution statement**

530   **Ussawit Srisakrapikoop**: Methodology, Investigation, Validation, Formal analysis, Writing –

531   original draft. **Tara J. Pirie:** Resources, Writing – review & editing. **Graham J. Holloway:**

532   Resources, Writing – review & editing. **Mark D.E. Fellowes:** Conceptualization, Methodology,

533   Supervision, Writing – review & editing.

534   **Declaration of competing interest**

535   The authors declare that they have no known competing financial interests or personal

536   relationships that could have appeared to influence the work reported in this paper.

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