

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

4 Ussawit Srisakrapikoop^{a,*}, Tara J. Pirie^a, Graham J. Holloway^b,

5 Mark D.E. Fellowes^a

6 ^a*People and Wildlife Research Group, School of Biological Sciences, University of*
7 *Reading, Whiteknights, Reading, Berkshire RG6 6AJ, UK*

8 ^b*Centre for Wildlife Assessment and Conservation, School of Biological Sciences,*
9 *University of Reading, Whiteknights, Reading, Berkshire RG6 6AJ, UK*

10
11
12 * Corresponding author. People and Wildlife Research Group, School of
13 Biological Sciences, University of Reading, Whiteknights, Reading, Berkshire
14 RG6 6AJ, UK; E-mail address: ussawit28@gmail.com

15 **ABSTRACT**

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

38 Keyword: Bean beetle, Host quality, Maternal effects, Mating competition, Oviposition
39 experience, Transgenerational effects

40 **1. Introduction**

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

47 Both species lay eggs on the surface of a bean; after the eggs hatch the larvae bore into
48 the bean where they develop and pupate (Giga and Smith, 1991). Thus, the whole immature
49 development takes place inside an individual bean seed (Giga and Smith, 1991; Tuda et al.,
50 2005). The adult beetles emerge from the host and require no food or water to complete their life
51 cycle (although providing nutrients can influence longevity and fecundity; Moller et al., 1989;
52 Srisakrapikoop et al., unpublished data), so adult traits are influenced by the natal host (Beck and
53 Blumer, 2014). Seed resources are limited, and therefore host species (and hence female choice)
54 affects offspring traits, such as development time, larval mortality, emergence mass, size (e.g.
55 pronotum width or elytral length), rate of adult emergence, adult longevity, and fecundity
56 (Timms, 1998; Paukku and Kotiaho, 2008; Mainali et al., 2015; Hosamani et al., 2018; Messina
57 et al., 2018).

58 Oviposition choice can be influenced by olfactory (Ajayi et al., 2015) and chemical cues
59 emanating from hosts (volatile and surface chemicals) (Giga and Smith, 1985; Gokhale et al.,
60 1990), the curvature of host seeds (Gokhale et al., 1990), seed size (Cope and Fox, 2003),
61 vibration from larvae already inside the seeds (Guedes and Yack, 2016) and chemical markers
62 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 $28 \pm 2^\circ\text{C}$ 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.

114 *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.

120 *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 [$4.38 \pm$
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

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

229

| 230 | Species and natal host | Focal host | N | % Acceptance | Mean \pm SE no. egg |
|-----|------------------------------|------------|----|--------------|-----------------------|
| 231 | <i>C. maculatus</i> (Lentil) | Lentil | 31 | 87.10 (27) | 10.89 \pm 1.62 |
| 232 | | Mung | 29 | 100 (29) | 25.90 \pm 1.20 |
| 233 | <i>C. maculatus</i> (Mung) | Lentil | 29 | 51.72 (15) | 7.33 \pm 2.00 |
| 234 | | Mung | 25 | 100 (25) | 18.32 \pm 1.58 |
| 235 | <i>C. analis</i> (Lentil) | Lentil | 30 | 53.33 (16) | 8.50 \pm 1.54 |
| 236 | | Mung | 29 | 100 (29) | 29.90 \pm 1.53 |
| | <i>C. analis</i> (Mung) | Lentil | 28 | 21.43 (6) | 4.17 \pm 1.45 |
| | | Mung | 27 | 96.30 (26) | 18.35 \pm 1.46 |

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

239

| 240 | Species and natal host | Experience | N | Focal host | % Acceptance | Mean \pm SE no. egg |
|-----|---------------------------------|------------|--------|------------|------------------|-----------------------|
| 241 | <i>C. maculatus</i> (Lentil) | Lentil | 31 | Lentil | 32.26 (10) | 0.45 \pm 0.13 |
| 242 | | | | Mung | 100 (31) | 19.65 \pm 1.77 |
| 243 | <i>C. maculatus</i> (Mung) | Mung | 29 | Lentil | 6.90 (2) | 0.07 \pm 0.05 |
| 244 | | | | Mung | 100 (29) | 12.24 \pm 0.74 |
| 245 | | Lentil | 29 | Lentil | 10.35 (3) | 0.10 \pm 0.06 |
| 246 | | | | Mung | 100 (29) | 22.69 \pm 1.54 |
| 247 | <i>C. analis</i> (Lentil) | Mung | 25 | Lentil | 8.00 (2) | 0.12 \pm 0.09 |
| 248 | | | | Mung | 100 (25) | 12.88 \pm 0.75 |
| 249 | <i>C. analis</i> (Mung) | Lentil | 30 | Lentil | 3.33 (1) | 0.10 \pm 0.10 |
| 250 | | | | Mung | 100 (30) | 32.27 \pm 1.32 |
| 251 | <i>C. analis</i> (Mung) | Mung | 29 | Lentil | 0 (0) | 0 |
| 252 | | | | Mung | 100 (29) | 16.34 \pm 1.12 |
| | | Lentil | 28 | Lentil | 7.14 (2) | 0.07 \pm 0.05 |
| | | | | Mung | 100 (28) | 23.68 \pm 1.77 |
| | Mung | 27 | Lentil | 3.70 (1) | 0.04 \pm 0.04 | |
| | | | Mung | 100 (27) | 18.11 \pm 1.00 | |

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

256

| Species | Dependent variable | Independent variable | Coefficient value ± SE | P-value |
|---------------------|--------------------|----------------------|---------------------------|---------|
| <i>C. maculatus</i> | 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 |
| <i>C. analis</i> | 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 |

264

265

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

268

| | Natal host | Focal host | % Acceptance | Mean \pm SE no. egg |
|-----|------------------------------|------------|--------------|-----------------------|
| 269 | <i>C. maculatus</i> (Lentil) | Lentil | 45 | 1.25 \pm 0.40 |
| 270 | | Mung | 100 | 15.60 \pm 1.11 |
| 271 | <i>C. maculatus</i> (Mung) | Lentil | 30 | 0.55 \pm 0.23 |
| 272 | | Mung | 100 | 7.95 \pm 0.76 |
| 273 | <i>C. analis</i> (Lentil) | Lentil | 60 | 1.50 \pm 0.39 |
| 274 | | Mung | 100 | 12.00 \pm 0.93 |
| 275 | <i>C. analis</i> (Mung) | Lentil | 15 | 0.15 \pm 0.08 |
| 276 | | Mung | 100 | 6.60 \pm 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

283 **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
 284 experiment). Number of emerged and un-emerged individuals, and emerged individuals by sex is given in parentheses. *G*-test for deviation from
 285 1:1 sex ratio.

286

| Parental host | Natal host | % Total Emerged | | Emerged | | G value | P-value |
|------------------------------|------------|-----------------|------------|------------|------------|---------|---------|
| | | Emerged | Un-emerged | % Female | % Male | | |
| <i>C. maculatus</i> (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 |
| <i>C. maculatus</i> (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 |
| <i>C. analis</i> (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 |
| <i>C. analis</i> (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 |

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294 3.2. Performance

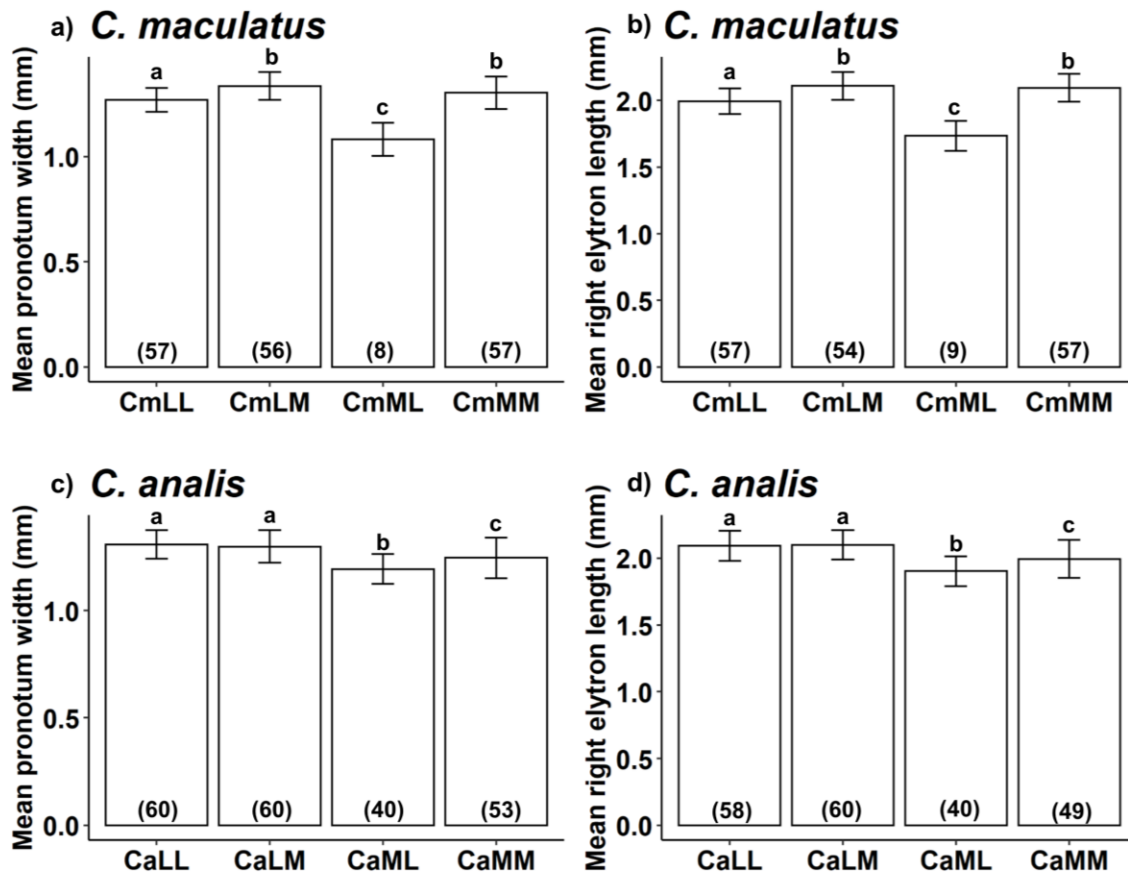
295 Overall the effect of parental host, natal host and sex was significant for both pronotum
296 width and right elytron length of both species (Table 6). Generally, females were larger than
297 males for both species [*C. maculatus* pronotum width: female 1.31 ± 0.01 mm (n = 80), male
298 1.28 ± 0.008 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 | |
|---------------------|-------------------------|------------------------------|----------------------|--------|
| <i>C. maculatus</i> | | | | |
| 311 312 313 | 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 |
| 314 315 316 | 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 |
| <i>C. analis</i> | | | | |
| 318 319 | 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 |
| 320 321 | 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 |

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

334

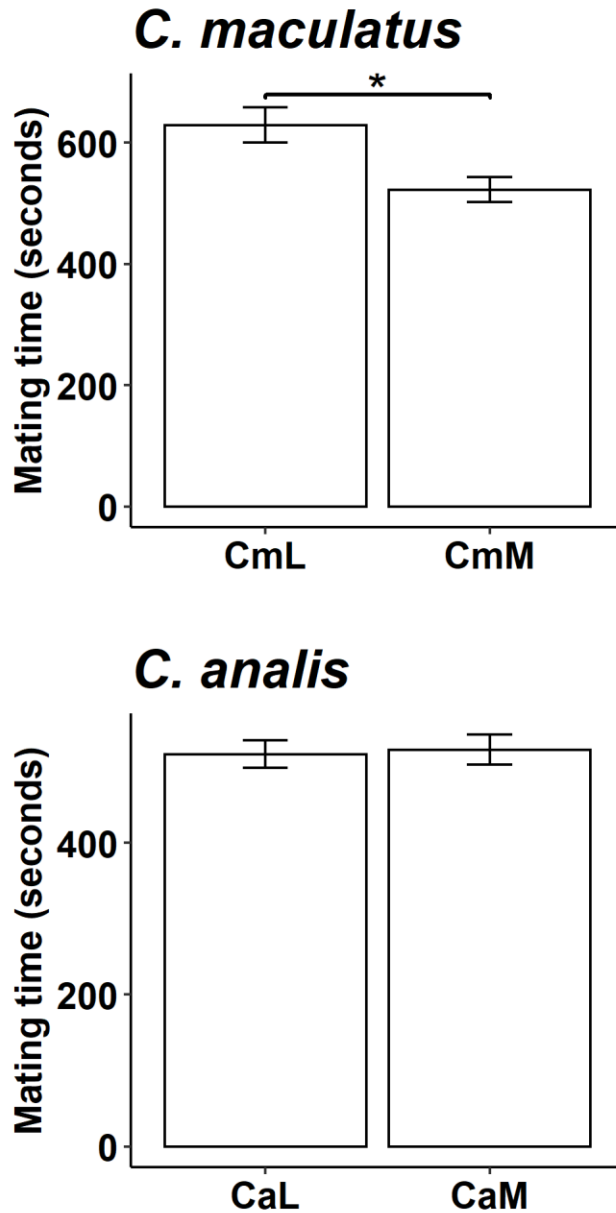
335 Males from lentil were more successful in competition for mates against males from
336 mung bean (Table 7). We hypothesized that size may influence the outcome of mating success
337 where larger males are more likely to outcompete smaller rivals; however, we found a reverse
338 size trend between 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

| 358 | Female and natal host | Percentage of male mating success | | <i>G</i> value | <i>P</i> -value |
|-----|------------------------------|-----------------------------------|-----------------|----------------|-----------------|
| | | Males from lentil | Males from mung | | |
| 359 | <i>C. maculatus</i> (Lentil) | 77.78 (21) | 22.22 (6) | 19.93 | <0.001 |
| 360 | <i>C. maculatus</i> (Mung) | 48.15 (13) | 51.85 (14) | 0.074 | 0.785 |
| 361 | <i>C. analis</i> (Lentil) | 72.72 (24) | 27.28 (9) | 15.28 | <0.001 |
| | <i>C. analis</i> (Mung) | 76.67 (23) | 23.33 (7) | 20.08 | <0.001 |

362



363

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

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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

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

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

386

387

388 **Table 9.** Mean \pm 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) |
|------------------------------|------------|----------------------------|-------------------------|
| <i>C. maculatus</i> (Lentil) | Lentil | 28.30 \pm 0.201 (56) | 37.70 \pm 1.170 (56) |
| | Mung | 27.60 \pm 0.174 (56) | 37.30 \pm 1.100 (56) |
| <i>C. maculatus</i> (Mung) | Lentil | 54.70 \pm 2.590 (9) | 37.80 \pm 2.540 (9) |
| | Mung | 29.40 \pm 0.439 (58) | 39.40 \pm 1.310 (58) |
| <i>C. analis</i> (Lentil) | Lentil | 28.40 \pm 0.130 (60) | 44.50 \pm 1.010 (61) |
| | Mung | 27.60 \pm 0.153 (58) | 41.60 \pm 1.170 (60) |
| <i>C. analis</i> (Mung) | Lentil | 29.50 \pm 0.196 (31) | 47.70 \pm 1.110 (41) |
| | Mung | 27.60 \pm 0.246 (52) | 37.60 \pm 1.420 (53) |

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 \pm 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) |
|---------------------------|--------|-----------------------|
| <i>C. analis</i> (Lentil) | Female | 46.00 \pm 1.12 (55) |
| | Male | 45.60 \pm 1.02 (47) |
| <i>C. analis</i> (Mung) | Female | 43.60 \pm 1.39 (51) |
| | Male | 36.50 \pm 1.09 (62) |

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407

408 **4. Discussion**

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

414 We found no effects of natal host and oviposition experience on overall oviposition
415 preference, with both preferring mung bean, but oviposition experience with lentil did increase
416 the chance of acceptance of lentil for future oviposition. Females of both species emerging from
417 lentil laid more eggs when the better host (mung bean) was provided. However, host switching
418 by *C. maculatus* from better (mung bean) to poor (lentil) quality hosts had a negative effect on
419 fitness (emergence rate, development time and size). Females were larger than males, and the
420 effect of parental and natal hosts affected offspring size. In *C. analis*, both parental and natal host
421 influenced observed offspring sex ratios, which were male skewed when the parental host was
422 mung and natal host was lentil, but female skewed when the parental host was lentil and the natal
423 host was lentil. No other combinations deviated from expected. Males from lentil tended to
424 outcompete males from mung bean in mating competition, with the exception of male *C.*
425 *maculatus* emerging from lentil which spent longer mating than males emerging from mung
426 bean, and female *C. maculatus* emerging from mung bean showed no preference between males
427 emerging from mung or lentil. No effect of natal host was found on male fitness, but was
428 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 compatibility during
480 mating (Weissman et al., 2008). A similar study system found that larger male *Sitophilus 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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