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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.

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

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 responsive to these cues, affecting host preference (Messina, 2004; Messina et al., 2018). Most studies show that females preferred their natal host when given a choice (Messina and Slade, 1997; Boeke et al., 2004; Paukku and Kotiaho, 2008; Rova and Björklund, 2011; Bergeron et al., 2019), suggesting a learned response, but some studies did not find a preference (Mainali et al., 2015; Bergeron et al., 2019). Therefore while many studies have demonstrated the capability of herbivorous insects to learn during oviposition (Jones and Agrawal, 2017), the existence of such a learned response in *Callosobruchus* is uncertain.

While studies generally focus on female fitness traits (typically measured as fecundity, as this links directly to pest status), little is known as to how host quality may affect male traits. Most bean beetle species show sexual size dimorphism, with females being larger than males (Guntrip et al., 1997; Savalli and Fox, 1999). In terms of male mate choice, male *C. maculatus* show no preference between females differing in size (Holme, 2019; Kirschke et al., 2019), but when two males compete for mating, larger males have an advantage (Savalli and Fox, 1998). However, it is not clear if natal host, by affecting the traits of emerging adults, also affects mate choice in *Callosobruchus*.

Studies have shown the existence of transgenerational effects in some insect taxa. These effects can affect offspring performance (Mbande et al., 2020; Tougeron et al., 2020), change offspring predator avoidance behavior (Keiser and Mondor, 2013), and alter resistance to pathogens and pesticides (Brevik et al., 2018; Schulz et al., 2019). For herbivorous insects transgenerational effects can be induced by variation in host plant quality (Mousseau and Fox, 1998). Although transgenerational effects are transmitted from the parental generation, where the environment experienced by the mother can influence offspring life histories, the environment is usually dynamic and the environment for the parental generation can change and consequently differ for the offspring generation. Therefore, the environment directly experienced by the offspring may be more important in determining their fitness.

Callosobruchus maculatus and *C. analis* both attack a range of legume hosts, and show notable differences in competitive behavior, in particular showing scramble (*C. maculatus*) and contest (*C. analis*) forms of competition (Giga and Smith, 1983), where with the former multiple adults emerge from a bean (but each is smaller) and with the latter form only one adult emerges from a bean (Toquenaga and Fujii, 1991). This difference in behavior may have profound effects on weevil life histories, causing different species to react differently on the same host. They therefore provide useful model systems to explore the effects of different stored products on the fitness of their most economically important insect pests.

In this laboratory study we ask: 1) if host preference shows evidence of transgenerational or maternal effects (parental host effects), and if these can be modified by experience (learning; natal host effects); 2) if performance is influenced by parental (transgenerational effects) and/or natal (current environment) hosts; and 3) if these effects are consistent across pest species with differing life histories.

2. Materials and methods

Callosobruchus maculatus and *C. analis* were cultured separately on either mung beans or lentils in a culture room at 28 ± 2°C with 40% relative humidity and constant light (termed culture room). This produced four cultures of the beetle; *C. maculatus* reared on mung (CmM), *C. maculatus* reared on lentil (CmL), *C. analis* reared on mung (CaM) and *C. analis* reared on lentil (CaL). CmM, CmL, CaM and CaL have been cultured on their hosts since 2010, 2016, 2011 and 2013, respectively. Twenty mated females of each species from each culture were placed together in a 90 mm Petri dish containing a single layer of the same bean from which they had emerged. They were left for two hours to lay eggs in the culture room to produce beans harboring a single egg. Each mung bean and lentil harboring a single egg was then selected and stored in a perforated Eppendorf tube before the beetles hatched. All subsequent experiments used only the beetles emerging from the beans harboring a single egg to exclude the confounding effect of larval competition.

2.1. Oviposition experience experiments

After beetles emerged from the seeds, any remaining seeds were discarded. Each beetle was sexed and a single male and female from the same culture were then placed in a 1 ml perforated Eppendorf tube for 48 hours to mate before experiments. All the following experiments were conducted in a controlled environment (CE) room at 28°C with 60% relative humidity.

2.1.1. No choice experiment (first oviposition, naïve)

A single mated female was put into a Petri dish containing 50 evenly dispersed seeds of either mung bean or lentil (termed the focal hosts). This was replicated with 32 females from each of the four cultures for both of the focal hosts, producing eight treatments in total. The beetles were left in the dark (mimicking storage conditions) to oviposit eggs for six hours (a time frame found to be suitable through personal observation). The number of eggs laid on each bean was then counted to determine host acceptance rate, and emergence rate was recorded three weeks after oviposition to allow all adults to emerge. This experiment also created an oviposition experience for the females on the given focal host (i.e., same or different to their natal host). Each female was kept individually in a perforated Eppendorf in the CE room before being used in the choice experiment 24 hours later.

2.1.2. Choice experiment (second oviposition, experienced)

Each female used in the no choice experiment was put into individual Petri dishes containing 100 evenly dispersed seeds (50 mung beans and 50 lentils; focal host) and allowed to oviposit for a further six hours in the dark. The number of eggs laid on each bean was then counted. Host acceptance rate and emergence rate were recorded as previously described.

2.1.3. Oviposition preference: quality or quantity?

Previous studies showed that *C. maculatus* oviposits more eggs on larger seeds (Cope and Fox, 2003; Yang et al., 2006; Paukku and Kotiaho, 2008); therefore, we performed a second choice experiment with 30 different mated females from each of the four cultures, under the same conditions as previously described. This time the females were offered fifteen small seed mung beans and fifteen lentils and allowed to oviposit for two hours. The number of eggs laid on each host were counted. Thirty randomly selected seeds of lentil and small seed mung bean were measured under a high-performance stereomicroscope (Leica MZ9.5), and a significant difference in size between lentil [5.18 ± 0.06 mm (n = 30)] and small seed mung bean [4.38 ± 0.06 mm (n = 30)] was confirmed (Wilcoxon rank sum test: W = 879.5, $n_1 = 30$, $n_2 = 30$, $P < 0.001$).

2.2. Development and survival time

Each bean from the no choice experiment harboring a single egg (eight groups [CmLL, CmLM, CmML, CmMM, CaLL, CaLM, CaML and CaMM]. 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.) was transferred into a 1 ml perforated Eppendorf tube with a unique code. These beans were kept in the CE room and were checked once a day, starting three weeks after oviposition, to record emergence date from which development time was calculated. The emerged beetles were kept in the 1 ml perforated Eppendorf tubes without resources and moved into a laboratory at room temperature where they were checked every twelve hours until death, to calculate adult survival time.

2.3. Performance

2.3.1. Size and sex of offspring from no choice experiment

Dead beetles from the survival experiment were sexed and the pronotum width and right elytron length were measured under a high-performance stereomicroscope (Leica MZ9.5).

2.3.2. Male-male competition

Two 24-hour old unmated males of the same species but emerging from different hosts (e.g., CmM vs CmL and CaM vs CaL), were placed in a 1 ml perforated Eppendorf tube at room temperature which contained a single 24-hour old unmated female that emerged from either a mung bean or lentil. Males were marked with a permanent marker to distinguish host origin. The two males were put into the Eppendorf tube at the same time to reduce bias. The beetles were continually observed until a successful mating occurred. The host origin of the successful male was recorded.

2.3.3. Copulation time and male fitness

Twenty-four-hour old bean beetles were used in this experiment. An unmated female from each of the four cultures was mated with an unmated male that had emerged from the same or a different host (8 groups in total) in a perforated Eppendorf tube at room temperature. Copulation time is defined here as the time since the male beetle started palpating the female until the time they separated. After copulation, each female was put in a 90 mm Petri dish containing a single layer of the same host bean that she had emerged from and was allowed to oviposit in the dark CE room at 28°C 60% relative humidity until she died. Forty-five days after the copulation, the Petri dishes were put in a freezer to prevent a new generation of beetles emerging. The number of bean beetles (less one; the original female) in each Petri dish was counted.

2.4. Statistical analysis

2.4.1. Oviposition experience, development and survival time

All analyses were performed using R 4.0.4 (R Core Team, 2021). Host acceptance rate and mean number of eggs oviposited on each host were calculated for no-choice and choice experiments. Emergence rate obtained from beans in no-choice experiment was calculated as well as sex ratio which was analyzed using *G*-tests with expected 1:1 sex ratio.

The number of eggs oviposited in the no-choice experiment for each species was modelled with zero-inflated negative-binomial model (ZINB) using *pscl* package (Zeileis et al., 2008) with natal and focal hosts as independent variables. Models were generated from a global model from dredge function in *MuMIn* package (Barton, 2019). Development and survival time were modelled with accelerated failure time models (AFT) using *survival* package (Therneau, 2021) with parental host, natal host and sex as independent variables. Models were selected with stepwise method using *MASS* package (Venables and Ripley, 2002) and validated by deviance residuals analysis (Achilonu et al., 2019). All models were selected based on Akaike's Information Criteria (AIC) (Burnham and Anderson, 2003). Collinearity was not detected as VIF values ranged from 1.00 to 2.28.

2.4.2. Performance

Three-way ANOVA was performed to examine the effect of parental host, natal host and sex on pronotum width and right elytron length of the offspring from each species. Copulation time and offspring number (male fitness) of each species were compared between host origin (from lentil or mung bean) of females and males using two-way ANOVA and the Scheirer-Ray-Hare test (non-parametric two-way ANOVA) from the *rcompanion* package (Mangiafico, 2021), respectively. Mating times for *C. maculatus* and *C. analis* were $\log_{10}$ and square root transformed respectively to meet normality assumptions. Competition between males from different natal hosts was tested using a *G*-test with expected mating success taken as equal. We hypothesized that size may contribute to mating success; therefore, we extracted the size data from the no choice experiment (only individuals that came from the same bean type for both parental and natal hosts (no host switching e.g. CmLL, CmMM, CaLL and CaMM)) and then a *t*-test was performed to quantify the differences in size between males and females of each species from lentil and mung bean in the male-male competition experiment.

3. Results

3.1. Oviposition experience experiment

In the no choice experiment, both bean beetles species more readily accepted and oviposited more eggs on mung bean regardless of natal host (Table 1). Our results showed that prior oviposition experience (no choice experiment) did not influence subsequent oviposition preference (choice experiment) in both bean beetles species as the percentage of host acceptance and numbers of oviposited eggs were higher on mung bean regardless of experience (Table 2). Both bean beetle species oviposited more eggs on mung bean as focal host [*C. maculatus*: lentil 6.73 ± 1.06 (n = 60), mung 22.40 ± 1.10 (n = 54); *C. analis*: lentil 2.78 ± 0.66 (n = 58), mung 24.00 ± 1.36 (n = 56)], but bean beetles emerging from lentils laid significantly more eggs than those emerging from mung bean (*C. maculatus*: lentil 17.4 ± 1.45 (n = 60), mung 10.5 ± 1.40 (n = 54); *C. analis*: lentil 17 ± 1.91 (n = 59), mung 9.13 ± 1.39 (n = 55); Table 3). In addition, when the beetles were given a choice between small seed mung bean and lentil, both beetle species still preferred to oviposit on mung bean, suggesting that host species (quality), rather than host size (quantity), mattered (Table 4).

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 ± 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

Emergence rate was high for all treatments (>88% emergence) regardless of parental or natal host, except for CmM (from mung), which performed very poorly on lentil with only 16% successfully emerging (Table 5). The sex ratio did not differ between cultures, except for CaL and CaM on lentil, which showed significant female (67%) and male (66%) bias, respectively (Table 5).

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

3.2. Performance

Overall the effect of parental host, natal host and sex was significant for both pronotum width and right elytron length of both species (Table 6). Generally, females were larger than males for both species [*C. maculatus* pronotum width: female 1.31 ± 0.01 mm (n = 80), male 1.28 ± 0.008 mm (n = 98); *C. maculatus* right elytron length: female 2.09 ± 0.016 mm (n = 78), male 2.02 ± 0.012 mm (n = 99); *C. analis* pronotum width: female 1.32 ± 0.008 mm (n = 104), male 1.22 ± 0.006 mm (n = 109); *C. analis* right elytron length: female 2.12 ± 0.012 mm (n = 104), male 1.94 ± 0.011 mm (n = 108)], and the offspring were larger when the parental host was lentil or natal host was mung bean for *C. analis* (Fig. 1). A significant two-way interaction between parental and natal hosts was detected only on *C. maculatus* (Table 6) where the beetles emerging from mung bean natal hosts were larger, but performance was very poor when beetles came from mung bean parental hosts and had lentil as natal host (Fig. 1).

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

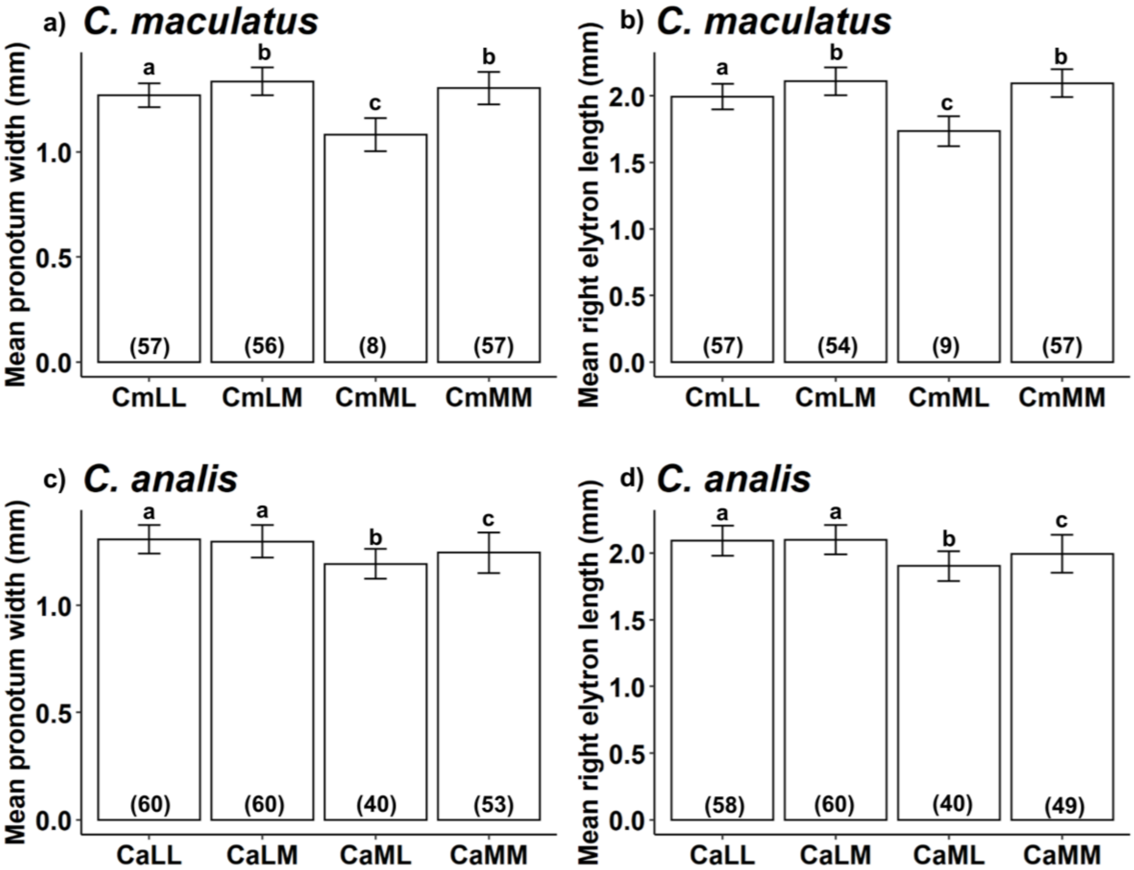

Fig. 1. Mean ± SD of *C. maculatus* a) pronotum width and b) right elytron length. Mean ± SD of *C. analis* c) pronotum width and d) right elytron length. The letters above bar represent significant differences between groups calculated from Tukey's test. The number of individuals in each group is given 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.

Males from lentil were more successful in competition for mates against males from mung bean (Table 7). We hypothesized that size may influence the outcome of mating success where larger males are more likely to outcompete smaller rivals; however, we found a reverse size trend between the two bean beetle species in both sexes. *Callosobruchus maculatus* was larger on mung bean (compared with *C. maculatus* from lentil), whereas *C. analis* was larger on lentil (compared with *C. analis* from mung bean) (Fig. 1; CmLL vs CmMM and CaLL vs CaMM). No significant terms were detected for *C. analis* (lentil: 516.62 ± 18.35 seconds (n = 60); mung: 522.61 ± 20.08 seconds (n = 60), Fig. 2). Male *C. maculatus* from lentil had significantly longer mating times than males which emerged from mung bean (lentil: 629.32 ± 28.78 seconds (n = 60), mung: 522.84 ± 20.86 seconds (n = 60), $F_{1,116} = 10.14$, $P = 0.002$). This was the only significant factor affecting mating time and mating times for lentil reared *C. maculatus* were longer than in *C. analis*. Our results also showed that male natal host did not affect male fitness in terms of offspring number in either species (*C. maculatus*: $H_{1,115} = 0.47$, $P = 0.495$; *C. analis*: $H_{1,116} = 3.1$, $P = 0.078$), but female natal host (from lentil or mung bean) did significantly affect fecundity (*C. maculatus*: $H_{1,115} = 29.32$, $P < 0.001$; *C. analis*: $H_{1,116} = 21.6$, $P < 0.001$). Females from mung bean had more offspring than females from lentil (*C. maculatus*: lentil: 44.37 ± 4.31 (n = 60), mung: 77.59 ± 2.97 (n = 59), Wilcoxon rank sum test: W = 751.5, $n_1 = 60$, $n_2 = 59$, $P < 0.001$; *C. analis*: lentil: 59.62 ± 4.96 (n = 60), mung: 92.40 ± 1.89 (n = 60), Wilcoxon rank sum test: W = 914.5, $n_1 = 60$, $n_2 = 60$, $P < 0.001$).

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

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

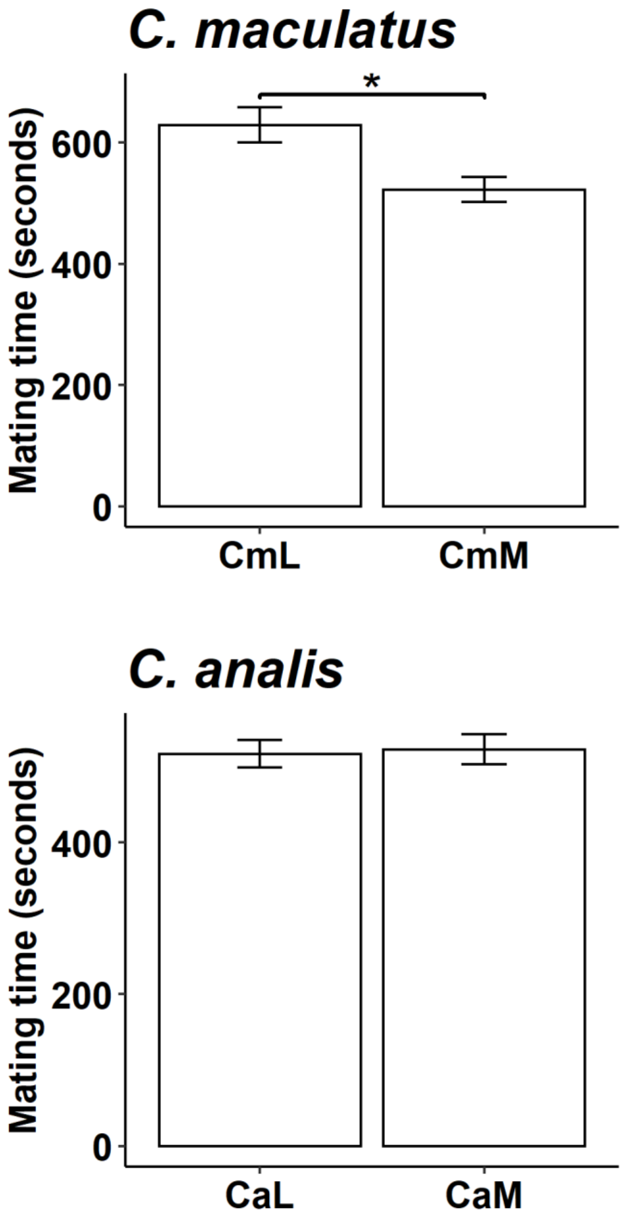

Fig. 2. Mean ± SE mating time in seconds of males of *C. maculatus* (above) and *C. analis* (below) that emerged from the two different hosts (mung and lentil). *Callosobruchus maculatus* reared on mung (CmM), *C. maculatus* reared on lentil (CmL), *C. analis* reared on mung (CaM) and *C. analis* reared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

3.3. Development and starvation resistance time

Callosobruchus maculatus with mung bean parental hosts had a longer development time than beetles with lentil parental hosts, and they showed a greater difference between different natal hosts (Table 8, 9). Beetles from lentil natal hosts had a longer development time, compared with those from mung natal hosts. We found similar results for *C. analis* development time (Table 8, 9), as having mung bean as a parental host caused longer development times, but having mung bean as a natal host decreased development time. Male beetles developed more quickly than females. An interaction between parental and natal host was detected and suggests that *C. analis* with mung bean as parental host and lentil as natal host had the longest development time (Table 9).

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**	

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

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)

We found no significant terms in the *C. maculatus* survival time model. For *C. analis*, having mung bean as parental host led to a longer lifespan (Table 8, 9). The interaction between parental and natal host was significant (Table 8). Having lentil as the parental host resulted in similar survival times regardless of natal host (Table 9). The interaction between natal host and beetle sex suggests that male *C. analis* with mung bean as both parental and natal host had the shortest lifespans (Table 9, 10).

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

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)

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 survival time. Generally, having mung bean as parental host resulted in increased development time while mung bean as natal host decreased development time of both beetle species.

Previous work has considered ovipositional experience of *C. maculatus*, but the study did not include the effects of natal host (Chiu and Messina, 1994). In no choice and choice experiments both beetle species, regardless of their natal hosts, clearly preferred to oviposit more eggs (in terms of focal host) on mung bean over lentil. Previous studies have suggested that *C. maculatus* preferred larger beans within (Cope and Fox, 2003; Yang et al., 2006) and between species (Paukku and Kotiaho, 2008). However, we found that both beetle species preferred ovipositing on smaller sized mung beans compared with lentils (which were larger in size compared to the small seed mung). Seed size is not the only factor determining bean beetle oviposition preference, which is also affected by chemical signals (Pouzat, 1981), smoothness (Sulehrie et al., 2003), curvature of seeds (Gokhale et al., 1990) and the presence of other eggs (Otake and Dobata, 2018). Our results suggest oviposition preference in bean beetles is not transgenerational as host quality comes before host quantity.

Lentil is considered to be an inferior host to mung bean (Messina et al., 2009). In terms of natal host, both beetle species emerging from lentil laid more eggs than those emerging from mung bean when a better host (mung bean) was provided. This result is consistent with a previous study showing that *C. maculatus* fecundity was enhanced when reared on lentil (Messina and Jones, 2009). Poor early life nutrition can lead to the thrifty phenotype (Hales and Barker, 2001), the characteristic which helps organisms to perform best under poor resource conditions by promoting fat storage and high glucose blood levels. This may lead to the accumulation of lipid storage in insects (Barrett et al., 2009; Jehrke et al., 2018) which is important in programmed cell death of fat cells contributing to ovary maturation and fecundity (Aguila et al., 2013). This may explain why beetles from lentil had higher fecundity.

Responses differed between species when they switched to a poorer natal host (lentil); while *C. maculatus* suffered from switching to the inferior host in terms of emerging adults, *C. analis* had no such response. This result is consistent with survival time results in this study, as *C. analis* survived for longer compared with *C. maculatus* with lentil as a natal host. In addition, the performance of *C. maculatus* offspring was also affected when the parental host was mung bean and natal host was lentil (Fig. 1). The poor performance seen in *C. maculatus* resulting from switching to the inferior host (lentil) may be linked to reduced expression of genes which help detoxify plant secondary metabolites (Rêgo et al., 2020).

In both beetle species, having lentil as the parental host resulted in larger offspring. Again, mothers already adapted to a poor quality host may invest more in fewer offspring, resulting in offspring more tolerant to poor quality hosts (Amarillo-Suárez and Fox, 2006), improving offspring fitness. In terms of natal host, mung bean is a better-quality host as emerged adults were larger than those from lentil. Overall, females were larger than males, following the general trend in insects (Stillwell et al., 2010; Teder, 2014).

In the absence of local mate competition and haplodiploidy, a 1:1 female: male sex ratio is favoured through natural selection (Trivers and Willard, 1973; King, 1987) We found a deviation in sex ratio from 1:1 only in *C. analis* when the natal host was lentil. Differences in parental host yielded different sex biases; where the parental host was lentil, the offspring had a female bias, while where mung bean was the parental host we saw a male bias. There is no evidence that bruchid bean beetles can directly control their offspring sex ratio, but deviations from a 1:1 ratio can occur through intraspecific competition and differential mortality between sexes (Cipollini, 1991; Ishihara and Shimada, 1993; Reece et al., 2005).

This study found males that emerged from lentil were generally more successful in gaining matings than those from mung bean regardless of species. Even though larger males tend to achieve more mating success by outcompeting other male competitors during direct conflict (Andersson, 1994), smaller males can gain more mating success through better mobility when acquiring females (Mclachlan and Allen, 1987) or better morphological compatability during mating (Weissman et al., 2008). A similar study system found that larger male S*itophilus oryzae* are preferred by females, demonstrated by reduced pairing time and increased mating time (Holloway and Smith, 1987). Higher mating success in larger male bean beetles can be explained only in the case of *C. analis* where males from lentil were also larger, but not for *C. maculatus* where males from mung bean were larger. Thus, in this study size may not fully explain the outcome of male-male competition. In this study, *C. maculatus* from mung bean seemed to be less active than those from lentil (pers. obs.) which provided an opportunity for the smaller males to mate.

Nutritional quality may influence male fitness in terms of number of offspring as shown in studies in other insects (Fricke et al., 2008; Morimoto and Wigby, 2016). In this study we found no difference in the number of offspring sired by the two male bean beetle species which emerged from different hosts. Male size is not likely to be a good proxy for male fitness (Savalli and Fox, 1999). *Callosobruchus maculatus* males that previously mated still provide many more sperm than females need (Eady, 1995). Hence, it seems that host quality could not account for a difference in offspring number among treatments as in this study we used unmated males.

Egg size varies both within and among females of *C. maculatus*, and individuals from larger eggs develop faster and emerge as larger adults (Fox, 1994). Developmental times were also found to be influenced by host; where mung bean was a parental host development rate was slower (whereas lentil as a parental host reduced development time) in both species. The effect of maternal rearing host on offspring is still unclear (Amarillo-Suárez and Fox, 2006); therefore, we remain cautious about the interpretation of the interactions between parental host and natal host on development time in this study. In contrast, both *Callosobruchus* species that developed in mung bean as a natal host had reduced development times. Mothers who are pre-adapted to poor food quality may change resource allocation to eggs resulting in offspring better able to tolerate poor quality food (Amarillo-Suárez and Fox, 2006). Thus, when offspring are reared on better quality food, they might in turn perform better. Interestingly, in *C. analis* whose parental host was mung bean and natal host was lentil showed the longest development time compared to other groups. This is similar to the reduction in performance seen in *C. maculatus*'s offspring when switching to the inferior quality host. This was not found in *C. analis*, but their increase change in development time suggests host quality also affects this species.

Studying adult lifespan is more complicated than we expected. We found no significant terms in the *C. maculatus* survival time model. While *C. maculatus* development time and emergence rates were affected by switching to lentil, host quality did not affect *C. maculatus* lifespan. In contrast, we found a significant effect of parental host on adult longevity for *C. analis*. Fox et al. (2004) also failed to detect the effect of rearing hosts on *C. maculatus* lifespan, which may be due to the use of two closely related hosts (*Vigna radiata* and *V. unguiculata*). Finding an interaction effect of parental and natal hosts on *C. analis* survival time was unexpected. Male *C. analis* with mung bean as both parental and natal hosts had a more reduced lifespan than females and males from other treatments, but why this is so is not known.

Overall, our results indicate that differences in larval seed host can greatly influence the fitness and life histories of bean beetles, but responses differ between species, making it difficult to draw generalities (Srisakrapikoop et al., 2021). Bean beetles preferred high quality over poor quality hosts, and this has profound effects both directly (natal host) and indirectly (parental host) on their behavior and fitness. Switching from poor to high quality hosts generally improves offspring performance but when switching from high to poor quality hosts, effects are species dependent. Our study provides insights into how host quality can affect offspring performance. Understanding how these pests may respond and adapt to the introduction of novel hosts provides us with a better understanding of both the fundamental biology of the system, and also how this knowledge can be applied to fundamental challenges in pest management.

CRediT authorship contribution statement

Ussawit Srisakrapikoop: Methodology, Investigation, Validation, Formal analysis, Writing – original draft. **Tara J. Pirie:** Resources, Writing – review & editing. **Graham J. Holloway:** Resources, Writing – review & editing. **Mark D.E. Fellowes:** Conceptualization, Methodology, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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