LAB-ADAPTED AND WILD STRAINS OF *Callosobruchus maculatus* (FABRIBIUS (COLEOPTERA: CHRYSOMELIDAE: BRUCHINAE) DIFFER IN HOST-SEED PREFERENCE AND LIFE HISTORY PERFORMANCE

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ABSTRACT

For decades, cowpea weevil, *Callosobruchus maculatus* F. has played a significant role in informing our knowledge on evolutionary behaviour of insects and has served as a model species in life-history studies. However, these studies have focused mainly on examining the weevil in specific experimental contexts with less interest in their behaviours as a pest. As an economic pest ravaging stored legume seeds, understanding the mechanisms that drive host selection in the wild and unlocking any potential link between the beetle's life-history performance and a host-seed type could help inform our pest management decisions and strategies. To test this hypothesis, this study examined the preference and life-history performance of female *C. maculatus* on five different bean types (adzuki beans, black-eyed beans, Borno-brown beans, mung beans and pinto beans). Two strains of the beetle were used for the study: a laboratory-adapted strain (model) and a wild type (pest). The strains were presented with a mixture of the five bean types (in a choice test) and to individual bean type (as a no-choice test). The results show strong variations in the choice of a bean type and differences on the life-history performance of the beetle strains. The lab-adapted strain-maintained preference for black-eyed bean (a familiar host), whereas the Wild-type laid more eggs on Pinto beans (an unfamiliar host). Beetles from the wild developed faster, weighed less and lived shorter, and adzuki bean had an antagonistic effect on the beetles by delaying their development and reducing their body weight.

Keywords: Bean, Cowpea weevil, *Callosobruchus maculatus*, Life-history studies, Preference, Performance

1.0 INTRODUCTION

Host preference and insect performance have enriched our understanding of the evolution of natural selection and its application in managing pests of economic importance (Dent, 2000). Preference and performance studies can be integrated as a component of pest management strategies (Nylin, 2001), and is important as it gives an understanding of how an insect pest interacts with a host. This relationship is often complicated, in most conditions, there is no clear interaction between host suitability and offspring fitness. However, when a strong correlation tends to exist, it will provide a clue on what drives a

choice of host. A poor relationship, on the other hand, could mean that the pest prefers a host that has a detrimental effect on offspring fitness. Interestingly, such a host-plant can be used as a trap crop in a mixed cropping system to reduce pest population level. Under conditions where there is no particular preference pattern (weak correlation) it could suggest that such females lay eggs indiscriminately and is common in insects with a very short life-span (Larsson and Ekbom, 1995).

The preference-performance hypothesis assumes that gravid females would prefer hosts that will increase their offspring's fitness, and the forces driving these "mother-knows-best" hypothesis have been suggested in many theories (Craig and Itami, 2008; Jaenike, 1990; Mayhew, 1997). Several studies have examined the interaction between a mother's choice and how it affects her offspring's wellbeing (Thompson, 1988b; Trivers, 1972). Work supporting (Barker and Maczka, 1996; Nylin and Janz, 1993) and contradicting (Faria and Fernandes, 2001; Fritz *et al.*, 2000; Underwood, 1994) the hypothesis have been reported although, there is a general notion that these contradictions can be explained by several factors including ecological and life-history variations (Craigs and Itami, 2008).

Host-quality status and the availability of a preferred host play a key role in the preference-performance interactions (Craigs and Itami, 2008): a plant with marginal diet quality may be preferred because it offers protection against competitors (Wise and Weinberg, 2002) and natural enemies (Björkman *et al.*, 1997). Aggregation of offspring may also affect offspring performance as females that lay eggs in clutches are assumed to have a stronger preference for high-quality hosts compared to females that lay eggs singly (Gripenberg *et al.*, 2010). This is important because choosing the wrong oviposition substrate is a risk for the former, while laying single eggs could be a risk-mitigation strategy by the latter (Hopper, 1999; Mangel, 1987). Progeny fitness can be affected by the potential of an insect to feed as an adult: adequate resource acquisition by developing larvae may be moulding preference in non-adult feeding females, thus a positive linkage between a mother's choice and her offsprings' wellbeing is highly likely. According to Thompson, (1988a), an insect's interaction with an unfamiliar host can trigger a weak or negative preference-performance relationship.

Hosts on the other hand have developed mechanisms ie resistant genes (Bergelson and Crawley, 1992) to deter herbivorous insects or suppress their infestation levels (Sarfraz *et al.,* 2006). Reduction in longevity, survival, body mass/weight, reproduction success, development time (which may increase their vulnerability to natural enemies) are some of plants' resistance features (Ebrahimi *et al.*, 2008; Sarfraz *et al.,* 2007; Sarfraz *et al.*, 2010; Syed and Abro, 2003). These modalities were summarised by Painter, (1951) as antixenosis, antibiosis and tolerance in plants. For example, the reproduction and population growth rate of the giant willow aphid, *Tuberolachnus salignus* varied across six willow clones, and the concentration of phenolic glucosides was suggested to be the cause of variation in aphid performance in willow plants (Kendall *et al.*, 1996). The compounds were also used by larvae of chrysomelid beetle, *Phratora vitellinae* as a defensive mechanism against its natural enemies (Rank *et al.,* 1998). Another study on

preference-performance showed that the oviposition preference, development rate and reproduction of the diamondback moth, *Plutella xylostella* varied between *Canola sp*. cultivars (Fathi, 2010). The study further proposed the chemical profile of the cultivars tested as the key source of variation. Studies reporting variations in host preference and performance among and within populations have also been documented (Scriber *et al.,* 1991; Jaenike, 1990; Tabashnik *et al.,* 1981). Strain differences are an important feature in an insect-plant relationship and is essential in understanding host selection strategies and the factors that mould them.

C. maculatus has been an important experimental tool in life-history studies as well as studies aimed at understanding the nature of traits underpinning those decisions. For instance, identification of traits driving cost of mating (Crudgington and Siva-Jothy, 2000); variation in population fecundity (Appleby and Credland, 2003); host discrimination (Beck and Blumer, 2014; Boeke *et al.*, 2003; Cope and Fox, 2003); effects of temperature and relative humidity on adult emergence (Howe and Currie, 1964) and the quality of available food on adults fitness (Kawecki and Mery, 2003) have been detected in the beetle. However, stocks/populations of this beetle have been reared in different laboratories and are known to differ in life-history traits such as mortality, reproduction and development rate (Dick and Credland, 1984). Differences in egg-spacing behaviour (Savalli *et al.*, 2000) and host-seed damage and larval respiration rate (Guedes *et al.*, 2003) have also been reported between strains. Despite its substantial representation in the life-history literature (resulting from its adaptations to exploiting stored products), few studies have examined this beetle in its pest context: such as host preferences and life-history trajectories in the wild with respect to the beetle's genetic background as well as natural host plants.

In the developing world, there is substantial geographic variation in local varieties of host plants affected by the beetle and therefore likely local adaptation by beetle populations. *C. maculatus* infests other legume cultivars (i.e. alternative hosts), and some substitute hosts result in sub-optimal development of the larvae (Gatehouse *et al*., 1990). Thus, a female is faced with the challenging task of detecting the right plant, at the right time and identifying a suitable oviposition substrate that is not already occupied; a critical and complex life-history choice that, if made incorrectly will be detrimental to offspring fitness.

Most life-history studies on *C. maculatus* use lab-adapted strains fed on commercially available black-eyed peas a contrast to the beetle's host preference behaviour in the wild as it's notorious with infesting several legume cultivars. Understanding what drives variation in life-history traits amongst individuals and how adaptations to environmental conditions affect individual fitness is important in pest control.

Consequently, this study examines the bean preference behaviour of two strains of *C. maculatus* and the effect of their choices on the fitness of their offspring using five agriculturally important bean types. The study hypothesized that the Wild strain would show greater plasticity while choosing an oviposition substrate, and that offspring's fitness between both strains will vary. The study aims to (a) examine the oviposition preferences of lab-adapted and wild strains of female *C. maculatus* on five agriculturally

important bean type (b) determine the effect of these choices on the performance (development rate, body weight and longevity) of emerging adult progenies.

2.0 MATERIALS AND METHODS

2.1 Insects

Two *C. maculatus* stocks were used: A wild strain (from a farmer's field in Taraba State, Nigeria, maintained in the lab for 3 months) and a lab-adapted strain (maintained in Sheffield for more than 3 decades). Both stocks were cultured by placing individuals from each strain separately into breeding containers (17 x 11.5 cm) containing 200 g of uninfested whole Borno-brown beans. The lids of the containers were perforated for ventilation. The cultures were kept in controlled climate conditions of 28 ± 2 ^{0}C and relative humidity of 30 ± 5 %.

2.2 Beans

Seeds of five bean types were used for this study: Borno brown, black-eyed bean (cultivars of *Vigna unguiculata* L. Walper), adzuki bean (*Vigna angularis* Wild), mung bean (*Vigna radiata* L. Wilzek) and pinto bean (*Phaseolus vulgaris* L.). With the exception of Borno brown from Nigeria, all were sourced from a local Whole Food Store (in Sheffield). Three kg of each bean type was frozen at -20 ^{0}C for 10 days to ensure they were free of infestation. Then, the beans were equilibrated for 2 weeks at 28 ± 2 ^{0}C and 60 ± 5 % relative humidity.

2.3 Bean Preference

Two different "choice" options were used to examine how female beetles would allocate their reproductive resources when faced with different ecological situations. In one, the females had access to different bean varieties in the same arena ("choice"). In the other, they were presented with only one type of bean (but different replicates were presented with different beans -"no choice"). The aims were to determine (a) what females preferences were when presented with several varieties (b) whether females could modulate this preference when presented with only one life-history option (c) to simulate a field (choice) and store (no-choice) conditions and (d) to identify what is possible against what is actual.

2.3.1 The "Choice" Experiment

In this study, ten (10) seeds from each of the five bean varieties were collected and mixed in a Petri-dish (8 cm diameter) and replicated 10 times. Newly emerging females from the wild and lab-adapted adults were collected and paired with a newly emerged (from the same culture) males within 24 h of emergence and introduced into each of the Petri-dishes. They were allowed to copulate and lay eggs for 24 h, and the total number of eggs laid was counted (Fig. 1).

2.3.2 The "No-choice" Experiment

Here, fifty (50) seeds from each of the five bean varieties were collected and placed in five Petri-dishes (8 cm diameter), respectively and replicated 10 times. Then, newly emerging females from the wild and lab-adapted adults were collected and paired with a newly emerged males within 24 h of emergence and introduced into each of the Petri-dishes. They were allowed to copulate and lay eggs for 24 h, and the total number of eggs laid was counted (Fig. 1).
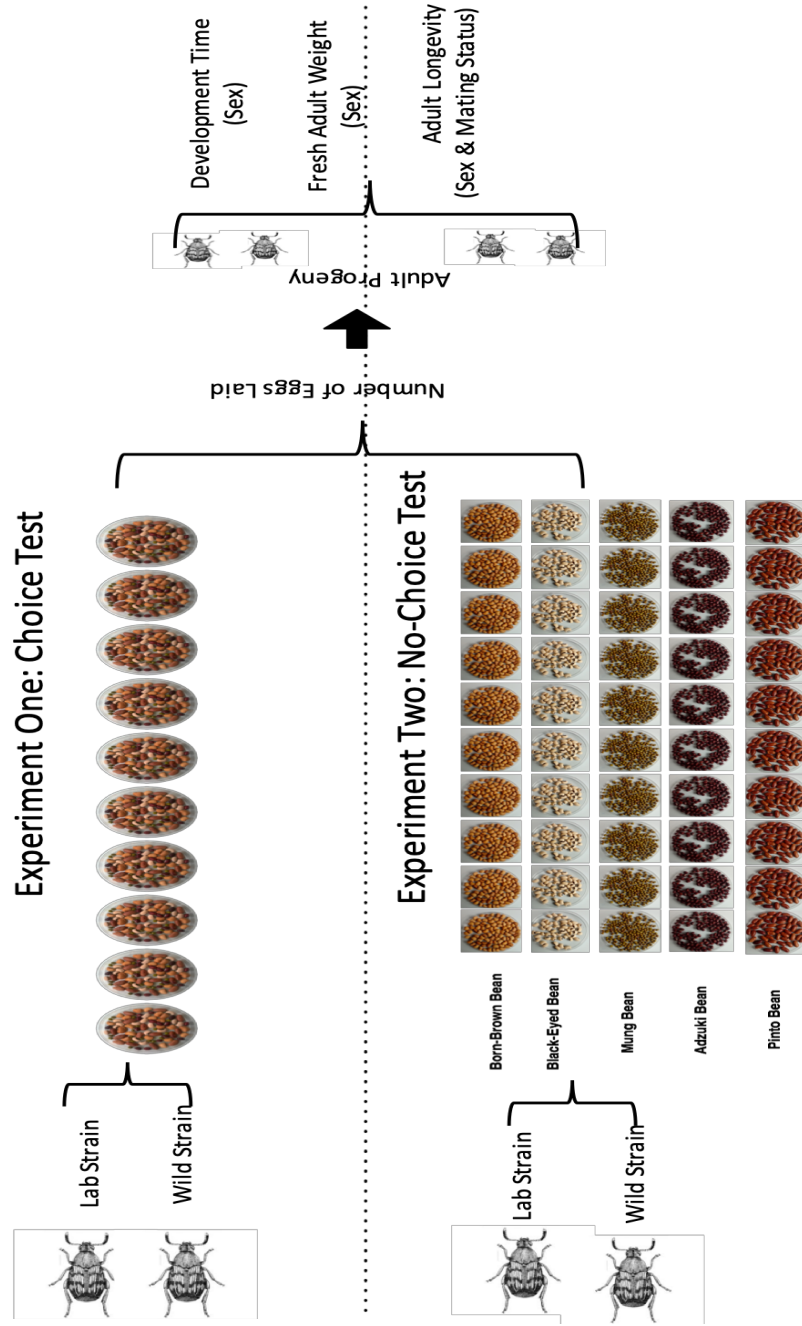
Approach

Experiment One: Choice Test

Lab Strain

Wild Strain

Experiment Two: No-Choice Test

Born-Brown Bean

Black-Eyed Bean

Mung Bean

Adzuki Bean

Pinto Bean

Lab Strain

Wild Strain

Number of Eggs Laid

Adult Progeny

Development Time
(Sex)

Fresh Adult Weight
(Sex)

Adult Longevity
(Sex & Mating Status)

Figure 1. Summary of the experimental layout.

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2.4 Measure of Progeny Fitness

The seeds were placed individually in an isolated cell in a grid box (greiner bio-one) to ensure emerging adults did not mate. Within 24 h of emergence, the date, sex and fresh body weight of the emerged adult were recorded. To obtain mated adults, a male and female from each bean type were paired, introduced into the experimental Petri-dishes and allowed to copulate for 24 hr. Virgin adults remained isolated. Longevity of both virgin and mated adults was then examined by daily monitoring of adults from emergence to mortality.

2.5 Statistical Analyses

Data collated were subjected to analyses of variance (ANOVA) and the differences between means separated using Tukey-HSD. R statistical software was used for the analyses.

3.0 RESULTS AND DISCUSSION

3.1 Bean Preference

In the "no-choice" bean preference test, there was no main effect of bean type ($F_{4, 90}$ = 1.53, P = 0.202; Table 1, Figure 2) and beetle strain ($F_{1, 90}$ = 3.36, P = 0.070; Table 1, Figure 2). Similarly, no interaction was detected in the number of eggs laid per bean type by the beetle strains ($F_{4, 90}$ = 0.73, P = 0.576; Table 1, Figure 2). In the "choice" bean preference test, there was no main effect of bean type ($F_{4, 90}$ = 1.47, P = 0.218; Table 1, Figure 2) and beetle strain ($F_{1, 90}$ = 1.05, P = 0.309; Table 1, Figure 2). However, there was a significant interaction between bean type and the beetle strains: The lab strain exhibited a strong preference for its familiar host (black-eye bean) whilst, the wild-type laid significantly more eggs on pinto beans (unfamiliar host) ($F_{4, 90}$ = 3.10, P = 0.019; Table 1, Figure 2). Mung beans were the least preferred as oviposition substrate by both beetle strains.

Furthermore, both strains did not prefer seeds of any bean type when compared to the cowpea cultivars (Black-eye bean and Borno brown).

Results of the "no-choice" test showed that both strains of *C. maculatus* laid eggs equally on the various bean types. This finding agrees with the result of Ofuya and Credland (1996), which reported that *Bruchidius atrolineatus* (Pic) laid equal number of eggs in a no-choice experiment. Similarly, no difference was found in oviposition by B. *atrolineatus* on seeds of various varieties of cowpea. This study showed that *C. maculatus* like other bruchids such as B. *atrolineatus* (Ofuya and Credland, 1996), *B. incarnatus* (Metwally, 1990), *Zabrotes subfasciatus* Boh. (Meik and Dobie, 1986), would lay eggs on bean types when beetles have no alternatives.

This findings revealed that when the beetles were presented with a mixture of bean types in the "choice" test, the lab strain showed a preference for black-eyed beans (its familiar host), whilst the wild-type laid more eggs on pinto beans but did not prefer it to Borno-brown beans (a familiar host). This is in line with earlier results of choice studies conducted between bean species which showed that *Callosobruchus* spp. prefer cowpea cultivars to other legume cultivars (Cope and Fox, 2003; Kawecki and Mery, 2003; Mainali *et al*., 2015; Messina, 2004; Paukku and Kotiaho, 2008). The strong preference for black-eyed beans displayed by the lab adapted strain may be due to selection in the lab that affected behavioural and physiological traits influencing host choice. It may also reveal a short association history with other bean types (Ofuya and Credland, 1996). The oviposition choice displayed by the wild-type could be due to reported evidence of decreasing preference for cowpea

by bruchids from West Africa to Asia (Kawecki and Mery, 2003). It could also be due to the new environment (laboratory condition) in which the beetles were reared as it differs from host selection conditions in the wild. The findings also showed that the number of eggs laid by both strains was lowest on mung bean, and earlier studies have revealed that choice of oviposition substrate is influenced by the difference in seed size (Cope and Fox, 2003; Kawecki and Mery, 2003) and seed surface area (Bhattacharya and Banerjee, 2001). Furthermore, use of chemical cues (Credland and Wright, 1989), sensory receptors on maxillary palps (Messina *et al*., 1987), or experience (Chiu and Messina, 1994), have also been reported to affect oviposition and discrimination among host species.

Table 1. Summary of ANOVA on the number of eggs laid by *C. maculatus* strains on different bean types

Sources of variance	Df	F-value	
		Choice test	No - choice test
Beetle strain	1	1.05^{ns}	3.36^{ns}
Bean type	4	1.47^{ns}	1.53^{ns}
Beetle strain x Bean type	4	3.10^{*}	0.73^{ns}

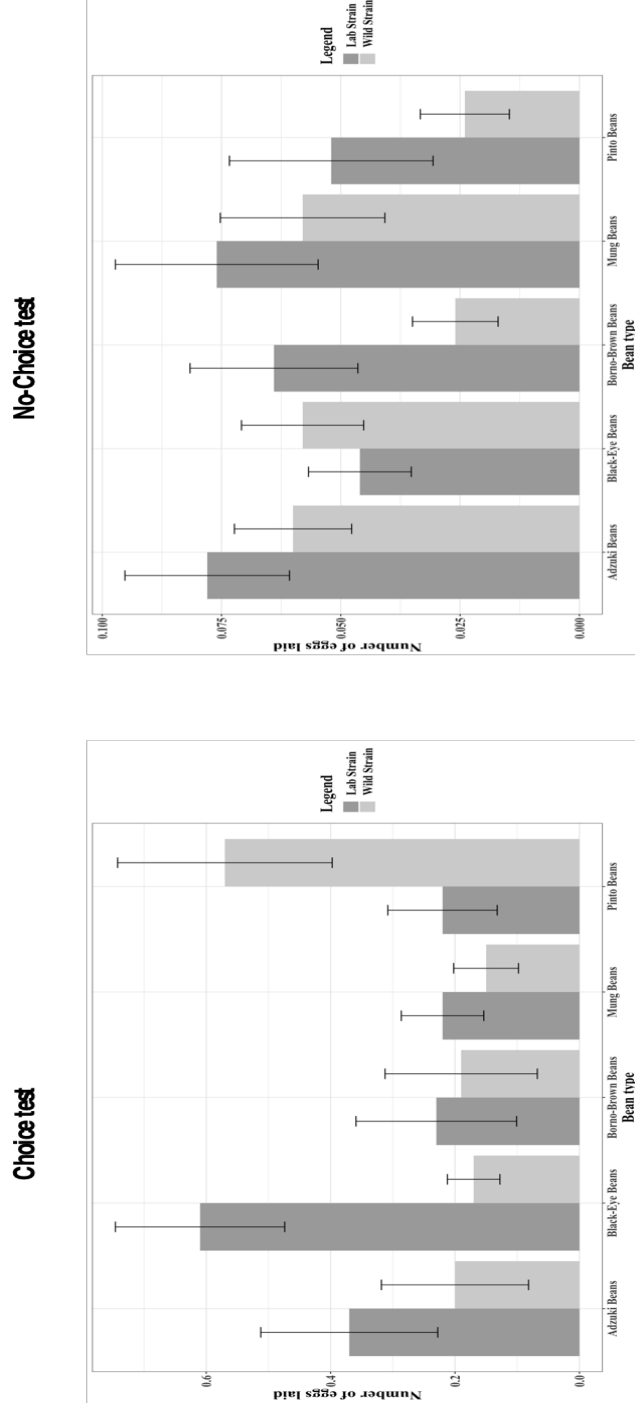* = Significant at 0.05
ns = not significant

Figure 2. Number of eggs laid by females of lab and wild strains of C. maculatus reared on different bean types. (Mean ± S.E.)

3.2   Development Rate

The development rate of adult *C. maculatus* in both "choice" and "no-choice" experiments were significantly affected by their sex, strain, and bean type, respectively.   Adults of the wild strain developed significantly faster than the lab strain in both "choice" ($F_{1, 80}$ = 156.92, P<0.001; Table 2, Figure 3) and "no-choice" ($F_{1, 80}$ = 106.21, P<0.001; Table 3, Figure 3) tests. The main effect of sex showed that males developed significantly faster than females in both "choice" ($F_{1, 80}$ = 6.68, P = 0.011; Table 2, Figure 3) and "no-choice" ($F_{1, 80}$ = 4.94, P = 0.028; Table 3, Figure 3) studies. The effect of bean type showed that the development of both beetle strains was significantly slower on adzuki beans compared to others in both "choice" ($F_{3, 80}$ = 122.99, P < 0.001; Table 2, Figure 3) and "no-choice" ($F_{3, 80}$ = 92.02, P < 0.001; Table 3, Figure 3) experiments.

Findings from this study showed that Borno-brown beans, black-eyed beans, adzuki beans and mung beans, all supported the successful development of *C. maculatus*, but pinto beans did not. However, it is worth noting that neither strain avoided pinto beans as a choice of oviposition substrate even though it was unsuitable for offspring development, indicating the beetles' inability to detect an unsupportive host. The toxicity of seeds of *Phaseolus vulgaris* on bruchid larvae had been reported many years ago. Toxicity exhibited by pinto beans on the strains of *C. maculatus* could be due to the presence of phytohaemagglutinin, a lectin present in most varieties of *P. vulgaris*. Non-protein and protein antimetabolites in legume seeds have been shown to have insecticidal properties against bruchids of economic importance (Gatehouse *et al.*, 1990). Further studies have

A significant interaction between beetle sex and strain showed that development rate was faster in males of the wild strain in the "no-choice" test ($F_{1, 80}$ = 4.70, P = 0.032; Table 3, Figure 3) but there was no interaction in the "choice" test ($F_{1, 80}$ = 1.78, P = 0.185; Table 2, Figure 4). A two-way interaction between sex and bean types indicated that adult development rate was significantly faster on male adults reared on black-eye beans, and slower on females from adzuki beans in choice ($F_{3, 80}$ = 6.62, P < 0.001; Table 2, Figure 3) and no-choice tests ($F_{3, 80}$ = 3.54, P = 0.018; Table 3, Figure 3). Pinto beans did not support the development of the beetles. There were no differences recorded in the three-way interaction involving the strain, bean type and beetle sex in "choice" ($F_{3, 80}$ = 0.71, P = 0.551; Table 2, Figure 3), and "no-choice" tests ($F_{3, 80}$ = 0.27, P = 0.848; Table 3, Figure 3).

also shown a-amylase inhibitor to be toxic to bruchids (Huesing *et al.*, 1991). The presence of toxic compounds within the testa (Simmonds *et al.*, 1989), and hardness of the testa (Thiéry *et al.*, 1994), have been found to prevent bruchids from penetrating seeds of most legumes.

The effects of bean type on larval development rate have also been reported (Boeke *et al.*, 2003). The Borno-brown beans, black-eyed beans and mung beans had a similar effect on the development rate of the beetles when compared to adzuki bean which delayed their development in both tests. This agrees with the work of Mainali *et al.*, (2015), which observed *C. chinensis* developing longer in adzuki bean when compared with cowpea and mung bean. Generally, the development rate was faster on wild strain compared to the lab type. Differences in development rates of both strains could be

due to variation in their genetic make-up as they were originally collected from two separate continents with different climatic conditions which make similarities in their life-history pattern not expected. The (Wild strain) faster development could also be a survival mechanism against natural enemies in the wild.
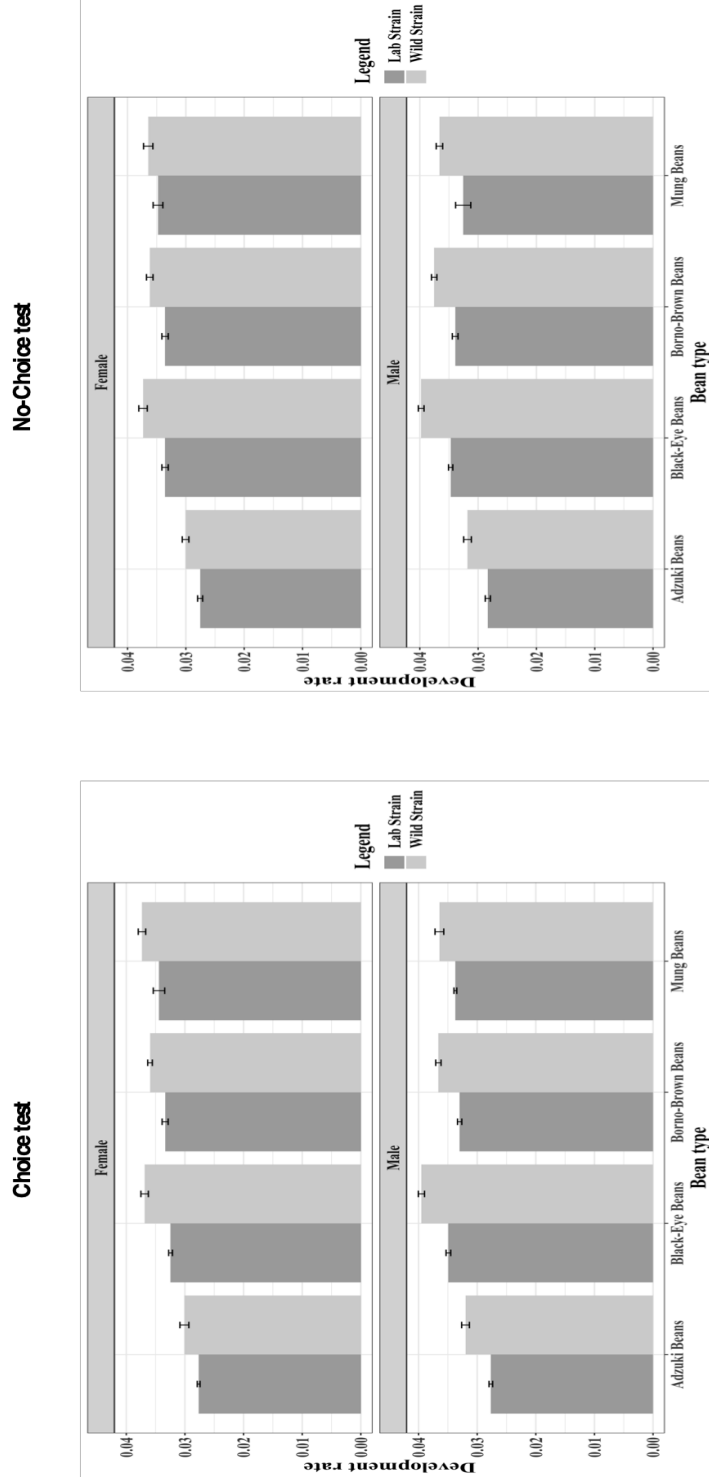
Figure 3. Development rate of males and females of lab and wild strains of *C. maculatus* reared on different bean types (Mean ± S.E.).

3.3 Fresh Body Weight

Beetle strain, sex and bean type, each showed a significant main effect on the beetles 'fresh body weight in both tests. A significantly higher fresh adult body weight was recorded by the lab strain in both "choice" ($F_{1, 80}$ = 529.47, P<0.001; Table 2, Figure 4) and "no-choice" tests ($F_{1, 80}$ = 507.01, P<0.001; Table 3, Figure 4). Female adults weighed more than males in both "choice" ($F_{1, 80}$ = 536. 80, P<0.001, Table 2, Figure 4) and "no-choice" (Figure 5.5; $F_{1, 80}$ = 477.21, P<0.001; Table 3, Figure 4), tests. The effect of bean type showed that the beetles that emerged from adzuki beans weighed significantly less compared to other bean types in both tests ("choice": $F_{1, 80}$ = 10.45, P<0.001, Table 2, Figure 4; "no-choice": $F_{1, 80}$ = 16.03, P<0.001, Table 3, Figure 4).

A significant strain and sex interaction showed that females of the lab strain recorded the highest fresh body weight in both "choice" ($F_{1, 80}$ = 18.56, P<0.001; Table 2, Figure 4) and "no-choice tests" ($F_{1, 80}$ = 11.51, P<0.001; Table 3, Figure 4). A significant interaction between beetle strain and bean type was also detected in the "choice" ($F_{3, 80}$ = 5.42, P = 0.001; Table 2, Figure 4) and "no choice" ($F_{3, 80}$ = 6.76, P <0.001; Table 3, Figure 4) investigations. However, no difference was recorded in a three-way interaction involving beetle strain, beetle sex and bean type in the "choice" ($F_{3, 80}$ = 1.06, P=0.370; Table 2, Figure 4) and "no-choice" ($F_{3, 80}$ = 1.69, P = 0.175; Table 3, Figure 4) experiments.

From the result, freshly emerged virgin adults from the lab strain weighed more than the wild-type, and females from both strains weighed more than the males. The findings are likely related to the longer development rate and longer longevity recorded by the lab strains against the wild-type, and the virgin females against the males, respectively. The fresh body weight of the lab strain suggests they are reared in a favourable condition, unlike the wild-type which is faced with challenges in the wild.
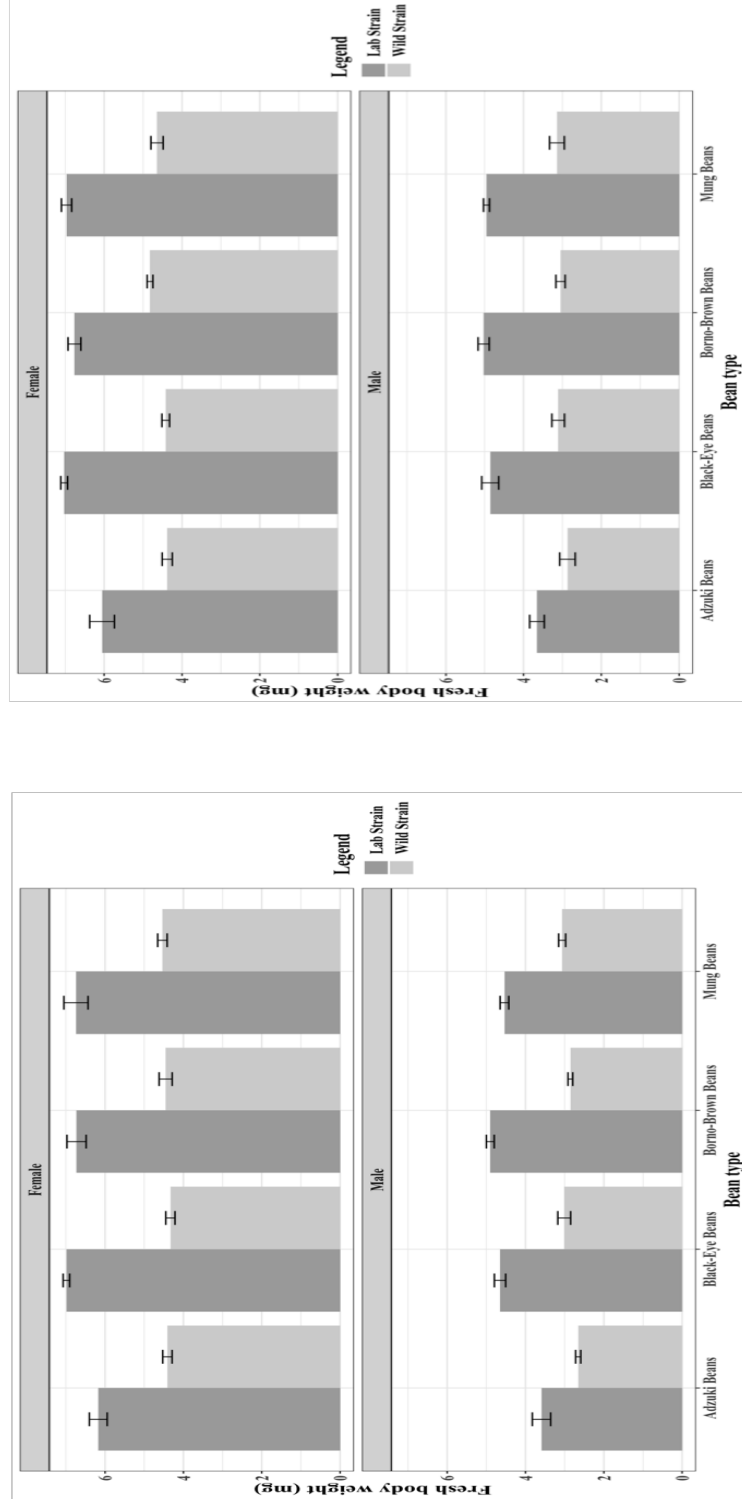
Figure 4. Fresh adult weight of *C. maculatus* strains reared on different bean types. (Mean ± S.E.).

3.4   Adult Longevity

The longevity of adult *C. maculatus* in the "choice" and "no-choice" test was significantly affected by main effects of mating status, sex and strain of the beetle, respectively. The results showed that lab strain lived significantly longer than the wild type in both "choice" ($F_{1, 64}$ = 150.21, P<0.001; Table 2, Figure 5) and "no-choice" ($F_{1, 64}$ = 234.56, P<0.001; Table 3, Figure 5) tests. Virgin adults lived significantly longer than mated adults in both "choice" ($F_{1, 64}$ = 387.45, P<0.001; Table 2, Figure 5) and "no-choice" ($F_{1, 64}$ = 565.44, P<0.001; Table 3, Figure 5) tests. Similarly, on main effect of sex, the result showed that female adults lived significantly longer than males in both "choice" ($F_{1, 64}$ = 84.49, P < 0.001; Table 2, Figure 5) and "no-choice" ($F_{1, 64}$ = 76.84, P < 0.001; Table 3, Figure 5) tests. A significant

Accordingly, the longevity of each strain was not affected by the different bean types. This is contrary to the findings of Mainali *et al.* (2015), which showed that longevity was higher on adzuki beans in a choice test. The lab strain lived longer than the wild-type suggesting there could be a trade-off between fresh body weight, development rate and longevity in a host-specific situation. This further explains that the ability of the wild-type to develop faster than the lab strain could be a fitness cost in their reduced longevity. According to Rolff *et al*. (2004), a decline in immune function investment is associated with a faster development rate. Fresh body mass has been found to have a positive correlation with body condition (fitness) suggesting why the lab strain and females lived longer than the wild-type and males, respectively. Variation in insect body condition has been linked with their rearing and/or environmental conditions:

interaction between mating status and strain indicated that longevity was highest in virgin adults of lab strain and lowest in mated adults of wild strain in both "choice" ($F_{1, 64}$ = 16.69, P<0.001; Table 2, Figure 5), and "no-choice" ($F_{1, 64}$ = 36.55, P<0.001; Table 3, Figure 5) tests. In both experiments, a significant sex and mating status interaction indicated that sex of both strains was not affected by the longevity of mated adults but, on the virgin adults. Furthermore, longevity was highest in female virgin adults, and lowest in mated male. A four-way significant interaction involving strain, sex, mating status and bean type indicated that virgin females of the lab strain reared on black-eye beans recorded the highest longevity in both "choice" ($F_{3, 64}$ = 3.88, P = 0.013; Table 2, Figure 5) and "no-choice" ($F_{1, 64}$ = 2.83, P = 0.045; Table 3, Figure 5) tests.

insects with better body condition have increased longevity (Petersen, 2003). Barone and Frank, (2003) reported that body condition can also be used as a yardstick for habitat quality. As the strain from the wild is exposed to several natural enemies including threats from extreme environmental conditions, a contrary life-history parameters with a lab adapted strain as reported in this study is inevitable. Variations in the life-history of both strains could also be due to genetically transferred traits in developing larvae which supports the prevailing rearing conditions.

The consequences of mating have been studied in insects (Crudgington and Siva-Jothy, 2000; Kotiaho and Simmons, 2003; Rolff and Siva-Jothy, 2002). Mating status of the strains was affected by their longevity as virgin adults lived longer than mated adults in both tests. The ability of the virgin adults to live longer than mated ones is attributed to the trade-off between mating and
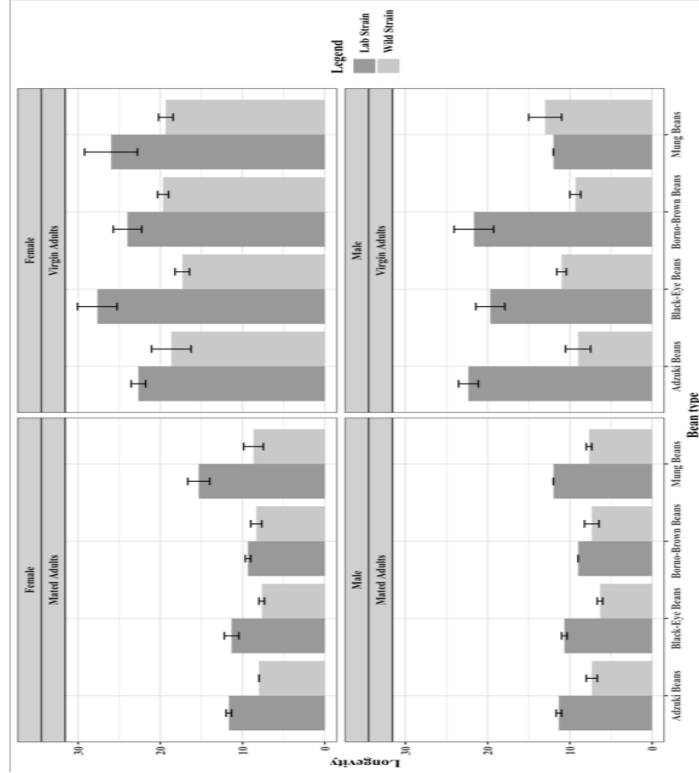
immunity as reported by Rolff and Siva-Jothy (2002), in mealworm beetle (*Tenebrio molitor*). A trade-off between mating and longevity in *C. maculatus* has also been studied (Paukku and Kotiaho, 2005). Early death recorded by mated adults could be due to the damage caused by male genitalia to the female genitalia during copulation, and the repeated kicks given to the male by the female as an act of defence (Crudgington and Siva-Jothy, 2000). The longevity of virgin adults was affected by the beetle's sex, but not on mated adults. On virgin adults, females lived longer than males which suggest there could be differences in resource acquisition during larval development.
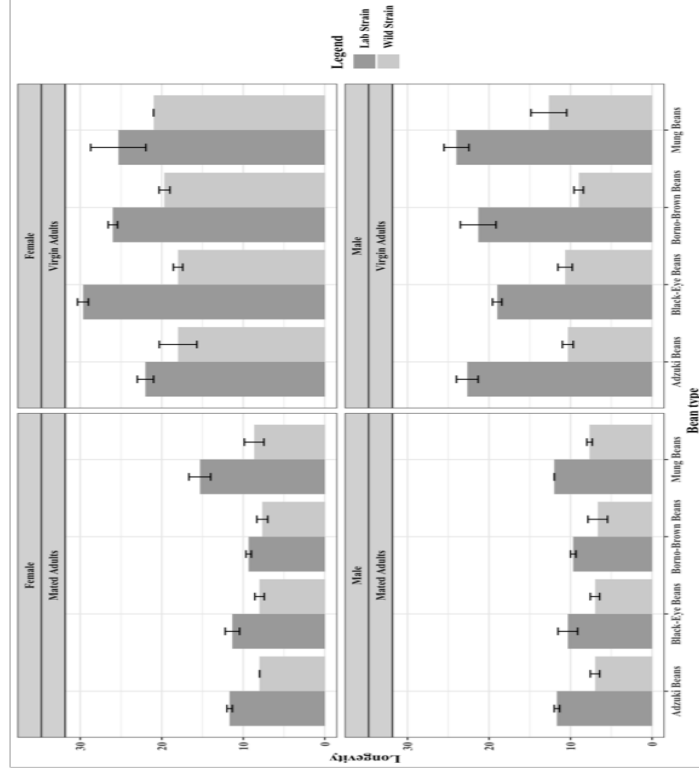
Figure 5. Longevity of mated and virgin adults of *C. maculatus* strains reared on different bean types (Mean ± S.E.)

Table 2. Summary of ANOVA on the life-history performance of *C. maculatus* strains on different bean types in the Choice test

Sources of variance	Df	F-value		
		Development rate	Body weight	Longevity
Beetle strain	1	156.92***	529.47***	150.21***
Bean type	3	122.99***	10.45***	0.374ns
Beetle sex	1	6.68*	536.08***	84.49***
Mating status	1			387.45***
Beetle strain x Bean type	3	1.82ns	5.24**	1.79ns
Beetle strain x Beetle sex	1	1.78ns	18.56**	1.04ns
Bean type x Beetle sex	3	6.62***	1.44ns	2.67ns
Beetle strain x Mating status	1			16.69***
Bean type x Mating status	3			3.19*
Beetle sex x Mating status	1			45.94***
Beetle strain x Bean type x Beetle sex	3	0.71ns	1.06ns	6.62***
Beetle strain x Bean type x Mating status	3			5.79**
Beetle strain x Beetle sex x Mating status	1			1.46ns
Bean type x Beetle sex x Mating status	3			0.66ns
Beetle strain x Bean type x Beetle sex x Mating status	3			3.88*

***, ** and * = Significant at 0.001, 0.01 and 0.05 probability levels.
ns = not significant

Table 3. Summary of ANOVA on the life-history performance of *C. maculatus* strains on different bean types in the No-Choice test

Sources of variance	Df	F-value		
		Development rate	Body weight	Longevity
Beetle strain	1	106.21***	507.01***	234.55***
Bean type	3	92.20***	16.03***	5.56**
Beetle sex	1	4.94*	477.21***	76.84***
Mating status	1			565.44***
Beetle strain x Bean type	3	1.23^{ns}	6.76**	0.24^{ns}
Beetle strain x Beetle sex	1	4.69*	11.51**	7.40**
Bean type x Beetle sex	3	3.54*	0.38^{ns}	2.28^{ns}
Beetle strain x Mating status	1			36.55***
Bean type x Mating status	3			1.06^{ns}
Beetle sex x Mating status	1			40.29***
Beetle strain x Bean type x Beetle sex	3	0.27^{ns}	1.69^{ns}	2.83***
Beetle strain x Bean type x Mating status	3			1.89^{ns}
Beetle strain x Beetle sex x Mating status	1			7.40**
Bean type x Beetle sex x Mating status	3			2.88*
Beetle strain x Bean type x Beetle sex x Mating status	3			2.83*

***, ** and * = Significant at 0.001, 0.01 and 0.05 probability levels.
ns = not significant

4.0   CONCLUSION

The bean types selected by both strains as oviposition substrate in the "choice" experiment had varying effects on the fitness of their progeny. Between strain, progeny development rate was slow on adzuki beans despite being next to the most preferred substrate by the beetles. Interestingly, the least preferred bean type (mung beans) together with the familiar substrates (Borno-brown and black-eyed beans) supported faster development of progeny. On the beetles' fresh body weight, again, adults that emerged from adzuki beans weighed less compared to other bean types, but the longevity of the adult progenies was not affected by any of the bean varieties. The performance (slower development rate and reduced body weight) recorded by the beetles that emerged from adzuki beans may indicate resistance against *C. maculatus,* and could suggest why it was not strongly preferred by both strains. Studies have shown that plants can cause a reduction in longevity, body mass and reproduction in adult progenies or indirectly increase an insect's risk to attacks by natural enemies *via* delayed emergence or developmental time (Syed and Abro, 2003; Sarfraz *et al*., 2007, 2010, Ebrahimi *et al.*, 2008). According to Sarfraz *et al*., (2006), plants that express antibiosis can suppress the pest population from causing economic damage.

Consequently, the performance of *C. maculatus* adults on adzuki bean could result in reduced infestation levels indicating its potential as a pest control tool, although further study is required to fully explore these findings. Furthermore, the ability of *C. maculatus* to oviposit, develop and survive on unfamiliar hosts as revealed in this study agrees with earlier findings that *C. maculatus* quickly modifies its egg-laying behaviour when presented with novel hosts (Fox, 1993; Wasserman and Futuyma, 1981). This could explain why the beetle successfully infests different bean types. Conclusively, this study revealed that (a) host-seed preference differed between a lab-adapted *C. maculatus* and the wild type (b) the beetles laid eggs equally on all bean types in a no-choice set up (c) the wild strain developed faster, weighed less and lived shorter compared to the lab-adapted type (d) a mother's choice of oviposition substrate affects the fitness of her progeny (e) adzuki beans showed antagonistic effect on the life-history performance of *C. maculatus.*

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