Ectoparasitoid Dinarmus basalis causes greater offspring loss to the winged morph of Callosobruchus maculatus

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Ectoparasitoid *Dinarmus basalis* causes greater offspring loss to the winged morph of *Callosobruchus maculatus*

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ABSTRACT

The pest cowpea weevil *Callosobruchus maculatus* (F.) (Coleoptera: Chrysomelidae) exhibits polymorphism with flight and flightless forms that differ in morphology and life-history. Flight forms are generally dispersers with lower fecundity that increase in frequency when population density and intraspecific competition are both high. *Callosobruchus maculatus* larvae can cause important damage to stored grains and the solitary ectoparasitoid *Dinarmus basalis* (Rondani) (Hymenoptera: Pteromalidae) is considered to be a good candidate biological control agent. However, whether morphs differ in the likelihood of their offspring surviving attack is unknown. Understanding this has implications for the pest status of the cowpea weevil following biological control. We found that attack by *D. basalis* lowered the number of emerging offspring produced by both morphs. The ectoparasitoid was most effective at reducing survival of larvae produced by flight morph parents, suggesting that there may be a further cost of dispersal for *C. maculatus*. Parental morph type did not influence *D. basalis* behavior or development when foraging, so the biological mechanism resulting in this difference remains unclear. Nevertheless, our study shows that *D. basalis* affects the offspring of both weevil morphs, as required for an effective biocontrol agent. These results contribute to our understanding of how intraspecific variation, including polymorphism, influences species interactions among biological control agents and their target insect pests.

1. Introduction

The cowpea weevil *Callosobruchus maculatus* (F.) (Coleoptera: Chrysomelidae: Bruchinae) is a major insect pest of pulses worldwide, including the agriculturally important legume, cowpea *Vigna unguiculata* (L.) Walp (Fabaceae). Cowpea and other legumes are high in protein, affordable, and an important part of the diet of many humans, particularly in tropical regions (Torres et al., 2016). However, *V. unguiculata* is at risk of infestation by *C. maculatus* at every stage of its production, from the field to storage, with the storage stage being the most affected (Tiroesele et al., 2015). Cowpea weevil populations can exponentially increase in size and infect up to 90% of stored cowpea beans in just three to six months, reducing bean weight by 30–60% (Caswell, 1981; Van Alebeek and Wau, 1996). A variety of control methods have been applied; however, for the past four decades chemical control methods have been preferred as they generally work and are easily accessible (Kalpna et al., 2022). However, these methods can be greatly affected by the temperature, strain and even the bean on which *C. maculatus* develops (Gbaye and Holloway, 2011).

Alternative biological control agents have also been tested to stop or reduce the impact of cowpea infestations including plant-derived biopesticides (Jayaram et al., 2022; Nisar et al., 2022; Ogunmefun et al., 2023) and parasitoids like the wasp *Dinarmus basalis* (Rondani) (Hymenoptera: Pteromalidae). *D. basalis* which has been identified as a potentially effective biological control candidate for *C. maculatus* (Akinbuluma and Chinaka, 2023; Ketoh et al., 2009), which could also control other storage pests such as the closely related Bruchid species *C. chinensis* (L.) (Hossain et al., 2014). This ectoparasitic wasp is a common natural enemy of *C. maculatus* in the field and in storage. The wasp oviposits its eggs on fourth instar larvae (the final larval stage of cowpea weevils), and the wasp's offspring then feed on the body fluids of the cowpea weevil larva until they are ready to emerge as adults (Qumruzzaman and Islam, 2005; Sankara et al., 2014). Although this biological control is only effective after cowpea beans are infected with *C. maculatus* larvae, *D. basalis* has been found to be highly successful at decreasing weevil population size, which could reduce bean loss. It is reported that the parasitoid is capable of suppressing up to 85% of the larvae of the cowpea weevil (Islam, 1998).

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Understanding pest biology is vital for developing effective management strategies (Barde et al., 2014; Bawa et al., 2017). *Callosobruchus maculatus* displays considerable intraspecific variation with two distinct morphs: an active, long-winged flight form; and an inactive, short-winged flightless form (Southgate et al., 1957). The ratio of these morphs is influenced by larval density with the flight morph more likely to occur in crowded conditions, but also responding to environmental triggers such as temperature, moisture, and photoperiod (Arnold et al., 2012; Sano, 1967; Utida, 1972). The morphs not only differ in their morphology but also show differences in life-history, behavior, and physiology (Sano, 1967). Flightless morphs are more fecund, have shorter life spans and reach sexual maturity earlier than their flight morph counterparts (Utida, 1972). The different traits between the two morphs are thought to be adaptations to the production process of cowpea beans, with the flight morph displaying dispersal traits most suitable to locate new sites in the field, whilst the flightless morph displays traits that are preadapted to natural pressures that are selectively beneficial (e.g. maximize reproduction) for life within artificial stores (Labeyrie, 1980). The trait differences are thought to be determined by genetic and environmental factors (Labeyrie, 1980) therefore there is likely to be some inheritance of morph traits from parent to offspring.

The presence of flight polymorphs is common to other insects (Arnold et al., 2012), and Appleby and Credland (2001) noted that polymorphisms could affect how populations respond to any control methods. Polymorphisms and other forms of variation among individuals of the same species represent intraspecific variation, which has been shown to influence population persistence (Kristensen et al., 2008; O'Grady et al., 2006; Vilas et al., 2006), growth (Pelletier et al., 2007), and may even affect species interactions (Libbrecht et al., 2007; Okuyama, 2008). Indeed, intraspecific variation in *C. maculatus* has been shown to influence their impact and response to resistant strains of cowpea (Appleby and Credland, 2003). Additionally, *C. maculatus* morphs have been shown to respond differently to infested beans, with the flight females significantly preferring infested to uninfested cowpea, whereas flightless females had no preference (Arnold et al., 2012).

Differences between *C. maculatus* morphs have potentially important consequences for the impact and management of this insect pest. For example, dispersal by the flight morph could result in wider spread of new infestations occurring, particularly in rural areas where sealed storage facilities are rare and unaffordable, whilst higher fecundity in the flightless form could lead to higher, but localized, damage in established infestations. Few studies (Appleby and Credland, 2003; Arnold et al., 2012; Oyeniyi et al., 2015) had evaluated the distinct impact from each morph. To our knowledge, no previous work has tested whether the offspring of these morphs vary in their susceptibility to the proposed biological control agent, *D. basalis*. In the present study, we address this question to determine if differences between the offspring of flight and flightless *C. maculatus* morphs affects biological control success of the larval parasitoid *D. basalis*. We assessed the fitness of flight vs. flightless morphs by comparing the performance of their offspring (population size, survival, development, and impact on stored beans) in the presence and absence of *D. basalis*. We also compared wasp performance (behavior, survival and population size) when parasitizing offspring from both morphs.

2. Material and methods

2.1. Experimental design

We used a laboratory colony of the Cameroon strain of *C. maculatus*. This colony has been kept at the University of Reading for ∼360 generations under controlled conditions (25–30 °C temperature, 55–60% relative humidity, and 12:12 h light:dark photoperiod). Since *C. maculatus* morph type is associated to interspecific competition (density dependent trait), we used subpopulation culture jars with varying amounts of cowpea beans (15, 45, 75, and 105 g) to encourage development of individuals of each morph. Culture jars were set up approximately 3.5 months prior to start of the experiment. To start the experiment, we selected beans with visible *C. maculatus* eggs from each culture jar. Each bean was then placed in a separate Eppendorf tube with a small air hole punctured at the top of the tube. These beans were checked several times a day for adult emergence, in order to obtain unmated individuals. Once an emerged adult was detected it was sexed, classified as either flight or flightless morph (Fig. 1, Tables A1 and A2 for classification protocols), and then stored into separate morph and sex stocks. If multiple adults were found together in an Eppendorf, all were removed from the experiment to ensure only unmated were used.

Once enough unmated males and females were starting to emerge, we prepared two Petri dishes (one per morph) and placed 250 female and 60 male unmated *C. maculatus* adults in each. These adults had emerged three to eight days prior to allow flight form adults to reach sexual maturity (Utida, 1972) and were then allowed to freely mate for 24 h. We used a 4.16 female:male sex ratio to reduce male-male competition. After 24 h, we placed six presumably mated females of the same morph into an experimental Petri dish containing ten cowpea beans (total bean weight 16.4–16.9 g). Females were allowed to oviposit for 24 h, after which they were removed. We created 20 replicate treatment Petri dishes per morph (totaling 120 females per morph), and also set-up 15 control Petri dishes containing only bean to evaluate bean weight loss in the absence of the weevils (Table A3).

Seventeen days after the weevil females had laid their eggs on the treatment Petri dishes (optimum larval stage for wasp oviposition; Kwasi Asante, unpublished data), we introduced two mated *D. basalis* females into each of 20 randomly selected treatment dishes in which *C. maculatus* females had laid eggs (10 dishes for each morph). Mated *D. basalis* females were randomly selected from a pool of ∼100 females and ∼100 males that had been allowed to mate for 48 h. All *D. basalis* had been reared under control condition (25–30 °C temperature, 55–60% relative humidity, and 12:12 h light:dark photoperiod) at the University of Reading for five generations from wild-caught individuals collected from Ghana in June 2019. Mated female *D. basalis* remained in the treatment dishes for 24 h. During the first 4.5 h, every 30 min we noted for each Petri dish if females were on or off the beans. If at least one female was on the bean, we recorded behavior classified as: drumming (otherwise referred to walk-antennating, where *D. basalis* was seen to palpate or "drum" the seed with its antennae in order to locate the host within the seed; Kumazaki et al., 2000; Mohamad et al., 2013), ovipositing (where the female was seen drilling through the seed with her ovipositor in order to make contact with the host and deposit her eggs; Kumazaki et al., 2000; Mohamad et al., 2013), or other.

After *D. basalis* females were removed, we separated and counted the number of *C. maculatus* eggs on each bean prior to placing each on an individually labelled Eppendorf with a small breathing hole punched at the top. Control beans were also placed in individual Eppendorf tubes to determine the average bean loss per Petri dish due to storage. We then checked daily for emerged *C. maculatus* and *D. basalis* in all wasp treatment beans and in six of the 10 beans in each no-wasp replicate (time constraints preventing daily monitoring of all beans). All emerged weevil and wasp adults were removed from the tubes, classified into a morph type (in the case of the cowpea weevils), sexed, and placed individually into a labelled Eppendorf with an air hole. All separated adults were monitored daily to record time of death. For the no-wasp beans that were not monitored daily we counted, identified the morph, and sexed all emerged adults at the end of the experiment. After six days of no new adult emergence, we assumed that all insects had emerged from the beans and we weighed each individual bean from each treatment and control replicates. The final bean weight of one replicate was incorrectly noted and this replicate was removed from analysis of bean loss.

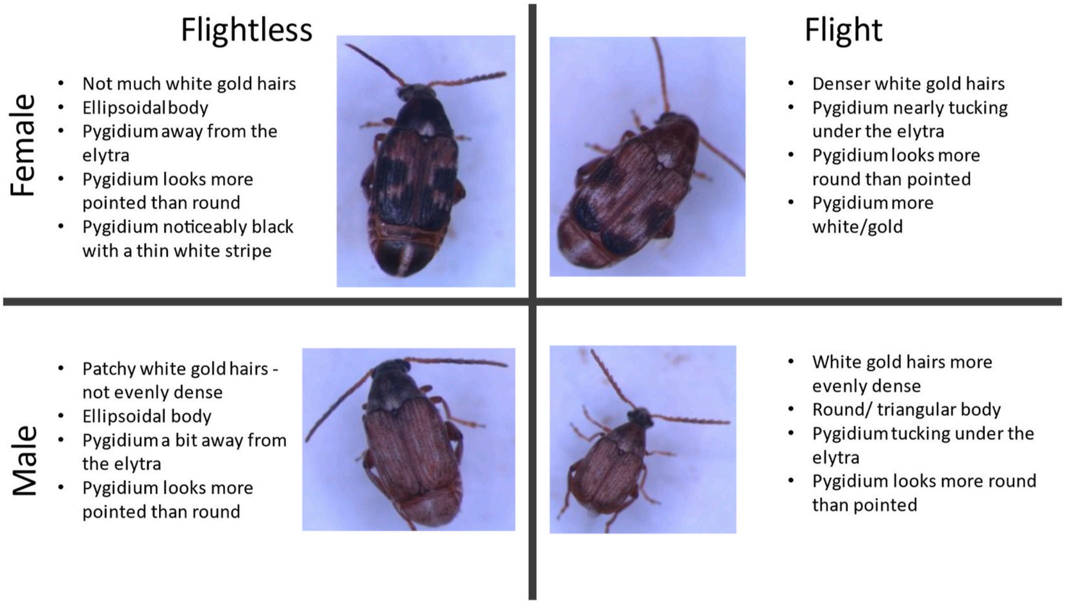

Fig. 1. Individual female and male of the flight and flightless morphs of *C. maculatus*. We list the traits used to differentiate flight vs flightless morphs (see Tables A1 and A2 for additional details).

2.2. Data analysis

We measured the following response variables for each of replicate: *total bean loss* (the difference between initial and final bean weight in grams which includes the weight loss due to weevil feeding and water loss. The average *water loss* was calculated as the average bean weight loss in control Petri dishes), *weevil population size* (the total number of emerged *C. maculatus* adults); and *per capita bean loss* (*total bean loss* divided by *weevil population size*). We also measured the following response variables per individual bean (Eppendorf) or per individual adult weevil: *weevil larval survival* (*weevil population size* divided by number of *C. maculatus* eggs), *weevil development period* (time in days from start of the experiment to adult emergence), *weevil adult lifespan* (time in days from adult emergence to death). The *egg number* (total number of *C. maculatus* eggs laid in each Petri dish treatment replicate), *offspring morph* (the morph of each individual offspring which emerged), and *proportion flightless* (the proportion of offspring which were of the flightless morph per replicate) were also noted. For *D. basalis* performance we calculated the following response variables for each Petri dish treatment replicate: *wasp population size* (the total number of emerged adult *D. basalis*), *drumming behavior* (the number of times drumming behavior was observed) and *ovipositing behavior* (the number of ovipositing behaviors was observed). Additionally, for wasp response variables per individual, we measured: *wasp development period* (time in days from when wasps were introduced to Petri dish treatment replicated to adult emergence) and *wasp adult lifespan* (time in days from adult emergence to death).

We used regression models to determine which factors influenced each response variable. The parent morph was included as a predictor in all models, and the presence of *D. basalis* was a predictor in all *C. maculatus* response models. For all responses except *total bean loss, per capita bean loss* and *egg number,* models included the number of *C. maculatus* eggs (total per Petri dish or per Eppendorf depending on how the response was measured) as a control fixed predictor (Tables A4 and A5). Other predictors included in individual models are described in. For each response we fitted two models: one with predictors as additive effects, and one testing the interaction between parent morph and presence of *D. basalis*. Models with interactions were considered to be supported if the interaction coefficient had a P-value <0.05. To account for variability within Petri dishes and Eppendorfs, models for response variables measured at the Eppendorf or individual level included Petri dish name as a random effect. Additionally, models for responses measured at the individual level included Eppendorf name as a random effect.

We used linear mixed effect regression models for *development period* and *adult lifespan* of both *C. maculatus* and *D. basalis* and used generalized linear mixed effects regression models for *C. maculatus larvae survival*, *D. basalis drumming* and *ovipositing behavior* and *offspring morph*. Models were fitted with the functions 'lmer' and 'glmer' (family binomial*)* from package *lme4* (Bates et al., 2015) in R version 3.4.3 (R Core Team, 2017). Variables measured at the Petri dish level did not include random factors, and were evaluated using generalized linear models fitting with the function 'lm' (*C. maculatus egg number, percentage flightless, bean loss* and *bean loss per capita)*, and 'glm' Poisson (*C. maculatus* and *D. basalis population size*) from *stats v3.6.2* package (R Core Team, 2017). We evaluated model assumptions (normality and heteroscedasticity) and potential outliers plotting residuals from tested models. Post-hoc tests were performed to evaluate differences between flight and flightless parent morphs, and presence and absence of *D. basalis* using functions 'difflsmeans' and 'lsmeansLT' from package *lmerTest* (Kuznetsova et al., 2017) for 'lmer' models, and 'emmeans' from the package *emmeans* (Lenth, 2022)or 'glmer' and 'glm' models.

3. Results

3.1. Effect of the parasitoid wasp on weevil responses

The presence of *D. basalis* affected most weevil offspring response variables, with some differential effects between the offspring of flight vs. flightless parents (Fig. 2; Tables 1 and 2). Wasps reduced offspring *population sizes* from both flight and flightless parents (Fig. 2A; Table 2), and reduced *larvae survival* for offspring produced by the flight morph, but not for offspring from the flightless morph (Fig. 2B; Table 2). When *D. basalis* were present, *C. maculatus* offspring from both parent morphs took longer to develop into adults (Fig. 2C; Table 1). We observed higher *total bean loss* and *per capita bean loss* in the presence of wasp, particularly for offspring from flight morph parents (Fig. 2A and B; Table 2). The observed bean loss (mean ± SD = 8.45% ± 1.23% of the original bean mass) reflected mostly damage caused by the weevil, as we found a small, estimated *water loss* of 0.25% ± 0.09% (mean ± SD per Petri dish)

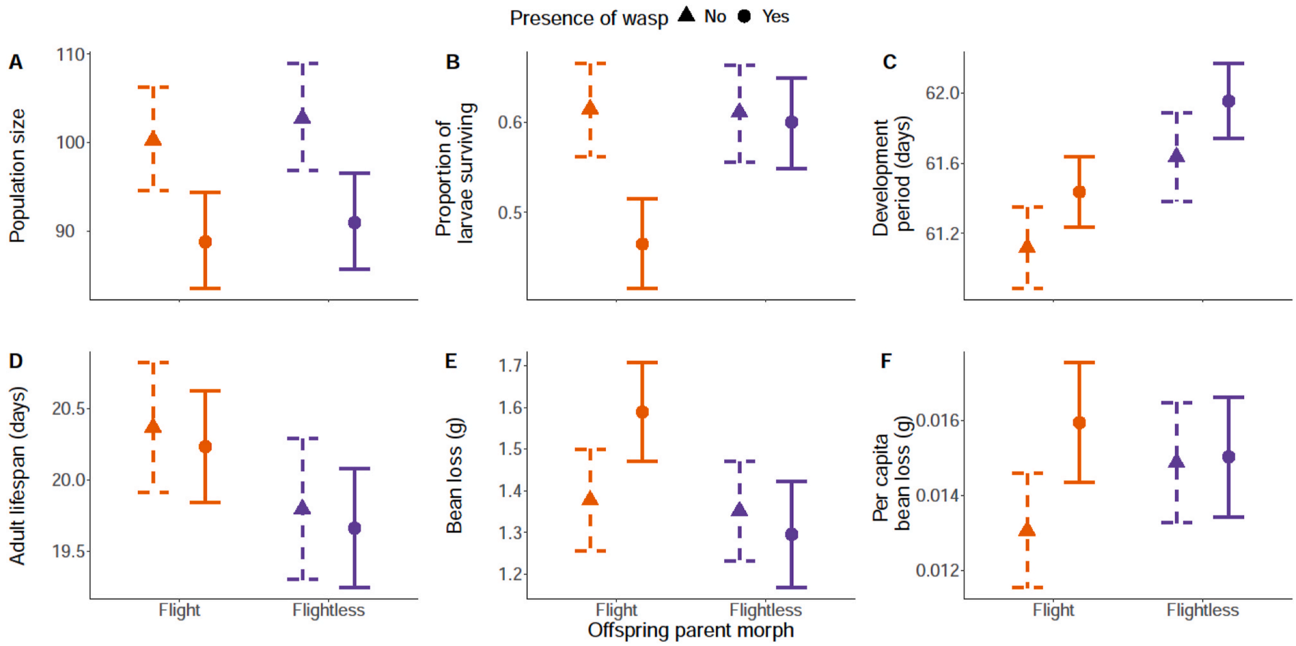

Fig. 2. Cowpea weevil *C. maculatus* performance traits. We show the estimated model mean (symbol) and 95% confidence intervals (lines) for each treatment. Dashed lines with triangle symbols represent treatments without *D. basalis*, and solid CI and round points represent treatments with *D. basalis*.

Table 1

Anova outputs for linear mixed effects regression models predicting cowpea weevil *C. maculatus* responses *development period* and *adult lifespan* as a function of the main predictors: parent morph (flightless or flight) and presence of *D. basalis* (yes or no). Some models also included as predictors: *C. maculatus* egg number and *C. maculatus* emergence morph. We report the F-value and P-value for each variable. Interaction terms are indicated by two variable names separated by a colon. Significant variables and interactions are highlighted in bold.

Variable	*F*-value	*P*-value
Development period		
Parent morph	**13.199**	**<0.0001**
Presence of wasp	**6.369**	**0.012**
Eppendorf no eggs	**7.250**	**0.008**
Adult lifespan		
Parent morph	**49.252**	**<0.0001**
Presence of wasp	0.297	0.586
Eppendorf no eggs	**4.201**	**0.041**
Weevil emergence morph	**43.995**	**<0.0001**

Table 2

Anova outputs for generalized linear mixed effects regression models predicting the *bean loss* and *per capita bean loss*, *weevil population size* and *weevil larvae survival*, as a function of the main predictors: *C. maculatus* parent morph (flightless or flight) and presence of *D. basalis* (yes or no). Some models also included as predictors: total *C. maculatus* count per Petri dish replicate, the ratio of flightless offspring per Petri dish replicate and *C. maculatus* egg number per Petri dish replicate. We report Chi-square statistic (Chisq) and P-value for each variable. Interaction terms are indicated by two variable names separated by a colon. Significant variables and interactions are highlighted in bold.

Variable	Chisq	*P*-value
Bean loss		
Parent morph	**4.683**	**0.030**
Presence of wasp	1.820	0.177
Total Petri weevil count	2.574	0.109
Petri percent flightless	2.005	0.157
Parent morph:Presence of wasp	**5.475**	**0.019**
Per capita bean loss		
Parent morph	0.300	0.584
Presence of wasp	**3.878**	**0.049**
Petri percent flightless	0.483	0.487
Parent morph:Presence of wasp	3.075	0.080
Population size		
Parent morph	0.370	0.543
Presence of wasp	**14.206**	**<0.0001**
Petri no eggs	**41.327**	**<0.0001**
Larvae survival		
Parent morph	**7.005**	**0.008**
Presence of wasp	**9.701**	**0.002**
Parent morph:Presence of wasp	**6.623**	**0.010**

on the control beans (without weevils). The presence of wasps (which affect the larval stage) did not alter *adult lifespan* of offspring from either flight or flightless parents (Fig. 2D; Table 1).

3.2. Wasp responses

The behavior and development of *D. basalis* were not affected by weevil parental morph (Fig. 3, Tables 3 and 4).

3.3. Variation between offspring of weevil morphs

Parental morph had a significant effect on several weevil offspring responses (Fig. 2), with flightless morph parents producing, on average, offspring with longer *development periods* and shorter *adult lifespan* (Fig. 2C and D: Tables 1 and 2). *Larval survival* and *bean loss* did not differ in the absence of the parasitoid wasps (Fig. 2B; Table 2). Parental morph did not influence offspring *population size* (Fig. 2A; Table 2), but as expected, the number of offspring emerging as adults was larger in replicates with higher initial egg counts (Table 2). We also observed that flight parents oviposited more eggs (mean ± SD: 18.45 ± 5.03) than flightless parents (14.00 ± 4.44) within 24 h (Figure A1A; Table A6). Offspring morph was partly influenced by parental morph, with flightless parents producing a higher percentage of flightless offspring, while flight parents were more likely to produce flight offspring (Figures A1B and A1C; Table A6 & A7).

4. Discussion

The parasitic wasp, *Dinarmus basalis,* has been proposed as a biological control for the pest species *Callosobruchus maculatus*

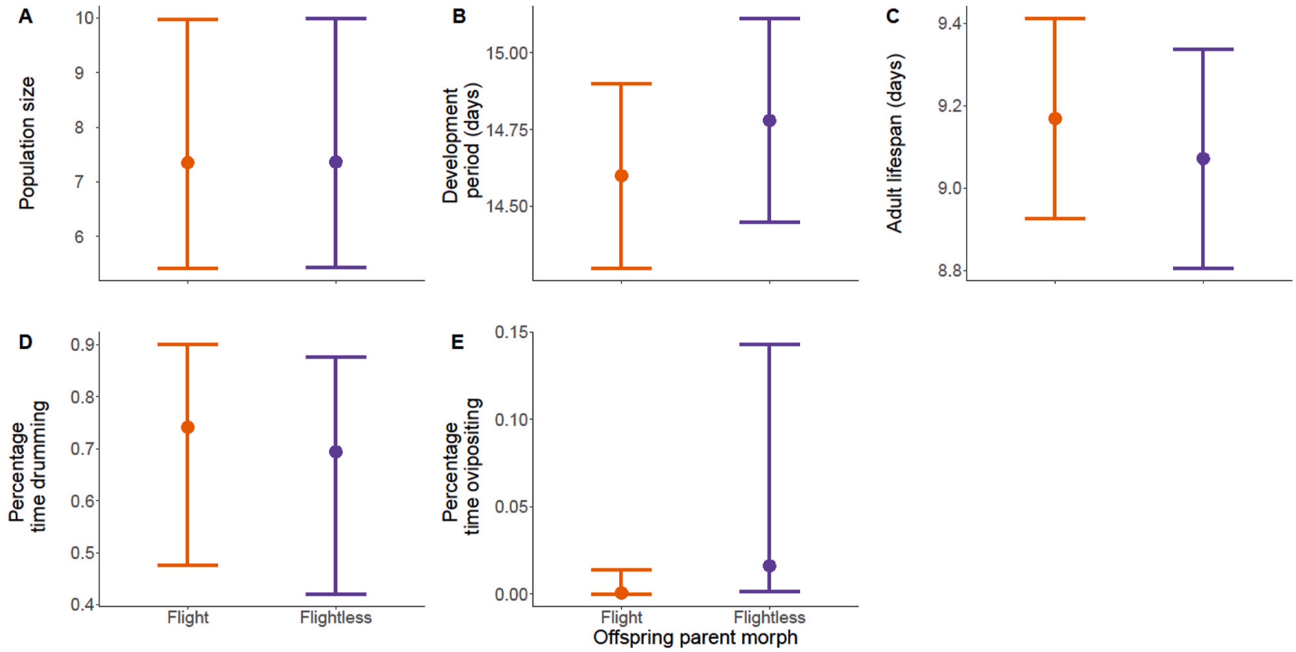

Fig. 3. Parasitoid wasp *D. basalis* performance on the offspring of flight and flightless *C. maculatus* parents. We show the estimated model mean (symbol) and 95% confidence intervals (lines) for each treatment.

Table 3
Anova outputs for linear mixed effects regression models predicting *D. basalis* responses *development period* and *lifespan*) as a function of the main predictors: *C. maculatus* parent morph (flightless or flight). Some models also included as predictors: *C. maculatus* egg number per eppendorf, eppendorf ratio of flightless offspring, eppendorf *D. basalis* count. We report the F-value and P-value for each variable. Interaction terms are indicated by two variable names separated by a colon.

Variable	*F*-value	*P*-value
Development period		
Parent morph	0.544	0.465
Eppendorf no eggs	0.450	0.506
Eppendorf percent flightless	1.533	0.223
Eppendorf wasp count	0.207	0.653
Adult lifespan		
Parent morph	0.243	0.623
Eppendorf no eggs	0.065	0.799
Eppendorf percent flightless	1.863	0.175
Eppendorf wasp count	1.980	0.162

Table 4
Anova outputs for generalized linear mixed effects regression models predicting *D. basalis* responses *population size*, *drumming behavior* and *ovipositing behavior* as a function of the main predictors: *C. maculatus* parent morph (flightless or flight). Some models also included as predictors: *C. maculatus* egg number per Petri dish replicate, ratio of flightless offspring per Petri dish replicate, and the mean number of *C. maculatus* eggs per Petri dish replicate. We report Chi-square statistic (Chisq) and P-value for each variable. Interaction terms are indicated by two variable names separated by a colon.

Variable	Chisq	*P*-value
Population size		
Parent morph	0.632	0.427
Petri no eggs	0.000	0.995
Drumming behavior		
Parent morph	0.059	0.808
Petri mean no eggs	0.059	0.808
Ovipositing behavior		
Parent morph	2.657	0.103
Petri mean no eggs	0.001	0.983

(Akinbuluma and Chinaka, 2023; Ketoh et al., 2002a) but to ensure its effectiveness it is important to consider how this wasp affects and is affected by polymorphism in this globally significant storage pest. Our study partly addressed this question showing that *D. basalis* can affect offspring produced by both the flight and flightless morphs, although we detected some important differences discussed below.

An effective biological control agent should reduce the pest population such that damage remains below the economic injury level (Pappas et al., 2017; Stiling and Cornelissen, 2005). We found clear positive effects of *D. basalis* as a natural enemy and biological control agent. Even with limited exposure (two *D. basalis* wasp females allowed to oviposit for 24 h) the parasitoid reduced *C. maculatus* population size by approximately 23% and lowered larval survival of offspring from flight parents by 15.2% and of offspring from flightless parents by 0.63%. General reduction in population size has been described in previous studies (Akinbuluma and Chinaka, 2023; Amevoin et al., 2007; Ketoh et al., 2002a; Sanon et al., 1998), but here we show that this occurs similarly in populations started by different weevil morphs.

Larval survival and development were affected by the wasp, but adult lifespan of uninfected *C. maculatus* larvae was similar in the control and wasp treatments, suggesting no indirect effects of *D. basalis*. Because parasitized larvae continue to feed until their forth instar, we did not expect or observe reduced bean loss (overall or *per capita*). However, we found greater loss in beans affected by the offspring of the flight morph in wasp treatments. Wasp presence resulted in slower development, which could reflect changes in resource strategy in response to varying competition when some larvae are parasitized. Future work will be necessary to unravel the mechanisms behind this pattern and to evaluate whether this short-term negative impact could reduce efficacy of this biocontrol in the longer-term.

Host variation has previously been shown to affect parasitoid fitness (Urrutia C et al., 2007). We therefore hypothesized that life-history, behavior and biochemical differences between the offspring from the two weevil morphs, such as water and crude fat content (Nwanze et al., 1976; Utida and Takahashi, 1958), could affect the development of *D. basalis* and its effectiveness as a biocontrol agent. Counter to our prediction, *D. basalis* performance and behavior was found to be similar, regardless of whether *D. basalis* was parasitizing offspring from flight or flightless parents. Offspring from different parental morphs may be relatively similar in the early stages and/or parasitoids may not exhibit strong preferences. Indeed, even if parasitoids prefer optimal size hosts, they have been shown to successfully parasitize and grow on hosts of varying sizes (Cohen et al., 2005; Morris and Fellowes, 2002).

Previous work reported differences between the flight and flightless morphs of *C. maculatus* (Caswell, 1960; Utida, 1972). In the present study, we found that the offspring of different parent morphs (flight or flightless) also perform differently in the absence of the parasitoid. For example, adult lifespan was longer in the offspring of flight parents and individuals that were morphed as flight, which agrees with previous literature (adults of the flight morph can live twice as long as flightless morph adults; Appleby and Credland, 2001). Having longer lifespans can enable individuals to disperse over longer distances and potentially infest bean storages in a wider range. While morph types partly reflect different environmental conditions during development, our results support partial heritability of morph type as previously suggested by Caswell (1960) and Utida (1974).

Flight morph weevils had longer development periods from egg to adult emergence. This pattern is consistent with descriptions by Caswell (1960) (Utida, 1972). However, on average, the offspring of flight parents had shorter development periods. Our results could reflect trade-offs between competition and dispersal (Burton et al., 2010): flight morphs are dispersers more likely to colonize new areas, therefore, longer development period could allow more time to develop wings. On the other hand, once a new location is reached, offspring benefit from faster development as competitive ability is beneficial in a new resource. Similarly, we also found that flight parents produced more eggs than flightless parents within a 24 h period, which could represent the initial stages of colonization of a new resource. Previous work found higher lifetime fecundity for the flightless morph ((Utida, 1972). These differences may reflect a trade-off between early exploitation of a new resource by dispersers (a rapid, early reproduction strategy) and competition by non-dispersers (a more constant, higher fecundity strategy). Future experiments will be needed to unravel potential trade-offs and distinct morph strategies.

Dinarmus basalis reduced the number of emerging adults from beans infected by both *C. maculatus* morphs, but was particularly effective at reducing survival in offspring produced by the flight morph. This may suggest a novel cost of dispersal in this pest species, which is worthy of further consideration. In the short term at least, *D. basalis* appears more effective at controlling the offspring of the flight, 'dispersal', morph (Messina, 1987). Therefore, *D. basalis* could be particularly useful in preventing or reducing *C. maculatus* infection of nearby stores. Future work will be needed to test efficacy over a longer time span and under natural conditions. However, if *D. basalis* is indeed more suitable to control new infestations, long-term and broad control could require combination with other known parasitoids of *C. maculatus* (Van Huis et al., 2002).

Polymorphism in pest insects needs to be considered when developing Integrated Pest Management strategies because, as shown here, different morphs can be differently affected by biological control agents. Adaptive management strategies that involve the use of different agents combined or in sequence targeting different stages could be a pathway for improved control. Previous work, which did not explicitly consider polymorphism, has found that combining different biocontrol agents can be beneficial (Kam et al., 2022) although not always (Berger et al., 2017). Biocontrol agents could also be combined with other approaches such as using plant oils as insecticides (Shaaya et al., 1997); however, some of these natural insecticides can have more negative impacts on the biocontrol agents than the pest insects (Ketoh et al., 2002b). In addition, to our knowledge whether natural insecticides affect the two morphs of *C. maculatus* is also unknown and should be explored. Overall, our study provides experimental evidence that intraspecific variation within pest species can influence biological control effectiveness and emphasize the importance of considering this variation when trialing potential methods of biological control for pest species, especially for those displaying distinct dispersal polymorphisms.

Author statement

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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.

Data availability

Data will be made available on request.

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Appendix A

Table A1
Traits used to assess flight and flightless morphs on day of emergence based on studies by Caswell (1960) and Utida (1972) (see Fig. 1 in the main text for photographs)

	Question	Options
1	Is the pygidium more tucked into the elytra than outside of the elytra?	Yes - Flight No - Flightless Unsure – go to 2
2	What is the body shape?	More round/triangular - Flight More ellipsoidal - Flightless

(*continued on next page*)

Table A1 (*continued*)

	Question	Options
3	Looks dark 'wholly black' ground colour	Yes - Flight No - Flightless

Table A2
Traits used to assess flight and flightless morphs when individuals are older based on studies by Caswell (1960) and Utida (1972) (see Fig. 1 in the main text for photographs)

	Question	Options
1	Is the pygidium more white/gold than the weevil's ground colour (red/brown/black)?	Yes - Flight No - Flightless Unsure – go to 2
2	Does the *C. maculatus* have denser white/gold hairs compared to the pygidium of a flightless morph?	Yes - Flight No - Flightless
3	What is the body shape?	More round/triangular - Flight More ellipsoidal - Flightless
4	Is the pygidium more tucked into the elytra than outside of the elytra?	Yes - Flight No - Flightless
5	Looks dark 'wholly black' ground colour	Yes - Flight No - Flightless
6	Is the pygidium more pointed than round?	Yes - Flightless No - Flight
7	Is the pygidium noticeably black with a thin white stripe (as opposed to all one colour)?	Yes - Flightless No - Flight

Table A3
Summary of sample sizes and treatments in the study

Treatment	Number of Petri dishes/repeats	Total number *C. maculatus* at start of experiment	Total number of *D. basalis* used for each treatment
Just Bean (control)	15	NA	NA
Flight Morph	10	310 virgin flight *C. maculatus* (250 F, 60 M) were used to create a 'flight morph mating dish'. Six females were then used per Petri dish for oviposition	NA
Flightless Morph	10	310 virgin flightless *C. maculatus* (250 F, 60 M) were used to create a 'flightless morph mating dish'. Six females were then used per Petri dish for oviposition	NA
Flight Morph + *D. basalis*	10	Six females from the 'flight morph mating dish' were used per Petri dish for oviposition	20
Flightless Morph + *D. basalis*	10	Six females from the 'flightless morph mating dish' were used per Petri dish for oviposition	20

Table A4
All C. maculatus models tested to analyze the effects of C. maculatus parent morph and presence of D. basalis on C. maculatus offspring performance: bean loss, *per capita* bean loss, population size, larvae survival, development period, adult lifespan, and additionally C. maculatus: egg number, percentage flightless and offspring morph. * indicates tested interactions and models used are highlighted in bold.

Model	Fixed predictors	Random Factors
Bean loss		
	Parent morph + presence of *D. basalis* + *C. maculatus* Petri count + *C. maculatus* Petri percentage flightless morph	NA
	Parent morph*presence of *D. basalis* + *C. maculatus* Petri count + *C. maculatus* Petri percentage flightless morph	**NA**
Per capita bean loss		
	Parent morph + presence of *D. basalis* + *C. maculatus* Petri percentage flightless morph	NA
	Parent morph*presence of *D. basalis* + *C. maculatus* Petri percentage flightless morph	**NA**
Population size		
	Parent morph + presence of *D. basalis* + *C. maculatus* Petri egg count	**NA**
	Parent morph*presence of *D. basalis* + *C. maculatus* Petri egg count	NA
Larvae survival		
	Parent morph + presence of *D. basalis*	**Petri dish**
	Parent morph*presence of *D. basalis*	Petri dish
Development Period		
	Parent morph + presence of *D. basalis* + *C. maculatus* Eppendorf egg count	**Petri dish: Eppendorf name**
	Parent morph*presence of *D. basalis* + *C. maculatus* Eppendorf egg count	Petri dish: Eppendorf name
Adult lifespan		
	Parent morph + presence of *D. basalis* + *C. maculatus* Eppendorf egg count + *C. maculatus* emergence morph	**Petri dish: Eppendorf name**

(*continued on next page*)

Table A4 (*continued*)

Model	Fixed predictors	Random Factors
	Parent morph*presence of *D. basalis* + *C. maculatus* Eppendorf egg count + *C. maculatus* emergence morph	Petri dish: Eppendorf name
	Parent morph**C. maculatus* emergence morph + presence of *D. basalis* + *C. maculatus* Eppendorf egg count	Petri dish: Eppendorf name
Egg number		
	Parent morph	**NA**
Percentage flightless		
	Parent morph + presence of *D. basalis* + *C. maculatus* Petri dish egg count	**NA**
	Parent morph*presence of *D. basalis* + *C. maculatus* Petri dish egg count	NA
	Parent morph**C. maculatus* Petri dish egg count + presence of *D. basalis*	NA
Offspring morph		
	Parent morph + presence of *D. basalis* + scale(*C. maculatus* Eppendorf egg count) + scale(*C. maculatus development period)* + scale (*C. maculatus adult lifespan)*	**Petri dish: Eppendorf name**
	Parent morph*presence of *D. basalis* + scale(*C. maculatus* Eppendorf egg count) + scale(*C. maculatus development period)* + scale(*C. maculatus adult lifespan)*	Petri dish: Eppendorf name
	Parent morph*scale(*C. maculatus development period)* + presence of *D. basalis* + scale(*C. maculatus* Eppendorf egg count) + scale(*C. maculatus adult lifespan)*	Petri dish: Eppendorf name

Table A5

All *D. basalis* models tested to analyze the effects of *C. maculatus* parent morph on parasitoid performance: *population size*, *development period*, *drumming behavior*, *ovipositing behavior* and *adult lifespan*. * indicates tested interactions and models used are highlighted in bold.

Model	Fixed predictors	Random Factors
Population Size		
	Parent morph + *C. maculatus* Eppendorf egg count	**Petri dish**
	Parent morph**C. maculatus* Eppendorf egg count	Petri dish
Development Period		
	Parent morph + *C. maculatus* Eppendorf egg count + *D. basalis* Eppendorf count + *C. maculatus* Eppendorf percentage flightless morph	**Petri dish: Eppendorf name**
	Parent morph**C. maculatus* Eppendorf egg count + *D. basalis* Eppendorf count + *C. maculatus* Eppendorf percentage flightless morph	Petri dish: Eppendorf name
	C. maculatus Eppendorf egg count**D. basalis* Eppendorf count + Parent morph + *C. maculatus* Eppendorf percentage flightless morph	Petri dish: Eppendorf name
	Parent morph**D. basalis* Eppendorf count + *C. maculatus* Eppendorf egg count + *C. maculatus* Eppendorf percentage flightless morph	Petri dish: Eppendorf name
Drumming behavior		
	Parent morph + *C. maculatus* Petri dish egg count	**Petri dish**
	Parent morph**C. maculatus* Petri dish egg count	Petri dish
Ovipositing behavior		
	Parent morph + *C. maculatus* Petri dish egg count	**Petri dish**
	Parent morph**C. maculatus* Petri dish egg count	Petri dish
Adult lifespan		
	Parent morph + *C. maculatus* Petri dish egg count + *C. maculatus* Eppendorf percentage flightless morph	**Petri dish**
	Parent morph**C. maculatus* Petri dish egg count + *C. maculatus* Eppendorf percentage flightless morph	Petri dish
	Parent morph**C. maculatus* Eppendorf percentage flightless morph + *C. maculatus* Petri dish egg count	Petri dish

Table A6

Anova outputs for linear regression models predicting cowpea weevil *C. maculatus* responses *egg number* and *percentage flightless* as a function of the main predictors: parent morph (flightless or flight). *Percentage flightless* also included the predictors: presence of *D. basalis* (yes or no) and *C. maculatus* egg number per Petri dish replicate. We report the sum of squares (sum sq), the arithmetic mean (mean sq), degrees of freedom in the numerator (numDF), degrees of freedom in the denominator (denDF), F-value and P-value for variables. Significant variables and interactions are highlighted in bold.

Variable	Sum sq	DF	*F*-value	*P*-value
Egg number				
Parent morph	**21669.000**	**1**	**20.063**	**<0.0001**
Percentage flightless				
Parent morph	**1041.260**	**1**	**12.037**	**0.001**
Presence of wasp	177.740	1	2.055	0.160
Petri no eggs	233.190	1	2.696	0.109

Table A7

Anova outputs for generalized linear mixed effects regression models predicting *offspring morph* as a function of the main predictors: *C. maculatus* parent morph (flightless or flight) and presence of *D. basalis* (yes or no), and also: *C. maculatus* egg number per Eppendorf, *C. maculatus development period* and

C. maculatus adult lifespan. We report Chi-square statistic (Chisq), degrees of freedom (DF) and P-value. Significant variables and interactions are highlighted in bold.

Variable	Chisq	Df	*P*-value
Parent morph	34.8957	1	<0.0001
Presence of wasp	1.1391	1	0.286
Eppendorf no eggs	**18.1779**	**1**	**<0.0001**
Weevil *development period*	**6.5734**	**1**	**0.010**
Weevil *adult lifespan*	**28.6874**	**1**	**<0.0001**

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