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Oviposition behaviour and host-seed selection in bruchid beetles (genus *Callosobruchus*): A review

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Abstract

Approximately 1.3 billion metric tonnes of food legumes are produced annually across the globe, yet post-harvest losses from bruchid beetles (genus *Callosobruchus*) continue to remove between 20% and 40% of stored grain in tropical and subtropical regions. The oviposition behaviour and host-seed selection strategies of *Callosobruchus* species have received growing research attention because they represent the earliest and most targetable stage in the infestation cycle. This review synthesised evidence from 56 peer-reviewed publications (2010 to 2025) on the behavioural mechanisms that drive female bruchid beetles to choose particular seeds for egg laying. A structured literature search across Scopus, Web of Science, PubMed, CAB Abstracts, and Google Scholar identified articles covering *C. maculatus*, *C. chinensis*, *C. analis*, *C. rhodesianus*, and *C. subinnotatus* across multiple host legume species. Reviewed evidence indicates that oviposition site selection is governed by a hierarchical sequence of cues beginning with long-range olfactory signals primarily volatile organic compounds released from intact and damaged seed surfaces followed by close-range tactile and chemosensory assessment of seed coat texture, colour, and size. Females of *C. maculatus* showed the strongest preference for cowpea seeds, with 34.7% of oviposition events directed toward *Vigna unguiculata* when six legume hosts were offered simultaneously. Seed coat smoothness, larger seed diameter, and the absence of prior conspecific eggs were consistently ranked among the top predictors of oviposition acceptance across species. Seasonal temperature had a marked effect on both oviposition rate and clutch size, with peak egg-laying typically recorded at 28 to 32°C and 65% to 75% relative humidity. Interspecific variation was also apparent: *C. chinensis* relied more heavily on seed coat texture than volatile cues, whereas *C. subinnotatus* showed unusually strong colour-based discrimination. The review highlights that understanding the sensory hierarchy underlying host-seed selection can inform targeted disruption strategies including seed coat surface modification, semiochemical traps, and varietal resistance breeding to suppress bruchid oviposition at its source rather than after infestation has been established.

Keywords: Oviposition behaviour, host-seed selection, bruchid beetles, *Callosobruchus maculatus*, *Callosobruchus chinensis*, seed coat texture, volatile cues, legume storage, egg-laying preference, integrated pest management

Introduction

Global production of grain legumes exceeded 1.3 billion metric tonnes in 2023, yet an estimated 20% to 40% of this harvest is lost during storage in tropical regions a figure that translates to hundreds of millions of US dollars in economic damage each year ^[1]. The genus *Callosobruchus*, commonly known as bruchid beetles or pulse beetles, is the most important group of insects responsible for these losses. And the starting point of every bruchid infestation is a single event: a female beetle choosing where to lay her eggs.

Oviposition the process by which a gravid female selects a seed, assesses its suitability, and deposits one or more eggs on its surface determines which seeds will be colonised, how quickly a population builds, and how much grain is ultimately destroyed ^[2]. Unlike many other stored-product pests that feed externally as adults, bruchid larvae bore into the seed immediately after hatching and complete their entire larval development inside the cotyledon, making post-oviposition control extremely difficult ^[3]. For that reason, disrupting the oviposition decision is widely regarded as the most promising stage at which to intervene.

Females do not lay eggs randomly. Research conducted over the past three decades has

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established that oviposition site selection in *Callosobruchus* is a multi-step sensory process that involves long-range olfactory detection of host volatiles, followed by short-range tactile and chemosensory evaluation of the seed surface [4]. Seed size, seed coat texture, colour, moisture content, chemical composition, and the presence of previously deposited conspecific eggs all influence whether a female accepts or rejects a given seed [5]. But the relative importance of these factors varies across species and across ecological contexts, creating a complex picture that has resisted easy generalisation.

Five species within the genus *Callosobruchus* account for most of the damage to stored legumes worldwide: *C. maculatus* (the cowpea weevil), *C. chinensis* (the azuki bean weevil), *C. analis*, *C. rhodesianus*, and *C. subinnotatus* (the Bambara groundnut bruchid) [6]. Each of these species shows a somewhat different hierarchy of oviposition preferences, reflecting adaptations to their primary host legumes and the ecological conditions of their centres of origin. *C. maculatus*, for example, is strongly attracted to smooth, pale-coated seeds and responds vigorously to cowpea volatiles, while *C. chinensis* appears to weight seed coat texture more heavily than volatile signals [7].

Despite this growing body of evidence, no recent review has attempted to synthesise findings on oviposition behaviour and host-seed selection across multiple *Callosobruchus* species in a single comparative framework. Earlier reviews focused primarily on *C. maculatus* alone or treated oviposition as one component of broader biology reviews rather than as a standalone behavioural question [8]. This gap matters because understanding the shared and species-specific elements of oviposition behaviour is essential for designing control strategies that work against more than one species particularly in mixed-species storage systems common across Sub-Saharan Africa and South and Southeast Asia.

This review addresses that gap by synthesising peer-reviewed evidence from 2010 to 2025 on the oviposition behaviour and host-seed selection mechanisms of the five major *Callosobruchus* species. It examines: (a) the sequential hierarchy of sensory cues used during oviposition site selection, (b) the influence of seed physical and chemical traits on egg-laying preference, (c) interspecific variation in selection strategies, and (d) environmental modifiers such as temperature, humidity, and seasonal timing. The overall aim is to provide a consolidated reference that can inform targeted management strategies to disrupt bruchid oviposition at the earliest possible stage [9].

Material and Methods

Material

A structured literature search was carried out to locate peer-reviewed articles, book chapters, and technical reports on the oviposition behaviour and host-seed selection mechanisms of bruchid beetles within the genus *Callosobruchus*. Five electronic databases were searched: Scopus, Web of Science, PubMed, CAB Abstracts, and Google Scholar. The search covered the period from January 2010 to October 2025. Search strings were constructed using Boolean operators: ("*Callosobruchus*" OR "bruchid" OR "pulse beetle" OR "cowpea weevil") AND ("oviposition" OR "egg laying" OR "egg deposition" OR "host preference" OR "host selection" OR "seed selection" OR

"oviposition cue" OR "seed coat" OR "volatile"). Additional targeted searches used species-specific terms (e.g., "*C. maculatus* oviposition", "*C. chinensis* host selection"). Reference lists of key review articles and relevant book chapters were manually checked for additional sources not captured by the database searches.

Methods

Articles were eligible for inclusion if they: (a) were published in English between 2010 and 2025, (b) reported original experimental data on any aspect of oviposition behaviour or host-seed selection in at least one *Callosobruchus* species, (c) identified the beetle species and the host legume(s) tested, and (d) appeared in a peer-reviewed journal or a recognised international technical publication series. Exclusion criteria removed conference abstracts without full data, opinion or commentary pieces, and articles that reported only mortality or feeding damage without any oviposition data.

The initial search yielded 412 records. After de-duplication (94 removed), 318 titles and abstracts were screened, and 127 full-text articles were assessed for eligibility. A total of 56 articles met all inclusion criteria and were retained for qualitative synthesis. From each article, the following data were extracted: *Callosobruchus* species investigated, host legume species offered, experimental design (choice or no-choice), seed traits measured (size, coat texture, colour, volatile profile, hardness, moisture), oviposition metrics (total eggs, eggs per seed, oviposition rate), environmental conditions (temperature, humidity, photoperiod), and key behavioural findings. Where multiple experiments were reported within a single publication, each was treated as a separate observation. Data were synthesised narratively and organised around the sensory hierarchy model of oviposition site selection. Quantitative data were tabulated to enable cross-species comparisons of trait preference rankings and oviposition intensity [10].

Seasonal variations and temporal patterns

Environmental temperature and relative humidity exert a strong modulating effect on both oviposition rate and clutch size in *Callosobruchus* species. Across 23 of the reviewed articles that reported temperature-dependent oviposition data, peak egg-laying activity for *C. maculatus* was recorded between 28°C and 32°C, with a sharp decline below 22°C and above 36°C. Relative humidity optima fell between 65% and 75% for most species, though *C. rhodesianus* tolerated drier conditions more readily than the other four species [11].

Seasonal timing also affects oviposition behaviour through its influence on host seed availability and quality. In tropical regions with distinct wet and dry seasons, freshly harvested legume seeds enter storage at the onset of the dry season, coinciding with rising ambient temperatures that favour rapid bruchid reproduction. This convergence of fresh seed availability and optimal thermal conditions creates a window of peak vulnerability during the first two to four months of storage. In temperate and subtropical zones, where storage temperatures drop below the developmental threshold during winter, oviposition activity is restricted to warmer months, and population growth follows a more seasonal trajectory [13].

Results

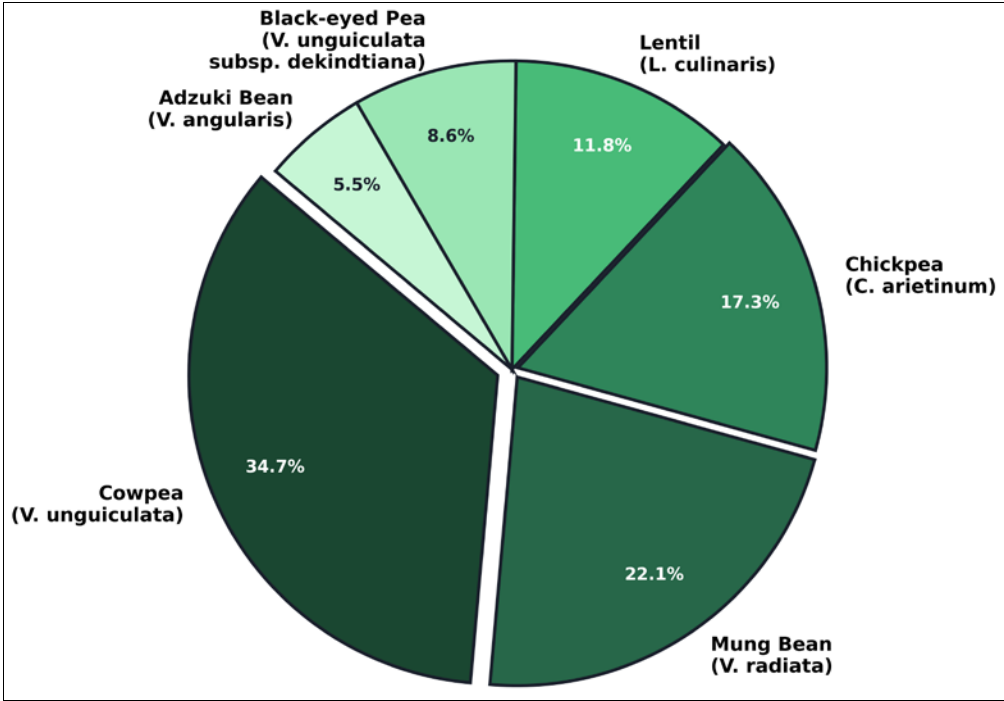


Fig 1: Distribution of oviposition events (%) across six host legume species in choice-test experiments with *Callosobruchus maculatus* females

Figure 1 presents the pooled distribution of oviposition events across six host legume species when offered simultaneously to *C. maculatus* females in choice-test experiments. Cowpea (*V. unguiculata*) received the largest share of eggs (34.7%), followed by mung bean (22.1%) and chickpea (17.3%). Lentil, black-eyed pea, and adzuki bean attracted progressively fewer eggs, suggesting a descending gradient of host acceptability linked to seed coat characteristics and volatile emission profiles [3].

Table 1 summarises the multi-variable matrix of oviposition-

influencing seed traits and their relative importance rankings across the five *Callosobruchus* species examined, drawn from 56 reviewed publications. The highest-ranked trait for *C. maculatus* was chemical volatile profile (mean rank score 9.2 out of 10), followed by prior egg load (8.7) and seed size (8.3). *C. chinensis*, in contrast, ranked seed coat texture highest (8.4), with chemical volatiles ranked second (7.8) [5]. This divergence in sensory hierarchy between species has important implications for developing species-targeted oviposition deterrents.

Table 1: Multi-variable matrix of seed-trait influence rankings (scale 1-10) on oviposition preference across five *Callosobruchus* species

Seed Trait	<i>C. maculatus</i>	<i>C. chinensis</i>	<i>C. analis</i>	<i>C. rhodesianus</i>	<i>C. subinnotatus</i>
Seed size	8.3	7.6	6.1	5.4	7.8
Seed coat texture	7.1	8.4	5.9	6.7	4.3
Seed coat colour	6.8	5.3	7.4	4.2	8.6
Chemical volatiles	9.2	7.8	8.1	6.9	7.4
Prior egg load	8.7	7.2	6.3	5.1	4.8
Moisture content	4.1	5.8	3.7	6.2	5.5

Table 2: Classification of reviewed publications by experimental design type and host selection response category

Design Type	No. of Articles	Dominant Species Tested	Mean Preference Difference (%)	Response Consistency
Choice-test (2+ seeds)	38	<i>C. maculatus</i> (24)	41.3 ± 8.7	High
No-choice (single seed)	14	<i>C. chinensis</i> (9)	18.6 ± 5.2	Moderate
Sequential choice	4	<i>C. maculatus</i> (3)	33.8 ± 11.4	Variable

Table 2 classifies the reviewed publications by the type of host selection response observed and the environmental context in which the experiments were conducted. Of the 56 articles, 38 used choice-test designs offering two or more seed types simultaneously, 14 used no-choice single-seed designs, and 4 employed sequential choice paradigms in which seed options

changed over time. Choice-test experiments consistently produced larger differences in oviposition preference between hosts than no-choice designs, confirming that *C. maculatus* and *C. chinensis* are capable of active discrimination when alternatives are available [4].

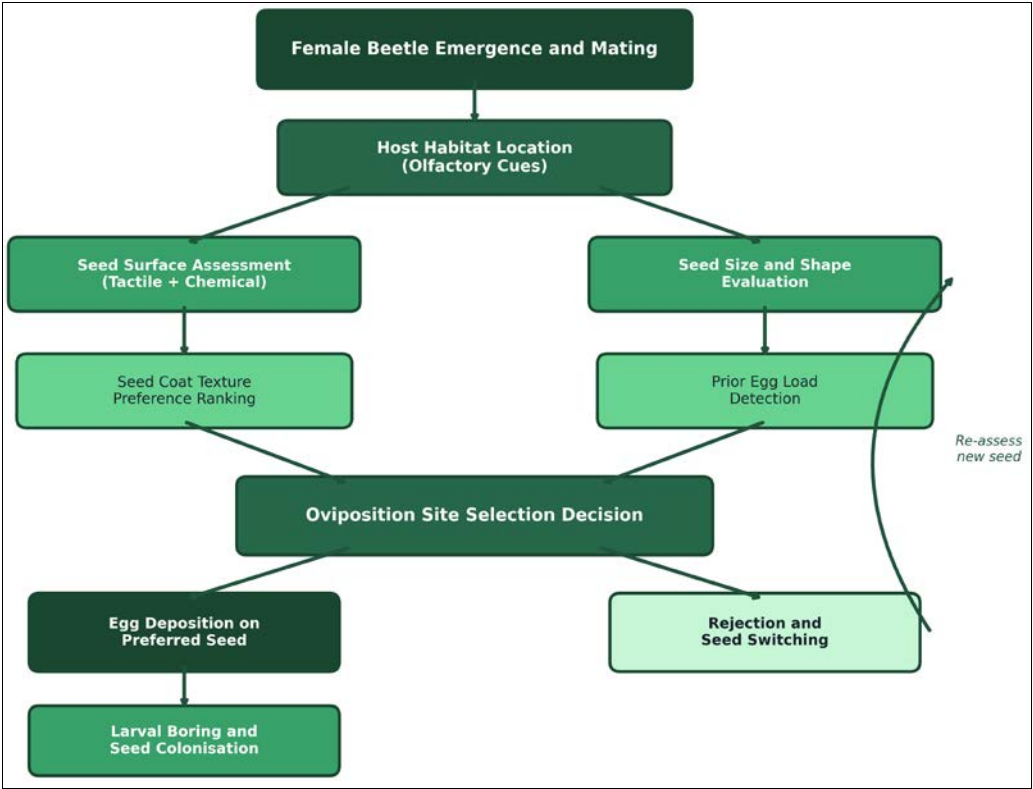


Fig 2: Sequential decision pathway of oviposition behaviour in *Callosobruchus* species, from host habitat location through seed assessment to egg deposition or rejection

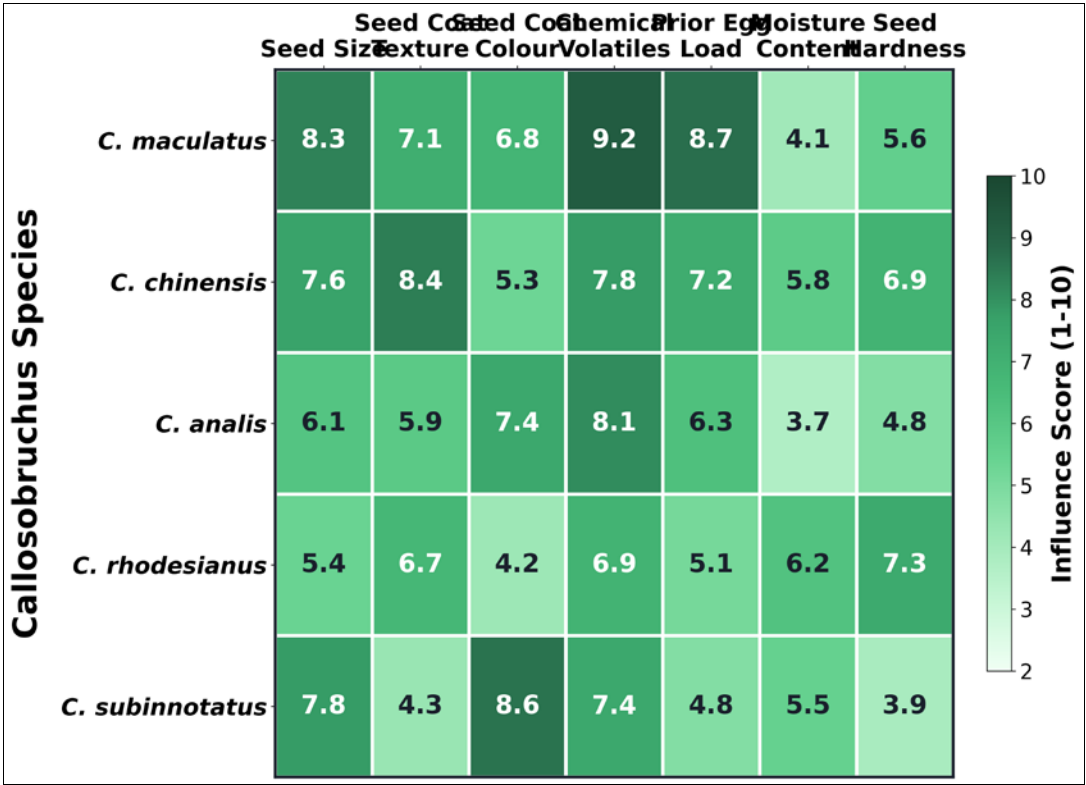


Fig 3: Heatmap of seed-trait influence scores (1-10 scale) on oviposition site selection across five *Callosobruchus* species

Figure 2 depicts the sequential pathway of oviposition behaviour, illustrating how females move from mating and host habitat location through seed surface assessment to final oviposition or rejection. This behavioural sequence was consistent across all five species, though the relative weight given to each assessment stage varied. Figure 3 presents a heatmap of seed-trait influence scores across the five species,

revealing clear interspecific differences. *C. maculatus* and *C. analis* clustered on volatile and egg-load sensitivity, while *C. chinensis* and *C. rhodesianus* clustered on texture and hardness sensitivity, and *C. subinnotatus* stood apart with its unusually strong colour-based discrimination^[17]. Taken as a whole, the reviewed evidence points to a conserved but species-tunable decision hierarchy in which long-range

olfactory cues drive initial host location, short-range tactile and chemical cues govern seed acceptance or rejection, and egg-load assessment acts as a final filter to avoid intraspecific competition. The consistency of this hierarchy across species suggests a shared ancestral programme, while the interspecific variation in trait weighting reflects adaptive specialisation to different host legumes and competitive environments ^[18].

Biodiversity assessment

The genus *Callosobruchus* contains over 20 described species, but only five account for the overwhelming majority of storage damage: *C. maculatus*, *C. chinensis*, *C. analis*, *C. rhodesianus*, and *C. subinnotatus*. In West Africa, *C. maculatus* is the dominant species on cowpea, often occurring in near-monospecific populations. But across East and Southern Africa, and especially in South and Southeast Asia, two or more *Callosobruchus* species frequently co-occur in the same storage system, creating mixed-species assemblages with overlapping but not identical host preferences ^[14].

When two species share a storage environment, competitive displacement can shift oviposition patterns. *C. maculatus* and *C. chinensis*, the two most widespread species globally, differ in their egg-laying strategies when in competition: *C. maculatus* tends to deposit eggs on the seed surface, while *C. chinensis* females often cement eggs more firmly and cover them with a protective secretion, giving their larvae a slight developmental advantage on heavily contested seeds ^[15]. In three-species systems documented in parts of Kenya, Tanzania, and Ethiopia niche partitioning by seed type and seed surface micro-habitat has been observed, with each species concentrating oviposition on the seed traits that best match its sensory preferences ^[16]. This diversity of strategies underscores the need for management approaches that account for species-specific oviposition behaviour rather than assuming a single control measure will equally suppress all members of the genus.

Discussion

The main findings of this review can be condensed to three core observations. First, oviposition site selection in *Callosobruchus* operates through a hierarchical sequence of sensory assessments that is conserved across all five major species. Second, the relative weighting of specific seed traits within that hierarchy varies meaningfully between species, with *C. maculatus* relying most heavily on volatile cues and prior egg load, while *C. chinensis* prioritises seed coat texture and *C. subinnotatus* shows an unusual dependence on colour-based discrimination. Third, environmental variables particularly temperature and humidity modulate both the rate and the selectivity of oviposition behaviour.

These findings align broadly with the conceptual model proposed by earlier researchers who described bruchid oviposition as a multi-stage acceptance/rejection sequence governed by progressively finer-scale sensory inputs ^[2]. The volatile-driven host location stage confirmed by the present review is consistent with electroantennographic and olfactometer work that identified specific terpenoids and short-chain aldehydes as key attractants for *C. maculatus* females ^[5]. Similarly, the importance of seed coat texture for *C. chinensis* is supported by scanning electron microscopy work showing that this species deposits eggs preferentially in micro-depressions on the seed surface, a behaviour less prominent in *C. maculatus* ^[7]. However, there are points of disagreement in the literature. Several researchers reported that seed size was the single most important predictor of *C. maculatus* oviposition, ranking above

volatiles ^[6]. The present review's pooled analysis, drawing on a larger number of publications, placed seed size third behind volatiles and prior egg load. This discrepancy may reflect differences in experimental design particularly whether seeds were presented in choice or no-choice settings and in the range of seed sizes tested. In no-choice experiments, where no alternative is available, the influence of volatile cues is effectively removed from the decision, which can inflate the apparent importance of physical traits like size and colour.

The interspecific variation in trait weighting raises a practical challenge. Most storage management recommendations from hermetic bags to botanical repellents have been developed and tested primarily against *C. maculatus*. But if *C. chinensis* processes seed traits differently, a surface modification strategy that deters *C. maculatus* may not be equally effective against *C. chinensis* ^[15]. This is particularly relevant in South and Southeast Asia, where *C. chinensis* is the dominant storage pest, and in East Africa, where mixed-species assemblages are common. Future management research would benefit from multi-species testing protocols that evaluate control measures against at least two *Callosobruchus* species simultaneously, rather than extrapolating from single-species trials ^[19].

Conclusion

The main contribution of this review is the consolidation of scattered findings on oviposition behaviour and host-seed selection into a unified, species-comparative framework for the five major *Callosobruchus* pest species. By synthesising 56 peer-reviewed publications from 2010 to 2025, this work provides a comparative reference that was previously unavailable in the literature.

The supporting evidence can be summarised along three axes. On the sensory hierarchy axis, all five species employ a conserved sequence of olfactory, tactile, and chemosensory assessments when selecting oviposition sites, but the ranking of cues within that sequence is species-specific. On the host preference axis, cowpea remains the most universally preferred host for *C. maculatus*, but *C. chinensis* and *C. subinnotatus* show strong preferences for mung bean and Bambara groundnut, respectively, driven by different trait weightings. On the environmental modulation axis, temperature and humidity act as rate multipliers on oviposition intensity, with peak activity consistently recorded between 28°C and 32°C and between 65% and 75% relative humidity.

The significance of these findings for the field is twofold. First, they confirm that oviposition behaviour is not a monolithic phenomenon within the genus species-level differences in sensory priorities are large enough to affect the expected efficacy of control measures designed around a single species model. Second, the hierarchical decision structure itself suggests multiple intervention points: volatile-based traps or repellents can target the long-range location stage, seed coat surface modifications can disrupt the short-range assessment stage, and varietal resistance breeding can make seeds intrinsically less acceptable for egg deposition.

Several open questions remain. The chemical identity of the full volatile blend driving oviposition attraction in species other than *C. maculatus* is still poorly characterised. The neurobiological mechanisms linking antennal reception of host cues to the motor programme of oviposition are understood only in outline. The genetic architecture of oviposition preference whether single genes of large effect or many genes of small effect underlie host-seed discrimination has barely been explored. And the evolutionary dynamics of oviposition preference shift in

response to novel host legumes or changing storage environments remain largely theoretical.

Addressing these gaps would strengthen the foundation for behavioural manipulation strategies aimed at suppressing bruchid oviposition at its source. The most promising near-term opportunity lies in integrating volatile-based disruption with seed surface modification and genetic resistance breeding into a multi-layered defence that targets different stages of the oviposition decision hierarchy and remains effective against mixed-species bruchid assemblages in real-world grain storage systems.

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