



Effect of field infestations of immature pigeonpea (*Cajanus cajan* (L.) Millsp.) pods on production of active (flight) and sedentary (flightless) morphs of *Callosobruchus chinensis* (L.)

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Abstract

A study conducted in Uganda on *Callosobruchus chinensis* showed that adults emerging from dry seed-infested and immature pod-infested pigeonpea differed in a number of morphological and biological characteristics in one or both sexes. Adults emerging from dry seed-infested pigeonpea were more or less uniform in a number of these characteristics; in contrast, adults emerging from green pod-infested pigeonpea differed depending upon when they emerged: the differences were greatest between those emerging during the 2nd to the 6th days from first emergence, and those emerging from the 8th to the last days of emergence. In one or both sexes, these differences were expressed in terms of elytral hue and size, body length, distance between the compound eyes, length of pygidium, body water content, pre-maturation periods, fecundity and adult longevity. We suggest that these differences are due to polymorphism, and specifically the predominance of flight forms among late emergers from pod-infested pigeonpea. The differences observed in the two morphs of *C. chinensis* and ascribed to the flight and flightless forms, are thought to be adaptations for survival and propagation under field and storage conditions, respectively. The predominance of emerged adults of the flightless forms from dry seed and the flight forms from green pods were associated with low moisture content in dry seed and high moisture content in green pods, respectively. These observations show that bruchid control measures are needed in the field as well as in storage. © 1999 Published by Elsevier Science Ltd. All rights reserved.

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1. Introduction

In many parts of the tropics, bruchid infestation on legumes starts in the field (Caswell, 1968; Southgate, 1978; Taylor, 1981; Nene and Sheila, 1990; Silim Nahdy, 1995) and is characterised by its insidious nature (Taylor, 1981); eggs are usually glued on green or drying pods, the young first instar larvae bore into the seeds and, at threshing, seeds either show slight or no apparent external damage (Booker, 1967; Caswell, 1968; Southgate, 1978). Although infestation and damage in the field are generally low, such infestation nevertheless has serious implications. This is because the insects multiply very rapidly within a short time, with very high consequent damage, once infested seeds are stored (Taylor, 1981). Though the major origin of storage infestation is from the field, cross infestation within stored commodities also occurs (Caswell, 1968; Singh and Jambunathan, 1990).

Studies conducted on *Callosobruchus* spp., especially *C. maculatus*, have shown that two distinct morphs of adults occur, one living out doors and infesting the crop in the field and the other multiplying and infesting stored seeds (Southgate, 1958, 1979; Utida, 1972; Messina, 1990). The field and storage forms have been referred to as the active or flight forms and the inactive-, non-flight, normal or sedentary forms, respectively. The occurrence of the flight and flightless forms of bruchids have been reported to arise from the differences in the ecological niches they occupy, flight forms being adapted to field conditions and the flightless forms to post-harvest seed storage conditions (Messina, 1990).

Among natural populations of *C. maculatus* and *Acanthoscelides obtectus* (Say), slower developmental rates have been associated with the active or flight morph stage, and faster development with the normal or flightless morph stage (Utida, 1972; Nwanze and Horber, 1976; Messina et al., 1987; Messina and Renwick, 1985, Gopal, 1986). Silim Nahdy et al. (1998) reported significant variation in mean incubation periods and adult emergence of *C. chinensis* following oviposition on immature pods at different pod developmental stages. In particular, the duration between the earliest and latest *C. chinensis* adult emergence varied greatly between pods infested at different development stages. They suggested that the differences were due to the varying proportions of *C. chinensis* morphs that developed in the pods. Silim Nahdy (1995) reported that at the start of pod formation (PR-1) and at early pod fill (PR-2), the variation in days between the earliest and latest adult emergence was very small (<7 days), and all adults emerged after a mean of 42 days of incubation. From the late pod fill (PR-3), mature green pod (PR-4), and mature yellow pod (PR-5), much wider variation in the days between the earliest and latest adult emergence was detected (>15 days). In addition, in PR-4 a bimodal emergence was observed (Fig. 1), with emergence generally well spread between 35 and 50 days, but concentrating between 35 and 41 days and between 42 and 50 days from oviposition. From seed-infested pigeonpea, the range between the earliest and latest adult emergence was wide (15 days), but most adults emerged very early (<40 days) and mean developmental period was only 38 days (Fig. 1). Silim Nahdy (1995) postulated that most, if not all *C. chinensis* that emerged from eggs laid in PR-1 and PR-2 stages may have been the active morphs because of the long incubation periods and those from eggs laid on pods at stages PR-3 to PR-5, may have been a mixture of the two morphs, with the non-flight forms emerging earliest and the flight forms emerging later.

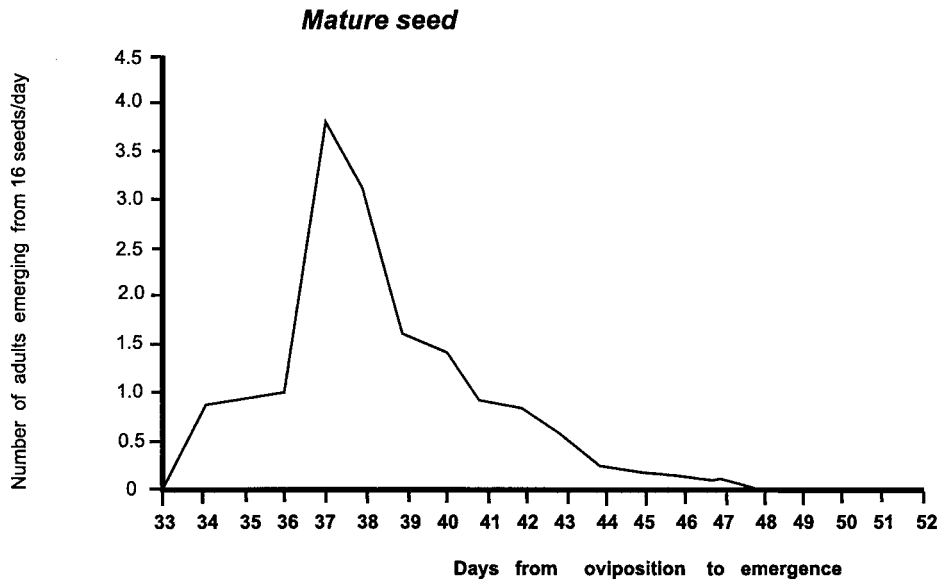
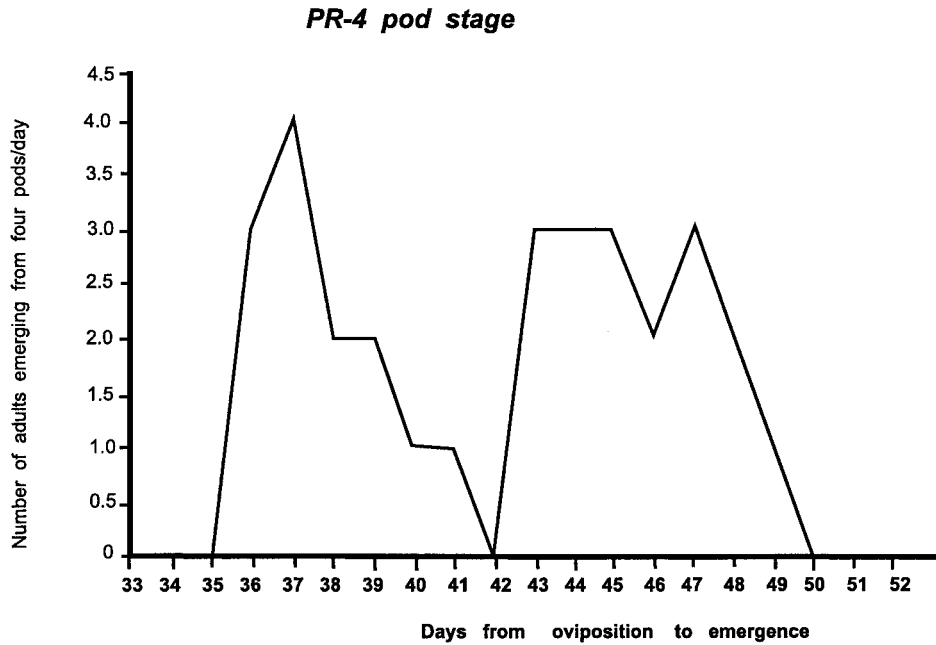


Fig. 1. Frequency distribution of emergence times of *C. chinensis* in pod- and seed-infested pigeonpea following oviposition on pods during PR-4 and mature seeds.

In *C. maculatus*, additional differences noted were in morphology, physiology, biology and behaviour (Utida, 1972, 1981; Nwanze and Horber, 1976; Messina et al., 1987; Messina and Renwick, 1985). Specifically, differences were noted in elytral colour patterns; body, wing and pygidium sizes and distance between the compound eyes; pre-maturation durations, fecundity, adult life-span, body fat and water content (Utida and Takahashi, 1958; Utida, 1981). Given that the wide variation in pre-imaginal development periods from infested pigeonpea pods (Silim Nahdy et al., 1998) was by itself insufficient to confirm the occurrence of the two morph forms, further investigations were conducted to determine whether there are differences in insects that emerge earlier or later from pod- and seed-infested samples.

2. Materials and methods

All investigations were conducted using adult *C. chinensis* cultured in the laboratory under ambient conditions (about 24°C) using pigeonpea seeds of the Uganda landrace variety “Apio-elina”. The original cultures were obtained from damaged seeds of “Apio-elina” and cultures were renewed after every two generations i.e. there was no selection by repeated laboratory culture. In all cases 2-day old adults were used to get maximum oviposition. Sexing was done using antennal shape (Southgate, 1958).

“Apio-elina” pigeonpeas originating from the Lira/Apac district of northern Uganda were sown in March 1994 at Kawanda Agricultural Research Institute (KARI), 12 km north of Kampala (0.4°N, 32.5°E and about 1150 m altitude). From emergence until maturity of the pigeonpeas, weeds were controlled by regular hand weeding. At the start of flowering, plants were tagged and stages of pod development monitored every 2 days. Mature green pods at developmental stage ‘PR-4’ (Silim Nahdy et al., 1998) were tagged.

In the field, pods still attached to plants were used for the study. Four pods per cluster at developmental stage ‘PR-4’ were caged using nylon sleeve cages. The treatment was replicated 20 times. Each cage measured 20 (length) by 8 cm (diameter). If pods older or younger than PR-4 interfered with those selected, they were removed prior to caging. Four pairs of 2-day old adult *C. chinensis* were introduced into each cage and allowed to lay eggs for 4 days, then removed. The pods were left attached to the plant within the cages. At maturity, pods from each cage were harvested and the four pods per cluster shelled separately in the laboratory. The seeds obtained from each cage (from four pods) were placed in separate glass vials and incubated under ambient conditions (23–26°C). As a basis of comparison, dry seeds (about 14% moisture content; mc) were placed in glass vials and infested at a similar rate and durations as the pods. The vials were examined daily for adult emergence.

Two trials were conducted for both pod- and seed-infested pigeonpea. Emerging adults from each trial were collected every 48 h and sexed. These were kept in separate plastic vials and labeled according to the source of infestation (pod or seed), day of emergence, and sex. The first set of adults (Trial 1) were investigated for morphological differences. The second set (Trial 2) were investigated for biological differences. Insects kept for biological studies were kept in pairs (males and females) within the same vial and in all cases, a minimum of 10 pairs of *C. chinensis* were used, classified according to the respective origin of infestation and per trial.

2.1. Trial 1: Morphological characteristics

The objective of this investigation was to determine whether or not there were differences in morphological characteristics between, (1) emerging insects whose infestation origin were pods and those whose infestation origin were seeds, and (2) between insects emerging on each subsequent day from the first day of emergence.

A number of morphological features were observed and recorded in both sexes for adults emerging on each day from first adult emergence. The features recorded were: elytral colour (both upper and lower), elytral wing dimensions (length and width), body length, pygidium length, distance between the compound eyes, and the percentage mc of individual adults.

The elytral colour was scored on a scale of 1–3 on a subjective basis, as follows: 1=very dark, 2=moderately dark, and 3=light. The frequency distribution for wing colour was graphically presented. Measurements of all dimensions were made under the binocular microscope using an eye-piece graticule. A two-stage mc measurement using the oven method was taken for individual adults from the first set of insects after all the observations were made. All data collected were subjected to one-way analysis of variance and mean measurements were plotted graphically.

2.2. Trial 2: Biological differences

From the second set of insects a number of biological factors were investigated to determine differences between (1) emerging insects from pod-infested and seed-infested pigeonpea; and (2) insects emerging on different days after the initial infestation. The factors measured were pre-maturation period (days taken from adult emergence to egg laying), fecundity (number of eggs laid in adult life time) of females, and adult longevity of both sexes.

Single pairs of newly-emerged adults were placed in glass vials containing 10 uninfested pigeonpea seeds. The seeds were examined every 12 h to determine the time of first egg deposition by each insect. The same adults were allowed to continue laying eggs. Seeds with eggs were carefully removed every 2 days, the egg number on the seeds counted and recorded and the exact number of seeds removed were replaced with uninfested seeds. This process continued until no further egg laying was recorded. Thus the total number of eggs laid per female was recorded.

Adult life span was determined by daily observations of the insects through glass vials, without disturbing them. Where inactivity or an unnatural position at rest of the adult was noted, the suspect insect was carefully removed to determine whether it was dead or alive by gently blowing air (from the mouth) on the insect and/or exposing it to heat and glare from a naked electric bulb. Daily mortality was recorded and tabulated until all insects had died. All data collected were subjected to one-way analysis of variance.

3. Results

3.1. Differences between adult *C. chinensis* emerging from seed- and pod-infested pigeonpea

There was a large variability in the morphology and biology of *C. chinensis* that emerged from pod- and seed-infested pigeonpea (Table 1). In the females, more than 80% of those emerging from seeds originating from infested green pods had moderately dark or very dark elytra, but the value was lower (about 60%) for those from infested mature seeds (Fig. 2). In the males, however, the opposite occurred; the elytral colour of adults emerging from infested mature seeds was always moderately dark or very dark, and over 50% of those emerging from seeds originating from infested green pods were light brown (Fig. 2). The female and male mean body and pygidial lengths, mean male elytral width and elytral lengths were significantly longer ($P < 0.05$) on adults emerging from pod-infested rather than from seed-infested pigeonpea. These data imply that active flight forms are larger than the sedentary flightless forms. The mean distance between the compound eyes was less ($P < 0.05$) in females but greater in males emerging from pod-infested than from seed-infested pigeonpea. The mean body mc of both sexes and fecundity of females, were lower ($P < 0.05$) in adults emerging from pod-infested than seed-infested pigeonpea, while the mean pre-maturation periods of females and adult longevity of both sexes were longer ($P < 0.05$).

Table 1

Comparison of characteristics of *C. chinensis* (males and females) emerging from pod- and seed-infested pigeonpea (see in parenthesis)

| Characteristics | Sex | Origin of infestation ^a | | <i>P</i> ^b |
|--|--------|------------------------------------|-----------------------|-----------------------|
| | | Infested green pods | Infested mature seeds | |
| 1. Elytral dimensions (mm) | | | | |
| -length | Female | 1.74 (0.010) | 1.72 (0.010) | NS |
| | Male | 1.61 (0.010) | 1.50 (0.010) | * |
| -width | Female | 0.77 (0.010) | 0.76 (0.010) | NS |
| | Male | 0.67 (0.018) | 0.51 (0.016) | * |
| 2. Body length (mm) | Female | 3.31 (0.056) | 3.09 (0.038) | * |
| | Male | 2.64 (0.160) | 2.27 (0.136) | * |
| 3. Distance between compound eyes (mm) | Female | 0.24 (0.003) | 0.25 (0.003) | * |
| | Male | 0.19 (0.002) | 0.17 (0.002) | * |
| 4. Length of pygidium (mm) | Female | 1.29 (0.016) | 0.88 (0.010) | * |
| | Male | 0.76 (0.010) | 0.54 (0.018) | * |
| 5. Moisture content (%) | Female | 48.70 (0.355) | 50.70 (0.411) | * |
| | Male | 47.00 (0.970) | 51.50 (1.296) | * |
| Pre-maturation period (days to egg laying) | Female | 2.46 (0.056) | 1.31 (0.107) | * |
| Fecundity (no of eggs) | Female | 44.52 (3.500) | 58.60 (3.520) | * |
| Adult longevity (days) | Female | 8.90 (0.201) | 8.18 (0.179) | * |
| | Male | 11.20 (0.402) | 10.21 (0.379) | * |

^a () = standard error.

^b *P* = level of significance (NS = not significant, * = significant at 5%).

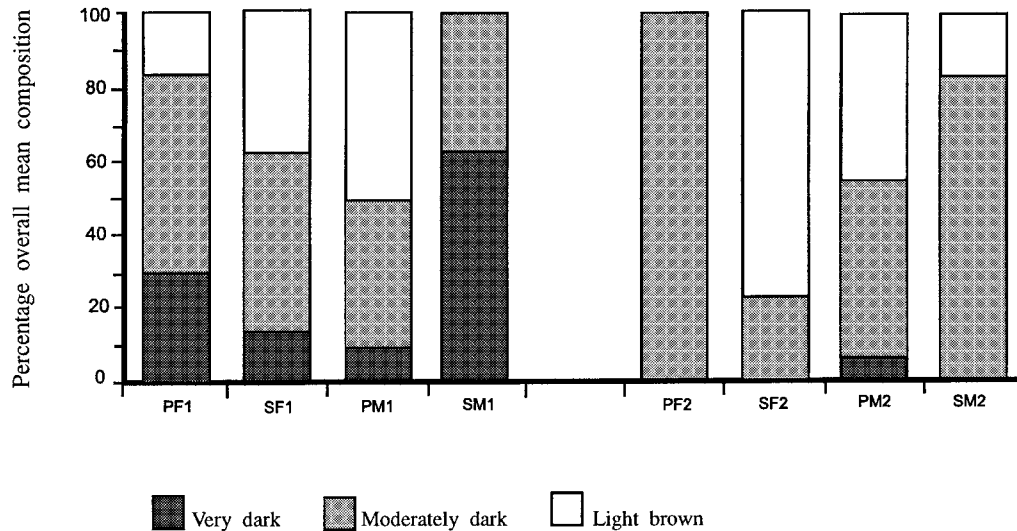


Fig. 2. Differences (mean) in elytral (1 = posterior; 2 = anterior) colour of *C. chinensis* emerging from pod-(p) and seed-(s) infested pigeonpea (M = male; F = female).

3.2. Differences between *C. chinensis* emerging on different days from seed and pod-infested pigeonpea

Among female and male adults emerging from seed infested pigeonpea, no significant differences (morphological or biological) were observed irrespective of when the adults emerged (means presented in Table 1, and in Fig. 3, as an example). From pod-infested pigeonpea, however, several differences were observed between those that emerged earlier and those that emerged later.

The posterior end of the elytra was darker among the early- than late-emerging adults, and the colour of the elytra was progressively lighter with each subsequent day of emergence from pod-infested pigeonpea (Fig. 3a, b). Anterior elytra of females were very dark in colour and did not change with delay in emergence (Fig. 3c), but in the males, the elytral colour became progressively lighter the later the emergence (Fig. 3d).

Measurements of the mean elytral lengths of female and male adults emerging from days 1–14 from pod-infested pigeonpea showed that they were significantly shorter (<1.74 mm, 1.59 mm, respectively) on those that emerged early, and became generally longer (>1.77 mm, 1.64 mm, respectively) for later-emerging adults (Fig. 4a). The differences was particularly noticeable around the 6th day of emergence, which coincided with the centre of the bi-modal emergence in Fig. 1. The mean elytral width of females was narrower ($P < 0.05$) for adults emerging on the first days (0.75 mm) than those that emerged later (0.80 mm) (Fig. 4b). Although there were no significant differences in mean elytral width between males emerging early and those emerging later (Table 1), there was a consistent increase in wing width throughout the period from 0.630 mm on the first day to 0.697 mm on the last (Fig. 4b).

Further observations showed that the mean body length of females emerging earliest was shorter (3.2 mm) than those emerging on subsequent days (3.4 mm) (Fig. 5). Although body

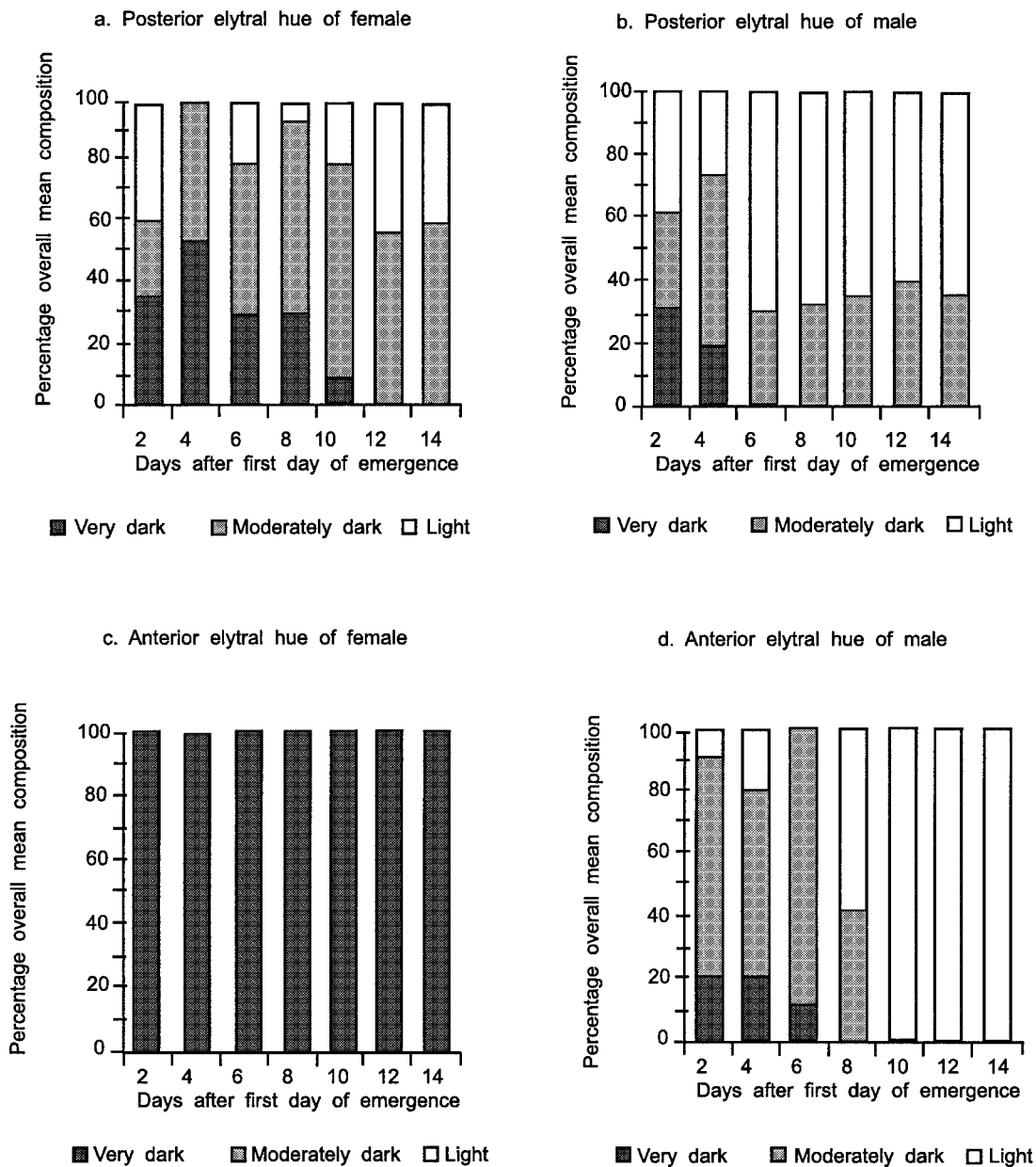


Fig. 3. Elytral hue (mean) variation in males and females of *C. chinensis* emerging from pod-infested pigeonpea 2–14 days after the first emergence.

length of adult males emerging on different days did not vary significantly, nevertheless the trend was that those that emerged earliest were generally shorter than those that emerged later, with a clear difference between the lengths of males emerging on the first 6 days and those emerging later.

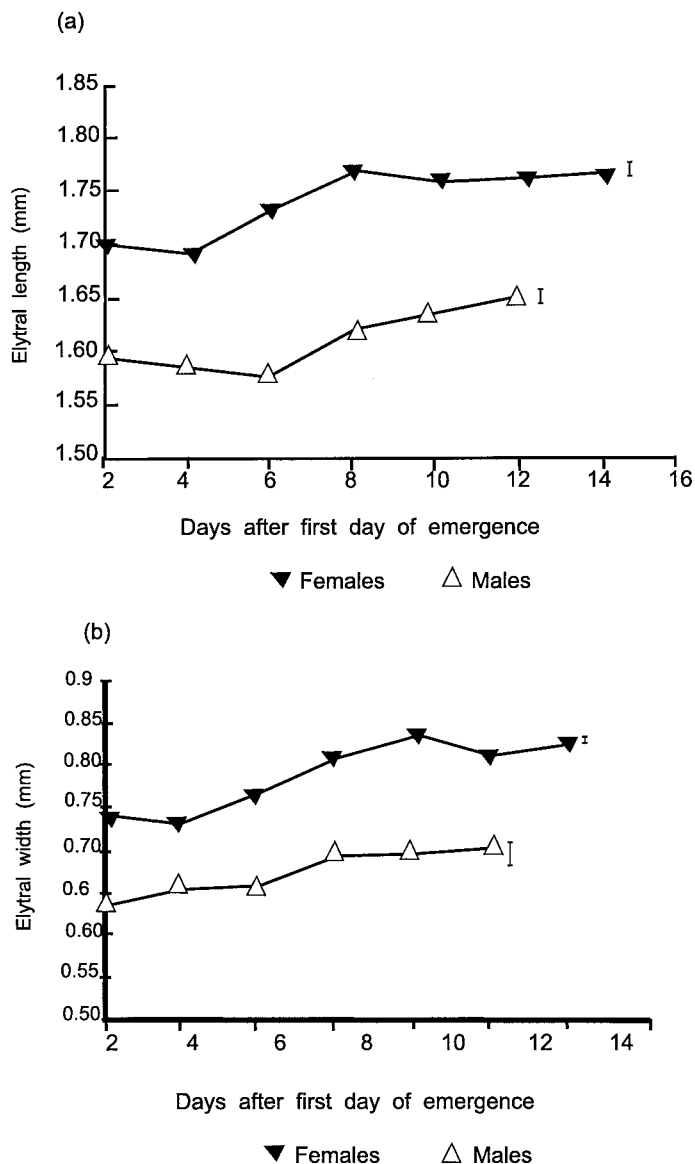


Fig. 4. Mean elytral (a) length and (b) width in males and females of *C. chinensis* emerging on different days from pod (PR-4) infested pigeonpea. Vertical bars are standard errors.

The results for these three characteristics suggest that adults emerging from pod-infested pigeonpea differentiate into small bodied and small winged, and large bodied and large winged adults, depending on the duration of development, with small bodied and small winged insects emerging earliest.

In both sexes, there was a negative and non-significant trend in the mean size of the gap between the compound eyes of insects that emerged on the first few days and those that

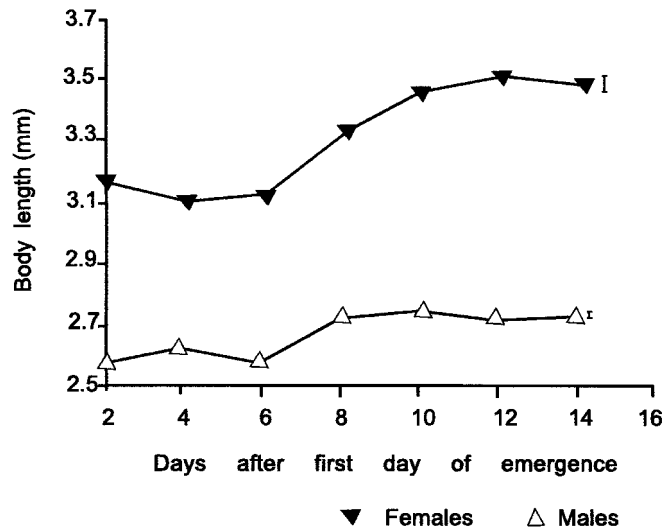


Fig. 5. Mean body length in females and males of *C. chinensis* emerging on different days from pod (PR-4) infested pigeonpea. Vertical bars are standard errors.

emerged later (Fig. 6). However, there was a successive and significant increase in the mean length of the pygidia of females, from 1.21 mm on the first days of adult emergence to about 1.44 mm on the last days (Fig. 7). The biggest pygidial length increase occurred after the 6th

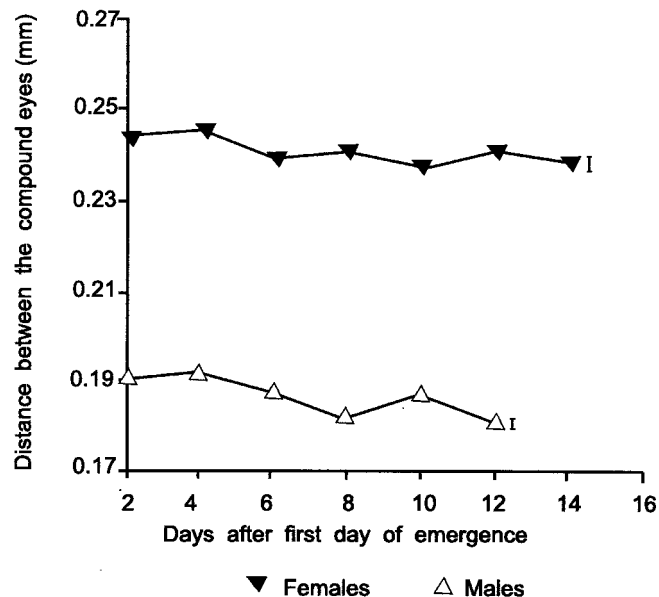


Fig. 6. Mean distance between the compound eyes in males and females of *C. chinensis* emerging on different days from pod (PR-4) infested pigeonpea. Vertical bars are standard errors.

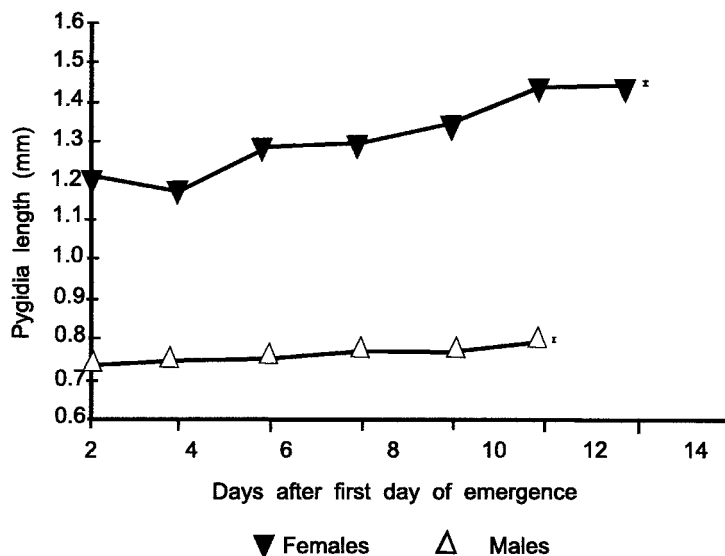


Fig. 7. Mean length of the pygidia in females and males of *C. chinensis* emerging on different days from pod (PR-4) infested pigeonpea. Vertical bars are standard errors.

day of adult female emergence. The pygidial length of adult males emerging on different days did not vary significantly (PNS).

In both sexes, the mean mc (Fig. 8) of adults emerging over the first 6 days was higher (about 50%) than that of adults emerging on each subsequent day (below 47%). There were significant differences among the pre-maturation periods of females of different emergence dates. The pre-maturation periods of females that emerged earliest were shorter than those that emerged later ($P < 0.05$) (Fig. 9), while the fecundity of females emerging earliest was greater

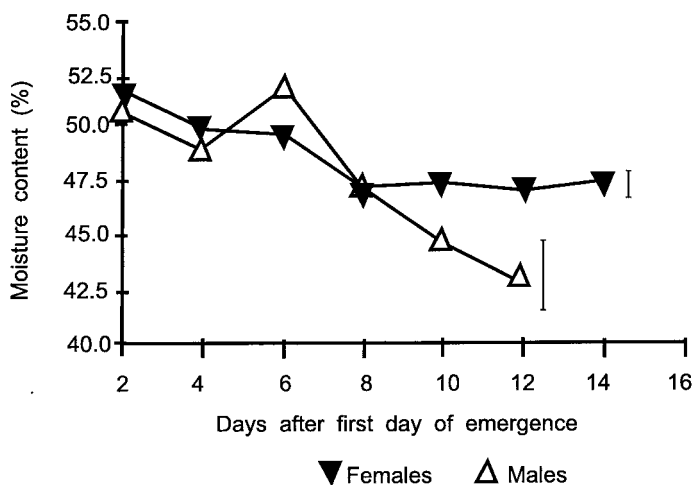


Fig. 8. Mean percentage moisture content of females and males of *C. chinensis* emerging on different days from pod (PR-4) infested pigeonpea. Vertical bars are standard errors.

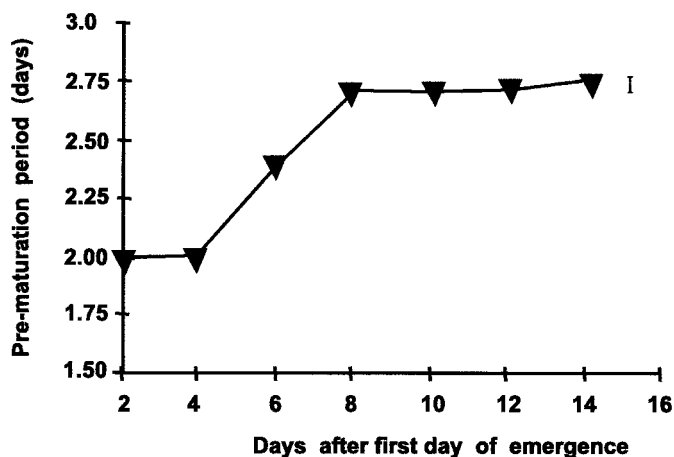


Fig. 9. Prematuration period of female *C. chinensis* emerging on different days from pod (PR-4) infested pigeonpea. Vertical bar is standard errors.

(about 54 eggs) than those that emerged later (about 38 eggs) ($P < 0.05$) (Fig. 10). The mean female longevity of *C. chinensis* emerging early from pod-infested pigeonpea was shorter than that of females which emerged later (Fig. 11), and these ranged from 7.6 to 9.8 days for earlier-emerged and later-emerged adults, respectively. The biggest difference in all the above cases occurred between adults that emerged on the first 6 days and those that emerged later. These results probably indicate that early-emerging adults need to lay as many eggs as possible

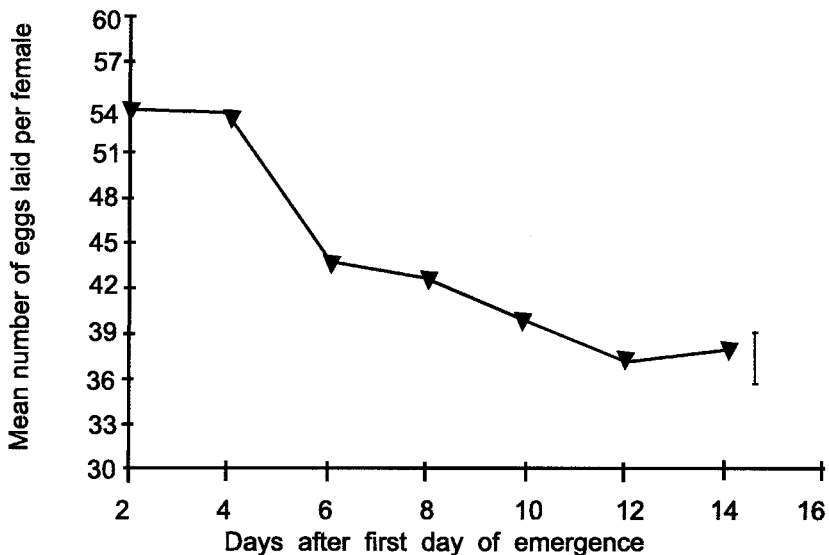


Fig. 10. Fecundity of newly emerged female *C. chinensis* emerging on different days from pod (PR-4) infested pigeonpea. Vertical bar is standard errors.

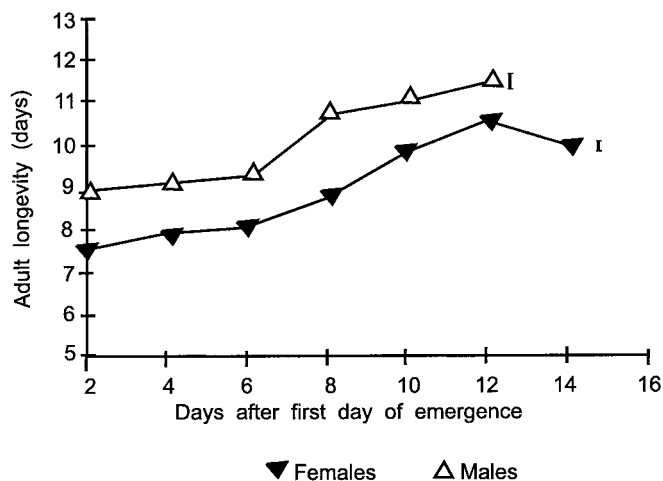


Fig. 11. Longevity of female and male *C. chinensis* emerging on different days from pod (PR-4) infested pigeonpea. Vertical bars are standard errors.

soon after emergence since they have shorter longevity, and conversely later-emerging adults delay egg laying and produce fewer eggs since they have greater longevity.

4. Discussion

Under natural conditions, two morphs of *C. maculatus* adults have been reported, one multiplying in stored beans which are “flightless”, or “normal” forms, and the other living out of doors in the crop which are “flight”, or “active” forms (Utida, 1954, 1972; Caswell, 1959; Ouedraogo and Huignard, 1981; Sano-Fujii, 1984). These two forms are not only morphologically different, but are also different in certain physiological and behavioural characteristics (Utida, 1954, 1956, 1972, 1981). In studies on *C. chinensis* (Silim Nahdy et al., 1998), where artificial infestation was done in the field on pods at developmental stage PR-4 (approximately 75% mc), adults that emerged showed a clear bimodal pattern of emergence, and in addition, there was a wider range (in days) between the earliest and latest adult emergence as compared to seed-infested samples (Fig. 1). This pattern was thought to be an expression of polymorphism.

In this study, where comparisons were made between *C. chinensis* adults emerging from pod-infested pigeonpea (stage PR-4) and seed-infested pigeonpea, it was found that the two populations were different in a number of morphological and biological characters, in at least one or both sexes (Table 1). The morphological differences observed in *C. chinensis* were in the elytral colour, the wing dimensions of males, the insect size, the width between the compound eyes, the pygidial length, and mc of adults (Table 1). The biological differences observed were in terms of the pre-maturation period, fecundity and adult longevity (Table 1). The fact that the differences observed in this study between adult *C. chinensis* emerging from seed- and pod-infested pigeonpea are, in many instances, comparable to differences observed in morph forms of *C. maculatus* (Southgate et al., 1957; Utida, 1972, 1981; Taylor and Agbaje, 1974) suggests

that such differences are probably expressions of polymorphism. If the observed differences, in *C. chinensis*, are due to the occurrence of the morphs, as in *C. maculatus*, then it appears that field pod infestation stimulates formation of a greater proportion of the flight morphs or conversely, development within dry seeds suppressed formation of flight forms. Thus from pod-infested pigeonpea, a greater proportion of the flight morphs emerged than in seed-infested pigeonpea where the flightless forms appeared to predominate.

In *C. maculatus*, Utida (1954, 1965) found that, among the environmental factors responsible for stimulating the production of the flight morphs, larval crowding is the most important. The seed temperature and mc increase due to the high larval population density, were the two factors found to be critical in the production of polymorphism (Utida, 1981; Sano-Fujii, 1984). If indeed immature pod infestation by *C. chinensis* stimulates the formation of the flight morphs as it appears in this study, then it is possible that the high bean mc in the immature pods acted as the greatest stimulus.

Observations conducted on adults emerging on successive days from pod-infested pigeonpea showed that adults emerging earliest were different in many ways from those that emerged later. The study showed that the elytra of the earliest-emerging insects (6 days or less) were generally darker in colour than those that emerged later (after 6 days). The colour variation is probably an adaptation, especially by the flight forms, to field conditions, where lighter colour offers appropriate camouflage within the field bio-system against numerous potential enemies. Under storage conditions, where there is almost constant darkness and fewer natural enemies, such camouflage is probably not necessary. Observations on wing and body dimensions showed that insects emerging on the last 8 days had larger wings and bodies than those that emerged earlier (Figs. 4a,b and 5). This trend was much more pronounced in the female than in the male wings, probably due to the need for greater mobility in the former to search for suitable oviposition sites. The accompanying body size increase could indicate a greater energy reserve that could be used in search for oviposition sites by flight forms. The pygidial length of late emerging female (flight) were longer than the early emerging ones (flightless), but the reason for this increase is difficult to explain without conducting abdominal dissections. In *C. maculatus*, however, it was found that, in the flight forms, the abdominal cavities in both sexes were filled with fat at adult emergence, whereas in the flightless forms, the abdominal cavity was filled with reproductive organs (Utida, 1972). If the above findings are applicable to *C. chinensis*, this extra fat in the larger pygidium of late emerging insects (thought to be flight forms) would supply more energy than the flightless form.

In male *C. chinensis*, the adults that emerged earlier (though to be flightless forms) had wider gaps between the compound eyes (smaller eyes) than those that emerged later (larger eyes), which is probably due to the greater visual needs of the flight form. In females, no variation in the size of the eyes was observed, probably because the initial location of the ovipositional sites requires senses other than vision.

Another difference lay in the mc which was higher in earlier than in later emerging adults. In *C. maculatus*, Utida (1972) observed that the crude fat content is higher in the flight than in the flightless forms while the water content was lower. The need to store more fat in the body and less water is probably a result of the greater energy required for mobility in flight forms under field conditions.

The biological differences observed in *C. chinensis* emerging on different days were in pre-

maturation periods, fecundity and adult longevity. In most cases the greatest difference occurred between adults emerging on the first 6 and the last days. Adults emerging earliest (flightless) had shorter pre-maturation periods and lower fecundity than those that emerged later (flight) (Figs. 9 and 10). Increased pre-maturation period in flight forms is thought to be another adaptation to field conditions, food reserves being available for mobility rather than the immediate maturation of reproductive organs. In the flightless forms (under storage conditions), where extended mobility is not necessary, it is probably more useful to devote all resources to rapid and increased reproduction.

From pod-infested pigeonpea, longevity was greater in late-emerging adults than earlier-emerging adults (Fig. 11). The longest adult longevity was recorded from adults emerging on the last days. Increased longevity in the flight form is, again, probably another adaptation to field conditions, where few or widely-dispersed oviposition sites and mating partners prevail.

From the above discussion, it is concluded that most of the differences observed are expressions of two morphs in *C. chinensis*. It is also concluded that a high percentage of adults that emerged from seeds originating from immature pod-infested pigeonpea were of the flight form, particularly those that emerged latest or developed slowest while those that emerged earliest or developed fastest were of the flightless form.

Studies by Wigglesworth (1954) on the physiology of insect metamorphosis emphasised that polymorphism could be regarded as different phases of development, the different metamorphic stages (larva, pupa and adult) representing successive expressions of polymorphism. Utida (1972) indicated that if this theory is applied to *C. maculatus*, then it can be assumed that the flightless form is a neotenus phenomenon, while the flight form is the more typical adult. If the theory is applied to *C. chinensis*, then the flightless forms (with shorter developmental period, and smaller bodies, wing dimensions and eyes) have undergone a slightly less complete metamorphosis than the flight forms. Infestation and development in dry seeds probably suppresses full metamorphosis, leading to the predominance of flightless forms in *C. chinensis*.

The natural occurrence of polymorphism in *C. chinensis* under field conditions, apart from showing the adaptability of the morphs to the two different niches, i.e. flight forms to field conditions, and flightless forms to storage conditions, may also have implications for long-term pest management strategies. In this case, pest management should aim at both morphs. Pest management in the field could employ both natural methods (i.e. plant resistance etc.) and chemical pest control techniques to reduce field populations in pods as they mature. This would probably help in breaking the cycle from field to storage and vice versa.

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