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Flight Activity of *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) in Relation to Population Density, Resource Quality, Age, and Sex

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Higher flight activity has been observed in aged, high-density cultures of Prostephanus truncatus (Horn) (Coleoptera: Bostrichidae), but adults in new, low-density culture jars showed less flight activity. In order to understand this change in behavior, the effects of population density, age, resource quality, and sex on the flight of P. truncatus were studied in a wind tunnel. While an immediate density on the release platform had no significant effect on flight, beetles from high-density cultures were more inclined to fly than those from low-density cultures. Resource quality exerted a major influence on flight; insects in food suitable for boring and oviposition seldomly exhibited flight, however, when food was absent or of inferior quality for boring and oviposition, the dominant behavior was flight. Also, insects maintained for a week in food suitable for boring and oviposition were less ready to fly than those maintained in food unsuitable for boring and oviposition. The optimum age range for flight activity was before the peak of reproduction and insects rarely flew before 4 days or after 32 days of emergence. There were no significant differences between the flight activity of males and that of females. Based on these results, we conclude that age and resource quality are major influences on the flight activity of P. truncatus and a hypothesis is proposed in which reproductively active male and female beetles disperse from habitats of low resource quality to those that support their reproductive behavior. The practical implications of these results and the possible role of the male-produced aggregation pheromone are discussed.

KEY WORDS: *Prostephanus truncatus*; larger grain borer; Coleoptera; Bostrichidae; flight; stored product insect.

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INTRODUCTION

Many external and internal factors have been implicated in the dispersal of insects. The majority of the research on the influence of such factors has been on migratory species of Lepidoptera, Hemiptera, Orthoptera, and Diptera (references cited by Johnson, 1969; Blackmer and Byrne, 1993). Among the beetles, the bostrichids represent an important family including many major field-to-store grain pests. However, little information is available on their flight behavior and dispersal mechanisms.

The larger grain borer *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) is an exotic species in Africa, where it has become a serious pest of stored maize and dried cassava (Hodges, 1986). Its distribution in Africa is still expanding and field trapping of the beetle has revealed its presence in the wild (Nang'ayo *et al.*, 1993). The lack of information concerning the influence of extrinsic and intrinsic factors on the insect's flight has, however, contributed to the difficulty in explaining pheromone trap catch patterns and prediction of its dispersal tendencies.

In the laboratory, adult *P. truncatus* in old, high-density culture jars have been observed to take off more than those in new and low-density culture jars (H. Fadamiro, personal observation). This observed high flight activity in old jars may be due to many factors including age of beetles, food quality, density in culture, immediate density, and pheromone. Which factors are most important?

This paper reports studies on the effects of population density, age, resource quality, and sex on the flight activity of *P. truncatus* as a part of the information needed to decipher its dispersal tendency. In an earlier paper (Fadamiro and Wyatt, 1995), we reported the optimum conditions of temperature, humidity, and time of day for flight activity and these optima have been taken into account in the design of the current experiments.

MATERIALS AND METHODS

Insects

Stock cultures of adult Tanzanian strains of *P. truncatus* [Natural Resources Institute (NRI), Chatham, Kent, UK] were reared on whole clean maize. Cultures for an experiment on the effect of age on flight were established on milled grains that passed through an Endecotts sieve of mesh size 3.35 mm for ease of removal of insects from culture. All cultures were maintained at $30 \pm 1^\circ\text{C}$ and $65 \pm 5\%$ RH under a 12:12 L:D photoperiod.

Beetles were sexed under a light microscope at $\times 50$ magnification examining the clypeal tubercles, which are more prominent and spaced farther apart in females (Shires and McCarthy, 1976).

Wind Tunnel

The wind tunnel used was a clear rectangular glass tunnel 160 cm long and 75 cm high and wide (Birch and White, 1988). Air was pulled out of the tunnel by a variable-speed extractor fan. Beetles were released onto a platform placed 20 cm from the downwind screen and 35 cm above the floor. The release platform consisted of a plastic petri dish 9 cm in diameter onto which was placed a plastic cone with sharp edges. The platform was roughened to enhance adherence and insects more readily took off from the cone than any other part of the platform (personal observation). Lighting was by four cool white fluorescent bulbs (85 W), mounted 5 cm above the wind tunnel, and air was warmed by electrical heating of the air in the room prior to tests. In a separate study, it was observed that *P. truncatus* took off more readily at higher light intensities (H. Fadamiro, unpublished data). Experiments were carried out in the wind tunnel at $28 \pm 2^\circ\text{C}$, $35 \pm 5\%$ RH, and 0.3 ± 0.1 m/s, at 10–12 h of the photophase (Fadamiro and Wyatt, 1995), under a light intensity of 3700 lux.

Effect of Population Density on Flight Takeoff

The influence of density on flight activity was studied in two ways: the effect of the immediate adult insect population density on the release platform and the effect of the density at which adults were reared (founding density). In the first experiment, the effect of insect population density on the release platform on takeoff was determined by selecting insects aged 5–15 days, unsexed from culture. The insects were then randomly placed into groups of 25, 50, 100, and 200 insects, giving four treatments. Each group was assessed for flight in the wind tunnel by counting the numbers of takeoffs for 10 min and the percentages of insect takeoff compared for all treatments. There were four replicates per treatment and the whole process of observation was randomized.

For the rearing density experiment, experimental densities were established by placing 5, 20, 100, or 500 adult *P. truncatus* in 250 g of whole maize in 500-ml culture jars. The founding insects were all sieved from the cultures 25 days later just before the adult progeny (F_1) started to emerge. There were many culture jars for each density. Fifty fully mature F_1 insects were randomly selected from each density treatment from 40 days after introduction of the founding insects and tested for flight in the wind tunnel. The numbers of F_1 insects taking off for 5 min from each density were counted and recorded. There were four replicates per treatment and a beetle was used only once. Flight tests in the tunnel were randomized and the flight observations were carried out over 2 days.

Effect of Resource Quality on Flight Takeoff

Resource quality in this study is defined in terms of the ability of maize forms to support insects' reproduction. The experiments were designed to inves-

tigate the readiness of *P. truncatus* to exhibit flight activity in different forms of maize and adult flight response after maintenance on different forms of maize for 1 week.

In the first experiment, stored maize was presented to adults in three forms: flour, kibbled maize, and whole maize. The important difference in these forms of maize is that whole maize supports insect boring and oviposition, while kibbled maize and flour are notably inferior in these respects (H. Fadamiro, data from a separate study shown in Fig. 4). Kibbled maize and flour were produced by milling whole fresh grains and sieving through Endecotts sieves of different mesh sizes: ≤ 710 and > 250 μm for kibbled maize and ≤ 250 μm for flour. The food was carefully presented to the beetles, making sure that the insects were not buried in the medium. Also, the quantity of each food treatment used was minimal (~ 50 ml). Twenty-five adult *P. truncatus* (mixed sex; aged 5–15 days) were selected at random and placed in 600-ml "flight jars" (described by Fadamiro and Wyatt, 1995) containing (~ 50 ml) the different treatments. The control jar contained no food. The jars were placed in the laboratory at 25°C and 40% RH for observation. The insects were allowed to acclimate in the jar for 2 h, and observations made in the 2 h before darkness. Flight activity was measured by counting takeoffs in each jar for 5 min. There were five replicates per treatment and a beetle was used only once (but could be counted more than once).

In another experiment, insects were maintained in the different forms of maize and flight activity was observed after 1 week. This was to test whether or not the quality of the medium in which *P. truncatus* is maintained or reared has an effect on its flight activity. The different food treatments were produced by milling whole fresh grains as described before. Newly emerged adults (aged 2–6 days; unsexed) were removed from cultures and randomly placed into three groups of 600 insects each. There were three treatments—flour, kibbled maize, and whole maize—and each group of insects was introduced into 20 g of food in a 250-ml glass jar. The jars were covered and placed in the culture room at $29 \pm 1^\circ\text{C}$ and $70 \pm 5\%$ RH. After 7 days, 50 insects were randomly selected from each jar and tested for flight activity on a release platform, without food, in the wind tunnel, counting the numbers of insects taking flight during 5 min. A beetle was used only once.

Effect of Age on Flight Takeoff

The effect of age on flight was studied in two experiments. First, newly emerged insects were tested for flight when 4 days old, then on day 10, and then at 10-day intervals until they were 40 days old. Cultures for this purpose were started by introducing known numbers of insects into half-milled maize grains (for ease of removal of newly emerged insects). All founding insects were removed 25 days after introduction. The cultures were then sieved 31 days after

introduction for newly emerged insects. Development from egg to adult took about 30 days at $30 \pm 1^\circ\text{C}$ and $70 \pm 5\%$ RH (H. Fadamiro, personal observation). Newly emerged insects (aged 1 day) identified by the lightly sclerotized cuticle were then carefully selected and 100 such insects were used per replicate in the experiment. The numbers of insects taking flight during 10 min in the wind tunnel were recorded and there were four replicates per treatment.

In another experiment, to narrow down the age range, newly emerged insects collected through the above procedure were tested for flight in the wind tunnel when 2 days old, then every 2 days till 32 days after emergence. One hundred insects were tested per replicate of each treatment, recording takeoff for 10 min, and there were four replicates per treatment.

Effect of Sex on Flight

Adult *P. truncatus* aged 7–15 days were removed from cultures and sexed. Forty adults of each sex were randomly selected and released for flight in the wind tunnel. The number of insects taking flight for 5 min was recorded. There were 10 replicates per sex and the order of observation was randomized.

Statistical Analysis

Data from the experiments were analyzed with Statview 4.0. Data for parametric tests (analysis of variance) were first normalized by transformation. The method of transformation was based on the results of exploratory analysis (i.e., skewness and kurtosis). The Mann–Whitney *U* test was used (for sex data) where the assumptions of parametric tests were not met (Martin and Bateson, 1993, pp. 125–136).

RESULTS

Population Density

Data for the effect of insect density on the release platform on flight were expressed as proportions and arcsine-square root transformed. The results showed that the number of insects on the release platform did not affect the proportion initiating flight ($F_{3,12} = 0.875$, $P = 0.48$) (Fig. 1).

Analysis of variance of square root transformed data for rearing density showed a significant, and positive, effect of rearing density on the proportion of the progeny taking flight ($F_{3,12} = 6.70$, $P = 0.007$). The proportion of the progeny flying correlated positively with the rearing density ($P = 0.0004$). Post hoc tests indicated that the progeny (F_1) of insects reared at a density of 500 adults per 250 g maize took flight significantly more often than those reared at the lower density of 5 adults per 250 g maize (Fig. 2).

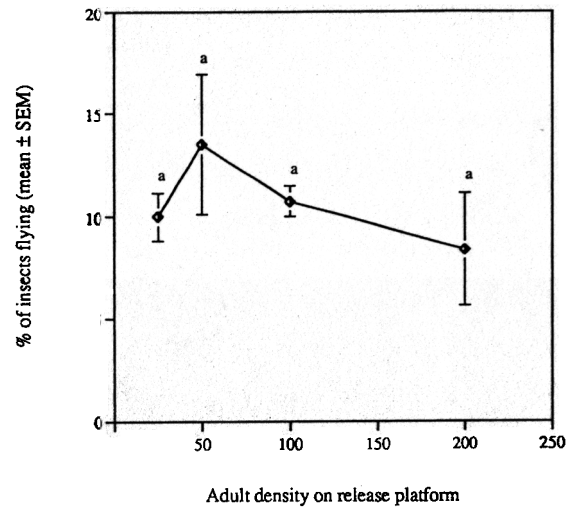


Fig. 1. Effect of population density of flight activity of *P. truncatus*: population density on release platform. Figure shows means of four replicates per treatment. *n* per treatment was unequal, hence the use of percentage flying. Observation period was 10 min ($P > 0.05$).

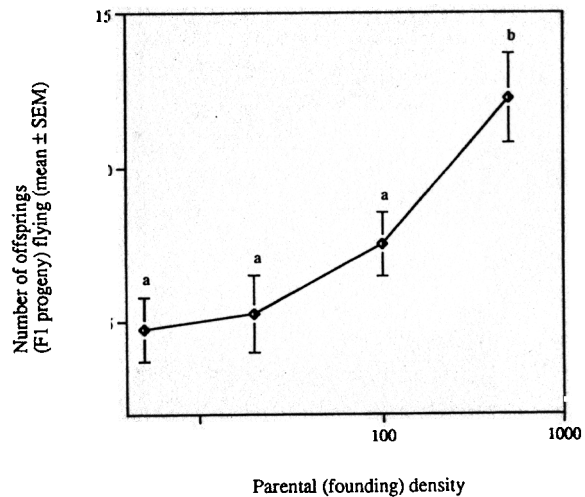


Fig. 2. Effect of population density on flight activity of *P. truncatus*: parental density in culture. Figure shows means of four replicates per treatment; 50 beetles were released per replicate for 5 min ($P < 0.05$). Here and in Figs. 3 and 4, means labeled with the same letter do not differ significantly.

Resource Quality

Data obtained on the readiness of *P. truncatus* to exhibit flight on the early colonization of different forms of maize were square root transformed [$x = \sqrt{(x + 0.5)}$] before analysis. Results show a significant effect of food quality on flight takeoff ($F_{3,16} = 35.44$, $P < 0.0001$, $n = 125$ per treatment). Takeoff was significantly higher in the control (no food) than in the treatments (Fig. 3). The least flight was recorded in the jars containing whole grains. The order of flight initiation in relation to maize form and quality was whole grains < damaged grains < dust < no food.

Data obtained on flight activity of adults after maintenance for 1 week on different forms of maize were also square root transformed. The form of the maize in which *P. truncatus* was maintained exerted a significant effect on its flight ability ($F_{2,45} = 14.17$, $P < 0.0001$, $n = 400$ per treatment) when tested on a platform without food. Post hoc tests showed significant differences between whole maize and both kibbled maize and flour. More flights were recorded for beetles maintained in flour and kibbled maize than in whole maize (Fig. 4).

Age

The data for the study of effect of age at 10-day intervals were log transformed [$x = \log(x + 1)$] before analysis. Age exerted a significant effect on

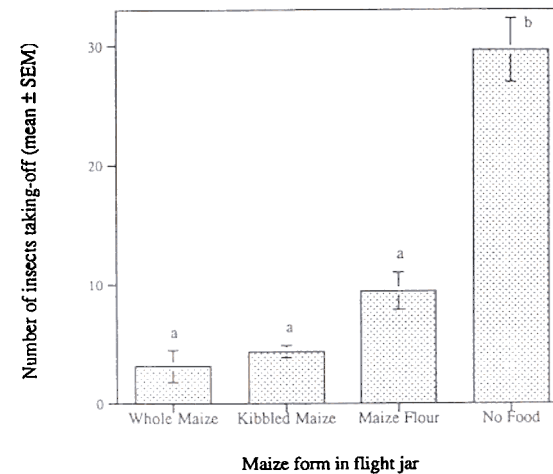


Fig. 3. Effect of immediate food form on release platform on the flight activity of *P. truncatus*, tested in "flight jars." Figure shows means of five replicates per treatment; 25 beetles were released per replicate for 5 min ($P < 0.05$).

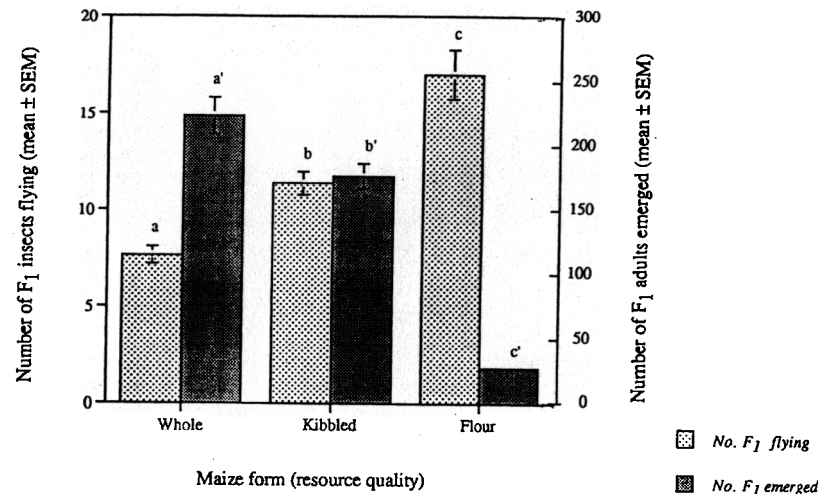


Fig. 4. Effect of resource quality on which *P. truncatus* was maintained on its development and flight activity, tested in a wind tunnel. Fifty beetles were released per replicate for 5 min for flight activity ($P < 0.05$).

flight ability ($F_{4,12} = 12.94$, $P = 0.0003$, $n = 400$ per age group). Insects aged around 10 days exhibited significantly more flight activity than those from other age groups (Table I). No flight was recorded for insects aged < 4 and > 30 days.

Data for effect of age of insects tested every other day were also log transformed [$x = \log(x + 1)$] and analyzed as a repeated-measures ANOVA (Martin and Bateson, 1993). The effect of age on flight was significant ($F_{15,45} = 39.61$, $P < 0.0001$, $n = 400$ per age), with significantly more takeoffs recorded for insects aged 8–12 days than for other ages (Fig. 5).

Table I. Flight Activity of *Prostephanus truncatus* in Relation to Age^a

| Age (days) | Number of insects flying (mean ± SE) |
|------------|--------------------------------------|
| 4 | 1.75 ± 1.11 c |
| 10 | 11.75 ± 2.50 a |
| 20 | 3.75 ± 1.75 b |
| 30 | 0.00 ± 0.00 c |
| 40 | 0.00 ± 0.00 c |

^aMeans of four replicates per age; 100 beetles were observed per replicate for 10 min ($P < 0.05$). Means followed by the same letter do not differ significantly.

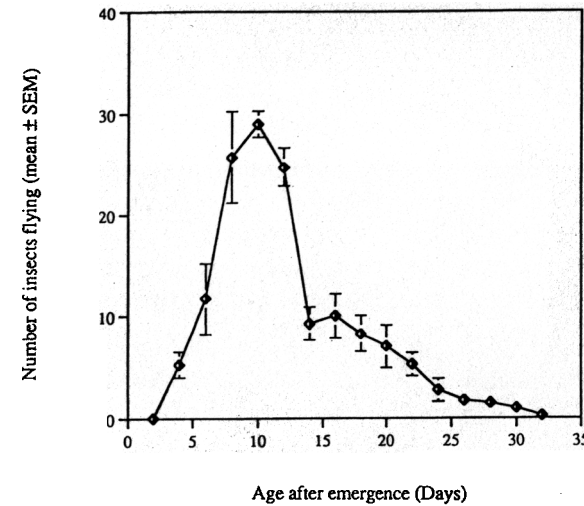


Fig. 5. Flight activity of *P. truncatus* in relation to age. Figure shows means of four replicates; 100 beetles were released per replicate for 10 min (repeated measures) ($P < 0.05$).

Sex

Analysis of sex data using Mann-Whitney U test showed no significant effect of sex on flight ($U = 43.00$, $P > 0.05$, $n = 400$ per sex). The numbers of male and female *P. truncatus* initiating flight were approximately equal (Table II).

DISCUSSION

The results of the experiments clearly implicate many extrinsic and intrinsic factors in the flight of *P. truncatus*. This is also true for many other insects (Blackmer and Byrne, 1993; Rankin and Rankin, 1980). Although flight duration

Table II. Flight Activity of *P. truncatus* in Relation to Sex

| Sex | Number of insects flying (mean ± SE) |
|--------|--------------------------------------|
| Female | 5.90 ± 1.07 |
| Male | 6.10 ± 0.71 |

^aMeans of 10 replicates per sex; 40 beetles were observed for 5 min for each replicate ($P > 0.05$, Mann-Whitney U test).

was not the theme of this study, most of the insects that initiated flight in the wind tunnel continued to fly until the end of the observation period (5–10 min) and, in a separate study, for up to 20 min or even more (personal observation). This performance may be a reasonable indication of long-duration flights which may lead to dispersal, especially as insects in the Coleoptera usually move about by walking (Rankin and Rankin, 1980). A preliminary flight mill study has also suggested that *P. truncatus* is capable of flying up to 24.8 km in 45 h (V. Pike, NRI, personal communication).

Results from the density experiments showed that while rearing density influenced flight activity, the immediate density of release had no influence on flight. In the rearing density experiment, beetles from cultures founded at high densities flew more readily than those raised in low-density cultures. This suggests that flight is rearing density dependent and immediate density independent. The flight of *Rhyzopertha dominica* (F.) was reported as dependent on rearing density, but only for a limited time (Barrer *et al.*, 1993). Tauber *et al.* (1984) report that density (or crowding) may be involved in the induction of diapause in some gregarious insects and that the influence of density may be associated with the effects of food quality and/or quantity. Flight, like diapause, is a way in which an insect population responds to environmental clues such as food quality and population density (Rankin and Rankin, 1980). The rearing density effect may be associated with a decline in food quality. By the time insect flight was tested almost half the weight of maize used in the culture started with 500 insects had been converted to flour, compared to only about a tenth as much flour produced in the culture started with 20 insects. The flour produced is inferior to whole maize in terms of ability to support oviposition and larval development (H. Fadamiro, data from a separate experiment but shown in Fig. 4). The observation that flight is independent of immediate density on the release platform suggests that the mechanism of the effect of density on flight is not direct and supports the premise that density may act by lowering food quality, which then leads to increase in flight activity (Tauber *et al.*, 1984). This is further supported by the results from the experiments on the form of maize in which *P. truncatus* was maintained or placed for flight tests; both affected the insect's flight activity, which is indicative of the major influence the behavioral response to food quality has on the flight activity of the larger grain borer.

In the first experiment on food, insects placed without food displayed greater flight activity than those placed in jars containing food. Flight activity also increased with decreasing suitability of the food for larval development, although this trend was not significant. Also, in the second experiment, insects maintained in whole maize showed less flight activity than those maintained in kibbled maize and maize flour. Food quality has been implicated in insect movements and insects respond to unfavorable conditions such as food depletion or decreas-

ing quality by flight. In many insects, migration is often associated with, and induced, by conditions such as poor food quality (Rankin and Burchsted, 1992). Cessation of flight in the presence of ample food has been reported in a seed bug, *Neacoryphus bicrucis* (Say) (Solbreck and Perhson, 1979), and in this study, while flight was the main behavior of insects placed in maize flour, the dominant behavior of insects placed in whole grains was tunneling. This tunneling activity may be important for reproduction since in this beetle eggs are laid in tunnels.

Results from the age experiments showed that newly emerged (1–3 days) and older (> 30 days) insects seldom fly and that the insects were most ready to fly when aged 8–12 days than at any other period in their life history. The flight muscles of some insects are not fully developed at emergence and increase in size subsequently (Johnson, 1969). Full sclerotization of teneral adults of *P. truncatus* does not occur in the first 3 days of emergence, when the insects are still very tender, and largely white-brownish in color, and do not fly or mate (personal observation). In *P. truncatus*, courtship begins about 4 days after emergence, and oviposition 6–8 days after emergence (personal observation). Egg production reaches a peak at about 20 days and thereafter gradually declines but may continue throughout the life span (Bell and Watters, 1982). This therefore means that flight activity reaches a peak before the egg production peak and may suggest that flight is linked to reproduction in the pest. In the beetle, *Sitona regensteiniensis* (Coleoptera: Curculionidae), the flight muscle apparatus was reported to autolyse upon aging, terminating flight (Danthanarayana, 1970). This may underlie the cessation of flight in very aged *P. truncatus* but we have not investigated this yet. Squire (1950) classified a population of *Glossina palpalis* into three age groups according to the wear and color of the hindwings. It could be argued that older insects with more wing fray are less likely to fly. Hindwing observations of insects classified into three age groups (<4, 10–20, and >30 days old) in this study, however, did not reveal any wear among any of the three groups. The absence of wear and tear of the hindwings in *P. truncatus* could be related to the protective role of the elytra. The hindwing of *P. truncatus* is nearly oval-shaped, with reduced venation. Hindwings of older insects seemed to be more sclerotized, with darker veins and margins. Although insects used in this study were mixed sex, the pattern is the same for members of both sexes.

Flight activity is not sex dependent in *P. truncatus*, as males and females displayed equal tendencies to fly. This is hardly surprising, as field studies involving the pheromone have recorded the trapping of both sexes (Tigar *et al.*, 1993). Most studies on the effect of sex on flight of insects have been done on the commonly known migratory species, with special attention to the oogenesis-flight syndrome in the female (Johnson, 1969). Since flight appears to occur

between bouts of oviposition, this phenomenon if present in the larger grain borer is not greatly pronounced, although flight activity reaches a peak before the peak of oviposition in the female.

A further variable we are studying is the possible role of a potential pheromone(s) buildup in old cultures, but the results of the experiments presented here suggest that the increased flight activity in old cultures can be explained largely by the decline in resource quality.

Relating these results to the natural environment of the pest, we are led to hypothesize that reproductively active adult beetles in the field and stores respond to depleting resource quality, characteristic of the end of the season in these habitats, by flying to a new environment with resources good enough for reproduction. The possible role of the male-produced aggregation pheromone may be to congregate males and females at a suitable resource for reproduction and thus we would predict that the insects caught by pheromone-baited traps are most likely to be reproductively active beetles seeking fresh resources. This behavior may be a factor responsible for the increasing range of the pest, especially in Africa, where environmental conditions are suitable for flight (Fadamiro and Wyatt, 1995) and food resource abundant.

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