Free flight capacity determination in a sustained flight tunnel: effects of age and sexual state on the flight duration of *Prostephanus truncatus*

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Abstract. Adult *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) steering anemotactically upwind to a pheromone source in a wind tunnel, respond normally to, and alter their ground speed according to the direction and speed of, the movement of ground patterns beneath them. By manipulating this optomotor reaction component of their behaviour, studies were conducted on their flight duration. The results show a great deal of individual variation in flight duration, and the general data on single flights were skewed towards short flights. Pre-reproductive and inter-reproductive male and female beetles flew significantly longer than older beetles that had passed their peak of reproduction. There was no significant difference in the flight duration of male and female beetles at any age. The overall results suggest that younger *P.truncatus* are capable of long-distance flights, and support the proposition that flight could be important in the spread of the beetle.

Key words. *Prostephanus truncatus*, larger grain borer, stored-product insect, Coleoptera, Bostrichidae, flight duration, pheromone, wind tunnel, optomotor anemotaxis.

Introduction

The ability to make long-distance flights has long been recognized as an important part of the life history of highly mobile, colonising insects (Dingle, 1986). This character is associated with migration and dispersal of most insects (Han & Gatehouse, 1993), and its thorough knowledge is critical to understanding a species' population and evolutionary ecology (Sappington & Showers, 1991).

Many techniques that allow insects to make prolonged flights have been employed in laboratory examinations of long-distance flights in insects. The most popular of these are the tethered-flight techniques (e.g. Dingle, 1965; Gatehouse & Hackett, 1980; Colvin & Gatehouse, 1993a; Rankin *et al.*, 1994). Gatehouse & Hackett (1980), however, discuss the problems associated with the use of these techniques for studying flight duration. Probably the most sophisticated method currently used to study insect migration is the 'air-treadmill' (Kennedy & Booth, 1963; David & Hardie, 1988; Blackmer & Phelan, 1991). This technique was developed principally for aphids, and it explores an insect's photokinetic and phototactic responses in a vertical wind tunnel. Miller & Roelofs (1978) described a sustained flight technique that can be adapted to study duration of free flight in insects.

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This apparatus was basically a horizontal wind tunnel with a variable-speed continuous belt installed on its floor. It allowed the manipulation of the ground speed of an insect responding to pheromone by moving the floor. In this way, anemotactic flights could be sustained. The authors recorded informative differences in the flight duration of individual *Argyrotaenia velutinana* using this technique.

One concept that has been studied frequently in research on insect migration is that of the 'reproduction-flight syndrome' proposed by Johnson (1969). This hypothesis recognizes that migratory flight and reproduction are usually mutually exclusive functions in insects, and proposes that migration is usually restricted to the post-teneral, pre-reproductive or inter-reproductive period in many insect migrants (Colvin & Gatehouse, 1993a, b; Gunn & Gatehouse, 1993; Rankin *et al.*, 1994). A review of the cost of migration in insects (Rankin & Burchsted, 1992), however, indicated a few studies in which this concept was refuted. The effects of other related factors on duration of flight have also been studied in many species: physiological factors (e.g. age, sex), food and flight resources (Rankin & Rankin, 1980; Armes & Cooter, 1991; Sappington & Showers, 1991; King, 1993), and environmental cues (Colvin & Gatehouse, 1993b).

Much of the available literature on long-distance flights in insects, however, concerns the well-known migratory species of the orders Hemiptera, Orthoptera, Coleoptera, Diptera and Lepidoptera (e.g. references cited by Johnson, 1969; Rankin &

Rankin, 1980; Han & Gatehouse, 1993). There is little information concerning long-distance flights in small beetles which are pests of stored-products, many of which must be capable of making relatively long flights from habitat to habitat since they occupy relatively temporary niches.

The larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae), is an exotic species with an ever-increasing range in Africa, where it is an important economic pest of stored maize and dried cassava (Hodges, 1986). Flight may be involved in the spread of *P.truncatus* in a number of ways (Fadamiro & Wyatt, 1995). Little is known, however, about its dispersal tendency.

In the present study the sustained flight tunnel technique described by Miller & Roelofs (1978) was adapted for the study of free flight duration in *P.truncatus*. The effects of age (or reproductive state) and sex on flight duration were examined. Based on available information on its biology, several hypotheses were tested including a hypothesis that pre-reproductive and inter-reproductive male and female beetles would exhibit a stronger tendency to fly longer than those that had passed their peak of reproduction. A second hypothesis was that both male and female beetles should be equally capable of long-distance flights. Finally, if the technique truly measures an insect's tendency to terminate flight ('settling' or 'landing') due to a gradual depletion of fuel (energy constraints) during flight, a decline in the duration of successive flights should occur, and thus it was hypothesized that the mean duration of all first flights would be greater than the mean duration of all second flights, which in turn would be greater than the mean duration of all third flights.

Materials and Methods

Insects. Prostephanus truncatus was reared on whole, clean maize at 30 ± 1°C and 65 ± 5% r.h. under a LD12:12h regime. The strain had originally been collected in Tanzania, Africa, and had been cultured in the laboratory for years. Beetles of known age were collected from cultures established on milled grain that passed through an Endecotts sieve of mesh size 3.35 mm to ease removal of beetles from culture (Fadamiro, 1995). Test beetles were collected 3 h before an experiment, cleaned with a soft brush to remove maize dust, pre-selected for flight activity (only beetles that displayed flight initiation were used for the experiments), and sexed (Shires & McCarthy, 1976).

Pheromone. The male-produced aggregation pheromone of *P.truncatus* consists of two components together known as 'Trunc-call'. The major and minor components were identified as 1-methylethyl(2E)-2-methyl-2-pentenoate (Trunc-call 1 or T1), and 1-methylethyl(E,E)-2,4-dimethyl-2,4-heptadienoate (Trunc-call 2 or T2) respectively (Cork *et al.*, 1991; D. Hall, personal communication). Pheromones (0.2 mg loading of T1 + T2 in the ratio of 1:1) used in this study were supplied by the Natural Resources Institute, Chatham, U.K., in polythene vial dispensers ($20 \times 9 \times 1.5$ mm thick). A 0.2 mg dose of the pheromone was used because this was the dose that gave the best attraction in the wind tunnel (Fadamiro, 1995). Upon receipt the vials were stored in a freeezer.

Wind tunnel. Experiments were conducted in a clear, rectangular glass, flight tunnel 160 cm long and 75 cm high and wide. The floor of the tunnel had a moveable pattern consisting of a white background scattered with 13 and 24 cm diameter black dots to provide visual feedback used by insects in monitoring upwind progress (Marsh *et al.*, 1978). The pheromone source was placed in the middle of the tunnel 30 cm from the upwind screen. Beetles were released onto a platform placed 100 cm directly downwind of the pheromone source. The release platform was placed 30 cm from the downwind screen. Both the platform containing the pheromone source and the release platform were placed at a height of 20 cm above the tunnel floor. Studies have shown that the beetles were less responsive to the moving floor patterns when released from greater heights (Fadamiro, 1995). The experimental set-up was calibrated by using ventilation smoke plumes of hydrochloric acid. Experiments were carried out at 28 ± 1°C and 30 ± 5% r.h. The wind speed was 20 ± 1 cm/s and beetles were flown at 9–12 h into the photophase under a light intensity of 3700 lux (Fadamiro, 1995).

Experimental protocol. The concept used to estimate flight duration in *P.truncatus* was based on the demonstration of 'optomotor anemotaxis' as a mechanism of flight orientation in the beetle (Fadamiro, 1995). This technique involved the movement of the visual pattern on the tunnel's floor beneath a flying beetle, to sustain and thus measure the duration and persistence of anemotactic flights in a pheromone plume.

Since single beetles released on the platform often did not take flight within 10 min (personal observation), up to five 'fliers' (beetles that initiated flight during a pre-test without pheromone) were released simultaneously in the tunnel. After the 'first' beetle had taken-off, the remaining beetles were carefully removed from the platform and placed in a marked petri-dish. When an orienting beetle (flying up a pheromone plume) had traversed an imaginary line drawn 50 cm upwind of the release platform (i.e. 50 cm to the pheromone source), the floor pattern was moved downwind and, consequently, the beetle decreased its airspeed accordingly and was drifted downwind. When the beetle reached the release platform (i.e. c. 30 cm to the downwind screen), the movement of the floor was stopped and, consequently, the beetle again resumed upwind flight to the pheromone source. By carefully manipulating the movement of the floor downwind, upwind, or keeping it stationary, it was possible to sustain the beetle's flight and prevent it from landing on the pheromone source. An orienting beetle could even be kept stationary for some time with zero net up-tunnel progress.

The duration of flight was timed using a stop-watch to the nearest 0.01 s from take-off until the beetle stopped flying. The beetle was then placed back onto the release platform where it could receive maximum exposure to the pheromone. By using a count-down digital clock with alarm, the beetle was given 3 min from the time the previous flight ended. If the beetle resumed flight within this time, the stop-watch was started again and the flight duration added to that of the previous flight duration (i.e. first flight). If the beetle resumed flight after 3 min but before 10 min, the flight duration was measured and counted as a 'second flight' (see Fig. 1). A beetle that did not resume flight again within 10 min of landing was recorded as, 'exhausted'. During a 'third flight', an alighted beetle was given only 3 min to resume flight.
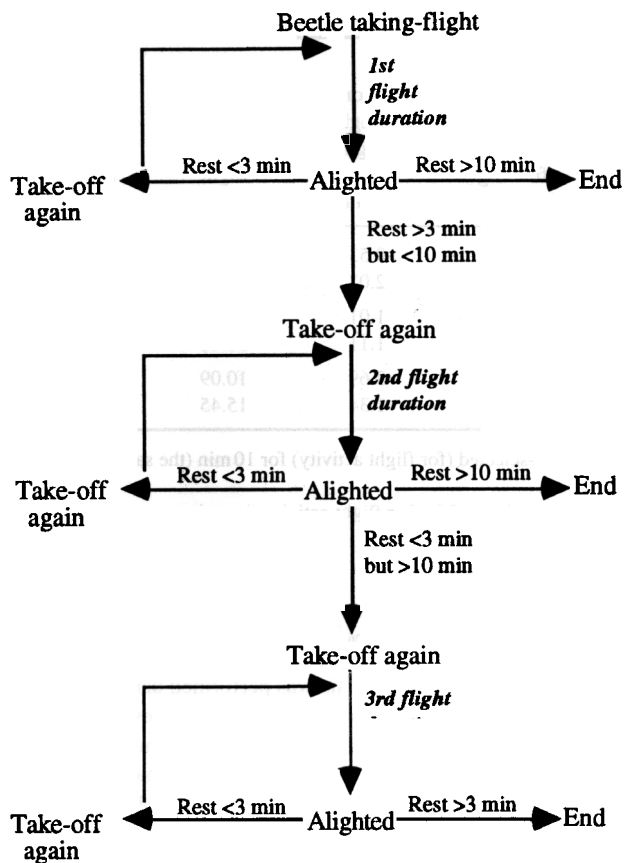
Fig. 1. Flow diagram showing the sequence of data recording for flight duration.

If it did not resume flight after this time, its behaviour on the platform was observed for a further 60 s. If it showed flight activity (wing-opening or take-off) within this period it was scored as 'inexhausted', but further flight duration was not measured. If it did not show flight activity during this period it was scored as 'exhausted.'

In this way, up to three successive flights by a beetle were measured where possible (Fig. 1). A single (continuous) flight was defined as the summation of flight time when flights were separated by less than 3 min, and a subsequent flight (second or third flight) was regarded as a flight that occurred between 3 and 10 min after the termination of the preceding flight. Any orienting beetle that landed on the pheromone source was discarded. Total flight duration was the summation of all measured flights (i.e. up to three single continuous flights with less than 10 min rest period in between). Due to time constraints, and since the technique was not automated, observations on one beetle continued for 60 min after which its flight was deliberately terminated. Such beetles were also scored as 'inexhausted.' These protocols were defined on the basis of observations during preliminary investigations.

The duration of flights were measured in beetles of known ages to give an indication of variation in flight duration in *P.truncatus*. Emphasis was placed on three different age groups of beetles: pre-reproductive (5–6 days old), inter-reproductive and just before peak of reproduction (15–17 days old), and those

that had passed the age at which peak of reproduction occurs (i.e. post-peak reproduction, 35–36 days old). Reproductive status was deduced from Bell & Watters's (1982) and Li's (1988) studies, in addition to personal observations (Fadamiro, 1995). The sex of beetles was determined to give an indication of any possible effect of sex on flight duration, and at least four beetles of each sex were flown per age group.

Statistical analyses. The data were analysed using GLM (SAS Institute, 1985). A linear regression model was fitted to the general data on the variation in flight duration with age. Data for comparison were log-transformed and the analysis of variance (two-way or MANOVA, as necessary) test was used to check for differences in flight duration between the three successive flights, the three age groups, and sexes. The Tukey test was used to compare means.

Results

Although individual variations in flight duration were recorded, the first hypothesis that pre-reproductive and inter-reproductive beetles would exhibit a stronger tendency to fly longer than those who had passed their peak of reproduction, and the second that both male and female beetles should equally be capable of long-distance flights were both supported by the data. Data from the experiments are summarized in Table 1.

General variation in flight duration

Fig. 2 shows the general variation in flight duration in *P.truncatus*. By using regression analysis, a significant negative linear relationship was found between age and flight duration ($F_{1, 40} = 26.26$, $P < 0.0001$, $r^2 = 0.40$). The r^2 value showed that 40% of the variation in flight duration could be explained by age. Fig. 3 shows that the distribution of single flights obtained in this study is skewed towards shorter flights.
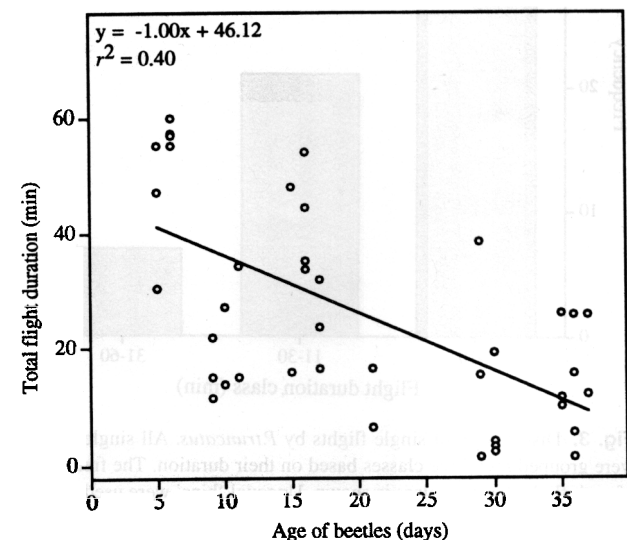

Fig. 2. General variation in total flight duration of *P.truncatus* in relation to age.

Table 1. Summary of the data on flight duration in *P.truncatus*.

Age class (days)	% take-off*	Sex of beetles	Total number beetles flown (n)	No. of beetles completing three flights	Total flight duration range (min)	No. of beetles completing only the first flight (min)	Shortest single flight duration (min)	Longest single flight duration	No. of beetles flown showing sign of exhaustion[1]
5–6	6	Female	4	4	30.5–>60.00	0	0.53	42.06	0
		Male	4	3	47.00–>60.00	0	2.07	57.27	0
		Female	5	5	16.05–35.23	0	1.01	20.06	2
		Male	4	3	16.53–53.89	0	1.11	38.48	2
		Female	4	0	5.45–12.01	2	3.69	10.09	4
		Male	5	4	1.34–26.12	1	1.34	15.45	2

* Approximated average take-off recorded when batches from each age group were pre-selected (for flight activity) for 10 min (the same conditions were used and both sexes were released together during all pre-tests).

[1] 'Exhaustion' in the above table denotes a condition in which a flown insect showed no signs of further flight activity (i.e. wing-opening, take-off) during a 1 min observation period after termination of flight duration.

Variation in successive flights

The trend was for successive flight durations to decrease ($F_{2, 26}$ = 2.92, P = 0.07). Fig. 4 shows that the mean duration of the first flight was twice as long as those of the second and third flights, although this was significant only at the P = 0.07 level. There was no difference between the mean durations of the second and third flights. This trend was similar for both sexes, and across all age groups: there were no significant interactions between flight succession and sex ($F_{2, 26}$ = 0.29, P = 0.75), age ($F_{4, 26}$ = 2.33, P = 0.08), or both age and sex ($F_{2, 26}$ = 1.49, P = 0.24). It should be noted that the above analysis was performed using only data on beetles that completed the three flights (i.e. beetles that stopped flying after the first or second flights were not included). The inclusion of all flown beetles (including those that did not fly during the second or third flight tests) would greatly exaggerate this trend and make first flight much longer than successive flights.
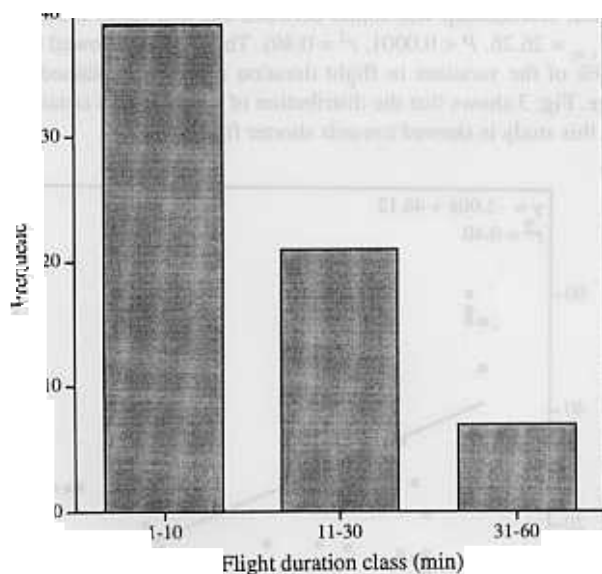
Effect of age on flight duration

Age exerted a significant and profound effect on total flight duration ($F_{2, 20}$ = 12.26, P = 0.0003). The Tukey test showed that while the difference between the mean flight durations of pre-reproductive 5–6-day-old beetles and that of inter-reproductive 15–17-day-old beetles was not significant, both of the younger age classes of beetles flew significantly longer than older 35–37-day-old beetles (Fig. 5). This observed effect was similar for both sexes; there were no interactions between age and sex ($F_{2, 20}$ = 0.07, P = 0.93). This trend was similar for each successive flight (since there were no interactions between flight succession and age). The data support the hypothesis that pre-reproductive and inter-reproductive adults of both sexes make longer flights than post-peak-reproductive adults.

Fig. 3. Distribution of single flights by *P.truncatus*. All single flights were grouped into three classes based on their duration. The frequency of each flight duration class is shown. Unequal 'bins' were used for the three flight duration classes because each of the three classes may have ecological implications: flights of less than 10 min duration could be classified as 'short' flights, while flights of duration greater than 30 min could be classified as 'long-duration' flights, especially in the Coleoptera.

Effect of sex on flight duration

There was no significant effect of sex on flight duration within each age group, thus, the data for the three age groups were pooled [($F_{1, 6}$ = 0.42, P = 0.54 (data for 5–6-day-old beetles)], [$F_{1, 7}$ = 1.17, P = 0.31 (data for 15–17-day-old beetles)], and ($F_{1, 7}$ = 0.24, P = 0.64 (data for 35–37-day-old beetles)). No effect of sex was found upon pooling the data ($F_{1, 20}$ = 0.46, P = 0.51). The mean flight duration of female was about 29 min compared to 37 min for male *P.truncatus*.
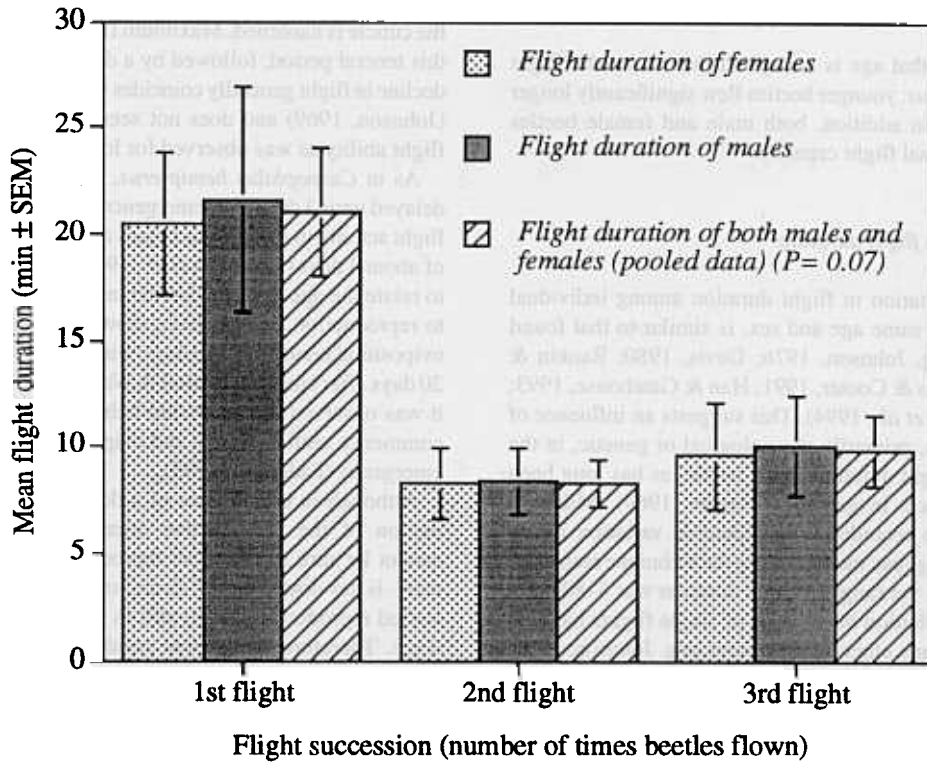
Fig. 4. Changes in the duration of successive flights by *P.truncatus*. Figure shows mean duration of single flights versus the number of flight. The difference was not significant (*P* = 0.07). *n* = number of beetles flown.
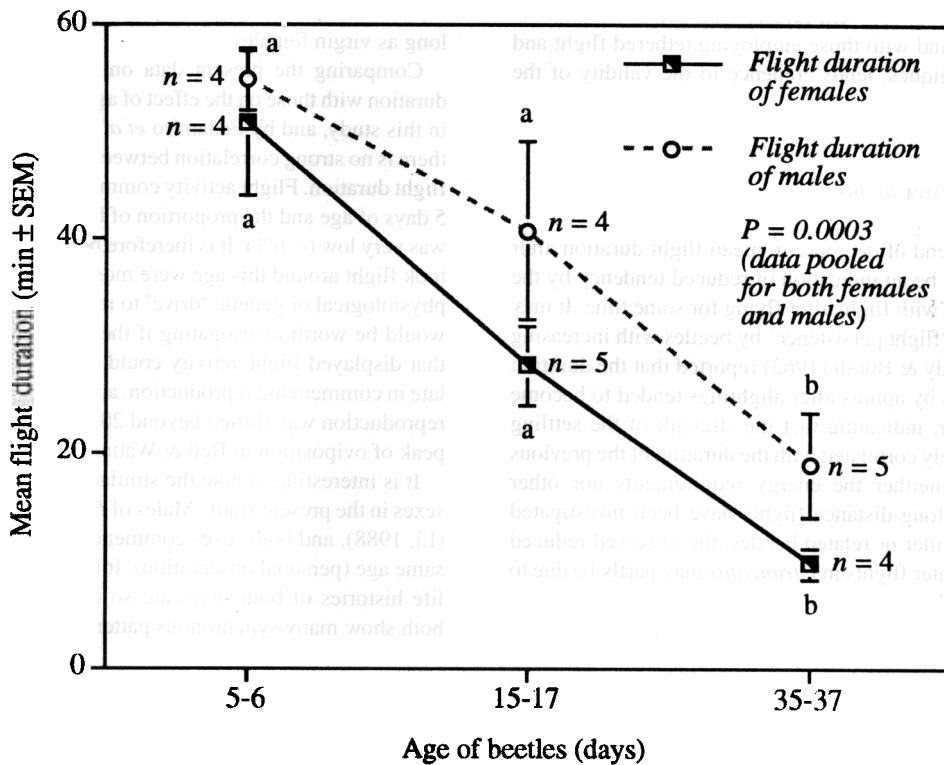

Fig. 5. Influence of age on the flight duration of *P.truncatus*. Two sets of data are shown: male and female. *n* = number of beetles flown. Means having the same letter are not significantly different (at *P* < 0.05).

Discussion

These results show that age is a major influence on the flight duration of *P.truncatus*: younger beetles flew significantly longer than older beetles. In addition, both male and female beetles displayed almost equal flight capacity.

General variation in flight duration

The observed variation in flight duration among individual *P.truncatus*, even of same age and sex, is similar to that found in other insects (e.g. Johnson, 1976; Davis, 1980; Rankin & Rankin, 1980; Armes & Cooter, 1991; Han & Gatehouse, 1993; King, 1993; Rankin *et al.*, 1994). This suggests an influence of several other factors, primarily physiological or genetic, in the determination of flight duration in the beetle, as has long been recognized for insects in general (Johnson, 1969). Miller & Roelofs (1978) also recorded a considerable variation in the flight duration of the gypsy moth by using the technique employed in the present study; the range of flight duration was 3–83 min.

The skewed distribution of duration of single flights has also been reported for many other insect species (e.g. Johnson, 1976; Rankin & Rankin, 1980). Frequently, only a small proportion of a resident population migrates, and this is influenced by environmental factors, or over longer time periods by differing selection pressure (Rankin & Burchsted, 1992). Davis (1980) concluded, based on evolutionary considerations, that short flights are probably adaptive most of the time for most individuals, since suitable habitats for colonization are likely to be close at hand.

The similarity of the present results with those of Miller & Roelofs's (1978), and with those employing tethered flight and other similar techniques, lends credence to the validity of the present results.

Variation in successive flights

The observed trend of decrease in mean flight duration after the first flight may be an indication of reduced tendency by the beetles to continue with flight after flying for some time. It may suggest a reduced 'flight persistence' by beetles with increasing flight time. Kennedy & Booth (1963) reported that the duration of later free flights by aphids after alightings tended to become shorter and shorter, indicating that the strength of the settling response is positively correlated with the duration of the previous flights. Although neither the energy requirements nor other potential costs of long-distance flights have been investigated in this or other similar or related beetles, the observed reduced flight duration of later flights in *P.truncatus* may partly be due to energy constraints.

Effects of age and sex

The present results recorded a strong effect of age on flight duration: flight duration decreased with age. Dingle (1985) summarized results showing that migratory behaviour in insects is a function of age after emergence: characteristically, flight is delayed in adult insects until the end of the teneral period when the cuticle is hardened. Maximum flight capacity is attained after this teneral period, followed by a decline in flight activity. This decline in flight generally coincides with the onset of reproduction (Johnson, 1969) and does not seem to result from changes in flight ability as was observed for locusts (Dingle, 1985).

As in *Carpophilus hemipterus*, in which flight activity was delayed until 3 days after emergence (Blackmer & Phelan, 1991), flight activity in *P.truncatus* begins after an average teneral period of about 4 days (Fadamiro *et al.*, 1996). There is strong evidence to relate the age-specific decline in flight activity in *P.truncatus* to reproduction. Studies have shown that the female has a pre-oviposition period of 6–10 days, with oviposition peaking around 20 days after emergence (Bell & Watters, 1982). In another study it was observed that courtship behaviour in both sexes did not commence until 4–5 days and oviposition until 8–12 days after emergence (Fadamiro, 1995).

Although in the absence of a detailed morphological examination of the reproductive organs during this period, one cannot be sure of the exact reproductive status of the beetles, there is no doubt that 5–6-day-old beetles are (if they have started reproduction at all) still in their very early reproductive stage. Therefore the present results show that beetles in pre-reproduction, early-reproduction, or inter-reproduction (before peak of reproduction) ages tended to exhibit longer flights than beetles that had passed the age at which reproduction peaks. This is in agreement with findings by several authors for many insect species (e.g. Colvin & Gatehouse, 1993a, b; Gunn & Gatehouse, 1993; Han & Gatehouse, 1993; Rankin *et al.*, 1994). King (1993), however, reports that mated females of the parasitoid wasp, *Nasonia vitripennis* (Hymenoptera: Pteromalidae) flew twice as long as virgin females.

Comparing the present data on the effect of age on flight duration with those on the effect of age on flight take-off recorded in this study, and by Fadamiro *et al.* (1996), it would seem that there is no strong correlation between probability of take-off and flight duration. Flight activity commenced post-tenerally around 5 days of age and the proportion of beetles taking-off at this age was very low (*c.* 6%). It is therefore possible that the beetles that took flight around this age were mostly those that possessed the physiological or genetic 'drive' to make long-distance flights. It would be worth investigating if the few 35–37-day-old beetles that displayed flight activity could possibly be those that were late in commencing reproduction, and as such, their peak age for reproduction was shifted beyond 20 days which was the time of peak of oviposition in Bell & Watters's (1982) study.

It is interesting to note the similar patterns observed for both sexes in the present study. Males of *P.truncatus* mate many times (Li, 1988), and both sexes commence reproduction at about the same age (personal observation). It is therefore possible that the life histories of both sexes are so closely associated that they both show many synchronous patterns of behaviour.

Migration and biology of P.truncati

Migration is one of those terms whose general meaning is widely understood, but whose precise definition is difficult (Southwood, 1981). Ecologically, migration involves departure

from the habitat (Southwood, 1981) or population redistribution by movement (Kennedy, 1992).

The duration of flights in the laboratory that can be indicative of migratory (or long-distance dispersal) behaviour in nature has not been ascertained and would seem to vary from species to species. Although it may be up to hours in some species, flight durations of up to 30 min could be considered as migratory in other species. Rankin & Rankin (1980) used a performance of 30 min tethered-flight by a beetle, *Hippodamia convergens*, as a reasonable indication of migratory behaviour. This may also be true for *P.truncatus*, since many beetles are said to fly only occasionally (Dingle, 1965). Going by the behavioural definition of migration as a persistent, straightened-out, undistracted movement (Kennedy, 1975), however, it may seem that the behaviour measured in the present study actually represents 'vegetative,' or the tendency of the beetle to remain lock-on to pheromone plume, rather than 'migratory' (T. C. Baker, personal communication).

Whether the flights measured in this study could be classified as migratory or not, it is obvious that younger beetles are capable of long-duration flights that could take them to a new habitat. In a separate study, the beetles were shown to orient to pheromone at an average ground speed of about 15–20 cm/s against a wind of 20–25 cm, making an air speed of 35–45 cm/s (Fadamiro, 1995). This suggests that a reasonable distance (i.e. 1260–1620 m/h in still air) could be covered in a few hours. Farrell & Key (1992) report that *P.truncatus* were able to disperse to pheromone traps in the field by upwind flight of up to a distance of 340 m in 24 h, and Rees *et al.* (1990) recorded a dispersal of over 250 m in 72 h. However, preliminary studies on flight capability of *P.truncatus* on a 'flight mill' have shown that distances equivalent of up to 25 km can be covered over a 45 h period (Pike, 1993).

The ability of pre-reproductive and inter-reproductive male and female *P.truncatus* to make long-distance flights could be regarded as an ecological adaptation ensuring the successful colonization of new resources. Southwood (1981) concluded that migratory behaviour is particularly important for species that occupy temporary habitats or habitats that become periodically unsuitable. During shortages of high-quality resources characteristic of the end of season in maize stores and the field, the larger grain borer must locate and colonize more suitable habitats. Indeed, movements of the beetles between stores have been observed (Hodges, 1986), and the natural environment (e.g. wood) has been reported as the major reservoir for the pest (Rees *et al.*, 1990; Nang'ayo *et al.*, 1993).

When in a suitable food source, male *P.truncatus* are known to secrete a pheromone that leads to the aggregation of both sexes on the source (Cork *et al.*, 1991). Considering this important role played by the male in the location and successful colonization of a new habitat, it is necessary that they are involved in any long-distance flights that can lead to dispersal.

The technique employed in this study seems to give a reasonable measure of flight duration in *P.truncatus*, although it should be stressed that the technique measures the persistence of the beetle's anemotactic flights to pheromone. Pre-reproductive and inter-reproductive beetles of both sexes are capable of flights that may at least lead to their dispersal. The results are consistent with the life history of the beetle. They support the proposition that flight could be involved in the continued spread of the larger

grain borer, especially in Africa, where environmental factors influencing its flight are optimal (Fadamiro & Wyatt, 1995).

Acknowledgments

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