ıid *Sitobion avenae* by
cological Entomology

Vratten & P. I. Sopp,
ıid *Sitobion avenae* by
l Ecology 31: 1–12.
opp, 1984. Evaluation
ble crop. British Crop
1: 271–276.
ıphids and their natu-
r, J. F. Darbyshire &
e cereal fields. Black-
233-257.

Entomologia Experimentalis et Applicata **75**: 273–277, 1995.

Flight initiation by *Prostephanus truncatus* in relation to time of day, temperature, relative humidity and starvation

Henry Y. Fadamiro[1] & Tristram D. Wyatt[1,2]
[1]*Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK*
[2]*Department for Continuing Education, University of Oxford, 1 Wellington Square, Oxford OX1 2JA, UK*

Accepted: October 27, 1994

Key words: *Prostephanus truncatus*, larger grain borer, Coleoptera, Bostrichidae, flight initiation, take-off, wing-opening, stored products insect

Abstract

Studies were carried out in the laboratory on the influences of time of day, temperature, relative humidity and starvation on flight initiation by *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae). Flight occurred throughout the 12 h photophase and at the beginning of the scotophase but peaked at 2–0 h before darkness. Temperature exerted a significant effect on flight. The frequency of flight take-off increased with temperature over the range 20–30 °C but declined sharply at 35 °C. Flight activity increased with starvation up to a maximum at 2 days after which it began to decline.

Introduction

Since being identified in Tanzania in 1981, *Prostephanus truncatus* (Horn), the larger grain borer, has become an introduced pest of great economic significance, attacking stored maize and dried cassava (Hodges, 1986), and has spread rapidly across Africa, now affecting both the east and west of the continent.

Little is known about the flight behaviour of *P. truncatus* (McFarlane, 1988; Tigar *et al.*, 1993) although this is an important part of both its biology and the knowledge needed for effective control. Flight is involved in the spread of the beetle in three ways. First, it is likely that *P. truncatus* moves locally from store to store by flight. Second, field trapping of flying beetles has revealed populations in maize fields far from farmers' stores, suggesting the beetle may be widespread outside farm buildings and that it may infest maize cobs still on the plant (Dendy *et al.*, 1989). Third, the presence of field populations both in maize fields and non-farmland (G. Hill, IIBC, Kenya, pers. comm.) suggests that wider dispersal by flight is possible. The relative importance of unaided dispersal by flight and long distance trade of commodities in the rapid spread of the beetle across the continent remains unknown.

The first step to learning more about the flight behaviour is to establish the basic conditions for flight. These are difficult to control in the field; hence this laboratory study, allowing systematic investigation under controlled conditions. This paper reports the effects of time of day, temperature, relative humidity, and starvation on flight initiation by adult *P. truncatus*.

Materials and methods

Culture method. Insects used in this study were adults of Tanzanian strains of *P. truncatus* (Natural Resources Institute, Chatham, Kent, UK) reared on whole, clean maize. Cultures were maintained at 30 ± 1 °C and $65 \pm 5\%$ r.h. under a L12:D12 photoperiod with no dusk or dawn.

General method. In this study, flight initiation was measured in still air, in incubators with a light intensity of 250 lux. Flight activity was measured by counting take-offs and wing-openings for 5 min.

Time of day and flight. Experiments were conducted in incubators at 30 °C and 65 ± 5% r.h. under a L12:D12 h photoperiod. The periods examined were 1–11 h of the photophase (i.e. 11–1 h before onset of darkness) at hourly intervals. Observations were also made at 0.5 h before and after darkness. Fifty adult *P. truncatus* (mixed sex, aged 5–20 days) were randomly selected and placed in a 600 ml 'flight' beaker. The base of the beaker was floored with white filter paper onto which was placed an upwardly projecting filter paper cone with saw-tooth edges from which the insects took-off most readily. The top of the flight beaker was covered with white filter paper and the whole apparatus was placed in an incubator with a glass inner door. Observations were made hourly over the test periods (unless otherwise stated). Flight activity was observed in the dark (where necessary) under red light with a light intensity of 10 lux. A total of 4 flight beakers were observed sequentially at each period (i.e. four replicates per observation) and the experiment was repeated over 5 days using the same insects. At the end of each day's observations, test insects were left in the beakers in incubators at 30 ± 2°C overnight without food. This procedure gave an insight into the possible effect of starvation on flight initiation.

Temperature and flight. The temperatures investigated were 20, 25, 30 and 35 °C. The experimental set-up was similar to the one described above. Four flight beakers each containing 50 adult insects (mixed sex and aged 1–20 days) randomly selected, were put into each incubator 2 h before observation, for acclimation. The relative humidity in all incubators was 65 ± 5% and observations were carried out at 2–0 h before darkness (based on the observed peak activity in this period in the experiment described above). The experiment was conducted over 4 days and at the end of each day's observations, insects were pooled, placed in a larger container (1000 ml) and kept in incubator at 30 ± 2°C overnight without food. This procedure also allowed the effect of starvation on flight to be measured. Each day, insects were removed from the pool and randomly distributed into jars for observation. Temperatures were also assigned to incubators randomly.

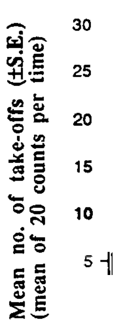
Relative humidity and flight. The effects of three relative humidities (25, 50 & 75%), representing dry, moderate, and wet environments respectively, were investigated. Normally, the relative humidity obtainable in the incubators used in this study was only 25%. Higher relative humidities of 50% and 75% were obtained by placing different amounts of water in containers into the incubators. The larger the surface area of water the higher the relative humidity. All experimental incubators were set at 29 °C and the relative humidity and temperature were checked with the aid of a thermohygrometer. Insects used in this experiment were first pre-selected for flight in a wind tunnel and those that displayed flight potentiality were selected for tests. This was done since low flight activity was generally recorded in a preliminary trial with this particular culture. Twenty five insects (mixed sex, aged 5–20 days) were randomly selected and introduced into each of four flight beakers as described before. After covering with filter paper, each beaker was randomly assigned to one of the incubators. The insects were allowed to acclimate to the incubator conditions for 3 h before the start of observations at 2–0 h before darkness. The order of observation of flight activity in the incubators was randomised. The experiment was conducted over 3 days of starvation and at the close of each day's observation, all insects were pooled into a large container kept at 30 °C, 60% r.h. overnight without food. On the following day, the insects were again randomly selected into beakers for another day's observation. This method again allowed measurement of the effect of starvation on flight and interactions between starvation and relative humidity. There were four replicates per treatment.

Statistical analysis. Data from the experiments were analysed on Statview 4.0 using the two-factor analysis of variance (ANOVA). Prior to analysis, raw data were transformed using the square root method ($x = \sqrt{(x + 0.5)}$), and for relative humidity data ($x = \sqrt{x}$) to make the variances independent of the means (Sokal & Rohlf, 1981). Scheffe's test was used to test for significance at 5% significance level.

Results

In this study, starvation was studied in combination with each of the three key factors: time of day, temperature, and relative humidity to investigate any interactions. In all the three experiments, wing-opening and take-off were strongly correlated ($r_{258} = 0.81$, $P < 0.0001$). Thus, only the data on take-off will be reported.

Time of day. Data for the five-day observations were expressed as numbers of take-offs for the 5 min test



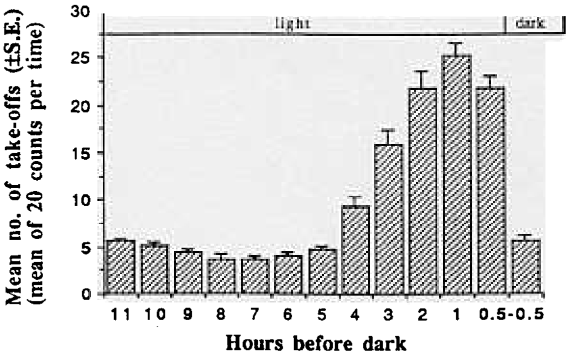


Fig. 1. Flight activity of *P. truncatus* in relation to time of day (Figure shows mean of 20 replicates per time, 50 insects were tested per replicate, P<0.05).

period (Fig. 1), and analysed as repeated measures (Martin & Bateson, 1993). Results showed significant differences in take-off by *P. truncatus* across the periods of day examined ($F_{12,180} = 146.24, P<0.0001$). *Post hoc* tests showed that flight initiation at 10–12 h of the photophase (2–0 h before darkness) was significantly greater (P<0.05) than that at other times. Flight began at the early hours of the day, dropped a little afterwards, reached a peak between 2–0 h before darkness and continued until 0.5 h of the scotophase when the observations stopped. There was significant interaction between time of day and starvation ($F_{48,180} = 1.78, P=0.004$). The effect of starvation seemed to be less pronounced at 2–0 h before darkness.

Temperature. Temperature significantly affected flight initiation ($F_{3,48} = 255.75, P<0.0001$), with insects flying more at 30 °C than at the other temperatures (Fig. 2). Insects flew more at 25 °C and 30 °C than at both extreme temperatures (20 °C and 35 °C) and insects took off more readily at 20 °C than at 35 °C. A significant interaction was recorded between temperature and starvation ($F_{9,48} = 2.16, P=0.04$). The general trend of the effect of starvation was not constant at all temperatures. The effect of starvation was less pronounced at 35 °C.

Relative humidity. The effect of relative humidity on take-off was not statistically significant ($F_{2,27} = 1.98, P=0.16$). The data suggest however, that flight initiation seemed to increase with relative humidity (Fig. 3). Although no significant interaction between relative humidity and starvation was recorded, starved insects seemed to respond more at a higher than at low relative humidity. Insects starved for up to

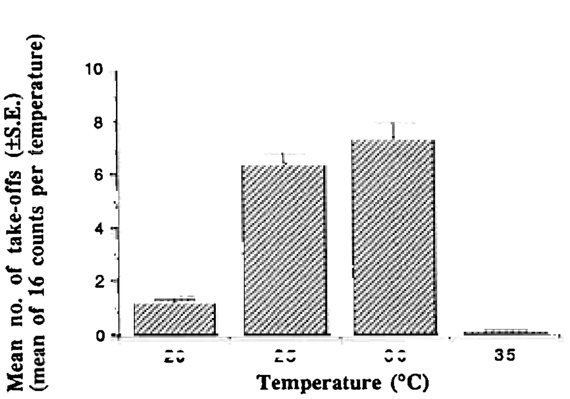


Fig. 2. Flight activity of *P. truncatus* in relation to temperature (Figure shows mean of 16 replicates per temperature, 50 insects were tested per replicate, P<0.05).

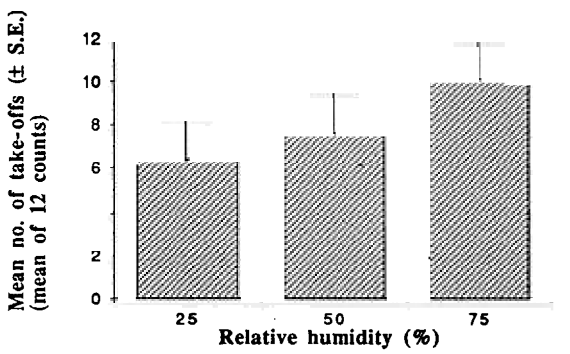


Fig. 3. Flight activity of *P. truncatus* in relation to relative humidity (Figure shows mean of 12 replicates per relative humidity, 25 insects were tested per replicate, P>0.05).

two days seemed to display less flight activity at 25% than at 75% r.h..

Starvation. The trend was similar in all the experiments: insects took off more readily on the second day of starvation than on the other days (Fig. 4). Although different lengths of starvation were studied in the three independent experiments, nevertheless, statistical analysis revealed a significant effect of starvation on take-off in all the experiments ($F_{4,1.80} = 4.52, P=0.01$) (data from time of day experiment), ($F_{3,48} = 18.13, P<0.0001$) (data from temperature experiment) and ($F_{2,27} = 3.71, P=0.04$) (data from relative humidity experiment).

Discussion

Time of day and temperature are major influences on flight activity in *Prostephanus truncatus*. In addition,

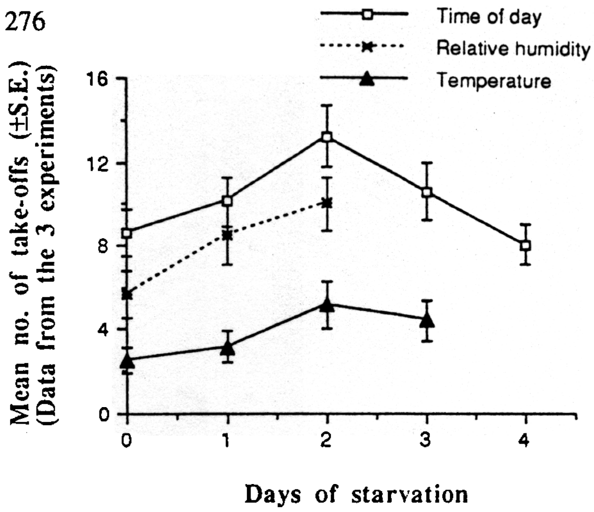


Fig. 4. Flight activity of *P. truncatus* in relation to starvation (Figure shows data collected from the three experiments (time of day, temperature and relative humidity) with unequal number of replicates, No. of insects tested in each experiment was also unequal, $P<0.05$ in all the experiments).

starvation may also be important in determining the likelihood of flight initiation. The data allow optimum conditions to be selected for laboratory flight studies.

Time of day. Flight activity showed a strong periodicity matching that recorded in the field (Tigar *et al.*, 1993): although flight activity was recorded throughout the periods examined, it peaked at 2–0 h before darkness. This period corresponded to the tail end of the photophase in the laboratory or dusk in the field (cultures being maintained on a 12:12 h light: dark period similar to field conditions). Similar results have been obtained on the closely related beetle *Rhyzopertha dominica* (F.) in the field (Leos-Martinez *et al.*, 1986) and laboratory (Barrer *et al.*, 1993). Tigar *et al.*'s (1993) study of the flight of *P. truncatus* in response to pheromones in the field reported, in addition to the early evening peak observed in this study, a smaller peak in the early hours of the photophase. This was also observed here but was not statistically significant. The small differences between the results of the present study and those of Tigar *et al.* (1993), may have arisen from differences between field and laboratory conditions. The present study suggests a circadian rhythm of activity in *P. truncatus* since insects flew more readily towards the end of the photophase in a laboratory environment with no dusk or dawn, or fluctuations in light, temperature and relative humidity characteristic of field conditions. The interaction between time of day and starvation suggests that at the peak hours of flight (2–0 h before dark), starvation was less important since both starved and unstarved insects exhibited similar flight propensity.

Temperature. Temperature had a very strong effect on flight activity with an optimum in the region of 25–30 °C and a dramatic drop at 35 °C. Flight behaviour of *P. truncatus* or other bostrichids in relation to temperature has not been documented previously. The optimum may accord with the dusk air temperatures in the field: the mean maximum air temperatures during the peak periods of *P. truncatus* trap catches at Matchakos, Kenya were less than 27 ° (G. Hill, IIBC, Kenya, pers. comm.). Similar optimum temperatures have been reported for other aspects of the biology of *P. truncatus*; the optimum for development has been reported as between 27 °C and 32 °C (Shires, 1979), while Subramanyam *et al.* (1987) reported more feeding by adult *P. truncatus* at 30 °C than at other temperatures. Starvation seemed to have less effect at higher temperatures.

Relative humidity. There seemed to be a trend for greater flight initiation with increased relative humidity but the effect was not statistically significant. The effects of low relative humidity may be especially marked for a small insect, with a small haemolymph volume (Unwin & Corbet, 1991) making water loss in flight particularly important.

Starvation. In the three separate experiments, the same pattern of flight activity in relation to starvation was observed. It was at a maximum after 2 days of starvation beyond which, flight tended to decline. This is in line with the observations made on *Rhyzopertha dominica* (Barrer *et al.*, 1993) and may mean that well fed insects fly less readily.

The results presented here may help explain the patterns of trap catch recorded in the field and underpin the more detailed laboratory studies underway to provide a deeper understanding of the flight behaviour of *Prostephanus truncatus*.

Acknowledgments

We thank the Rhodes Trust for financial support (HYF) and Dr Rick Hodges (NRI, Chatham, UK) for advice, beetles, and maize. We thank Dr Martin Birch for very helpful comments on the ms and, together with Dr Peter Miller, for support, encouragement, and advice. Drs David Rogers and David Goulson are thanked for
beetles were
UK licence r

References

Barrer, P. M., N
tors influenc
(Coleoptera:
29: 1–5.
Dendy, J., P. D
Trapping the
fields using
et Applicata
Hodges, R. J., 1
tus (Horn) (C
with an incr
22: 1–14.
Leos Martinez,
& W. E. Bu
lesser grain b
dominicalure
1138.

thanked for critical reading of the manuscript. The beetles were reared in the laboratory under a MAFF, UK licence number PHF 1231A/286/122.

References

Barrer, P. M., N. T. Starick, R. Morton & E. J. Wright, 1993. Factors influencing initiation of flight by *Rhizopertha dominica* (F.) (Coleoptera: Bostrichidae). Journal of Stored Products Research 29: 1–5.

Dendy, J., P. Dobie, J. A. Saidi, J. L. Smith & B. Uronu, 1989. Trapping the larger grain borer *Prostephanus truncatus* in maize fields using synthetic pheromones. Entomologia Experimentalis et Applicata 50: 241–244.

Hodges, R. J., 1986.The biology and control of *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) – a destructive storage pest with an increasing range. Journal of Stored Products Research 22: 1–14.

Leos Martinez, J., T. A. Granovsky, H. J. Williams, S. B. Vinson & W. E. Burkholder, 1986. Estimation of aerial density of the lesser grain borer (Coleoptera: Bostrichidae) in a warehouse using dominicalure traps. Journal of Economic Entomology 79: 1134–1138.

Martin, P. & P. Bateson, 1993. Measuring behaviour: an introductory guide. Cambridge University Press, 220 pp.

McFarlane, J. A., 1988. Pest management strategies for *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) as a pest of stored maize: present status and prospects. Tropical Pest Management 34: 121–132.

Shires, S. W., 1979. Influence of temperature and humidity on survival, development period and adult sex ratio in *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae). Journal of Stored Products Research 15: 5–10.

Sokal, R. R. & F. J. Rohlf, 1981. Biometry. W. H. Freeman & Company., New York, 859 pp.

Subramanyam, Bh., L. K. Cutkomp & B. Kouable, 1987. Effects of short term feeding by adults of *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) on shelled maize. Journal of Stored Products Research 23: 151–155.

Tigar, B. J., G. E. Key, M. E. Flores-S & M. Vazquez-A, 1993. Flight periodicity of *Prostephanus truncatus* and longevity of attraction to synthetic pheromones. Entomologia Experimentalis et Applicata. 66: 91–97.

Unwin, D. M. & S. A. Corbet, 1991. Insects, Plants and Microclimate. Richmond Publishing Co. England, 68 pp.