Influence of stimulus dose and wind speed on the orientation behaviour of *Prostephanus truncatus* (Coleoptera: Bostrichidae) to pheromone

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Abstract

Wind tunnel studies were conducted on the influence of pheromone dose and wind speed on the response behaviour of the larger grain borer, *Prostephanus truncatus* Horn to its male-produced aggregation pheromone. The pheromone did not increase the proportion flying and non-optimal dosages reduced flight initiation. Beetles flew at progressively lower airspeed and net upwind velocity as the pheromone dose was increased from 0.02 mg to 4 mg. Also, at the higher doses, the latency of take-off was longer. However, at the intermediate dose of 0.2 mg, take-off latency was significantly shorter, and the proportion of beetles exhibiting phototaxis at this dose was at a minimum. Wind was necessary for the beetles' orientation to pheromone, supporting the pheromone-induced anemotaxis hypothesis. Flying beetles increased their airspeed and net upwind velocity and therefore flew faster at the higher wind speeds. These results suggest that pheromone dose and wind speed are major influences on the flight behaviour of *P. truncatus*, and the implications of this on the interpretation of field pheromone-baited trap catch data are discussed.

Introduction

Much literature on semiochemicals concerns the responsiveness of male moths to the female produced sex pheromone (e.g. Charlton *et al.*, 1993; Willis & Baker, 1994) and although several hypotheses have been proposed, the strategies employed by flying moths and other insects to locate distant odour sources are the subject of continuing debate. It is generally presumed that pheromone initiates flight in insects, or increases the proportion of 'fliers' and this concept is probably central to the use of pheromone-baited traps to monitor insect pests.

An important factor that can influence the flight responsiveness of an insect to pheromone is the dose, and the effects of pheromone doses/concentrations on many flight parameters have been reported for moths (see for example, Kuenen & Baker, 1982; Charlton *et al.*, 1993). Roelofs (1978) suggests that the sequence of behavioural responses resulting in upwind flight will be elicited by concentrations bounded by a lower threshold for flight activation and by an upper threshold for disorientation or upwind flight arrestment.

The male-produced aggregation pheromone of the larger grain borer *Prostephanus truncatus* Horn (Coleoptera: Bostrichidae) is a two-component mixture (Cork *et al.*, 1991). It is currently employed in the monitoring of this storage pest especially in Africa, where it has continued to spread since it was introduced in the early 1980s from its native Central America (Hodges, 1986). Results from different field trapping studies (Dendy *et al.*, 1991; Farrell & Key, 1992; Tigar *et al.*, 1993) have been far from consistent, and trap catches are generally low and difficult to interpret. There is little information about the recommended dose for trapping and this is probably because to date, no detailed laboratory flight bioassays have been conducted on the responsiveness of the insect to different doses of the pheromone: a walking bioassay was used to assess the beetle's attraction to synthetic compounds (Cork *et al.*, 1991).

In earlier papers (Fadamiro & Wyatt, 1995; Fadamiro *et al.*, 1996), the role of extrinsic and intrinsic factors on the flight activity and hence trap catches of *P. truncatus* were reported. Another ecological factor that potentially may affect the flight behaviour and hence trap catches of the larger grain borer is wind speed. Based on casual

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observation, it was suggested that trap catches of *P. truncatus* appeared to be lower during periods of high winds (Tigar *et al.*, 1993). However, the effect of wind speed on the response of *P. truncatus* to pheromone remains otherwise uninvestigated.

In this paper, the results of flight tunnel studies on the influence of stimulus dose and wind speed on response behaviour of *P. truncatus* to pheromone are reported.

Materials and methods

Beetles

Stock cultures of adult Tanzanian strains of *P. truncatus* (Natural Resources Institute, Chatham, Kent, UK) were reared on whole clean maize. To collect beetles of known age, cultures were established on milled maize that passed through an Endecotts sieve of mesh size 3.35 mm to ease removal of beetles from culture. All cultures were maintained at 30 ± 1°C and 65 ± 5% r.h. under a L12:D12 photoperiod. Beetles were sexed under ×50 magnification by examining the clypeal tubercles (Shires & McCarthy, 1976).

Wind tunnel

Studies were conducted in a clear, rectangular, glass flight tunnel, 160 cm long and 75 cm high and wide with moveable visual floor patterns (Fadamiro, 1995). Air was pulled through the tunnel with a variable speed extractor fan. Beetles were released onto a platform placed 25 cm from the downwind screen and 23 cm above the floor, facing the upwind direction. The release platform consisted of a plastic Petri dish 9 cm in diameter onto which was placed a plastic cone with sharp edges. A smoke plume from a cigarette was used to determine the best position of the release platform in relation to the pheromone source (Fadamiro, 1995). The platform was roughened to enhance adherence and insects more readily took off while on the cone than any other part of the platform (personal observation). Lighting was provided by four cool white fluorescent bulbs (85 W), mounted 5 cm above the wind tunnel. Warming of the air that passes through the tunnel was done by heating the air in the room with an electric heater prior to each observation. Pheromone contamination of the laboratory was kept to a minimum as the air flowing through the wind tunnel was exhausted to the exterior outside. Contamination of surfaces within the tunnel was managed by rinsing (before and after each test) all surfaces that may possibly come in contact with the pheromone source or the plume (i.e. glass sides, release platforms, metal clamp holders etc.) with 70% ethanol. Insects were removed from a culture 3 h before flight observations, cleaned with a soft brush to remove maize dust, examined for damage, sexed, and allowed to acclimate in tunnel conditions for 20 min. Studies in the wind tunnel were carried out at 29 ± 1°C, 30 ± 5% r.h., during the last 2 h of the photophase under a light intensity of 3700 lux (Fadamiro & Wyatt, 1995; Fadamiro *et al.*, 1996). All observations and recordings were made manually.

Pheromone

Male *P. truncatus* produce a two-component aggregation pheromone known as 'Trunc-call'. The major and minor components are 1-methylethyl(*E*)-2-methyl-2-pentenoate (T1), and 1-methylethyl(*E,E*)-2,4-dimethyl-2,4-heptadienoate (T2) respectively (Cork *et al.*, 1991; Dendy *et al.*, 1991). The pheromone components T1 and T2 were synthesized at the Natural Resources Institute, UK and supplied in polythene vial dispensers (20×9×1.5 mm thick) which were impregnated with pheromone by adding a solution of the components (in a ratio of 1:1 to give a release rate of 10:1 in the air) in 0.1 ml pentane, allowing the solvent to evaporate and closing the lid (D. Hall, personal communication). Four different pheromone loadings (0.02, 0.2, 2 and 4 mg) were used, and upon receipt the dispenser packages were stored at −50°C until needed. Vials containing solvent blank were also supplied and stored seperately at −50°C.

Influence of pheromone dose on flight behaviour

Five pheromone treatments were tested: 0, 0.02, 0.2, 2 and 4 mg. For each treatment, 20 beetles (10 females+10 males) of known age (6–15 days old) were randomly selected and released together 100 cm downwind of a pheromone dispenser. A block of treatments was run daily using beetles of the same age. Each beetle was used only once and flight tests were carried out daily during the last 2 h of the photophase. There were eight replicates per treatment and the treatments were randomized. Tests were carried out at a wind speed of 20 ± 1 cm/s (Fadamiro, 1995). Observation of each treatment lasted 10 min. A period of 15 min was then allowed between observations when the tunnel and whole apparatus were cleaned with 80% ethanol and fast moving hot air blown through. Also, platforms were changed for each treatment. A preliminary study confirmed the absence of contamination using this procedure.

The quantified flight parameters for all treatments in this and the second experiment below were: number of beetles taking-off, number exhibiting phototaxis (defined as a straight upward flight in the direction of the light source), number of beetles orienting to source (defined as a directional upwind flight at the level of the plume and to within 10 cm distance of the source), number of beetles landing on the source (defined as landing on the platform holding the dispenser, or landing on the dispenser itself), latency of take-off (or time to first insect take-off, measured from the time when a group of beetles were released until the first take-off was recorded from the group), time taken by an orienting beetle to complete a 100 cm distance (T100) (i.e. time taken by a flying beetle from take-off to landing on source), net upwind velocity (*c.* distance traversed (100 cm) by an orienting beetle divided by the time taken to traverse that distance) (Kuenen & Baker, 1982), and air speed (*c.* sum of net upwind velocity and the prevailing wind speed, 20 cm/s, with the assumption that the beetles fly in straight tracks). All time measurements were made with a stop-watch to the nearest 0.01 s.

Effect of wind speed on the response of beetles to pheromone

Beetles were tested at four different wind speeds (0, 20, 25 and 32 (± 1 cm/s)) in the presence of a 0.2 mg pheromone source. Twenty beetles (10 females+10 males) aged 8–15 days old were randomly selected and released in each test. A block of treatments was run daily using beetles of

the same age. There were eight replicates per treatment and a beetle was used only once. Observation of beetles in each treatment lasted 7.5 min and a period of 15 min was allowed between observations when the tunnel and the whole apparatus were cleaned as described above. Observation parameters were similar to those described above, and in addition, the number of beetles exhibiting in-flight dropping (defined as a condition in which a flying (orienting) beetle suddenly dropped down in the middle of the tunnel) was also recorded.

Statistical analysis

Data from the experiments on time measurements and speed were expressed as actual numbers, transformed as necesssary (mainly by square root transformation) and analysed using ANOVA. Data on take-off were expressed as a proportion of the numbers of beetles released, while those on orienting, landing, phototaxis and other observed parameters were expressed as a proportion of the 'fliers', transformed using the arcsine-square root method and subjected to weighted (by n) analysis of variance using the GLM procedure (SAS Institute, 1985). This approach took into account the effect of unequal numbers of observations (n) (i.e. unequal numbers of 'fliers' within treatments). The Tukey test was used to compare means.

Results

Influence of pheromone dose

A significant difference in the proportion of beetles taking-off was recorded at the different pheromone doses ($F_{4,35}$=4.17, P=0.007) though *post hoc* testing did not indicate the nature of this significant variation (fig. 1). The raw data suggest, however, that at none of the pheromone doses tested was take-off higher than in the solvent blank control (odour free air).

Similarly, fig. 1 also shows the significant difference recorded in the proportion of beetles exhibiting phototactic flight at the five pheromone treatments ($F_{4,35}$=8.10, $P < 0.0001$). More beetles flew to the light when exposed to the solvent blank control and 0.02 mg pheromone doses than when exposed to the 0.2 mg vials.

A higher proportion of beetles oriented to the pheromone dispensers than to the solvent blank vial ($F_{4,35}$=24.13, $P < 0.0001$), but the difference was only significant between the solvent blank control and the 0.2 mg dose (fig. 2). Moreover, a significantly higher proportion of beetles landed on the 0.2 mg vials than on the vials containing the 0.02 mg dose or the solvent blank control ($F_{4,35}$=22.80, $P < 0.0001$). Generally, not all the beetles that took flight oriented to the pheromone treatments and not all beetles that oriented landed on the treatments (fig. 2).

Figure 3 shows that the latency of take-off was significantly shorter with the 0.2 mg vials than with 2 mg or 4 mg vials ($F_{4,35}$=4.51, $P < 0.005$).

Significant differences were also recorded for the time taken by beetles to fly 100 cm ($F_{4,40}$=8.24, $P < 0.0001$), net upwind velocity of beetles ($F_{4,40}$=16.13, $P < 0.0001$), and beetles' airspeed ($F_{4,40}$=16.00, $P < 0.0001$). The time taken by beetles to fly 100 cm was longer to the 4 mg vials than to the 0.2 mg, 0.02 mg or the solvent control vials (fig. 4),

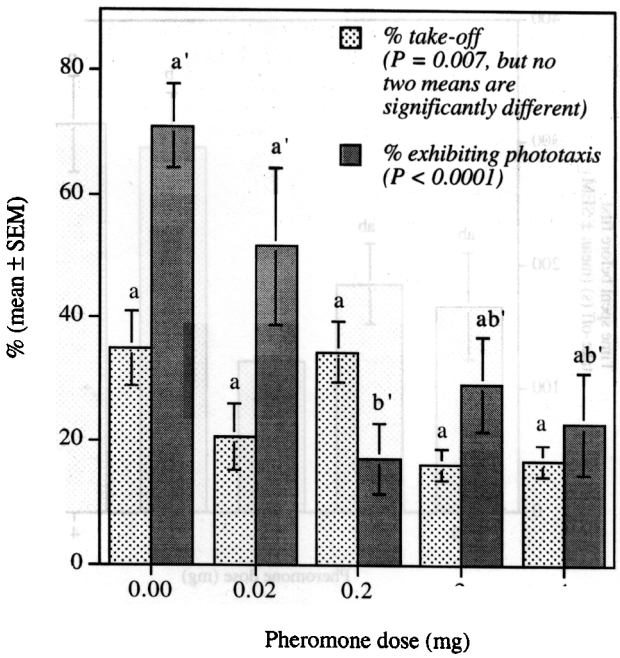

Fig. 1. Influence of pheromone dose on take-off and phototactic flight by *Prostephanus truncatus*. Figure shows mean proportions of take-off (total number of beetles released per treatment=160), and 'fliers' flying upwards to light. In this, and related subsequent figures 0.00 pheromone dose=control solvent blank; means having the same letters are not significantly different at $P < 0.05$.

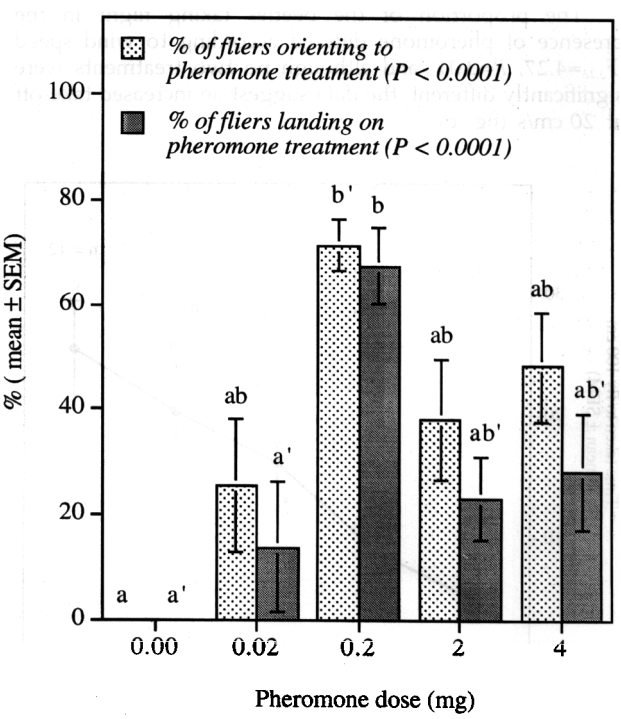

Fig. 2. Influence of pheromone dose on orientation and landing by *Prostephanus truncatus*. Figure shows mean proportion of fliers orienting to, and landing on the different treatments. None of the flying beetles landed on the solvent blank control (0.00 mg pheromone dose).

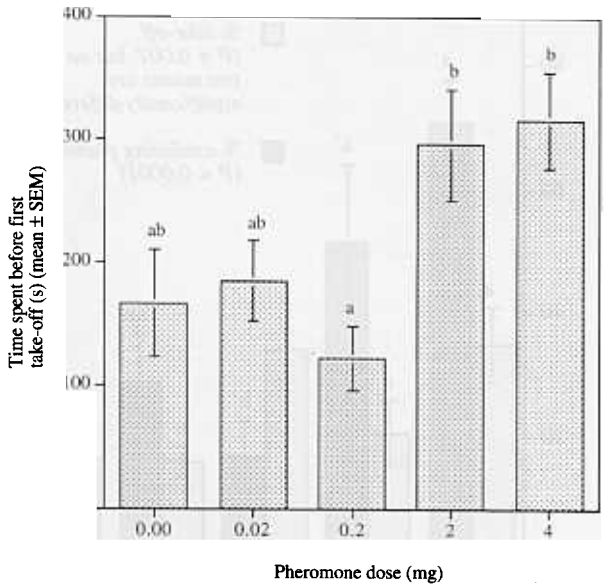

Fig. 3. Influence of pheromone dose on latency of take-off by *Prostephanus truncatus*. Figure shows mean time spent in seconds ($P < 0.005$). Data were recorded for eight beetles per treatment.

and flight speeds were significantly slower to the 4 mg vials than to the 0.02 mg or the control vials (fig. 5).

Effect of wind speed on response to pheromone

The proportion of the beetles taking flight in the presence of pheromone differed according to wind speed ($F_{3,28}$=4.27, P=0.01) and although no two treatments were significantly different, the data suggest an increased take-off at 20 cm/s (fig. 6).

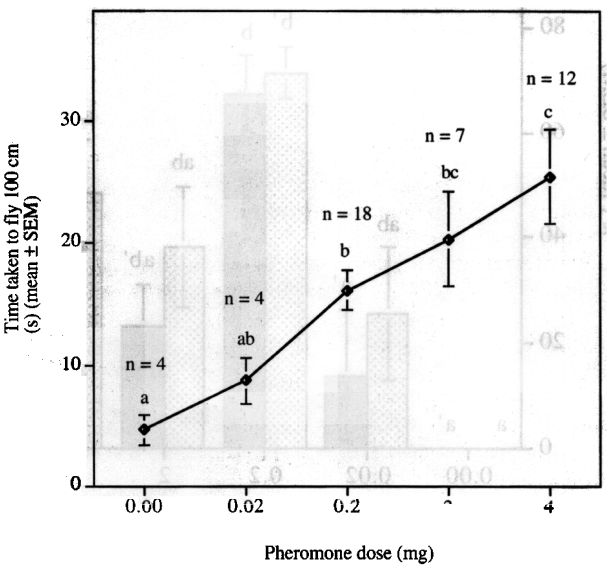

Fig. 4. Influence of pheromone dose on time taken by flying *Prostephanus truncatus* to traverse a distance of 100 cm upwind. Figure shows mean time in seconds ($P < 0.0001$). Unequal numbers of beetles were observed per treatment.

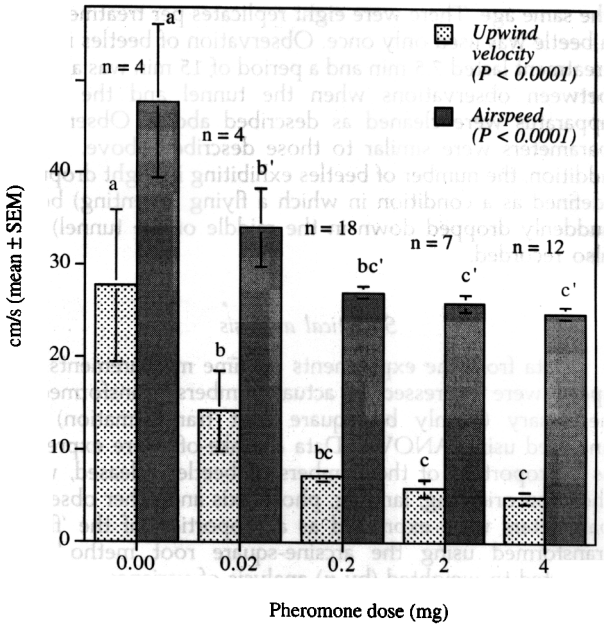

Fig. 5. Effect of pheromone dose on the flight speeds of *Prostephanus truncatus*. Figure shows mean speeds in cm/s. *n*=unequal for treatments but same at each treatment for both parameters.

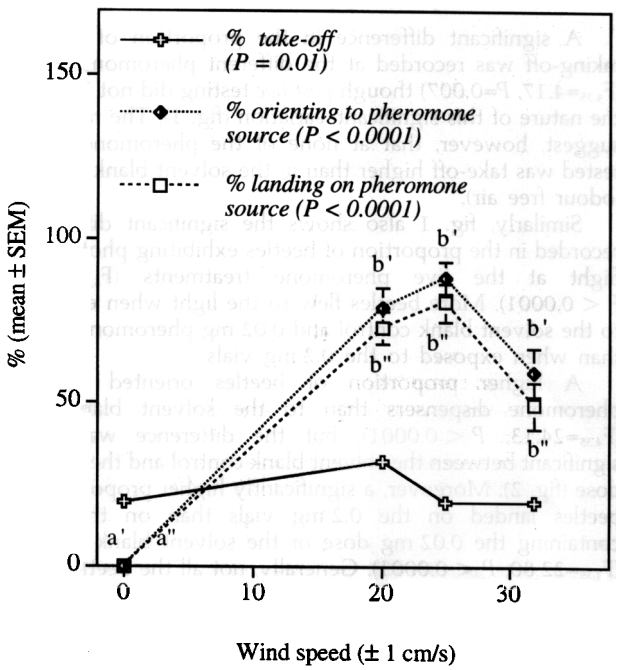

Fig. 6. Effect of wind speed on the response of *Prostephanus truncatus* to pheromone. Figure shows mean proportions of beetles initiating flight, and those of 'fliers' orienting to and landing on the pheromone source. The pheromone dose used in this and related subsequent figures was 0.2 mg. For take-off, total number of beetles released at each wind speed was 160. *n* for proportions orienting and landing were unequal because number of beetles taking-off was different at each wind speed.

Table 1. Effect of wind speed on some flight parameters of pheromone-modulated flight behaviour of *Prostephanus truncatus*.

Flight parameter	Wind speed (cm/s) 0	20	25	32
Latency of take-off (s) (P=0.77)	120.63 (±14.95) a	140.00 (±27.76) a	131.25 (±12.91) a	111.25 (±22.79) a
% exhibiting phototaxis (P=0.008)	23.8 (±8.2) a′	2.1 (±2.1) a′	6.7 (±4.5) a′	21.9 (±6.9) a′
% dropping in-flight ($P < 0.005$)	*	8.5 (±3.2) a″	7.7 (±3.8) a″	30.1 (±5.2) a″
% leaving pheromone source after landing (P=0.51)		1.6 (±1.6) c	4.6 (±3.0) c	4.2 (±4.2) c

Table shows mean values (±SEM). Treatments having the same letter are not significant at $P < 0.005$. *=no data collected.

At the different wind speeds, significant differences were also recorded for the proportions of beetles orienting to ($F_{3,28}$=38.58, $P < 0.0001$), and landing on ($F_{3,28}$=47.91, $P < 0.0001$) the pheromone source; the differences in both cases being between still air (0 cm/s) and each of the other wind speed treatments (fig. 6).

Also, an overall significant difference was recorded for the frequency of beetles exhibiting phototactic flight ($F_{3,28}$=4.76, P=0.008) but no difference between any two pairs of treatments was significant (table 1).

Since no orientation to, or landing on, the pheromone source were recorded at 0 cm/s (still air), the proportions of beetles suddenly dropping during directional flight to the pheromone (i.e. in-flight dropping) and those leaving the pheromone source after landing were compared only for three of the four wind speed treatments (i.e. 20, 25 and 32 cm/s). The results showed a significant difference in the proportion dropping during oriented flight ($F_{2,21}$=6.86, $P < 0.005$), while the frequency of leaving after landing on the pheromone source was not significantly different ($F_{2,21}$=0.70, P=0.51) for any of the three wind speeds (table 1). Also, latency of take-off did not differ with wind speed ($F_{3,28}$=0.37, P=0.77) (table 1).

None of the beetles that took flight at 0 cm/s oriented to the pheromone source and therefore values for time taken to traverse 100 cm (T100), net upwind velocity and airspeed were compared only for three treatments (i.e. 20, 25 and 32 cm/s). Nonetheless, T100 ($F_{2,36}$=2.55, P=0.09), and net upwind velocity ($F_{2,36}$=2.91 P=0.07) did not significantly differ at the three wind speeds although the data showed a trend of decreasing T100 (fig. 7), and hence an increasing net upwind velocity (fig. 8) with increasing wind speed. Airspeed significantly increased with increase in wind speed ($F_{2,36}$=77.10, $P < 0.0001$) (fig. 8).

Discussion

The results show that both pheromone dose and wind speed are major influences on the pheromone-mediated

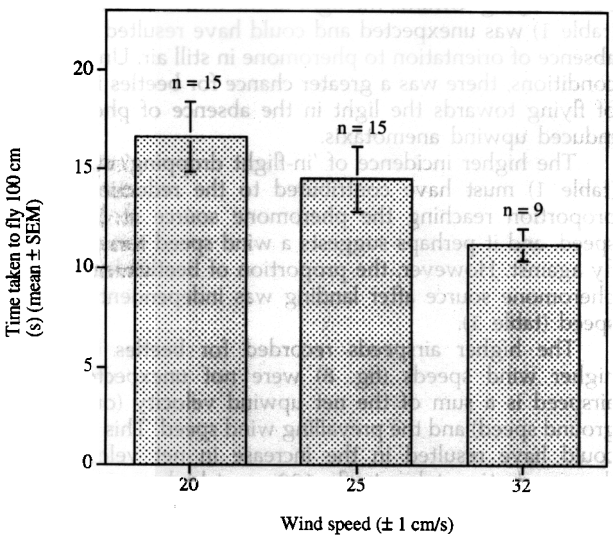

Fig. 7. Effect of wind speed on time taken by *Prostephanus truncatus* to traverse a distance of 100 cm upwind in response to pheromone (0.2 mg dose). The difference between treatments was not significant (P=0.09).

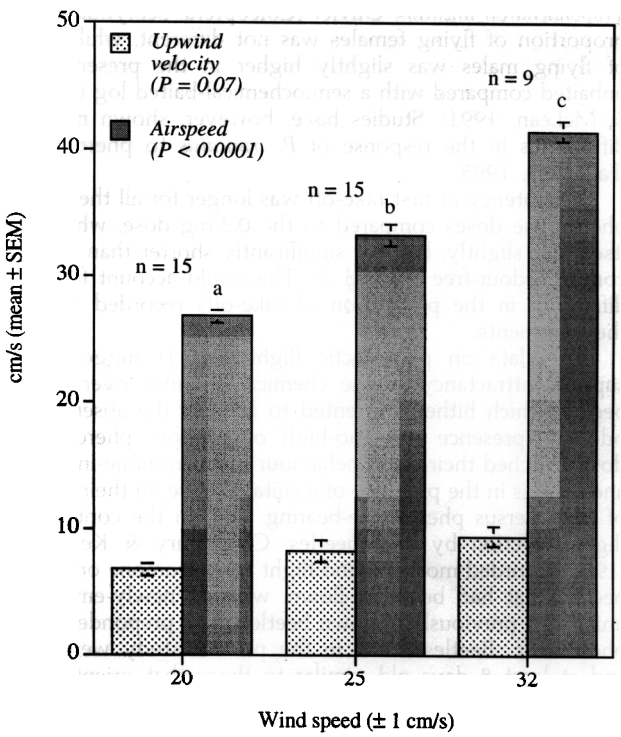

Fig. 8. Effect of wind speed on flight speeds of *Prostephanus truncatus* orienting to pheromone (0.2 mg dose). Figure shows mean speeds in cm/s. *n*=unequal for treatments but same at each treatment for both parameters.

response behaviour and possibly trap catches of *P. truncatus*.

Influence of pheromone dose

The presence of pheromone did not increase the proportion initiating flight; in fact, slightly fewer take-offs were recorded at most pheromone doses (except at 0.2 mg) than in odour-free air (fig. 1). This suggests that pheromone or a chemical stimulus is not necessary for flight take-off and that flight initiation occurs independently of pheromone. This observation has been confirmed in another study in which 'non-fliers' were released in the presence of a suitable pheromone dose (0.2 mg). The percentage take-off was not different from the control (odour-free air) (Fadamiro, 1995) and it means that the likelihood of a beetle initiating flight depends more on its physiological state than on the presence of an attractant. This is in agreement with the dispersal-dependent, pheromone-positive behaviour suggested generally for beetles (Borden, 1977), in which physiologically 'ready' insects in appropriate environmental conditions having initiated dispersal flights make a transition from dispersal to pheromone orientation on encountering a pheromone odour.

Most studies on the sex pheromones of moths have not compared flight initiation in odour free air (no pheromone) with that in pheromone-laden air. For instance, Sanders *et al.*, (1981) did not measure take-off in their study; they, however, recorded no moths fanning, locking-on (i.e. entrance into, and response to, the odour plume) or making flights of more than 150 cm in the absence of pheromone in their wind tunnel. In the scolytid beetle, *Trypondendron lineatum* Olivier (Coleoptera: Scolytidae) the proportion of flying females was not different, while that of flying males was slightly higher in the presence of unbaited compared with a semiochemical-baited log (Salom & McLean, 1991). Studies have, however, shown no sex differences in the response of *P. truncatus* to pheromone (Fadamiro, 1995).

The latency of first take-off was longer for all the other pheromone doses compared to the 0.2 mg dose, which in itself was slightly, but not significantly shorter than in the control (odour-free air) (fig. 3). This could account for the difference in the proportion of take-offs recorded within the treatments.

The data on phototactic flight (fig. 1) suggest the superior attractancy of the chemical stimulus over light; beetles which hitherto oriented to light in the absence of odour or presence of a 'too-high' or 'too-low' pheromone dose switched their flight behaviour to pheromone-induced anemotaxis in the presence of a suitable dose. In their study of light versus pheromone-bearing wind in the control of flight direction by bark beetles, Choudhury & Kennedy (1980) recorded more upwind flight to pheromone only for beetles that had been pre-flown, whereas newly-emerged unfed and previously unflown beetles were preponderantly phototactic. Beetles flown in the present study were fed and at least 8 days old, similar to those that oriented to pheromone in Choudhury & Kennedy's (1980) study.

The observations of decreases in net upwind velocity and air speed, and consequently, an increase in time taken to fly 100 cm with increasing pheromone dose (figs 4 and 5) have also been reported for moths (e.g. Cardé & Hagaman, 1979; Sanders *et al.*, 1981; Kuenen & Baker, 1982; Charlton *et al.*, 1993). Charlton *et al.* (1993) suggest that the reduction of airspeed is a result of the adoption of a more upwind heading by insects flying at higher pheromone doses.

Interestingly, the pheromone dose used in most laboratory bioassays and field trapping studies on *P. truncatus* (Obeng-Ofori & Coaker, 1990; Dendy *et al.*, 1991; Farrell & Key, 1992, Tigar *et al.*, 1993) was 2 mg and the results of this wind tunnel study showed lower response to this dose. Clearly, further studies should be carried out, particularly on the emission rates at different wind speeds and active distance boundaries of the pheromone of *P. truncatus*. It is therefore recommended that the selection of the dose of the pheromone to be used for monitoring the pest should be based on the knowledge of the emission rates and boundaries of the active distance which may be different in different habitats (i.e. stores, and field).

Effect of wind speed on response to pheromone

Percentage take-off in the presence of the pheromone was higher at 20 cm/s than at other wind speeds (fig. 6). Orientation to, and landing on, the pheromone source were only recorded in the presence of wind (fig. 6): none of the beetles released in still air conditions flew upwind to the pheromone source suggesting that upwind flight toward pheromone source was anemotactic not chemotactic (Choudhury & Kennedy, 1980). Contrasting results however, have been reported for *Trypondendron lineatum* in which the frequencies of beetles locking-on and landing on a semiochemical-baited simulated log were higher in still air than at other wind speeds (Salom & McLean, 1991). The authors' interpretation of this result was, however, based purely on casual observation and not on quantitative data: random flights in still air could bring the beetles close to the bait by chance leading to their arrestment. They also suggest the possibility of arrestment due to the visual attraction of the simulated log.

The overall significant difference in the proportion of beetles flying towards the light at the different wind speeds (table 1) was unexpected and could have resulted from the absence of orientation to pheromone in still air. Under these conditions, there was a greater chance for beetles in still air of flying towards the light in the absence of pheromone-induced upwind anemotaxis.

The higher incidence of 'in-flight dropping' at 32 cm/s (table 1) must have contributed to the reduction in the proportion reaching the pheromone source at this wind speed, and it perhaps suggests a wind speed too strong to fly against. However, the proportion of beetles leaving the pheromone source after landing was independent of wind speed (table 1).

The higher airspeeds recorded for beetles flying at higher wind speeds (fig. 8) were not unexpected since airspeed is a sum of the net upwind velocity (or upwind ground speed) and the prevailing wind speed. This probably could have resulted in the increase in net velocity and decrease in time taken to fly 100 cm at higher wind speeds (fig. 7). This suggests that the beetles are capable of increasing their flight speed to compensate for increases in wind speed in order to locate a pheromone source.

These wind tunnel results, at least, show the effects of dose and wind speed on the long-range orientation of *P. truncatus* to pheromone. The results may find application

in the field monitoring of the pest, although attraction in the field may involve greater distances from the pheromone source.

Acknowledgements

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