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Behavioural Response of *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) to the Individual Components of its Pheromone in a Flight Tunnel: Discrimination Between Two Odour Sources

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Abstract—The flight response of *P. truncatus* to its major pheromone component (T1), minor pheromone component (T2), and a 1:1 mixture of T1 and T2 was investigated in a wind tunnel. Single-source and two-choice experiments were conducted to determine which of the two components is more important in the medium-close-range (≥100 cm) behaviour of the beetle. In single-source experiments, either of the two components could attract the beetles, and the mixture was only slightly, but not significantly, more attractive than either of the components. In two-choice flight experiments, *P. truncatus* were able to discriminate between two simultaneously presented odour sources separated by 12.5 cm, and displayed significant preference for the mixture, or T2 over T1, suggesting that T2 may be more important than T1 in the medium-close-range behaviour of *P. truncatus*. These results contrast with some previously published data and possible reasons are discussed. There were no differences in the sex ratios of beetles attracted to the three pheromone treatments (T1, T2, or the mixture), suggesting that neither of the two components specifically functions as a sex attractant. The results are discussed in relation to the existing concepts for the multicomponent sex pheromones produced by females of many moth species. Copyright © 1996 Published by Elsevier Science Ltd

Key words—larger grain borer, *Prostephanus truncatus*, aggregation pheromone, discrimination, flight tunnel, Coleoptera, Bostrichidae

INTRODUCTION

The larger grain borer, *Prostephanus truncatus* (Horn), is a pest of stored grains in Central and South America that was introduced into Africa in the early 1980s. It was first identified in Tanzania (Hodges *et al.*, 1983) and has since spread to many countries in East and West Africa (Hodges, 1994). The male beetle produces an aggregation pheromone and this was identified and synthesised by Cork *et al.* (1991). Traps baited with the synthetic pheromone are now widely used for

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monitoring for this pest and for *Teretriosoma nigrescens* (Lewis) (Coleoptera: Histeridae), a predator of *P. truncatus* which is also attracted by the pheromone (Hodges, 1994).

The aggregation pheromone of *P. truncatus* was shown to consist of two components (Cork *et al.*, 1991; Dendy *et al.*, 1991). The major, or most abundant component was identified as 1-methylethyl (*E*)-2-methyl-2-pentenoate and was given the trivial name Trunc-call 1 (T1). This component was found to be attractive to the beetles in the laboratory (Cork *et al.*, 1991), and was used singly in lures in traps for monitoring beetle populations in the field (Dendy *et al.*, 1989, 1991). A second component of the pheromone was identified recently as 1-methylethyl (*E*,*E*)-2,4-dimethyl-2,4-heptadienoate and given the trivial name Trunc-call 2 (T2) (D. Hall, unpublished). Both components are esters sharing the same alcohol, but different acid groupings. However, being 3-carbons shorter, T1 is more volatile, and thus released faster than T2. The male beetle releases T1 and T2 in approximately 10:1 ratio (unpublished), and hence T2 is referred to as the "minor component".

In tests carried out in maize fields in Tanzania, traps baited with mixtures of T1 and T2 in 1:1 or 1:4 ratios were significantly more attractive to the beetles than traps baited with T1 alone (Dendy *et al.*, 1989). Dendy *et al.* (1991) also carried out tests in small maize stores in Tanzania and recorded significantly higher catches by traps baited with mixtures of T1 and T2 in 4:1, 1:1 or 1:4 ratios than traps baited with T1 alone. In addition, they observed that traps baited with T2 alone caught fewer beetles than traps baited with T1, although this difference was not significant. In contrast, Leos-Martinez *et al.* (1995) recently reported that in Mexico, flight traps baited with a 1:1 mixture of T1 and T2 or with T2 alone caught significantly more *P. truncatus* than traps baited with T1 alone, and there was no significant difference between catches with T2 and the mixture.

The work reported here aimed to study the effects of the two pheromone components alone and in blends on the flight behaviour of *P. truncatus* in a laboratory wind tunnel. This work was carried out before the appearance of the paper by Leos-Martinez *et al.* (1995), and, although it does not completely resolve the apparent difference in the results of these authors and those of Dendy *et al.* (1991), the present studies confirm that either of the two components can singly attract beetles at medium-close-range, and that the mixture is only slightly more attractive than either of the components alone. The results may find practical use in the current efforts aimed at improving trapping methods for *P. truncatus*.

MATERIALS AND METHODS

The beetles

Beetles were adults of a Tanzanian strain of *P. truncatus* reared on whole, clean maize at 30 ± 1°C and 65 ± 5% r.h. under a L12:D12 photoperiod with no dusk or dawn. They were removed from a culture 3 h before flight observation, cleaned with a soft brush to remove maize dust, examined for presence of all parts, and sexed after Shires and McCarthy (1976). Adults used in this study were 8–15 days old, but beetles of the same age were used in the daily replication of all the treatments in order to avoid possible effects of age on response (Fadamiro, 1995).

Wind tunnel

Experiments were conducted in a wind tunnel of dimension 160 × 75 × 75 cm at 29 ± 1°C, 30 ± 5% r.h., 20 ± 1 cm/s wind speed, under a light intensity of 3700 lux as described in Fadamiro (1995). Beetles 10–12 h into the photophase (Fadamiro and Wyatt, 1995) were allowed to acclimatise in wind tunnel conditions for 20 min. Beetles were released on to a platform placed 25 cm from the downwind screen, 20 cm above the floor and 100 cm downwind of the pheromone source. The pheromone source was attached to a 20 cm-high retort stand placed centrally, directly upwind from the beetles' release platform. A period of 15 min was left in between observations when the whole tunnel was cleaned with ethanol and the source stands changed to avoid contamination. Plume characterisation was by smoke plumes of HCl (as described in Fadamiro, 1995).

Pheromones

The pheromone components T1, T2 and the mixture were synthesised at Natural Resources Institute, Chatham (NRI) and were ⩾ 98% pure by capillary gas chromatography. They were

dispensed from polythene vials (20 × 9 × 1.5 mm thick) impregnated with 0.1 mg of T1 or T2 or 0.2 mg of a 1:1 mixture by weight of T1 and T2, and an equal quantity of 2,6-*di-tert*-butyl-4-methylphenol (BHT) as antioxidant. In previous studies, the 0.2 mg loading of the mixture proved more attractive than 0.02 or 2.0 mg loadings (Fadamiro, 1995). The three treatments were stored separately at − 50°C until use. 'Blank' vials treated with hexane solvent were also used and stored separately also at − 50°C.

Single-source experiments

The responses of beetles to each of T1, T2, and the mixture were compared separately. Twenty (10 males + 10 females) randomly selected beetles were released in the presence of each pheromone treatment. The parameters observed during a 10-min observation period in this, and the two-choice experiments included: (a) number of beetles taking flight, (b) number of beetles exhibiting phototaxis, defined as a directional upward flight towards light resulting in hitting the tunnel roof (not monitored during two-choice experiments), (c) number of beetles orienting to treatment source, defined as a directional upwind flight at the level of odour plume and to within 10 cm of the source, and (d) number of beetles that landed on treatment source, defined as landing on the clamp holding the pheromone dispenser, or the dispenser. The beetles that landed on each treatment were sexed. At least one block of treatments was run daily and the order of observation was randomised. There were ten replicates per treatment and a beetle was used only once. A control experiment was run daily to check if beetles were responding to solvent blank vials as a test for contamination in the tunnel.

Two-choice experiments

In this set of experiments, the ability of flying beetles to discriminate between two simultaneously presented different odour sources was examined. The two sources were held horizontally separated by 12.5 cm cross wind. Smoke plumes of hydrogen chloride emanating simultaneously from the two sources overlapped at a distance of 60–70 cm downwind. The beetles' release platform 100 cm cross-wind was thus in both plumes.Twenty (10 males + 10 females) beetles were released together for each test. There were three main tests involving the following pheromone pairs: T1 versus T2, T1 versus mixture, and T2 versus mixture. Prior to these tests, however, each treatment was paired in turn with a solvent blank vial to determine whether or not the beetles could show discrimination between two sources separated horizontally by 12.5 cm. Throughout this study, any two sources were alternated between observations to control for possible effects of uneven lighting, wind direction, etc., and the initial positioning of the treatments was randomised. The orientation behaviour of the beetles to the two sources was recorded in addition to the behavioural parameters listed earlier. Fresh pheromone vials were used during each observation and a beetle was used only once. Each test was replicated at least eight times.

Statistical analysis

Data from the single-source experiments on phototaxis, orientation and landing were expressed as a proportion of the 'fliers' (i.e. beetles taking flight), transformed using the arcsine-square root method and subjected to weighted (by number of fliers) analysis of variance using the GLM procedure (SAS Institute, 1985). This approach took into account the effect of unequal numbers of observations (i.e. different number of 'fliers' in each test). The Tukey test was used to compare means. Chi-square (χ^2) was used to compare the sex ratio of those beetles that landed on each treatment.

For the two-choice experiments, chi-square was used to make comparisons within each pairing. Goodness-of-fit test was used for data on frequencies of orientation and landing while degree of association (using 2 × 2 table) was tested for the data on the sex ratio of beetles that landed on the treatments (Parker, 1979). Fisher's exact test (SAS Institute, 1985) was used to analyse data where the expected frequencies were below a lower limit of five.

RESULTS

Single-source experiments

Although the beetles showed a slightly greater response to the mixture than to the individual components, this was not significant: there were no significant differences in the proportions of

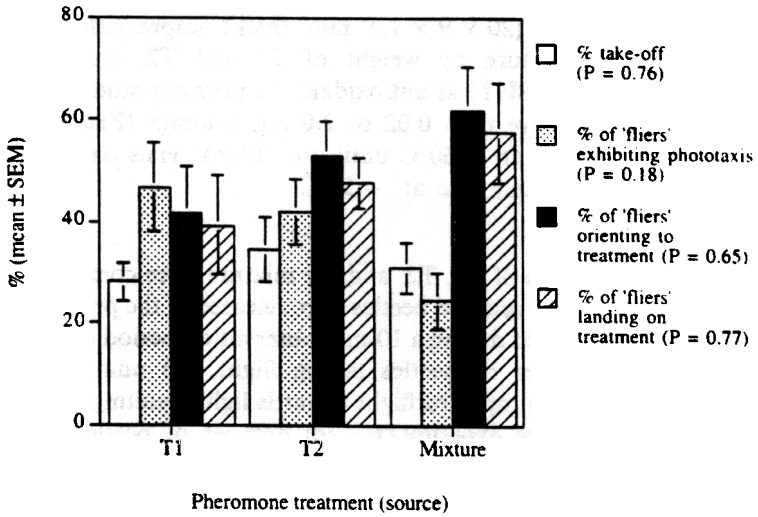

Fig. 1. Response of *P. truncatus* to individual components of its pheromone, and the mixture (data from single source experiments). Figure shows mean % of beetles exhibiting the different behaviours in the presence of each pheromone treatment. Ten replicates were run for each treatment. None of the observed behaviours showed significant differences between treatments (at $P < 0.05$). In this and Fig. 2, the mixture consisted of T1 + T2 in the ratio 1:1.

beetles taking-off ($F_{2,27} = 0.28$, $P = 0.75$), exhibiting phototaxis ($F_{2,27} = 1.81$, $P = 0.18$), orienting to odour source ($F_{2,27} = 0.45$, $P = 0.64$), and landing on odour source ($F_{2,27} = 0.27$, $P = 0.77$) between the three treatments (T1, T2, and mixture) (Fig. 1). Figure 2 shows that the sex ratio of the beetles that landed on each of the three treatments did not deviate from unity (i.e. 1:1) ($\chi^2 = 0.38$, $P > 0.5$, for T1; $\chi^2 = 0.14$, $P > 0.5$, for T2; and $\chi^2 = 0.03$, $P > 0.5$, for the mixture). In previous studies, *P. truncatus* showed no (0%) orientation or landing behaviour when presented with solvent blank vials (Fadamiro, 1995).

Two-choice experiments

In the choice experiments between pheromone and solvent blank control sources, although there was a general decrease in response when compared to the single-source experiments, or the two-choice tests involving two pheromone treatments, the beetles that responded were all attracted to pheromone rather than to solvent blank control vials. In no case did beetles orient to or land on the blank vials, suggesting the absence of visual attraction to the polythene vials. This showed

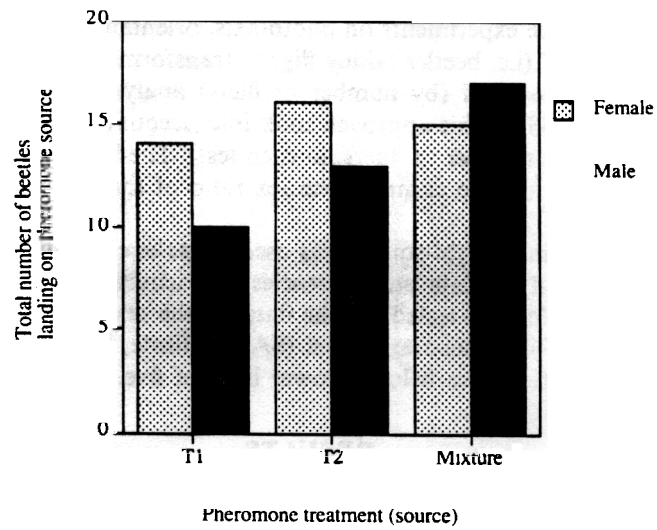

Fig. 2. Sex distribution of *P. truncatus* that landed on the three pheromone treatments (data from single source experiments). No significant effect of sex was recorded for the three treatments (at $P < 0.05$).

that *P. truncatus* were able to discriminate between an odour source (T1, T2, or mixture) and a solvent blank vial separated horizontally by 12.5 cm.

Description of discrimination behaviour during orientation

In the presence of two simultaneously presented odour sources, responding beetles that took-off upwind directly from the release platform seemed to be flying at the level of both plumes up to a distance of 30 cm upwind, after which they began to display discrimination between the two plumes. This stage was marked by a conspicuous change of course by the beetles, orienting to, and landing on, the source of their preferred odour. Out of a total of 108 oriented beetles in the two-choice tests, only one beetle oriented between both odour sources, and only two other unusual cases were recorded. In the first, a beetle that first landed on T1 left the source, flew cross-wind and landed on T2. In the second, a beetle that first oriented to T2 reaching approximately 5 cm from the source and hovered round it, and then suddenly flew cross-wind to the mixture, and landed on it.

T1 versus T2

Data from this test showed that significantly more beetles oriented to ($\chi^2 = 6.30$, $P < 0.05$), and landed on ($\chi^2 = 8.26$, $P < 0.01$), T2 than on T1 (Table 1). There was no significant difference in the sex ratio of the beetles that landed on both odour sources ($\chi^2 = 0.51$, $P > 0.1$) (Table 1).

T1 versus mixture

Significantly more beetles oriented to, and landed on, the mixture than on T1 (orientation: $\chi^2 = 29.17$, $P < 0.01$; landing: $\chi^2 = 26.69$, $P < 0.05$) (Table 2). No significant difference was recorded for the sex ratio of beetles attracted to both pheromone sources ($\chi^2 = 2.27$, $P > 0.1$) (Table 2).

T2 versus mixture

No significant differences were recorded in the number of beetles attracted to T2 or the mixture

Table 1. The responses of *P. truncatus* to simultaneously presented pheromone stimuli. The beetles were presented with a choice of two pheromone sources in each of three experiments (1–3). T1 versus T2

Response parameter	Frequency of response		*P*-value
	T1	T2	
Orientation to source			$P < 0.05$
Landing on source			$P < 0.01$
Sex distribution of attracted beetles (female:male)			$P = 0.38$*

Table 2. T1 versus mixture (complete blend)

Response parameter	Frequency of response		*P*-value
	T1	Mixture	
Orientation to source			$P < 0.01$
Landing on source			$P < 0.05$
Sex distribution of attracted beetles (female:male)			$P = 0.14$*

Table 3. T2 versus mixture (complete blend)

Response parameter	Frequency of response		*P*-value
	T2	Mixture	
Orientation to source			$P > 0.1$
Landing on source			$P > 0.1$
Sex distribution of attracted beetles (female:male)			$P > 0.5$

Table shows total number of beetles responding to each source in each pairing. Values in the same row followed by the same letters are not significantly different (at $P < 0.05$). The mixture consisted of T1 + T2 in the ratio 1:1. *Data analysed using Fisher's exact test.

(orientation: $\chi^2 = 0.57$, $P > 0.1$; landing: $\chi^2 = 0.63$, $P > 0.1$) (Table 3). Similarly, the sex distribution of the beetles that landed on both treatments was not different ($\chi^2 = 0.16$, $P > 0.5$) (Table 3).

DISCUSSION

The results of the studies described here, the first to test wind tunnel flight responses of this species, confirm that *P. truncatus* adults are highly attracted to dispensers containing the individual pheromone components or the mixture and that blank dispensers are completely unattractive. When presented with a single source, the beetles show similar orientation and landing behaviour towards either pheromone component or a 1:1 blend of the two components. The responses to T2 were greater than those to T1, and the responses to the mixture were greater than to either single component, but these differences were not significant. When response levels are high to all treatments, simultaneous presentation is needed to allow possible discrimination. When presented with two sources separated across wind by 12.5 cm, the beetles could discriminate between the two sources. They showed a clear preference for T2 or the 1:1 mixture of T1 and T2 when these were paired with T1, but showed no significant preference for T2 or the mixture when these were paired.

These results are not necessarily contradictory. Although either pheromone component singly or a blend of the two can elicit high degrees of upwind flight and landing by *P. truncatus*, when given a choice the beetles prefer T2 or mixtures containing T2 over T1. However, it is difficult to interpret these results in terms of possible roles of the two pheromone components. Two theories have been proposed to describe the responses of males to multi-component female sex pheromones in Lepidoptera. The earlier 'component' hypothesis proposed that the major, most abundant component alone determines the dimensions of the active space of the blend, while the minor components function only to initiate such close-range behaviours as landing and courtship and are not important for long-distance attraction (e.g. Cardé *et al.*, 1975). The more recent 'blend' hypothesis implicates the whole blend of components in the entire response range and stresses that several components in a blend act synergistically to effect a full response (e.g. Linn *et al.*, 1986; Linn and Roelofs, 1989). It appears that the two components of the aggregation pheromone of *P. truncatus*, under these conditions, conform to neither of these hypotheses in that either component can apparently elicit the same range of orientation and landing behaviour when presented alone or in a blend of the two.

Furthermore, the sex ratios of the beetles landing on the different sources did not differ significantly from 1:1, confirming that the pheromone is primarily an aggregation pheromone. Presumably it also functions to bring both sexes together for mating, and it was thought possible that the sexes might respond differently to the different components. Although there were no significant differences, the raw data suggested that a higher proportion of males landed on T1. More work is necessary to confirm this observation.

The present results offer the first characterisation of flight responses of *P. truncatus* to its pheromone components under controlled conditions. They offer a context in which to discuss contrasting field trapping results reported in the literature. The first tests with both pheromone components were carried out in small village stores in Tanzania by Dendy *et al.* (1991) using crevice traps made from corrugated cardboard impregnated with permethrin. As it was impossible to test all treatments in a single store, the experimental design involved three traps in each store. One trap was baited with the test blend, another placed 60 cm away from the first was baited with T1 and a third, unbaited control trap was placed midway between the other two. Catches in the trap baited with the test blend were expressed as a proportion of the total catch in the baited traps to allow for different populations in the different stores. In these trials, catches in traps baited with 4:1, 1:1 and 1:4 blends of T1 and T2 caught significantly more *P. truncatus* than the traps baited with T1, and traps baited with T2 alone caught less, although not significantly so. Dendy *et al.* (1989) had previously found that traps baited with mixtures of T1 and T2 caught over ten times more beetles than traps baited with T1 alone which caught only slightly more beetles than unbaited traps. However, T2 alone was not tested in this trial.

Recently, Leos-Martinez *et al.* (1995) reported the results of trapping tests carried out in Mexico. In tests to compare different pheromone blends, Lindgren funnel traps (Lindgren, 1983) with eight

funnels were used. Four traps were placed along a wall, 5 m apart, baited with T1, T2, a 1:1 blend of T1 and T2, or a blank dispenser. The trap baited with T2 alone caught more beetles, although not signficantly more than that baited with the mixture. However, both caught over twenty times more beetles than the trap baited with T1 alone, which itself caught significantly more beetles than the unbaited trap.

Although these trials all showed that more beetles were caught in traps baited with mixtures of T1 and T2 than in traps baited with T1 alone, Dendy *et al.* (1991) reported that catches with T2 alone were similar to those with T1 alone, while Leos-Martinez *et al.* (1995) found that T2 alone was at least as good as a 1:1 mixture of T1 and T2, implying that T1 contributes little or nothing to the attractiveness. Despite the geographical separation, it is presumed that the beetles do not actually differ in the two locations, since *P. truncatus* populations in Tanzania were probably introduced from Central or South America within the last 20 years.

The reason for this apparent disparity between the results of the two studies is not clear, but may be related to differences in experimental design. Dendy *et al.* (1991) used crevice traps, and traps baited with the test blends were always paired with a trap baited with T1 alone 60 cm away. Thus these tests measured responses of crawling beetles in maize stores where any plume structures would have been very different from those in a wind tunnel or open field. Leos-Martinez *et al.* (1995), on the other hand, used multifunnel flight traps, so responses of flying beetles were measured. The traps were 5 m apart in a Latin Square design so that the different blends were further apart than in the experiments of Dendy *et al.* (1991), although there is still likely to have been significant interference between the plumes (Wall, 1989). Furthermore, the pheromone dispensers used by Leos-Martinez *et al.* (1995) tests were thin-walled polythene vials containing 25 μl (approx. 20 mg) of pheromone, and laboratory studies (unpublished) have demonstrated that release rates of the pheromone components are more than ten times the release rates from the vials containing 2 mg of pheromone used by Dendy *et al.* (1991). In fact, wind tunnel studies showed that responses of *P. truncatus* to the pheromone were dose-related being reduced at high release rates (Fadamiro, 1995). It is therefore conceivable that very high release rates of the more volatile T1 in both the trap baited with T1 alone and that baited with the mixture actually reduced catches with these treatments in the experiments in Mexico.

The results described here measured responses of flying *P. truncatus*, but in the confines of a wind tunnel within 1 m of the source. The single-source experiment showed good responses, which were not signficantly different to T1, T2 or the mixture, in contrast to those of both trapping trials above which at least agreed that the mixture of the two components was significantly more attractive than T1 alone. The two-choice experiment demonstrated that *P. truncatus* can distinguish between two sources 12.5 cm apart, which is probably closer than was used in either of the trapping experiments. In the wind tunnel, T2 or the mixture were markedly preferred over T1, similar to the results with 'single' sources of Leos-Martinez *et al.* (1995), but in contrast to those of Dendy *et al.* (1991) with sources closer together.

Clearly further laboratory and field work is required to check for any differences in responses of walking and flying beetles. The field experiments in stores and open field should be repeated with similar protocols and lures to make direct comparisons possible, and further laboratory and field studies of the responses to different release rates of the pheromone and its components should help to define the behavioural roles of the pheromone components and blends of these.

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