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Laboratory Studies on Behavioural Interactions of *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) with Conspecifics, Synthetic Pheromone and the Predator *Teretriosoma nigrescens* (Lewes) (Coleoptera: Histeridae)

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Abstract—A bioassay method was devised to test the responses of adult *Prostephanus truncatus* (Horn) to conspecific adults or synthetic pheromone and to observe the response of the predator *Teretriosoma nigrescens* (Lewes) to adult or larval *P. truncatus* or the synthetic pheromone of this species. The results confirmed earlier observations that male *P. truncatus* are the source of a pheromone attractive to both males and females, *P. truncatus* adults (in this case virgin females) are disinclined to leave food in response to the pheromone and maize itself is relatively unattractive to *P. truncatus*. For the first time it has been demonstrated that males are not attracted to females, females repel or avoid each other and males are less attracted to the naturally produced pheromone secretion than are females. In view of the fact that unmated females will not leave food to locate a calling male it was concluded that the female response to the pheromone is primarily a means of locating a food source, rather than a sexual partner. In contrast, males release their secretion to attract females. When adult *P. truncatus* were tested against grains treated with the synthetic pheromone the response of males and females was apparently identical, in contrast to the lower response of males when tested against conspecific males. It seems probable that the amounts of pheromone used when testing the synthetic mixture are greater than would be produced naturally by a calling male and that this may mask the apparently lower sensitivity of males to the natural pheromone. The pheromone of *P. truncatus* is known to be a kairomone for *T. nigrescens*, but in the bioassay this species was not attracted to synthetic pheromone and responded more strongly to empty maize grains than to adult or larval *P. truncatus*. It would appear that when walking, adult *T. nigrescens* are unwilling to approach closely to *P. truncatus*. The possible significance of this is discussed.

Key words—*Prostephanus truncatus*, *Teretriosoma nigrescens*, bioassay, pheromones

INTRODUCTION

Prostephanus truncatus (Horn) is an important pest of farm stored maize and dried cassava in Africa and Central America (Hodges, 1986; Markham *et al.*, 1991). Host selection by this

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species is believed to be initiated by males (Hodges, 1994). Once suitable food is located, males release a pheromone attractive to both sexes and known to consist of two components, Trunc-call 1 (T1) and Trunc-call 2 (T2) (Cork *et al.*, 1991; Dendy *et al.*, 1989, 1991). This secretion is also a kairomone for a specific predator of *P. truncatus*, the beetle *Teretriosoma nigrescens* (Lewis) (Boeye *et al.*, 1992).

There have been numerous studies on the behavioural response of *P. truncatus* to synthetic pheromone sources when they are walking in the laboratory (Hodges *et al.*, 1984; Obeng-Ofori and Coaker, 1990; Cork *et al.*, 1991; Broughton and Fadamiro, 1996; Scholz *et al.*, 1997b), when flying in the laboratory (Fadamiro, 1995; Fadamiro *et al.*, 1996), when walking in a store (Hodges *et al.*, 1984; Dendy *et al.*, 1989, 1991) and when flying in the field (Leos-Martinez *et al.*, 1995; Hodges *et al.*, 1998). However, there is relatively little detailed information on those interactions between males, females and food sources that are involved in the successful selection and exploitation of hosts, although some interesting phenomena have come to light. For example, it was demonstrated that *P. truncatus* is not, or is only very weakly, attracted to maize grain (Wright *et al.*, 1993; Tigar *et al.*, 1994), that once present in a food source few, if any, *P. truncatus* adults will respond to the pheromone (Pike, 1993) and that males respond to the arrival of a female at a food source by ceasing pheromone production (Smith *et al.*, 1996). Similarly, details of the interactions that lead the predator *T. nigrescens* to find its prey are also lacking. The aim of this work was to develop a simple bioassay technique for walking beetles and to use this to investigate interactions between various combinations of *P. truncatus* adults in the presence and absence of food sources, responses of *P. truncatus* and *T. nigrescens* to synthetic pheromone and interactions between *T. nigrescens* and the larvae and adults of *P. truncatus*.

MATERIALS AND METHODS

General method

The method employed an arena (Fig. 1) at the centre of which there was an assembly constructed from two hollow maize grains held end on 'in-tandem' by solvent-free glue (UHU Ltd). The grains were drilled to create a blind-ending chamber (about 1.5 cm long and 2 mm wide). The treatment under test was placed in the tandem grain at the centre of an arena. Test beetles, either *P. truncatus* or *T. nigrescens*, were released at the arena edge and their success in reaching the central tandem grain recorded. In order to reduce the probability of the released beetle arriving at the central grains by chance, rather than by any attraction, the floor of each arena was provided with 37 evenly spaced non-edible refuges (described below) with blind-ending tunnels in which the beetles could take shelter. Release at the edge of the arena was in one of three ways—the beetles were placed there freely, placed there in another 'in-tandem' maize grain assembly, or placed there in a non-edible refuge.

Construction of the arena

A sheet of cardboard (29 cm × 29 cm) was covered with aluminium foil. A filter paper circle (24 cm) was stuck to the foil-covered board using spray-mount adhesive (3 M Ltd). The outer rim of the arena was formed by an aluminium ring (19.5 cm diameter and 3.5 cm high) sealed to the filter paper around its outer circumference with Blu-tak mastic (Bostik Ltd). Thirty-seven non-food refuges prepared from polystyrene blocks, each about 1.5 cm × 0.75 cm × 0.75 cm, were then attached to the filter paper with wood glue. These were arranged in roughly three concentric circles on the filter paper and evenly spaced covering all but the central area where the tandem maize grains were to be placed. Each block had a blind-ending tunnel, 2 mm wide and about 1.5 cm deep, formed by probing the block with a hot metal rod. The blocks were all orientated so that the holes faced inwards towards the central maize grains. This facilitated easy inspection and removal of beetles at the end of a test.

A few hours before testing, the central maize grains, with their test beetles, larvae or synthetic pheromone components inside, were attached by Blu-tak to a section of filter paper, backed with aluminium foil. The aluminium backing was sprayed with spray-mount adhesive just before

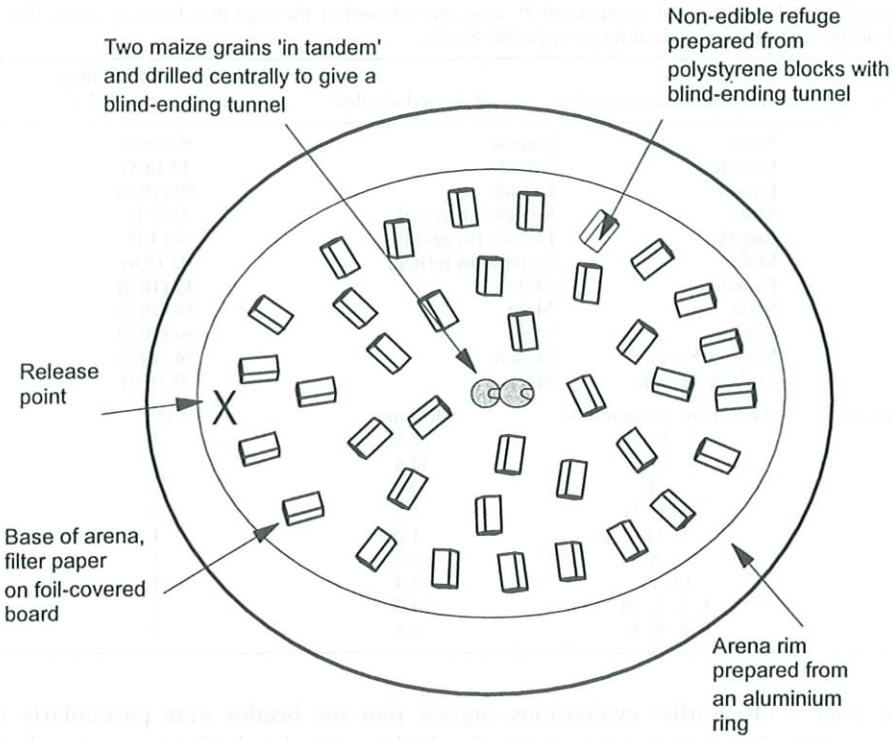

Fig. 1. Bioassay arena for testing the responses of adult *P. truncatus* and adult *T. nigrescens*.

testing, so that the whole assembly could then be attached or detached from the arena as required. The aluminium backing helped to prevent contamination of underlying filter paper of the arena with material from maize or beetles. When the arenas were in use the open top of the aluminium ring was covered by an aluminium foil lid.

Preparation of the test beetles

All *P. truncatus* were from a Tanzanian strain cultured on maize at 27°C and 70% r.h. Very young beetles, prior to emergence from pupal cells, were carefully removed from maize grains to ensure that they were unmated and of known age (0–2 days old). These beetles were placed singly on wheat flour in 5 cm × 2.5 cm glass vials closed with foam stoppers. When the beetles were 9–10 days old they were sexed using the characteristics of the clypeal tubercles (Shires and McCarthy, 1976). Only those that conformed to extremes of the male and female clypeal character were selected for the test to ensure a very high success rate in determining sex. Once sexed, the beetles to be confined to the central 'tandem grains' or released from 'tandem grains' or non-edible refuges were placed in the appropriate material whilst those to be released freely were placed in a glass vial with a small piece of filter paper to which the beetles could cling. On the following day they were tested in the arena.

T. nigrescens was collected in 1991 from Mexico and reared in the laboratory, feeding on *P. truncatus* at 27°C at 70% r.h. The strain used was the same as that released for the biological control of *P. truncatus* in Kenya (Giles *et al.*, 1996). To obtain *T. nigrescens* of known age, cultures of *P. truncatus* were prepared on kibbled maize. *T. nigrescens* adults (P1) were added to the culture and then removed after 30 days. After a total of 45 days, cultures were examined at two-day intervals and adult F1 removed manually and placed on maize flour without *P. truncatus*. When 10–20 days old these beetles were used in bioassays; they were removed from the maize flour and starved for 24 h before testing.

Experimental procedures and analysis

The various test combinations of beetles released and the treatments in the central tandem grains are shown in Tables 1–3. Tests described in Tables 1 and 2 were initiated at 15:30 h and

Table 1. Percentage of 10–13-day-old virgin adult *P. truncatus* released at the edge of a bioassay arena that entered and remained in the central grains containing conspecific beetles

Treatment No.	In grain at arena centre	Released at edge	% of beetles reaching central grain (SE)	
1	Male	Female	92 (5.6)	
2	Female	Female	13 (6.8)	
3	Empty	Female	50 (10.2)	
4	Male	Female (in grain)	0 (0.1)	
5	Empty	Female (in grain)	4 (4.1)	
6	Male	Female (in refuge)	92 (5.6)	
7	Female	Male	42 (10.0)	
8	Male	Male	54 (10.2)	
9	Empty	Male	46 (10.2)	
10	Male & Female	Female	54 (10.2)	
11	Male & Female	Male	38 (9.9)	
Key comparisons	Treatment combination	Deviance	d.f.	*p*
1	1, 3, 6	15.5	2	0.0004
2	1, 2, 3	34.6	2	0.00001
3	1, 10	9.2	1	0.0024
4	7, 8, 9, 11	1.5	3	0.6823
5	8, 11	1.4	1	0.2367
6	1, 8	9.2	1	0.0024
7	10, 11	1.4	1	0.2367
8	1, 2, 3, 10	34.7	3	0.00001
9	7, 8, 9, 11	1.5	3	0.6823

terminated after 3.5 h. Earlier evaluations suggest that the beetles were particularly responsive during this period. The tests listed in Table 3, which involved only *T. nigrescens* released at the edge of the arena, were similarly initiated at 15:30 h but terminated after only 2.5 hours, since this beetle responded somewhat more quickly than *P. truncatus*. At the end of all tests the central maize grains were checked to see whether or not the beetles released at the edge had reached the centre.

Table 2. Percentage of 10–13-day-old virgin adult *P. truncatus* (LGB) or 10–20 day old adult *T. nigrescens* (TN) released in a bioassay arena that entered and remained in the central grain treated with synthetic pheromone

Treatment No.	Maize grain at arena centre	Released at edge	% of beetles reaching central grain (SE)	
1	Grain + T1	Female LGB	62.5 (9.9)	
2	Grain + T2	Female LGB	91.7 (5.6)	
3	Grain + mix (T1 + T2)	Female LGB	95.8 (3.9)	
4	Grain + T1	Male LGB	79.2 (8.3)	
5	Grain + T2	Male LGB	91.7 (5.6)	
6	Grain + mix (T1 + T2)	Male LGB	91.7 (5.6)	
7	Grain + T1	TN	54.2 (10.2)	
8	Grain + T2	TN	54.2 (10.2)	
9	Grain + mix (T1 + T2)	TN	41.7 (5.6)	
10	Grain + solvent	Female LGB	50.0 (10.2)	
11	Grain + solvent	Male LGB	70.8 (9.3)	
12	Grain + solvent	TN	58.3 (10.0)	
Key comparisons	Treatment combination	Deviance	d.f.	*p*
1	1, 2, 3, 10 Females			
	Main effects T1	1.009	1	0.2943
	Main effects T2	19.734	1	0.0001
	Interaction of T1 and T2*	0.027	1	0.8625
2	4, 5, 6, 11 Males			
	Main effects T1	0.317	1	0.5734
	Main effects T2	4.987	1	0.0255
	Interaction of T1 and T2	0.130	1	0.7184
3	7, 8, 9, 12 TN			
	Main effects T1	0.673	1	0.412
	Main effects T2	0.669	1	0.4134
	Interaction of T1 and T2	0.165	1	0.6846

*Where the performance of T2 without T1 is compared with the performance of T2 with T1 (difference between treatments 2 and 10 compared with difference between 3 and 1). Other interactions likewise.

Table 3. Percentage of 10–20-day-old adult *T. nigrescens* (TN) released at the edge of a bioassay arena that entered and remained in the central grain containing adult or larval *P. truncatus* (LGB)

Treatment No.	Maize grain at centre	Released at edge	% of beetles reaching central grain (SE)	
1	Male LGB	TN	37.5 (9.9)	
2	Female LGB	TN	50.0 (10.2)	
3	Larval LGB	TN	66.0 (9.6)	
4	Empty grain	TN	75.0 (8.8)	
Key comparisons	Treatment combination	Deviance	d.f.	*p*
1	1, 2, 3, 4	8.5	3	0.0367

In cases where the beetles released at the edge of the arena might be confused with the beetles involved in the treatment in the central grain, those released at the edge were marked with non-toxic red fluorescent dust (Sterling Industrial Dyes Ltd, London, UK) prior to adding them to the arena.

The tests were undertaken in the dark in a CTH room set at 27°C at 70% r.h. Each treatment was replicated 24 times, with equal numbers of replicates on each test occasion. The synthetic pheromone components T1(1-methylethyl (*E*)-2-methyl-2-pentenoate) and T2 (1-methylethyl (*E*2,*E*4)-2,4-dimethyl-2,4-heptadienoate) were prepared at NRI and were at least 95% isomerically and chemically pure by GC analysis. Solutions in dichloromethane were used containing the single components at 10 ng/μl or the 1:1 mixture at 20 ng/μl total. In the bioassay 10 μl of pheromone solution (i.e. 100 ng of each component) or solvent blank was added to a maize grain with a micro-syringe. In tests requiring *P. truncatus* larvae in the central grain, two small or medium sized larvae were placed gently in the cavity of a tandem grain using soft-tipped forceps. Some fine maize flour, prepared specially from uninfested grain, was added on top of the larvae to provide ready access to food and so reduce mortality related to handling stress. The larvae were in the grain for 7–9 days prior to testing.

The data were analysed by logistic regression using the SPSS statistical package. Relevant treatment comparisons were made and significance probabilities determined. Treatment results were considered unlikely to have arisen by chance where the probability of their occurrence was less than 5% ($p < 0.05$).

RESULTS

Test 1—Responses of adult P. truncatus *to conspecifics*

The bioassay responses of *P. truncatus* adults to conspecifics are shown in Table 1. Shown in the same table are statistical comparisons, based on selected treatment combinations, which test the significance of relevant beetle interactions. These have been divided into key comparisons from which biological factors can be interpreted directly and additional comparisons which give background information. The following conclusions may be drawn from the results in Table 1:

Female responses. Females released freely at the edge of the arena or released in a refuge, entered grains containing males significantly more frequently than empty grains (comparison 1, $p = 0.0004$).

Females released at the edge of the arena in a grain did not leave it to seek a male in a grain at the centre (treatment 4—zero, compared with treatment 1—92%, no statistics necessary).

Females released freely at the edge of the arena entered the centre grains significantly less frequently when a female was already present than if the grain was empty or if there was a male present (comparison 2, $p = 0.00001$). This suggests that females may repel each other.

Females released freely at the edge of the arena entered central grains with a resident pair significantly less frequently than when only a male was present (comparison 3, $p = 0.0024$).

Male responses. Males released freely at the edge of the arena were no more attracted to grains containing males or females than they were to empty grain (comparison 4, $p = 0.68$). It should be noted however that previous studies have shown that males are responsive to the pheromone.

Males released freely at the edge of the arena entered central grains with a resident pair less frequently than they would enter grains containing only a male but this difference was not statistically significant (comparison 5, $p = 0.24$).

Comparison of male and female responses. Females released freely at the edge of the arena were attracted significantly more strongly to males in the central grain than were males released in the same way (comparison 6, $p = 0.0024$). There is no significant difference in the frequency with which males or females released freely at the arena edge entered grains containing a resident pair although only 38% of males entered grains compared with 54% of females (comparison 7, $p = 0.24$).

Test 2—Response of adult P. truncatus *or* T. nigrescens *to synthetic pheromone components*

The bioassay responses of adult *P. truncatus* and *T. nigrescens* to synthetic components of *P. truncatus* pheromone are shown in Table 2. The responses of male and female *P. truncatus* to the components and mixture were broadly similar although male response to empty grain, which in this case had also been treated with solvent, was somewhat higher than in the previous test and suggests that the combination of solvent and grain may be attractive in some measure. Clearly for both male and female *P. truncatus*, T2 alone or the mixture (T1 + T2) was significantly more attractive than empty grain. However, the addition of T1 to T2 did not significantly improve the performance of T2 while T1 alone was not significantly more attractive than empty grain. For *T. nigrescens* none of the treatments was any different from the empty maize grain suggesting that synthetic components or mixture were either unattractive or *T. nigrescens* adults might be unwilling to approach *P. truncatus*. To investigate this further the next series of bioassays tested the response of *T. nigrescens* to adult and larval *P. truncatus*.

Test 3—Response of T. nigrescens *to adults and larvae of* P. truncatus

The bioassay responses of adult *T. nigrescens* to adult and larval *P. truncatus* are shown in Table 3. Adult *T. nigrescens* in this bioassay showed a stronger response to maize grain than to adult or immature *P. truncatus*. Empty grains were more attractive to *T. nigrescens* in this test than in the previous test. The difference between the tests is that in the earlier one, solvent had been added to the empty grain; so it seems possible that the addition of solvent may reduce the response of these beetles, although Test 2 suggested the reverse appears to be true for male *P. truncatus*. There were significantly fewer *T. nigrescens* entering grain with male *P. truncatus* than entering empty grain ($p = 0.011$) which is the reverse of what would be expected, as flying *T. nigrescens* are known to be attracted to the male produced aggregation pheromone. This result suggests that walking adult *T. nigrescens* do indeed avoid approaching a source of pheromone.

DISCUSSION

The results confirm earlier observations that male *P. truncatus* are the source of an attractant pheromone for male and female conspecifics, *P. truncatus* adults (in this case virgin females) are disinclined to leave food in response to the pheromone and maize itself is relatively unattractive to *P. truncatus*. For the first time, it has been demonstrated that males are not attracted to females, females repel or avoid each other and males are less attracted to the naturally produced pheromone secretion than are females, at least when walking in close proximity to pheromone sources.

The reluctance of virgin females to leave a source of food, despite exposure to the male pheromone, suggests there is a strong hierarchy of behavioural cues and that females do not seek males when they are already on food, even if they are unmated. Response to the attractant may only occur once feeding or other conditions are unfavourable and a 'decision' to disperse and find a new host has been made. This interpretation is supported by the observations of Fadamiro (1995) who demonstrated that the presence of a pheromone source does not initiate flight behaviour but that the pest orientates to the pheromone once in flight. Thus it may be suggested that for females the primary function in responding to pheromone is the location of a suitable food source and oviposition site. Most dispersing females are already mated (Scholz, 1997; S. Addo, personal communication) thus finding a male is not crucial. A mated female can

lay fertile eggs for up to 46 days (Li, 1988) by which time some of her progeny would have reached adulthood and could mate with her and each other, thereby perpetuating a small colony. Locating a male may, however, be advantageous since matings prior to dispersal may have been only with siblings while males in the new habitat are probably unrelated, so the offspring would have a wider genetic base.

In this study, male response to conspecific males was numerically greater than that of males to empty grain but this difference was not statistically significant, while females were significantly more attracted to males than to empty grains. Scholz *et al.* (1997b), in a study using a four-choice olfactometer and synthetic pheromone, also found that male response was less pronounced than that of the female. However, in the present study, when adult *P. truncatus* were tested against grains treated with synthetic pheromone, the responses of males and females were much the same. A similar finding was reported by Broughton and Fadamiro (1996) after investigating the reaction of walking beetles to synthetic pheromone. It is not clear why these studies have provided conflicting evidence, but it may be related to the amounts of pheromone to which the beetles were exposed. After placing a male on a food source the production of pheromone is less than 10 ng/day during the first 3 days (D. Farman and D. R. Hall, personal communication), thus in the current study it is probable that the synthetic sources (100 ng) were releasing a much greater quantity of pheromone than the beetles. This may mask a lower sensitivity of males to the pheromone. As physiological sensitivity to pheromone, as measured by electroantennography, has been reported to be similar between the sexes (Cork *et al.*, 1991; Scholz *et al.* in press) any differences are therefore probably behavioural. Either males are less willing to approach a source of pheromone or only a certain portion of the male population responds actively to it. A lowered behavioural response on the part of males could account for the fact that in pheromone baited flight traps only 35% of captures were male (Scholz *et al.*, 1997a; Hodges *et al.*, 1998). In traps for walking beetles (crevice traps) only 25% of captures were male; even though the beetles in the infestation source had a 1:1 sex ratio (Hodges *et al.*, 1998). The more limited response of males to the pheromone is also consistent with the proposition that the function of pheromone released by the males is for attraction of the female rather than aggregation of males and females (Hodges, 1994), a suggestion supported by the fact that males respond to the presence of females by ceasing pheromone production (Smith *et al.*, 1996).

As males cease pheromone production in the presence of a female, it would be expected that free males and females would enter grains with resident pairs less frequently than grain containing only a male. This was the case with both free females and free males but only with the females was this statistically significant, presumably because only with females was attraction to single males strong enough to make a significant contrast with the numbers entering grains containing a resident pair. However, it is not possible to state that this effect is due only to a reduction in pheromone production by paired males since female/female repellency observed in these tests might be a contributing factor. If female repellency is active, even when there is a male present, then it is clear that male-produced attractant is the stronger of the two stimuli since four times as many females entered grain with resident pairs than grain holding only a single female. The function of female repellency remains to be established but would most likely be a means of limiting competition either between females for oviposition sites and food or between their offspring, where the resident female's progeny are likely to be more advanced and hence dominant competitors. Attempts to extract a repellency chemical from females using dichloromethane and to test this extract in bioassay have so far been unsuccessful.

The current study demonstrated little or no function for the T1 pheromone component either alone or when mixed with T2, since T2 alone was as highly attractive as the mixture. In earlier studies T1 was reported to attract *P. truncatus* in the laboratory (Hodges *et al.* 1984; Cork *et al.* 1991). However, studies in grain stores using crevice traps that capture walking beetles, indicated that the T2 component was a little less attractive to the pest than T1 and that a blend of the two in a 1:1 ratio was much more attractive than either component alone (Dendy *et al.*, 1991). In contrast, studies with flight traps showed T2 alone to be much more attractive than T1 and not significantly less attractive than the 1:1 mixture (Leos-Martinez, 1995). These differences in performance, between the pheromone components depending on their use in traps for walking or for flying beetles, have recently been confirmed by Hodges *et al.* (1998). The bioassay

used here resembles the crevice trap in that the response of walking beetles is being tested, but the results of the bioassay are similar to those of the flight trap, i.e. T2 and the mixture show similar performance. However, the conditions of the bioassay and the crevice trap are different since it is likely that beetles would experience much higher pheromone concentrations for much longer walking towards a crevice trap baited with a lure containing 2 mg of pheromone than towards the lure in the bioassay which was only 100 ng of pheromone. The bioassay appears to share one particular feature with the flight trap, in both cases the beetle locates the pheromone source rapidly giving a relatively short exposure period. Thus it may be that only when there is long exposure to high concentrations of T2 is the pheromone component T1 required for accurate location of the pheromone source.

The failure of synthetic pheromone to attract *T. nigrescens*, which also appeared to respond more strongly to empty maize grain than to adult or larval *P. truncatus*, was unexpected and apparently contrary to the known fact that this beetle will fly (Boeye *et al.*, 1992) or walk (Rees *et al.*, 1990) into traps baited with the synthetic pheromone mixture. However, the same lack of response was observed when *T. nigrescens* was placed in a four-choice olfactometer with an airflow containing synthetic pheromone to which *P. truncatus* itself did respond (personal communication quoted in Scholz *et al.*, 1997b). It would appear that there are complexities in the response of *T. nigrescens* to *P. truncatus* that have still to be understood. The evidence to date suggests that a substantial portion of the adult *T. nigrescens* population is unlikely to approach close to a source of *P. truncatus* pheromone. As adult *P. truncatus* are active borers such behaviour might offer some protection to the eggs of *T. nigrescens*. This possibility could be checked by further experimental work.

The results of this study indicate that for *P. truncatus*, and presumably other species, observations on the natural pheromone secretion and its synthetic components are required in bioassays and field trials before a clear description of the behavioural interactions and responses can be given. For a better understanding of these interactions and responses further research should include investigation of female repellency and a determination of whether lowered male response to the pheromone results from fewer beetles being responsive and/or reluctance to approach the pheromone source. A study of the complexities of the reaction of *T. nigrescens* to the pheromone of *P. truncatus* would also be worthwhile.

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