Host selection or mate selection? Lessons from *Prostephanus truncatus*, a pest poorly adapted to stored products

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Abstract

Prostephanus truncatus (Horn) is primarily a wood boring insect that is pre-adapted to infest only certain stored products, specifically maize and dried cassava. Little is known about host selection of its typical woody hosts. However, a number of studies of its response to food materials, pheromone biology and sexual interactions have shed light on how stored-product hosts are colonised. Primary host selection is achieved by either males or females at random using a 'land and choose' behaviour while secondary selection occurs as either sex is attracted to the pheromone produced by males that have found food. Females and males are preferentially attracted to the pheromone released by particular males although on contact females select mates according to other features. For females, host location would appear to motivate response to the pheromone although mate selection could be an additional advantage of being able to distinguish between the pheromone secretions of different males.

Aggregation pheromones are a common feature of many of the Coleoptera found infesting stored products. Compared with other species, *P. truncatus* is relatively poorly adapted to the exploitation of stored products, and may therefore offer some insights into the early stages of the evolution of a well-adapted storage pest.

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INTRODUCTION

Prostephanus truncatus (Horn) (Coleoptera: Bostrichidae) is a well known pest in farm storage although generally restricted to only maize and cassava. It was introduced into Africa from Meso-America in the late 1970s and since then has spread widely in that continent (Hodges, 1994) where it has been the cause of substantial food losses. *P. truncatus* appears to differ from many of the well known storage pests in that it has large populations away from storage systems where it is believed to live on woody hosts. Observations in both Kenya (Nang'ayo *et al.*, 1993) and Mexico (Ramirez-Martinez *et al.*, 1994) confirm that this pest can reproduce on dead wood, and in a laboratory study Nang'ayo (1996) demonstrated variable ability to breed on the wood of 24 species of tree, belonging to eight families, at moisture contents ranging from 8.5% to 14.8%. However, despite considerable efforts it has rarely been found in the wild, even in places where high catches in pheromone traps indicate that the beetle is abundant. In both Mexico and Kenya it has been suggested that common hosts of *P. truncatus* include branches of trees that have fallen victim to girdling cerambycids (Ramirez-Martinez *et al.*, 1994; Nang'ayo, 1996).

Evidence that *P. truncatus* is poorly adapted to the infestation of stored products
The strong association of *P. truncatus* with woody hosts has led biologists to conclude that it has evolved as a wood borer (Chittenden, 1911; Nang'ayo *et al.*, 1993; Ramirez-Martinez *et al.*, 1994). It is known that many typical storage pests, including the closely related species *Rhyzopertha dominica*, are strongly attracted from considerable distances to the odours of stored products (Barrer, 1983), a behaviour which they do not share with *P. truncatus* (Hodges, 1994). *Prostephanus truncatus* would, therefore, appear to be a forest species that in some measure is preadapted to life in maize and dried cassava should it reach them by chance. Its exploitation of stored products is sporadic and concentrated within relatively few stores where it can cause enormous damage (Hodges, 1986 and 1994; Markham *et al.*, 1991) compared with well-adapted storage pests such as *Sitophilus zeamais*, *Tribolium castaneum*, *Ephestia cautella* and *Rhyzopertha dominica*, which pose a constant threat of infestation and which may attack a wide range of food lots within a given locality.

A tentative host selection hypothesis for *P. truncatus* has been proposed by Hodges (1994). An important component of this hypothesis is the aggregation pheromone released by the male. There have been some recent studies on the sexual behaviour of *P. truncatus*

(Birkinshaw, 1998) and new observations on the pheromone interactions of this pest (Smith *et al.*, 1996; Scholz *et al.*, 1997 a&b; Hodges *et al.*, 1998; Hodges and Dobson, in press). It is therefore timely to update the host selection hypothesis to include the latest observations and, at the same time, to consider what role pheromone attraction may have in the development of beetle aggregations at the host and/or in mate selection by females.

Selection thinking

Stored product entomologists have not always followed the logic of modern evolutionary thinking when discussing the adaptive function of features such as aggregation pheromones. We wish here to emphasise the central tenet of modern evolution: that the unit of selection is the individual insect or gene and not the group, population or species. Loose arguments along the lines of 'aggregation pheromone has evolved to help other members of the species find food' (implicitly suggesting group selection) are untenable for one simple reason: group-selected traits are not evolutionarily stable and will be rapidly replaced by mutant traits that benefit the individual rather than the group. We will illustrate this general principle by reference to the possible functions of aggregation pheromone.

Suppose that all individuals in a population produce a pheromone when they find food. This pheromone attracts unrelated individuals of both sexes to the food, and this somehow benefits other members of the species but is of no benefit to an individual producing the pheromone (a signaller). The signaller may suffer reduced fitness in absolute terms (perhaps because energy used to synthesise pheromone is not available for growth and reproduction, or because a predator is attracted by a kairomonal effect). The signaller will certainly suffer a reduction in *relative* fitness because unrelated individuals (competitors) will have their fitness increased. A mutation causing an individual not to produce pheromone would, therefore, increase the fitness of the mutant *relative to other members of the population*, and the mutation would inevitably spread through the population.

It is therefore clear that pheromone signalling can only be maintained in the face of mutation if there is a benefit to the individual signaller. This benefit might be, for example, *via* inclusive fitness (if close relatives were attracted to food more frequently than unrelated individuals, i.e. kin selection), or *via* 'conditioning' to improve the quality of the food medium through communal feeding (Wood 1982), or *via* attraction of a potential mate (Birkinshaw 1998). Whatever the proximate mechanism, there must be an ultimate benefit in

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terms of increased individual fitness. This logic is known as 'selection thinking' (Charnov, 1982) and has been expressed very lucidly and forcibly by Dawkins (1976).

PRIMARY HOST SELECTION

In *P. truncatus*, dispersal away from stored product hosts occurs as adult *P. truncatus* walk or fly from food sources, especially when these are depleted or insect population density is high (Hodges, 1986; Fadamiro, 1995a; Scholz, 1997). Most flight activity of the beetle is concentrated around dusk (Tigar *et al.*, 1993), but there is also sometimes a peak at dawn (Novillo, 1991). Such flight would not appear to be required for the act of mating itself since mating can occur in the tunnels of the food source (Birkinshaw personal observation) and most dispersing females are already mated (Scholz, 1997; S. Addo unpublished). Female *P. truncatus* have an extended reproductive period and have been found to mate multiply with the same and different partners (Birkinshaw, 1998). It is therefore likely that such flight is primarily intended for dispersal to a new food source, but also provides an opportunity for the selection of new mates.

One of the first surprises for entomologists investigating *P. truncatus* was that the adult beetles are not specifically attracted to stored products over a long range (Wright *et al.*, 1993; Tigar *et al.*, 1994). For primary host selection, male and female beetles alight on a surface and make test burrows in search of suitable food (Figure 1). The test burrows are usually not more than about 1 cm in depth and may be made into almost any solid material, such as wood, soap, leather, plastic, etc., that is not too hard to penetrate. Short-range attraction to some plant odours might help guide the beetle in making test burrows (Detmers, 1990; Wright *et al.*, 1993; Scholz *et al.*, 1997b) but the indiscriminate nature of test-boring behaviour suggests that specific chemical/visual cues are not a prerequisite to tunnelling behaviour. If a beetle fails to find food in its test burrow then it will back out and continue the search.

It is not certain which food materials *P. truncatus* is most in search of. It can digest cellulose (Vazquez-Arista *et al.*, 1997), but it would seem that starch is a particularly important component of the diet (Detmers, 1990; Ramirez-Martinez *et al.*, 1994; Nang'ayo, 1996: Borgemeister *et al.*, 1998). Starch can support the high rates of population increase observed when maize and dried cassava roots are infested, the latter being almost entirely starch. Starch is not volatile and is normally hidden below layers of plant matter that would emit

Beetles disperse by flying or walking

Pheromone detected   Pheromone not detected

Beetle selects substrate for boring

Beetle makes test burrow in search of food

Male locates food   Female locates food   Food not located

Pheromone released   Eggs laid   Backs out of burrow

Beetles arrive at pheromone source

Males arrive   Females arrive   Increase in population density, decrease in food quality

Pheromone production continues

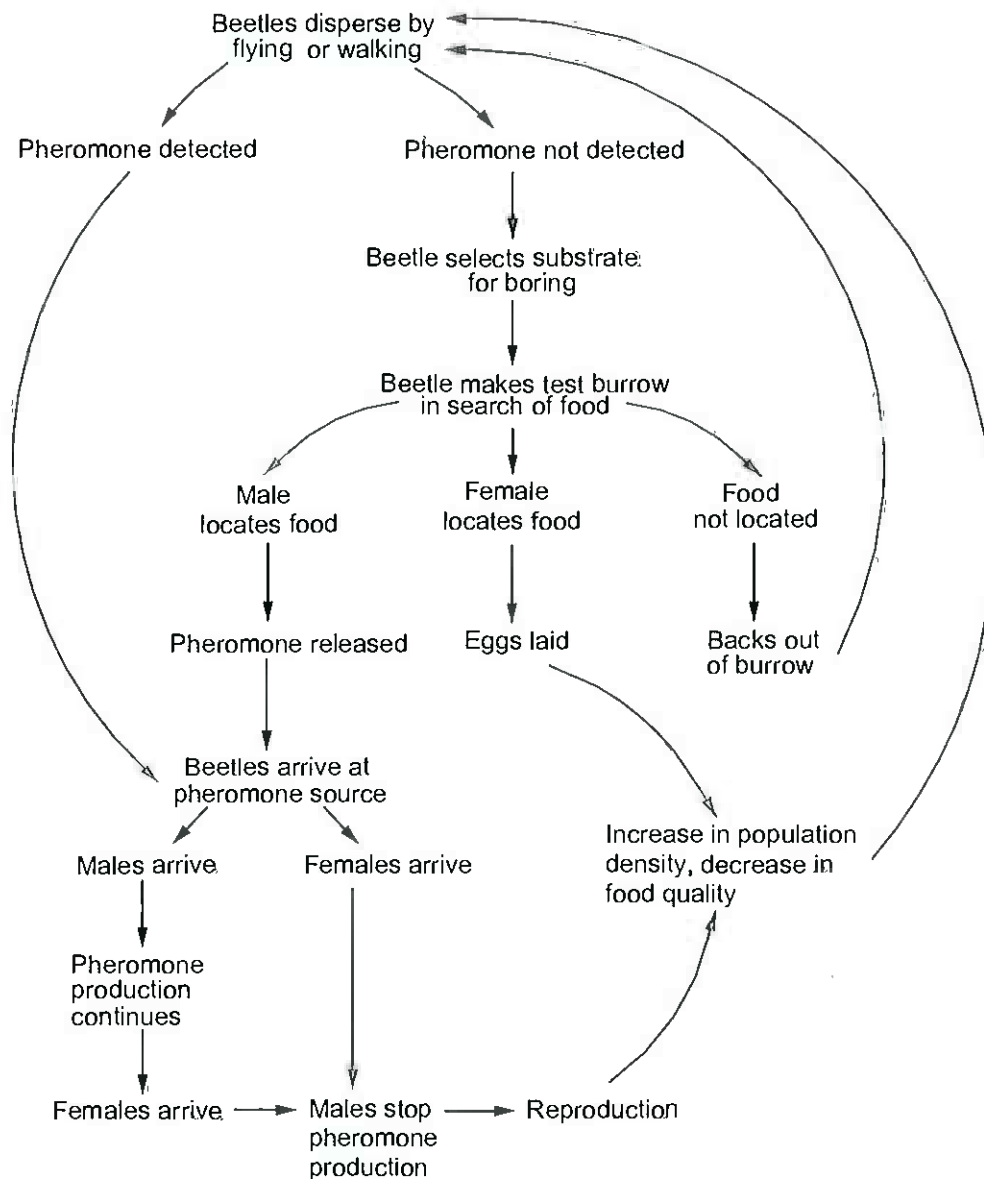Females arrive ⟶ Males stop pheromone production ⟶ Reproduction

Figure 1 - Strategy for the selection of stored products hosts (maize or cassava) by *Prostephanus truncatus*

commonly encountered volatiles. These volatiles would thus be no sure sign of the presence of suitable food. It is probably for this reason that maize volatiles do not appear to influence the orientation of *P. truncatus* in flight (Fadamiro *et al.*, 1998). The possibility that the volatiles emanating from other stored product insects might also attract *P. truncatus* has been studied by Scholz *et al.*, (1997b) with no conclusive results. However, these researchers plan to extend their studies to typical forest pests such as girdling cerambycids, which might well provide more positive results since *P. truncatus* is believed to favour the hosts that cerambycids have attacked.

Once primary host selection has taken place, a female can exploit the food reserve by herself as she would be able to lay fertilised 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 the small colony. On the other hand, male *P. truncatus* can not create a colony in the absence of females, so as soon as they locate a food source they release an aggregation pheromone. Unlike conventional sex pheromones, which attract only the opposite sex to that of the signaller, aggregation pheromones are attractive to both sexes (Borden, 1985) and in the case of *P. truncatus*, initiate the process of secondary host selection.

SECONDARY HOST SELECTION

The aggregation pheromone released by male *P. truncatus* is a blend of two components called Trunc-call 1 and Trunc-call 2 (Cork *et al.*, 1991; Dendy *et al.*, 1989, 1991). Males release their pheromone from within the host, and this diffuses to the exterior through the small holes made by the beetles' tunnelling. Pheromone collected from solitary males on maize grain is variable, amounting to a daily total for both components ranging for 1.0μg to 4.0μg with consistent differences between males in both amount and ratio of components (Hodges and Farman, unpublished). It would appear that only beetles in the process of dispersal respond to pheromone since, once inside a host, neither males nor females will leave it in response to pheromone released close by (Pike, 1993 a&b). In experimental studies, even virgin females would not respond to males once inside maize grain (Hodges & Dobson, 1998). Similarly, Fadamiro (1995) found that the presence of the pheromone will not stimulate beetles to fly; only when in flight do beetles orientate towards the pheromone.

In a period of one night in the field (Ghana), a single male *P. truncatus* feeding on maize has been observed to attract up to 35 other *P. truncatus*, although the median number of beetles attracted during this experiment was only two (Birkinshaw, 1998). Interestingly, the sex ratio of these beetles was significantly in favour of females (64%). Maize cobs initially baited with a single male, and left for one week, accrued an average population of about 60 beetles, whose sex ratio was also significantly female biased (65%) (Scholz *et al.*, 1997b). In flight traps or crevice traps baited with synthetic pheromone, designed to catch flying or walking beetles respectively, the preponderance of the catch was female (Hodges *et al.*, 1998); 65% in flight traps and 76% in crevice traps. Samples of beetles from the population being trapped

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with the crevice traps had an equal sex ratio. Fadamiro (1995) reported no differences in flight activity or duration of flight between the sexes. However, Scholz (1997) found that traps loaded with greater quantities of pheromone lure showed greater sex ratio distortion in favour of females and so suggested that male landing behaviour may be mediated by a lower pheromone concentration threshold than that for females. It is therefore possible that males, although attracted to the pheromone, settle at a greater distance from it than females, and hence are under-represented in traps. In view of similar observation on sex ratio distortion of the catch in crevice traps (Hodges *et al.,* 1998), where the beetles would locate the trap by walking rather than flying, this effect may not be confined solely to landing behaviour.

Successful host selection by males depends either on finding food and attracting a mate or on responding to the signal of another male. In the latter case, they may have to compete for both females and food. For males the lowest risk may be to respond to another male since this will enable a rapid location of a food source and may improve the chances of attracting a female since there will now be multiple pheromone signals from one location. In practice, a male needs to be close enough to benefit from the combined signals, but remain far enough away to avoid competition with other males for any female that is attracted to him. Whether or not males actually settle at a specific optimal distance from each other could be easily tested by further experimental work or field observation. While males appear to keep their distance from other males, females also appear to avoid or repel each other (Hodges and Dobson, in press): perhaps in both cases the behaviour is to limit same-sex competition. Although males respond to the pheromone signal of other males, the opportunity for them to do so may be brief as, once a female arrives in close proximity to a male, pheromone production declines rapidly (Smith *et al.,* 1996; Scholz *et al.,* 1997a; Hodges and Dobson, in press). This behaviour is mediated by a female factor that is non-volatile: males will respond to it even after antennal amputation (Smith *et al.,* 1996).

The findings that only males produce aggregation pheromone, that the sex ratio of beetles attracted in the field is female-biased, and that males cease to signal in the presence of adult females, are all indications that aggregation pheromone signalling is indeed intimately tied to the reproductive biology of *P. truncatus*. Sex-specific ornaments, be they visual, acoustic, or in this case, chemical, are often instrumental in determining differences in the relative reproductive success of individuals. Classic examples of such sexually selected traits include the elaborate peacock's tail and the large antlers of male deer. Perhaps aggregation

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pheromone signalling in male *P. truncatus* owes its origins and current maintenance to processes similar to those that have produced these other ornaments. Sexually selected traits are notoriously variable (Andersson, 1994). If responding beetles show a variable response to different male signallers then the identity of colonising males could be an important determinant of host selection.

Field trials have demonstrated that males and females are preferentially attracted to particular males (Birkinshaw, 1998). This has been interpreted as a preference for their particular pheromone secretion, which is known to vary in quantity and quality between males (Hodges and Farman, unpublished). It has also been observed that some *P. truncatus* males consistently secure more matings than others if they are presented in pairs to females in a mating arena however, these males were frequently not those selected at a distance, i.e. not always those selected on characteristics of their aggregation pheromone. Thus the aggregation pheromone signal appears not to be the main determinant of mate choice when contact has been made between the sexes (Birkinshaw, 1998). This is in direct contrast to the behaviour of the cockroach *Nauphoeta cinerea* (Moore *et al.*, 1997), where variation in the pheromone signal is the basis for mate selection on contact. Male *P. truncatus* would appear to increase their reproductive success by manipulating beetle distribution through pheromone signalling but, once beetles make contact, males are selected on other characteristics.

Observations of tunnelling *P. truncatus*, in artificial plant hosts sandwiched between two glass plates, have shown that males form temporary pair bonds with an ovipositing female and mate repeatedly with that female (Birkinshaw, 1998). When not copulating with the female, *P. truncatus* males tend to sit in the entrance to the tunnel system, a behaviour they share with some species of scolytid (Kirkendall, 1983). Tunnel guarding and shut-down of the aggregation pheromone signal, in the presence of females, could be adaptations to limit loss of paternity from other male suitors and to reduce the risk of predation. The latter is a particular risk as the aggregation pheromone is also a kairomone for the predatory histerid beetle *Teretrius nigrescens (Lewis)*, formerly *Teretriosoma nigrescens*, (Rees *et al.*, 1990; Boeye *et al.*, 1992).

In summary, host selection would appear to proceed as follows. It is initiated when beetles take flight in response to a declining food source or increased population density. Thereafter, there may be primary selection, which involves the response to as yet unidentified

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behavioural cues causing the beetle to orientate, land and initiate test-burrows until a suitable food source is found. Such land-and-choose behaviour, without response to host volatiles, is well known in those scolytid beetles responsible for killing trees (Raffa *et al.*, 1993). Secondary host selection results from the attraction of both males and females to the pheromone released by males that have already found a food source. When males releasing pheromone come into contact with a female, pheromone production is stopped; similar behaviour is shown by certain scolytids (*Ips* spp, Borden, 1982). It seems probable that the release of the pheromone by males evolved to attract only females, while males and females respond to the pheromone both to locate a host and potential mates. If females encounter the aggregation pheromone released by closely located males then preliminary screening of potential mates is possible. However, as dispersing females are normally already mated and as even virgin females will not respond to the pheromone once they are in a suitable food source, it seems likely that host location motivates the response to the pheromone. Mate selection is a possible additional advantage of females being able to distinguish between signals from different males.

THE ROLE AND EVOLUTION OF SEX AND AGGREGATION PHEROMONES IN THE LIFE HISTORIES OF STORAGE PESTS

Burkholder (1982, 1990) noted that the reproductive biology of short-lived (<30 days) and non-feeding adult storage insects, such as the moths and a few storage Coleoptera, is mediated by (sex) pheromones that result in the attraction of only the opposite sex. In contrast, long-lived adult pests (>30 days) that feed, such as most of the storage Coleoptera, rely on (aggregation) pheromones which lead to assemblages of both sexes. The logic of the short-lived strategy is that the priority of the adults is to locate the opposite sex and mate rather than to find food. The female then spreads her eggs in an area perceived to be suitable for the development of larvae (Barrer and Jay, 1980) or after a certain time, in the absence of host cues, just scatters the eggs. The female is responsible for releasing the sex pheromone. In contrast, the adults of longer-lived species feed as adults on the same host as the developmental stages and produce pheromone when feeding on such hosts. Generally, the male produces the pheromone that leads to the aggregation. Most storage pests fall into one or other of these categories: *P. truncatus* clearly into the second. However, there are several exceptions listed by Levinson and Levinson (1995).

Levinson and Levinson (1995) viewed aggregation pheromones in storage insects as a means

"of creating an aggregation that provides benefits of optimal feeding, oviposition sites, suitable mates as well as physical protection", and presumed that sex pheromones evolved from aggregation pheromones. The use of the male pheromone in *P. truncatus*, a relatively poorly adapted storage pest, might well give some clues as to the means by which insect aggregation evolved in those species which have stronger associations with stored products. In *P. truncatus*, it would appear that the male releases pheromone in order to attract females. Females respond to the pheromone to locate a host and may discriminate between different males' signals in order to obtain high quality mates and/or hosts. Males also respond to the pheromone as a means of locating a host but the signaller does not emit its signal for the benefit of other males since signalling is terminated once a female has arrived. It is therefore probable that other males are exploiting the signal to gain food resources and mates and aggregation is achieved as an unintentional by-product of the response to a sex attractant. This is also considered to be the case in bark beetles (Scolytidae) where pheromones that lead to aggregation probably evolved in the sexual context of courtship and male-male competition and were elaborated further to the benefit of both senders and receivers (Raffa *et al.*, 1993). *P. truncatus* would appear to fit the pattern of a male calling from its food source to attract a mate and incidentally attracts other males.

In summary, we suggest that aggregation pheromones first evolved as sex-attractant pheromones (in contrast with the views of Levinson and Levinson, 1995), and that the response by other males is part of the struggle for survival. It would be worth attempting to reinterpret the role of the aggregation pheromones of other storage pests in this light.

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