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SHORT COMMUNICATION

Host selection behaviour by adults of legume and cereal breeding populations of *Sitophilus oryzae* (Coleoptera: Curculionidae)

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Introduction

Host preference is a significant feature of any organism's life history. Indeed, for some species, 'the host plant is not merely something fed on, it is something lived on' (Jermy, 1984). This is certainly the case for the rice weevil *Sitophilus oryzae* (Linnaeus) (Coleoptera: Curculionidae) where, in addition to feeding on their hosts, adults will meet members of the opposite sex and mate, females will oviposit and larvae will feed. The entire life cycle is therefore dependent on the suitability of the host. Historically, *S. oryzae* has been associated with stored cereals (Chu & Wang, 1975), but more recently some populations have displayed an ability to utilize certain types of legumes for breeding and feeding (e.g. Champ & Dyte, 1976; Pemberton & de Rodriguez, 1981; Holloway, 1986). Most populations of *S. oryzae* are unable to feed on legumes due to the toxic secondary compounds produced by the plants (Coombs *et al.*, 1977; Holloway, 1986; Holloway & Mackness, 1988; Delobel & Grenier, 1993). A move by some populations to breed on legumes can be viewed as a major host shift.

The acceptance of a new host plant requires both behavioural and physiological adaptations (Wassermen & Futuyma, 1981), each involving complex sets of traits some or all of which may be under genetic control (Futuyma & Peterson, 1985). For example, behaviourally, the host must be found and recognized as food, whilst physiologically the effects of any anti-nutritional or toxic compounds must be overcome. For phytophagous insects such as *S. oryzae*, oviposition and food choice decisions are essentially the same (Singer *et al.*, 1992). Inappropriate decisions could prove very costly for both adults and juveniles alike. In particular, selection pressure on ovipositing females is likely to be high in a species that does not invest in parental care (Jaenike, 1978). As a result, it has been proposed that behavioural and physiological adaptations should co-evolve (Wasserman & Futuyma, 1981). There is some evidence that oviposition preference and offspring performance can be correlated with heritable variation existing for oviposition preference (e.g. Singer *et al.*, 1988; Fox, 1993).

Sitophilus oryzae that have been bred for long periods of time on cereal or legume each display certain characteristics that optimize their fitness in their respective habitats (Holloway *et al.*, 1990a; Povey & Holloway, 1992). Specifically, in the case of legume breeding *S. oryzae* a genetically based ability to overcome the legume toxins has evolved (Thind & Muggleton, 1981; Holloway & Smith, 1985; Grenier *et al.*, 1997). However, it must be the case that some cereal feeding populations have extended their range of acceptable foodstuffs either because cereal was absent or through choice. To recognize a legume, such as yellow split-pea *Pisum sativum* L. (Fabaceae) as potential food represents a major behavioural change and it has been proposed that once such a step has been made the diet of phytophagous insects could expand to include other unrelated species (Gould, 1979) or those chemically dissimilar (Courtney *et al.*, 1989; Dobler *et al.*, 1996). This is particularly possible if the potential food hosts were found in similar natural or artificial ecological settings, for example for *S. oryzae* where cereals were replaced with legumes in a storage facility. Stored legumes have their own pest species, such as Bruchidae. Even so, such a large proportion of the world's human population relies on legumes that if *S. oryzae* were to become a pest of stored legumes as well as cereals the result could be disastrous. *Sitophilus oryzae* is considered to be the most serious insect pest of stored cereals in the world (Champ & Dyte, 1976).

The purpose of this study was to determine whether legume feeding *S. oryzae* selectively seek out legumes in

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preference to cereals and whether wheat-bred insects will accept yellow split-pea as an alternative host.

Materials and methods

Three strains were studied: Trinidad bred on wheat *Triticum aestivum* L. (Poaceae) (TW), Trinidad bred on yellow split pea (TP), and Indian bred on wheat (IW). All populations had been bred on their respective foodstuff for in excess of 150 generations and so displayed a high degree of adaptation. Throughout the study for each strain two replicate lines were used. These replicate lines had been separate from each other for over 150 generations.

Only whole grains of wheat and yellow split-pea were used during the study since cracked wheat grains are known to release more volatiles than whole grains (Trematerra *et al.*, 1999). As a result, cracked grains are more attractive to *S. oryzae*, possibly because they offer easier access to feeding. English soft wheat and yellow split-pea variety Century were used. Experimental food was frozen at –30°C for two weeks prior to use. The moisture content of all grain was adjusted to 14.5 ± 0.1% by adding the appropriate amount of distilled water (Richards, 1947). This was done because grain moisture content can greatly affect certain life history parameters (Holloway, 1985).

Three identical choice chambers were used during the study. Each chamber consisted of five Perspex cubicles, 7 cm in diameter and 4 cm deep. One cubicle was located centrally with the remaining four positioned equidistantly around it. Each cubicle had a removable lid, again made of Perspex, with a 1 cm hole drilled in the centre. The central cubicle was connected to the outer cubicles by a 2.5 cm length of clear plastic tubing flush with the floor of the cubicle. The design allowed air to be drawn in through the lids of the outer cubicles by attaching a vacuum pump to the lid of the central cubicle. The pump was set at a constant flow rate of one litre of air per minute. This level of suction had been identified as sufficient to prevent chemical saturation in a similarly designed chamber used to examine the response of the greater grain borer *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) when exposed to both food and pheromones (Birkinshaw, 1998). The flow rate was insufficient to suck any insects out of the cubicles or to interfere which their environment. Finally, the chamber was glued to a firm plastic base to make it robust enough for cleaning and repeated use.

Adult insects aged between 7 and 14 days were collected from stock jars held in a constant temperature and humidity room (28°C and 70% relative humidity). The experimental insects were sexed according to sexually dimorphic rostrum characters (Halstead, 1963). All experimental insects were starved for 24 h prior to the experiment. All experiments were conducted in the constant temperature and humidity room. All insects of the genus *Sitophilus* have been shown to be predominantly photo-negative (Richards, 1951). To ensure that directional light within the constant temperature and humidity room did not affect the behaviour of the insects, each choice chamber was completely covered with light impenetrable material.

Before use, each choice chamber was thoroughly washed and air dried to remove any contamination. Fluon was applied to the inner surfaces of the walls and the lids of each cubicle to prevent the insects from climbing from the floor of the chamber. Five grams of wheat were placed into one of the outer cubicles. In a second cubicle 5 g of yellow split-pea were placed, and the remaining two contained 5 g of glass beads (2.5 mm diameter) and nothing, respectively. The latter two cubicles were therefore acting as controls. The glass beads used roughly mimicked the size of the food grains. The positioning of these choices relative to one another was randomized prior to each trial.

Table 1. Mean numbers (± SE) of *Sitophilus oryzae* in each cubicle type within the choice chamber after different periods of time during the experiment for Trinidad on pea (TP) population, Trinidad on wheat (TW) population and Indian on wheat (IW) population.

Minutes after introduction	Mean number of individuals on			
	Pea	Wheat	Glass beads	Nothing
TP population				
15	16.6 (±2.9)	14.8 (±1.8)	13.4 (±2.1)	7.7 (±1.3)
60	28.0 (±4.1)	21.3 (±2.4)	12.3 (±1.8)	8.2 (±1.4)
360	35.9 (±3.6)	33.1 (±2.5)	9.6 (±2.4)	3.8 (±0.7)
1440	39.2 (±3.9)	45.7 (±3.4)	4.8 (±0.9)	3.9 (±0.9)
2880	42.5 (±3.8)	46.7 (±3.5)	2.1 (±0.5)	4.5 (±0.9)
TW population				
15	13.0 (±1.6)	16.3 (±2.3)	10.5 (±1.4)	13.1 (±1.5)
60	22.1 (±3.0)	30.0 (±3.3)	10.4 (±1.9)	8.8 (±1.2)
360	26.0 (±3.7)	45.0 (±4.1)	7.7 (±1.9)	6.3 (±1.2)
1440	17.8 (±2.8)	67.3 (±4.1)	4.1 (±1.3)	2.7 (±0.7)
2880	15.6 (±3.8)	74.9 (±2.4)	3.8 (±1.0)	2.0 (±0.5)
IW population				
15	19.0 (±2.1)	29.6 (±3.2)	10.2 (±2.6)	5.4 (±0.8)
60	19.6 (±4.1)	42.5 (±3.8)	10.9 (±1.8)	3.6 (±1.4)
360	18.9 (±2.7)	61.0 (±4.1)	5.5 (±1.4)	2.7 (±0.5)
1440	17.2 (±3.3)	68.0 (±3.5)	4.3 (±0.9)	2.5 (±0.6)
2880	9.0 (±1.2)	77.0 (±2.8)	5.1 (±1.2)	4.0 (±1.0)

Total of 100 individuals present in each choice chamber (NB only insects wholly within the experimental cubicles counted).

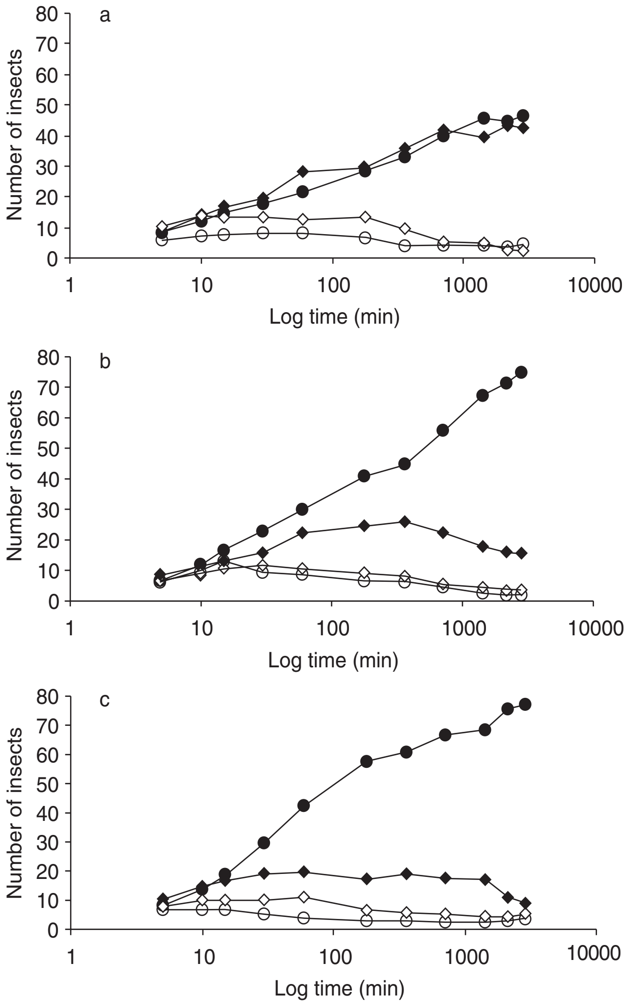

Fig. 1. Change in mean number through time of *Sitophilus oryzae* individuals from the Trinidad yellow split pea breeding strain (a), Trinidad wheat breeding strain (b) and Indian wheat breeding strain (c) in experimental cubicles containing yellow split-pea (◆), wheat (●), glass beads (◇) and nothing (○). Standard error bars have been omitted for clarity.

At the start of each test 100 adults starved for one day were placed into the central cubicle. The distribution of the adults was recorded at time intervals of 5, 10, 15, 30, 60, 180, 360, 720, 1440, 2160 and 2880 min post introduction. Only insects that were entirely within one of the four outer cubicles were counted. Insects in any of the connecting tubes or in the central cubicle were ignored. At the end of each trial, all insects, beads and food were disposed of and the chamber was washed and prepared for use again.

No information was available prior to the start of the trials as to whether males and females were likely to respond differently to the experimental conditions. As a result, tests were conducted using 100 males, 100 females, or 50 males plus 50 females mixed together. For each population line three separate tests were conducted in unison, one for each of the above three sex categories, and each line by sex category was replicated five times.

Statistical tests were carried out using Minitab (Release version 13.1). Only data from the final responses (i.e. at 2880 min) were statistically analysed. Both nested and un-nested analysis of variance tests were performed.

Results and Discussion

No significant differences were observed either between the lines within a population ($F_{36,288} = 0.81$, not significant (ns)) or among the different sex categories within a population ($F_{24,288} = 0.56$, ns). The data from both lines and from the three sex categories were pooled for further analyses (table 1). After 48 h, significant variation was found in the distribution of insects among the various cubicles for all populations ($F_{9,288} = 227.7$, $P < 0.001$) (fig. 1). Cubicles with food contained significantly more insects than the controls after 30 min. The data demonstrate that the commodity to which a population is adapted can have a significant effect on host selection. The TP population has been bred for a long time on yellow split-pea. However, the insects were still able to breed on wheat, which is not surprising since *S. oryzae* is very well adapted to exploiting various types of cereals (Dent, 2001). Consequently, there was no difference in the level of acceptance of wheat versus yellow split-pea for the TP population ($F_{1,58} = 0.08$, ns). However, after 48 h (2880 min), many more TW and IW insects were found on wheat than yellow split-pea ($F_{1,58} = 375.2$, $P < 0.001$ and $F_{1,58} = 489.6$, $P < 0.001$, respectively) (table 1, fig. 1). There was no difference between the numbers of TW and IW insects found on wheat after 48 h ($F_{1,58} = 0.31$, ns). As a result of this behavioural difference among populations there was a significant interaction between population and host selection ($F_{6,348} = 52.27$, $P < 0.001$). Whilst the wheat breeding populations are either unable to breed on pea (IW) or do so very poorly (TW) (Dent, 2001), it is clear from fig. 1 that the suitability of yellow split-pea as a potential food was being sampled. In both cases the numbers of animals initially built up on pea, but then after 360 min began to decline (fig. 1). In the case of IW, the numbers on pea were significantly higher than the numbers on either of the controls until 2880 when there was no significant difference between pea and glass bead numbers ($t = 1.62$, 58 df, ns) and just a marginally significant difference between pea and 'nothing' numbers ($t = 2.27$, 58 df, $P < 0.05$). For TW, there were significantly higher numbers of insects on pea than the controls throughout, although the decline in numbers on pea from a peak of 26 individuals after 360 min down to a mean of 15.6 individuals at 2880 min is clear (fig. 1). The data offer no evidence that the insects were responding to food volatiles operating over more than a few millimetres, otherwise they would have orientated almost immediately towards the favoured foodstuff. Instead, the results suggest that the beetles wander until they come across something that can be sampled at close quarters. At that stage the material is either accepted, as was the case for wheat (as well as yellow split-pea for the TP population), or rejected (yellow split-pea for the TW and IW populations). At the end of the experiment, equally low number were found in the cubicles containing glass beads and nothing for all three populations (TY: $F_{1,58} = 3.63$, ns; TW: $F_{1,58} = 2.8$, ns; IW: $F_{1,58} = 0.47$, ns).

The behaviours described in the current study have relevance to the evolution of legume feeding ability in *S. oryzae*. It is known that the ability to feed and breed on yellow split-pea is genetically determined (Thind & Muggleton, 1981; Holloway & Smith, 1985; Grenier *et al.*, 1997) and it is likely that these genetic changes influence the detoxification capabilities of the insects (Holloway & Mackness, 1988). However, it still remains necessary for *S. oryzae* carrying the mutations enabling legume feeding to recognize pea as a potential food source in order for the character to spread. The populations used here appear to sample the material offered to them and then decide whether to accept (and stay) or reject. Mohan & Field (2002) also noted *S. oryzae* movement away from ground pea and pea protein after 24 h of exposure, but not after 1 h. This observation is again consistent with a period of sampling by the insects prior to making a decision to depart. If this sampling behaviour were widespread in *S. oryzae*, it would facilitate the spread of legume feeding in this species. The mechanism used by the TW and IW *S. oryzae* to reject yellow split-pea is not clear, but may involve a physiological response either to ingesting toxic phytochemicals or to non-volatile surface chemicals. If a tolerant animal samples yellow split-pea and remains to breed, it is known that the life history of the population begins to evolve (Holloway *et al.*, 1990b; Povey & Holloway, 1992) increasing the fitness of the population rapidly (Dent, 2001). The ensuing increase in fitness can continue for a long time and still be measured after 100 generations (Dent, 2001).

The ability of some populations of *S. oryzae* to feed on certain legumes has been known of for some time (Cotton, 1920), but it was treated as a curiosity. Coombs *et al.* (1977) were the first to highlight the importance of the legume feeding ability. Nevertheless, the amount of work carried out on legume feeding and breeding in *S. oryzae* remains relatively small given the potential consequences should *S. oryzae* develop into a serious pest of certain legumes as well as cereals. In some parts of the world, for example Queensland, Australia (D. Rees, personal communication), the practice of using the same bin to store cereal and later in the same year switch to legume is increasing. In addition, there has also been a suggestion that pea protein fractions could be used to protect cereals from *S. oryzae* attack (Fields *et al.*, 2001). The mixing of legumes and cereals, either sequentially or concurrently, coupled with the host selection behaviour described here could facilitate the spread of legume breeding in *S. oryzae*.

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