Diet consumption, weight loss of cotton fibre and oothecal production under 4 balance	ced or carbohydrate-deficient dietary regimes
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Group*	Regime	Mean total diet consumed per insect (g \pm SD)	Mean total weight loss of fibre per insect (mg \pm SD)	Mean total number of oothecae per insect (\pm SD)
1	Dog food	2.7281 ± 0.6198		18.32 ± 8.75
	Cotton fibre		19.1 ± 13.1	
2	Dog food	2.6237 ± 0.1014	-	15.08 ± 5.55
3	Carbohydrate-deficient [»] diet	1.1828 ± 0.2306		6.16 ± 3.41
	Cotton fibre		9.5 ± 7.3	
4	Carbohydrate-deficient [®] diet	1.1618 ± 0.2313		9.30 + 1.70

*25 Insects per group.

^bCompounded from casein protein (86% by weight), yeast extract (10%) and Hawk-Owser salt mixture (4%).

the dry weight loss of fibre and oothecal numbers (Figure 2B; r = +0.003). As a control Group 2 received the same diet, but no fibre. Comparing Groups 1 and 2, no significant differences in the means of total diet consumption or of total oothecal numbers per insect were found.

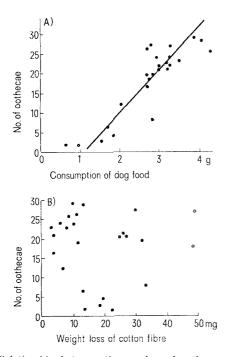


Fig. 2. Relationship between the number of oothecae produced during an 18-week period and A) consumption of dog food, B) dry weight loss of cotton fibre. Each dot represents the data from 1 insect.

Group 3 was maintained on a carbohydrate-deficient diet, with fibre provided. A control group again received the same diet, but no fibre (Group 4). No significant difference in the mean total consumption of the diet was found, but the experimental group produced fewer oothecae. Although this difference in mean oothecal numbers is relatively small, it is sufficient to be significant (p < 0.01). Both groups receiving carbohydrate-deficient diet produced significantly smaller mean total numbers of oothecae than the group maintained on dog food (p < 0.01). In addition the mean total dry weight loss of fibre was significantly less for insects maintained on the carbohydrate-deficient diet than for those provided with dog food (p < 0.01).

A number of deposited oothecae from each group were incubated in a moist container. Hatching was observed in each case.

Conclusions. The dry weight loss of fibre was greatest in groups receiving a balanced diet. Even in this case, however, the weight loss was less than 1% of the weight of diet consumed despite the fact that the dental roll became considerably roughened in appearance as a result of gnawing. Although it is not possible to distinguish by this gravimetric method between fibre displaced and fibre ingested, the provision of fibre did not increase the number of oothecae produced, irrespective of whether the diet was balanced or deficient in a carbohydrate source. The degradation of cellulose in the alimentary canal does not, therefore, appear to be of significance to reproductive performance in the female cockroach. The possibility remains that gnawing may provide the insect with materials for covering the deposited ootheca, but no clear evidence exists to support this thesis. The probable explanation of gnawing activity is that it prepares a suitable site for oothecal deposition, or is correlated with a physiological event not directly related to the nourishment of the fertile female.

Sex Attractant Responses of Male Oriental Fruit Moths to a Range of Component Ratios: Pheromone Polymorphism?¹

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Summary. Attraction of male Grapholitha molesta to different ratios of an attractant blend is not correlated with individuals or behavioural classes optimally responsive to different mixtures.

Intraspecies pheromone polymorphism has been documented in several insects. Certain halictine bees utilize individual specific odours both to distinguish nest mates (other females) from conspecific intruders and for male recognition of previously non-receptive females³. In *Drosophila melanogaster* genetic variation among the courtship pheromone bouquet is a requirement for stimulation of either sex^{4,5}, and this negative assortative mechanism appears to minimize inbreeding. In the pyralid moth *Ostrinia nubilalis* both geographical and intrapopulation differences in the attractiveness of *cis*-11- and *trans*-11tetradecenyl acetate admixtures have been hypothesized to reflect genetic variation within a single species⁶, and hence indicate the potential for rapid evolution of new pheromone systems. (But some of the variation in pheromone response may be due to semi- or sibling species statuses of the *cis* and *trans* strains⁷⁻⁹.)

Differences in the relative attractiveness of slightly altered blends of a pheromone medley are common to all field tests, but the basis of this variation is enigmatic. Optimum male attractancy for the Oriental fruit moth, *Grapholitha molesta* (Lepidoptera: Tortricidae), occurs with approximately 7% trans¹⁰ in cis-8-dodecenyl acetate¹¹, with slightly higher (<20%) and lower ratios (>2%) producing reduced trap catches¹². The question of whether such variation in pheromone response represents either broad sensory tuning about an optimum blend or the specific responses of several phenotypes has not been tested.

We investigated variation in the responses of G. molesta males to 3 cis: trans ratios in Geneva, N.Y. using a new attraction-marking-reattraction technique with wild males. Males from the natural population were attracted to 9 cm diameter circular dishes containing a thin layer of powdered fluorescent dye (Dayglo[™] red, yellow, or blue) situated within special non-sticky Pherocon $1C^{TM}$ traps for protection from the elements. Rubber septa chemical dispensers containing one of three attractant blends were positioned in the centre of the dish containing a dye colour-coded to that blend. The blends were 10 µg of either 3, 8, or 11% trans in cis-8-dodecenyl acetate, plus 10 µg of dodecyl alcohol (a component mediating close range orientation, landing, and precopulatory display^{13,14}). The relative attractiveness of these blends in previous field tests was 3:5:2 respectively¹². Wild males landing within 4.5 cm of the attractant dispenser contacted a dye before flying off, thus establishing their 'carte de visite'.

Marking devices were set out on a 20×20 m spacing in an apple orchard in a randomized complete block design of 16 replicates (1 device every other tree). After 2 days the marking devices were replaced with 16 replicates of sticky PheroconTM 1C traps baited with one of the 3 blends and deployed randomly on trees between the marking positions. If the variation in attractiveness to slightly altered blends represented disparate phenotypes, males marked at one dispenser type should tend to be captured at that blend. Conversely, if the differences in attraction to subtle blend changes represented a normal distribution of responses about an optimum mixture,

Captures of males marked at devices baited with 3, 8 and 11% trans in cis-8-dodecenyl acetate at similarly baited traps during test conducted July 22 to 25, 1975

	Marking Blend (No. expected with null hypothesis)						
	Blue (3%		Red (8%	trans)		llow % trans)	Total
Capture Blend							
3% trans	32	(34)	56	(50)	12	(15)	100
8% trans	88	(81)	108	(117)	37	(35)	233
11% trans	18	(22)	34	(32)	11	(10)	63
Total	138		198		60		396

Multiply-marked males pooled with singly-marked males: $\chi^2 = 3.99$, 4 d.f., with 0.25 < P < 0.50 and n = 396. Percentages of multiply-marked males were 21, 34 and 30% for the 3, 8 and 11% treatments, including 41 blue and red, 42 red and yellow, and 6 blue and yellow-marked individuals. The occurrence of many multiply-marked males and the directions of the deviations in 2 of 3 cases from those expected argues against discrete behavioural classes. Two additional field tests yielded identical trends.

then males should be reattracted to all blends in the same relative proportions.

Our data support the latter interpretation, since each class of colour-coded males was distributed among the 3 attractant blends in a statistically indistinguishable manner (Table). This indicates that the differences in attraction to altered blends cannot be readily ascribed to phenotypic variation. Also, the occurrence of many males (ca. 30%) marked with at least two different dyes argues against discrete behavioural classes.

A significant amount of genetically-determined variation in pheromone production and response implies nonrandom mating and possibly sympatric divergence. However, we submit that differences in trap catch distribution commonly found in field trials of pheromone blends cannot be used with certainty to infer possible behavioural classes in the responders, perhaps since attraction is a complex, sequential process¹³⁻¹⁵ and a trapping technique offers an organism no 'second chance'.

Pheromone polymorphism may be related to premating dispersal and the likelihood of inbreeding, an hypothesis also proposed by AVERHOFF¹⁶. In groups such as the moths, which typically disperse prior to mating, negative assortative mating and individual recognition would appear superfluous, whereas homogeneity of long-range attractant blend production and response would seem important for efficient mate location. In butterflies (which rarely use attractants) pheromones can serve for close-range conspecific sex perception¹⁷ and perhaps pheromonal polymorphism for recognition of individuals occurs among territorial species. Although the present evidence in \check{G} . molesta suggests that for the attractant system tested the responders are essentially homogeneous, the problem is worthy of further study. If appreciable variation occurs in some species, then control programmes based on the mass trapping technique likely should employ enough pheromone blends to reflect the natural variation in the responders. Otherwise, rapid selction of resistance would be enhanced.

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- ³ E. M. BARROWS, W. J. BELL and C. D. MICHENER, Proc. natn. Acad. Sci. USA 72, 2824 (1975).
- ⁴ W. W. AVERHOFF and R. H. RICHARDSON, Behav. Gen. 4, 207 (1973).
- ⁵ W. W. AVERHOFF and R. H. RICHARDSON, Proc. natn. Acad. Sci. USA 73, 591 (1976).
- ⁶ J. A. KLUN, Envir. Entom. 4, 891 (1975).
- ⁷ J. KOCHANSKY, R. T. CARDÉ, J. LIEBHERR and W. L. ROELOFS, J. chem. Ecol. 1, 225 (1975).
- ⁸ R. T. CARDÉ, J. KOCHANSKY, J. F. STIMMEL, A. G. WHEELER, JR. and W. L. ROELOFS, Envir. Entom. 4, 413 (1975).
- ⁹ J. LIEBHERR and W. L. ROELOFS, Ann. ent. Soc. Am. 68, 305 (1975).
- ¹⁰ M. BEROZA, G. M. MUSCHIK and C. R. GENTRY, Nature, Lond. 224, 149 (1973).
- ¹¹ W. L. ROELOFS, A. COMEAU and R. SELLE, Nature, Lond. 224, 723 (1969).
- W. L. ROELOFS and R. T. CARDÉ, Envir. Entom. 3, 586 (1974).
 R. T. CARDÉ, T. C. BAKER and W. L. ROELOFS, Nature, Lond.
- 253, 348 (1975).
 ¹⁴ R. T. CARDÉ, T. C. BAKER and W. L. ROELOFS, J. chem. Ecol. 1, 475 (1975).
- ¹⁵ J. S. KENNEDY and D. MARSH, Science 184, 999 (1974).
- ¹⁶ L. EHRMAN, W. W. AVERHOFF and R. H. RICHARDSON, Am. Sci., in press (1976).
- ¹⁷ T. E. PLISKE, Ann. ent. Soc. Am. 68, 935 (1975).