scotophase and differential rejection due to size was seen even with those males approaching from the rear, where female vision was obstructed.

In the debate concerning the evolution of female preference, some authors emphasize the possibility of sexual selection for the display alone[6], while others invoke the need for an adaptive benefit associated with the male trait being preferred[4]. If female discrimination in *E. elutella* is based on male odor, as our data suggests, then it is possible that the preference for large males evolved from a mechanism whose initial function was to prevent mating mistakes with either non-conspecifics or males from differentially adapted populations. Many sympatric species in the phycitine stored-product complex, including *E. elutella,* show high levels of interspecific attraction to female pheromones, with males of some species showing similar levels of response to non-conspecifics as to conspecifics[14]. Poor reproductive isolation along this and other long-distance parameters points to a greater reliance on less efficient short-range factors. Males of most of these species emit short-range pheromones[11, 13, 15–18] that in some cases have been demonstrated to function in reproductive isolation. Since small *E. elutella* males emit less pheromone, females may be able to distinguish between conspecific males of different sizes using the same mechanism that allows the avoidance of interspecific matings. Thus, the high potential for interspecific matings in this group may have triggered a sexual selection process for the co-evolution of a male chemical display and a female preference for that display. Females discriminating in favor of larger conspecific males that have a better display would accrue an extra benefit from the increased number of offspring and the production of sons with a higher probability of mating. While intersexual selection may be distinguished from ethological reproductive isolation, it must be emphasized that they share the same underlying mechanism of mate discrimination. Indeed, Fisher[7] clearly recognized that female avoidance of matings with males from different populations or from other species could be the initial fitness-related preference that may or may not lead to a 'runaway' form of intersexual selection (but see Thornhill and Alcock[4] and West-Eberhard[19]).

In summary, female *E. elutella* demonstrate a mating preference for large males, possibly using male chemical displays that are also important in reproductive isolation. By mating with large males, these females increase their fecundity and produce sons with a higher probability of mating. This is the first empirical evidence, to our knowledge, for female choice in moths, and one of the few cases in all animal groups where the demonstrated preference results in increased fitness for the female.

1 We thank Drs N. Ellstrand, D. Hare, K. Haynes, L. Nunney and C. Sassaman for critical review of the manuscript.
2 Present address: Department of Entomology, The Ohio State University, Ohio Agricultural Research and Development Center, Wooster, Ohio 44691.
3 Darwin, C., The Descent of Man and Selection in Relation to Sex. J. Murray, London 1871.
4 Thornhill, R., and Alcock, J., The Evolution of Insect Mating Systems. Harvard University Press, Cambridge, MA 1983.
5 Halliday, T. R., in: Mate Choice. Ed. P. Bateson. Cambridge University Press, Cambridge, MA 1983.
6 Lande, R., Proc. natn. Acad. Sci. USA *78* (1981) 3721.
7 Kirkpatrick, M., Evolution *36* (1982) 1.
8 Boake, C., Science *227* (1985) 1061.
9 Fisher, R. A., The Genetical Theory of Natural Selection. Dover Publications, New York 1958.
10 Phelan, P. L., and Baker, T. C., Anim. Beh., submitted.
11 Krasnoff, S. B., and Vick, K. W., J. chem. Ecol. *10* (1984) 667.
12 Ryan, T. A., Psychol. Bull. *57* (1960) 318.
13 Phelan, P. L., Silk, P. J., Northcott, C. J., Tan, S. H., Baker, T. C., J. chem. Ecol., in press.
14 Phelan, P. L., and Baker, T. C., Envir. Ent., in press.
15 Grant, G. G., and Brady, U. E., Can. J. Zool. *53* (1975) 813.
16 Grant, G. G., Ann. ent. Soc. Am. *69* (1976) 445.
17 Barrer, P. M., and Hill, R. J., Experientia *34* (1978) 343.
18 McLaughlin, J. R., Envir. Ent. *11* (1982) 378.
19 West-Eberhard, M. J., Q. Rev. Biol. *58* (1983) 155.

0014-4754/86/11/121291-03$1.50 + 0.20/0
© Birkhäuser Verlag Basel, 1986

Monitoring insecticide resistance with insect pheromones[1]

K. F. Haynes, T. A. Miller, R. T. Staten[2], W.-G. Li[3] and T. C. Baker

Division of Toxicology and Physiology, Department of Entomology, University of California, Riverside (California 92521 USA),
12 February 1986

Summary. A novel pheromone-baited sticky trap laced with insecticides proved to be a simple and effective means of monitoring insecticide resistance in the pink bollworm moth. Adult males from fields treated frequently with pyrethroid insecticides showed up to 20-fold resistance to permethrin and up to 14.5-fold resistance to fenvalerate.
Key words. Pectinophora gossypiella; pink bollworm moth; insecticide resistance; pheromones; sticky traps; permethrin; fenvalerate.

Resistance to insecticides in one of the most serious problems facing agriculture today[4–7]. The problem is often noticed by a loss of effectiveness of an insecticide in controlling a population, but by then genes conferring resistance have spread throughout the population. Recently, because of the pressing need for control of insecticide resistance, labor-intensive methods have been used to detect emerging resistance in field populations, but there is an immediate need for quick and effective methods for monitoring resistance[5].

Pheromones already have proven to be invaluable for monitoring population levels, timing insecticide sprays, and disrupting mating[8]. We report here a novel use of pheromone traps for detecting the buildup of resistance to insecticides in field populations. This new concept of insecticide-laced sticky traps for monitoring resistance in *Pectinophora gossypiella,* a major pest of cotton, has a significant advantage over labor-intensive methods for detecting resistance[9–11], and is compatible with widespread use of pheromone to monitor population levels in *P. gossypiella.* Information from the resistance-monitoring traps could be used to time the rotation of other chemical, cultural, or biological means of insect control. With effective monitoring and management of insecticide resistance, one could decrease the insecticide burden on the agroecosystem by maintaining susceptible individuals in pest populations.

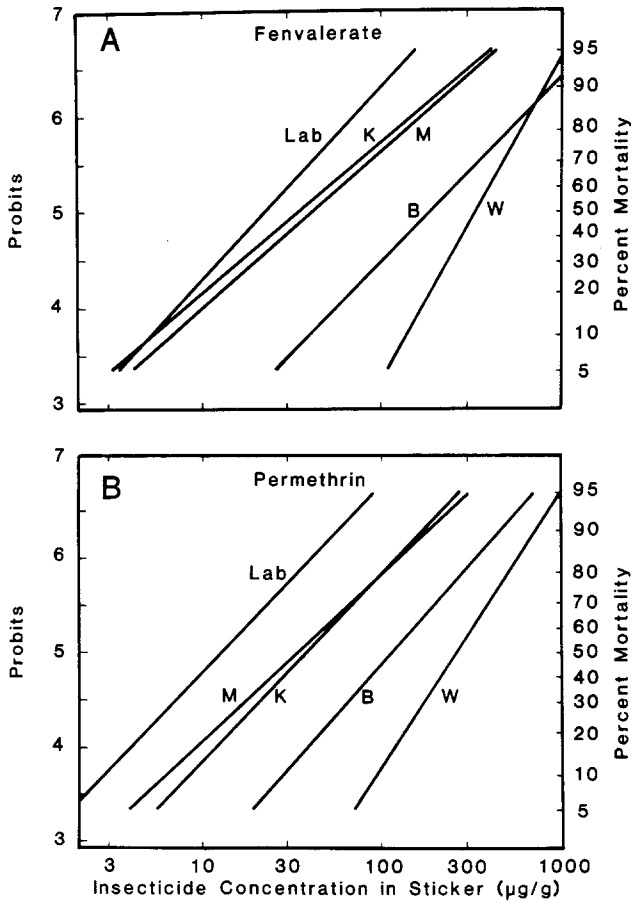
The emulsifiable concentrates of permethrin (Pounce®3.2 EC, FMC Corp., Philadelphia, Pennsylvania, USA) and fenvalerate (Pydrin®2.4 EC, Shell, Modesto, California, USA) were serially diluted in 90% hexane/10% ethanol. 1 ml of each solution was thoroughly mixed into 100 g of sticker (Tangle-trap, Tanglefoot Co., Grand Rapids, Michigan, USA), resulting in a series of sticker-insecticide mixtures from 1.6 to 1000 µg active ingredient per g of sticker. In addition, 1 ml of hexane-ethanol was added to

Results of probit analysis of mortality in sticky traps run for laboratory and field populations of *Pectinophora gossypiella*

Insecticide	Population	n[a]	LC_{50} (95% CI[b]) µg/g	LC_{90} (95% CI[b]) µg/g	Slope (± SE)	Resistance ratio LC_{50} pop/LC_{50} lab
Fenvalerate	Laboratory[c]	355	23 (17–30)	100 (69–179)	2.0 ± 0.28	1.0
	Mexicali,[d] Mexico	2,277	42 (38–47)	262 (219–323)	1.6 ± 0.07	1.9
	Kearny,[e] Arizona	80	36 (17–81)	244 (102–2,837)	1.6 ± 0.43	1.6
	Blythe,[f] California	415	193 (149–275)	927 (560–2,120)	1.9 ± 0.25	8.4
	Westmorland,[g] California	1,656	332 (298–370)	806 (696–966)	3.3 ± 0.24	14.5
Permethrin	Laboratory[c]	365	13 (9–17)	60 (43–99)	2.0 ± 0.28	1.0
	Mexicali[d]	1,916	35 (31–39)	189 (156–238)	1.7 ± 0.09	2.6
	Kearny[e]	217	38 (25–55)	170 (107–376)	2.0 ± 0.34	2.9
	Blythe[f]	504	117 (94–153)	485 (328–866)	2.1 ± 0.23	8.8
	Westmorland[g]	1,508	266 (236–299)	742 (623–929)	2.9 ± 0.23	20.0

[a] Total number of males captured; [b] 95% confidence intervals; [c] Original population collected from Coachella Valley before 1979. No exposure to pyrethroid insecticides; [d] The Mexicali field population had no direct exposure to pyrethroids in 1985; [e] The Kearny population was treated 3 times with pyrethroids in 1985; [f] In 1985 the Blythe population was exposed to 9 applications of pyrethroids before our test; [g] In 1985 the Westmorland population was exposed to 5 applications of pyrethroids before our test.

100 g of sticker serving as the control sticker. Approximately 5 g of sticker was evenly coated over a 9.5 by 17 cm wax-coated card that fitted into, and formed the inner bottom surface of a sticker-free delta trap (Sandia Die and Cartridge, Albuquerque, New Mexico). The traps were baited with the sex pheromone of *P. gossypiella* (1 mg of gossyplure on a rubber septum), and set out in cotton fields in a randomized complete block design with at least 20 m between traps. Five replications of each treatment (6 concentrations and 1 control for each insecticide) were run in each field, except the experiment near Blythe where the highest and lowest concentrations were not included. Cotton fields were selected for different histories of pyrethroid use (table). Male *P. gossypiella* on sticky cards were retrieved at sunrise of the following day, and were incubated at 21 °C until 08.00 h two days later, at which time mortality in the sticker was evaluated by gently probing each male and checking for any movement. Males from a susceptible laboratory colony were flown in a wind tunnel[12] and trapped in identical set of sticky traps. By carefully controlling excessive exposure to heat, mortality in the sticky traps without insecticides usally could be kept below 10%.



Insecticide concentration versus mortality lines (probit transformation) for fenvalerate (A) and permethrin (B) in sticky traps. Field sites were cotton fields near Kearny, Arizona (K), Mexicali, Mexico (M), Blythe, California (B), and Westmorland, California (W).

The traps successfully identified field populations of male *P. gossypiella* having resistance to two pyrethroid insecticides. A field population near Blythe, California had 8.4-fold resistance to fenvalerate and 8.8-fold resistance to permethrin (table). The highest level of resistance was found in a field near Westmorland, California where there was 14.5-fold resistance to fenvalerate and 20-fold resistance to permethrin. 80 km away from the Westmorland site males were captured on the same night in a cotton field near Mexicali, Mexico with no historical exposure to pyrethroid insecticides. Pyrethroids are rarely used in this area because of their expense. These males had a resistance ratio of only 1.9 to fenvalerate and 2.6 for permethrin. The log-concentration probit lines (fig.) illustrate clearly the difference between these populations. A fenvalerate or permethrin dose sufficient to kill 95% of the susceptible laboratory population is essentially non-toxic to the most resistant field population.

The high correlation between LC_{50}'s for fenvalerate and permethrin ($r=0.985$, 3 df, $p<0.01$) suggests cross resistance between pyrethroids for this species. Cross resistance is common for the pyrethroids[7], but independent evolution of resistance cannot be excluded because the two most resistant field populations come from areas with histories of both fenvalerate and permethrin use. Further support for cross resistance between pyrethroids comes from the most resistant field population (Westmorland) that was not treated with either fenvalerate or permethrin in 1985, but rather was treated with cypermethrin and flucythrinate (two other pyrethroids).

Using these pheromone traps pest controllers can easily and effectively detect local resistance to pyrethroids. Management of insecticide resistance may be accomplished by rotation of several classes of insecticides[5,7], thereby minimizing the duration of selection pressure imposed by a single compound. Without an effective technique for monitoring resistance at its early stages, the switch to a new control agent would have to be on a scheduled basis. With a reliable resistance monitoring method, rotation to a new insecticide or other control tactics could become a routine pest management decision. The pheromone trap for resistance monitoring in *P. gossypiella* should allow cotton growers to make rational decisions in selection of control tactics.

The compatible combination of resistance monitoring with population level monitoring would aid the grower by allowing more judicious use of insecticides and use of a material that remains effective at low application rates. This technique is ideally suited for *P. gossypiella* where treatments are targeted at the adult stage[13]. Resistance monitoring with sticky traps can be adapted to other insecticides, to other species that use pheromones in mate-location, to species that rely on specific host odors for food location, and to insects that orient to well-defined visual cues. In fact many of the major agricultural pests are amenable to monitoring of insecticide resistance using traps. For many species it will be important to establish the relationship between the toxicity of the insecticide to the adult and larval stages, since resistance may only be found in the targeted stage[14]. The need to preserve effective and environmentally sound pest control tactics is of paramount importance, and is providing the impetus for management of insecticide resistance.

1 We thank C.A. Beasley, E. Quintero, R. Vetter and R. Weddle. The Cotton Pest Control Board, Pest Management Division of the California Department of Food and Agriculture, Shell Development Co., CIBA-Geigy and Wellcome Research Laboratories provided support to the Resistance Management Laboratory at U.C. Riverside, which enabled these methods to be developed. Mention of any propietary products does not imply endorsement.

2 USDA, APHIS, PPQP, 4125 E. Broadway, Phoenix (Arizona 85040, USA).

3 Visiting scientist from Shanghai Institute of Entomology, Academia Sinica, Chungkin Road (S.), Shanghai (P.R.C.).

4 Adkisson, P.L., Niles, G.A., Walker, J.K., Bird, L.S., and Scott, H.B., Science *216* (1982) 19.
5 Dover, M., and Croft, B., Getting Tough, Public Policy and the Management of Pesticide Resistance, World Resources Institute, New York 1984.
6 Forgash, A.J., Pest. Biochem. Physiol. *22* (1984) 178.
7 Georghiou, G.P., and Saito, T., Pest Resistance to Pesticides. Plenum Press, New York 1983.
8 Silverstein, R.M., Science *213* (1981) 1326.
9 Bariola, L., Cotton Insect and Production Meeting, 1985, p. 11.
10 Suckling, D.M., Penman, D.R., Chapman, R.B., and Wearing, C.H., J. econ. Ent. *78* (1985) 204.
11 Riedl, H., Seaman, A., and Henrie, F., J. econ. Ent. *78* (1985) 692.
12 Haynes, K.F., and Baker, T.C., Archs Insect Biochem. Physiol. *2* (1985) 283.
13 Reynolds, H.T., in: Pink Bollworm Control in the Western United States, p. 35. ARM-W-16, USDA, Oakland 1980.
14 Dittrich, V., Luetkemeier, N., and Voss, G., J. econ. Ent. *73* (1980) 356.

0014-4754/86/11/121293-03$1.50 + 0.20/0
© Birkhäuser Verlag Basel, 1986

Ivermectin prevents head eversion in the blowfly *Calliphora vomitoria* L.

L. Strong*

Department of Zoology, The University, Bristol BS8 1UG (Great Britain), 3 February 1986

Summary. Failure to complete adult development after treating final-stage larvae of *Calliphora vomitoria* with ivermectin is due mainly to the inhibition of head eversion in the pupal stage.
Key words. Diptera; head eversion; ivermectin; larvae; metamorphosis.

Ivermectin, a product of the soil microorganism *Streptomyces avermitilis*, is used against nematode and arthropod parasites of livestock[1]. It acts upon inhibitory neuromuscular synapses, stimulating the release of the transmitter gamma-aminobutyric acid (GABA), enhancing the binding of GABA to muscle membranes, resulting in hyperpolarisation of the muscle[1,2]. 1-2 µg of ivermectin prevents final-stage, post-feeding larvae of *Calliphora vomitoria* from forming puparia, while 0.1 µg allows pupariation but hinders adult development[3]. The neuromuscular events in pupariation[4] might be expected to be susceptible to ivermectin, but the disruption of adult development is obscure. This paper shows why development fails after ivermectin treatment.

500 post-feeding larvae of *Calliphora*[3] were used 2 days before pupariation. 100 were untreated; 100 were given 1 µl of ethanol; 300 were given 0.3 µg ivermectin in 1 µl ethanol applied topically to the posterior region of the abdomen. The larvae were allowed to form puparia in glass jars at room temperature which took about 14 days. While most of the controls completed development, only 48% of the treated insects produced flies. The remaining puparia were dissected to assess adult development, and the observations are shown in the table.

Untreated and ethanol-treated controls produced adult flies almost completely, but 52% of the puparia from ivermectin-treated larvae failed to do so. 2% had died, as had 2% of the ethanol-treated controls: no significance is attached to this finding. 15% of the puparia contained normal-looking pharate adults with a functional ptilinum and moving limbs. Whether these flies would have emerged eventually is not known, but as similar delayed adults were not found in the controls, ivermectin clearly impedes the emergence of flies that otherwise appear to be normal.

A dramatic finding was that 35% of the puparia contained flies that lacked heads (fig.). The abdomen and thorax (with wings and legs) were present, but nothing anterior to the respiratory horns. This was not simply a deformity of the head: the latter was not present as such in any of these insects. Some abdomens were white and pupal-like (fig., a), while others were clearly adult, segmented, and covered with setae (fig., b and c). A constant feature was that the insects were packed into the anterior part of the puparium, with the thorax occupying the region where the head should have been: this left a space posterior to the abdomen.

Developmental fates *Calliphora vomitoria* treated with 0.3 µg ivermectin as final-stage, post-feeding larvae

	Puparia produced	Undeveloped adults (%)	Headless adults (%)	Pharate adults (%)	Normal adults (%)
Untreated controls (100)	99	0	0	0	100
Ethanol-treated controls (100)	99	2	0	0	98
Ivermectin-treated (100)	294	2	35	15	48

Ivermectin was given topically in 1 µl ethanol. Ethanol-treated controls were given ethanol only. Numbers in parantheses indicate number of larvae treated.