the upper end (plug) permitted by the apparatus, and selection pressure was small. Realized heritabilities (7), with 7 degrees of freedom each, were:
For H1: $h^2 = 0.199 \pm 0.020$ ($p < 0.001$). For H2: $h^2 = 0.172 \pm 0.010$ ($p < 0.001$). For L1: $h^2 = 0.035 \pm 0.071$ (not significant). For L2: $h^2 = -0.013 \pm 0.053$ (not significant).
Selection for diminishing pupation height was ineffective, although minor differences from the base population seemed to occur (fig. 2).
Although limits to selection were not, in fact, attained, and selected lines were not homozygous, some crosses were carried out to gain information about pupation height determination. The table gives the mean pupation heights of the H1, H2, L1, and L2 lines, as well as the values of the H1 × L1 and H2 × L2 crosses (and their reciprocal ones), all of which were obtained in a single generation (with 6 replicates each). The pupation heights of the crosses were lower than the midparent values, which suggested some grade of dominance for low pupation sites. No differences between H1 × L1 and its reciprocal cross were apparent, but a lower pupation height appeared for the ♂ H2 × L2 ♀ cross than for the ♀H2 × L2 ♂ cross, a result which might come from maternal effects as well as from sex-linkage.
When artificial selection has been applied, most quantitative traits have responded to it, and very few failures have been reported[8]. Pupation height in *D. simulans* is not an exception, as our data show. The population analyzed here showed considerable additive genetic variation for pupation height, which contradicts Ringo and Wood's hypothesis. We think that the failure of these authors in selecting for pupation height lies in the small selective pressure they applied and in the great sensitivity of this character to environmental factors. In relation to our failure for selecting for low pupation sites in *D. simulans*, we consider the finding of a negative correlation between pupation height and duration of larval development to be of some importance[9]; this fact causes a certain lack of correspondence between genotype and phenotype for pupation site choice.

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Male-size-related courtship success and intersexual selection in the tobacco moth, *Ephestia elutella*[1]

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Summary. In *Ephestia elutella* males, mating success is positively correlated with size. Experimental manipulation of males demonstrated that this is due to females actively discriminating against small males, the first direct evidence for female mate-choice in moths. Furthermore, this female preference is associated with increased fitness in that, by mating with larger males, females are more likely both to produce larger offspring and to increase their fecundity.
Key words. Sexual selection; mate choice; male pheromone; mating success; courtship; Pyralidae.

Since Darwin[3] introduced his theory of sexual selection, *intra*-sexual selection (i.e., competition between males) has been generally accepted as playing a key role in the evolution of male secondary structures and displays; however, the question of *inter*sexual selection due to female mating preferences remains unresolved due to two fundamental issues. First, despite the increased interest in this area during the past decade, unambiguous examples of differential mate selection by females remain relatively few. In insects, most cases of non-random mating are primarily due to intrasexual competition between males either for direct access to females or for possession of territories or resources necessary for mating[4]. Furthermore, in many mating systems, it is very difficult to partition the confounding effects of intra- and intersexual selection[5]. The second issue concerns the selective basis for the evolution of female choice. Has the female preference for a male character evolved due to its association with a higher Darwinian fitness[4], by a non-fitness-directed process leading to a linkage disequilibrium between the preference and the preferred character[6-8] or both[9]? We report that female tobacco moths *(Ephestia elutella)* show a mating preference for large males and that this preference results in a higher fitness for the females through increased fecundity and the production of larger offspring that will, in turn, enjoy reproductive advantages in the next generation.

The weight distribution of a population of 400–600 laboratory-reared *E. elutella* was characterized by weighing random samples of 30 4–5-day-old pupae of each sex ($\pm$ 0.1 mg). From this population, categories of small [$< (\bar{x} - 0.5$ SD)] and large [$> (\bar{x} + 0.5$ SD)] males and females were chosen for each sample. 20 courtships of each of the four size combinations using one male and one female were video-recorded[10] and analyzed for courtship success, duration of courtships, and duration of female receptivity. Females of six randomly chosen pairs from each size category were allowed to oviposit into containers holding an excess of artificial diet that were then maintained together at 23($\pm$ 1) °C. After approximately 37 days, the resulting pupae (4–5 days old) were segregated by sex and weighed.
Mating in *E. elutella* entails a sequence of interactive behaviors that gives the female considerable control over the outcome of the mating attempt[10, 11]. When approaching a female emitting pheromone, males fan their wings and expose scent-emitting glands on their forewings. Upon attaining a head-to-head position with the female, the male rapidly curls his abdomen over his head and strikes the female on the head and thorax with it. This brings a second set of scent structures located on the male's abdomen close to the female's antennae. The female responds by elevating her abdomen, thus making it accessible to the male's ensuing copulatory attempt. If the attempt is unsuccessful, the

sequence is repeated, with each repetition defining a courtship bout. The number of times that *E. elutella* males can attempt copulation during a courtship is limited, as females show a significant decline in sexual receptivity after only a few courtship bouts, and may terminate courtship[10]. In the present study, male courtship success showed a significant positive correlation with male size, irrespective of the size of the female (table 1). Combining the two classes of female size, small males were successful in courtship only 63% (25/40) of the time, compared to 98% (39/40) for the larger males. Three possible mechanisms for reduced mating success in small males are: 1) small males may be of lower general vigor and unable to perform their courtship movements properly; 2) small males may be less able to copulate with uncooperative females, and/or 3) females may be actively discriminating against small males. Although vigor is difficult to assess, the behaviors and apparent intensity of courtship in the two groups of males were indistinguishable in frame-by-frame analysis of video-recordings. Differential success through forced copulation of the female was also not supported. Small males were as unsuccessful with small females as with large females, and the size ratio between small males and small females was similar to that between large males and large females. Furthermore, females were rarely uncooperative with large males. There was, however, evidence for active female discrimination. Unsuccessful courtships with small males were always the result of female termination; no courtships were prematurely ended by the male. In addition, females showed rejection behavior during 53% (21/40) of the courtships with small males, whereas such behaviors were observed during only 8% (3/40) of the courtships with large males (table 1). Rejection behaviors by females included covering the abdomen with the wings, kicking the male, and flying or walking away from the male. In some instances, males successfully copulated with females either in spite of such behaviors, or because, through persistence by the male, the female became more receptive.

If females were in fact taking an active role in the reduced courtship success of small males, this would be evidenced by the females reducing the duration of their receptivity. Successful courtships with large males were not significantly longer in duration than those with small males (table 1): however, the length of these courtships grossly underestimates the female's true window of receptivity since successful copulation prematurely terminates the female's receptivity and a large proportion (50%) of males copulated within two courtship bouts. To obtain this measurement more accurately, a single abdominal clasper was removed from males; this permitted normal courtship, but made copulation impossible. Males were segregated according to pupal weight as before; however, within 12 h of emergence from the pupal stage, males were cold-anesthetized and their left clasper removed at the base. These males appeared unaffected by the surgery, and two days later they were allowed to court individually females of random weights. Females courted by de-claspered large males first displayed rejection behaviors after 11.9 ± 2.0 ($\bar{x}$+SE, $N = 15$) bouts, whereas rejection occurred after only 2.4 ± 0.9 bouts ($N = 15$) in females courted by declaspered small males ($p < 0.001$ after $\sqrt{x+0.5}$ transformation). It is clear then, that in *E. elutella* courtship, females actively discriminate between large and small males with the result that small males mate at a much lower frequency than large males. Parental size had a significant effect on the offspring size, with large parents producing larger offspring (table 2). Partitioning of effects by two-way ANOVA with replicates of log-transformed data shows that paternal size accounted for 13% of the variance in the pupal weight of sons ($F = 5.1$, $p < 0.05$), while maternal size accounted for 52% of this variance ($F = 17.9$, $p < 0.005$). Similarly, mean daughter pupal weight was affected by both paternal weight (11% of variance component, $F = 5.0$, $p < 0.05$) and maternal weight (29% of variance component, $F = 11.6$, $p < 0.005$). Parental weight effects were additive for son weight, but there was a significant interaction (26% of variance component, $F = 5.8$, $p < 0.05$) betwen parental weights for daughter weight. Parental size also affected the number of pupal offspring, with matings between small males and small females producing significantly fewer offspring than matings between large males and large females (table 2); paternal size contributed more to this result (40% of variance component, $F = 6.7$, $p < 0.025$) than did maternal size (19% of variance component, $F = 3.7$, $p > 0.05$). Thus, females that mate with large males, on average, benefit over those that mate with small males in three ways: 1) they produce larger sons, who have a higher probability of mating in the next generation; 2) they produce more offspring; and 3) they produce larger daughters, who will also produce larger sons and daughters. Although these benefits are realized in the second generation, it is not known whether they are genetically based or are due to extra-chromosomal factors. It is also not known what cues females use to differentiate male size; however, we hypothesize that discrimination is based on male odor. We have previously demonstrated the importance of male pheromones in *E. elutella* courtship success[10,13]. A blend of compounds, *(E)*-phytol, γ-decalactone, and γ-undecalactone, identified from glands on the forewings of *E. elutella* males evokes female receptive behaviors in the absence of males; removal of these glands significantly reduced male mating success by causing female rejection early in courtship[13]. In the present study, small males experienced a similar early rejection with 11 of 21 rejections occurring before the first copulatory attempt. Furthermore, quantification of pheromone levels from individual males does indeed show that small males have significantly less *(E)*-phytol than do large males (11.9 ng $\pm$ 1.32(SE)/male for 10 males of $\bar{x}$ pupal wt = 13.8 mg and 19.1 ng $\pm$ 2.1(SE)/male for 10 males of $\bar{x}$ pupal wt = 19.9 mg, $p < 0.02$). Stimuli associated with wing size, such as auditory cues from vibrating wings, are apparently not important, as removal of most of the forewing while leaving the wing gland intact does not alter mating success[13]. Primary reliance on visual cues for male-size determination also does not seem likely as mating occurs during

Table 1. Courtship success, probability of rejection by females, and length of courtship of large or small males individually courting large or small females (n = 20/size category)

	Courtship success	Rejection by females	Duration of female receptivity (No. bouts ± SE) Successful courtships	Unsuccessful courtships
Sm♀ × Sm♂	60%b	50%a	1.50 ± 0.55(12)	0.75 ± 0.29(8)
Sm♀ × Lg♂	95%a	10%b	2.74 ± 0.45(19)	1.00 ± 0.00(1)
Lg♀ × Sm♂	65%b	55%b	1.31 ± 0.26(13)	1.71 ± 0.33(7)
Lg♀ × Lg♂	100%a	5%b	4.25 ± 1.07(20)	—

Percentages within a column followed by the same letter are not significantly different at $p = 0.05$ by Ryan's [12] multiple test for proportions. A courtship bout is defined as one repetition of the courtship sequence. No significant differences were found in the duration of receptivity by Duncan's New Multiple-Range Test. Values in parentheses indicate number of males.

Table 2. Relationship between parental weight and offspring weight and number

	$\bar{X}$ pupal weight ± SE (mg) Parental Female	Male	Offspring Female	Male	Number of pupal offspring
Sm♀ × Sm♂	15.6	12.8	15.9 ± 0.5b	13.4 ± 0.5c	53.8 ± 12.6b
Sm♀ × Lg♂	14.8	16.7	17.8 ± 0.5a	14.7 ± 0.5b	73.3 ± 15.0ab
Lg♀ × Sm♂	19.3	13.2	18.4 ± 0.2a	15.5 ± 0.3ab	72.0 ± 16.9ab
Lg♀ × Lg♂	19.6	17.1	18.2 ± 0.1a	16.1 ± 0.2a	112.0 ± 14.6a

Offspring values based on all individuals from six randomly selected females of each size combination in table 1. Mean pupal weight for parental populations: female, 17.5 mg; male, 15.0 mg. Values within a column followed by the same letter are not significantly different at $P = 0.05$ by Duncan's New Multiple-Range Test (n = 6).

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.

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Monitoring insecticide resistance with insect pheromones[1]

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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