(two sites and two distances at each) is shown in figure 1. It is clearly seen that in each case the second signal (440 Hz) needed the least energy for transmission through the mole rat tunnel. Consequently we conclude that it is the optimal one of all the signals tested for transmission through the ground. All other signals had to be broadcast at a stronger intensity in order to produce a sound of the same magnitude. The 60 db curve of the second site at 2 m (fig. 1) flattens at points 5 and 6 as a result of a better signal-to-noise ratio in this recordings, compared with the other intensity curves.

The sonograms (fig. 2) show clearly that frequencies higher than 440 Hz were filtered out during the passage of signals through the tunnels. Signals 1 (220 Hz) and 2 (440 Hz) were fully transmitted. In signal 3 only the lowest (440 Hz) frequency was fully transmitted at all distances in the two localities, whereas the frequency of 880 Hz was transmitted only across 2 m distance and faded away at a distance longer than 5 m. For signal 4, 880 Hz was noticeable at a distance of 2 and 5 m but disappeared at 7 m, whereas 1760 Hz was recorded only at the shorter distance in Daliyat el karmil. For signal 5, 1760 Hz was noticeable only at 2 m, whereas 3520 Hz completely disappeared. For signal 6 (3520 Hz) no transmission whatsoever was recorded at any distance.
*Discussion.* Our results suggest that low frequency sounds are transmitted better than high frequency ones in the air of underground tunnels, for all intensities and distances tested. This is probably because low frequency sounds (consisting of long wavelength) collide less than high frequency ones (short wavelength) with the tunnel walls, and therefore are less absorbed. The 440 Hz frequency was the best transmitted through the tunnel out of all tested frequencies and needed the least energy for transmission, in comparison to either higher (880–3520 Hz) or lower (220 Hz) frequencies. Frequencies higher than 440 Hz are probably more absorbed in the tunnel walls, whereas the lowest tested frequency (220 Hz) seems to be weaker due to reflection from the walls and therefore also less intensely transmitted. These results match well with the main (approximately 500 Hz) frequency of the mole rat courtship sound[15], with other vocalizations of mole rats[7] and with the hearing ability of mole rats (report in preparation).

The intensity of the mole rat courtship call was found to be about 50 db[15] (approximately the same as the lowest intensity tested here). Signals of that magnitude faded in the present study across a distance of more than 2 m. Considering the efficiency of vocal transmission through the air in the tunnels, it is apparent from the results that acoustical communication of mole rats is efficient only across a short range, i.e. not more than 5 m. Therefore mole rat calls seem not to be effective for longer distances. The distance between individual mole rats is generally large since they live in nature in solitary neighboring territories.

A long-range acoustical communication system that exists between mole rats, probably for territorial defence and reproductive functions, may well use other means, such as thumping the head against the ceiling of the tunnel (report in preparation) which produce vibrations transmitted directly through the earth. When confrontation between individuals does occur (for courtship, mating or aggression), it is from a short range. Thus we conclude that the moe rat's low frequency calls, which are most efficient for vocal transmission across short range, are adaptive to communication in underground tunnels and are presumably molded by natural selection.

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# On selecting for pupation height in *Drosophila simulans*

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*Summary.* Selection for high and low pupation height has been carried out in a base *D. simulans* population derived from recently collected isofemale lines. Only the selection for increased pupation height was successful. At generation 8 around 50% of the individuals in the high lines attained the upper end permitted by the apparatus, and selection was stopped. The mean realized heritability was 18%. The finding of additive genetic variation for pupation height in *D. simulans* settles the question posed by a previous failure of selection reported in this species.
*Key words.* Pupation height; *Drosophila simulans;* directional selection.

The choice of suitable pupation sites by *Drosophila* larvae should be considered as an important fitness component in view of the direct repercussion this behavior has on pupal viability[1]. Genetic control for pupation behavior has been demonstrated in several *Drosophila* species[2–4], and parallelism between field observations and laboratory performance has been noticed recently for some larval patterns of behavior[3]. Strains of *D. melanogaster* quickly responded to selection for pupation height in the upward direc-

Mean pupation heights shown by the selected lines after 8 generations of selection and by some crosses between them. Comparisons between observed pupation heights and expected midparent values were carried out by Student's t-tests (23 df)

| Selected lines | Pupation height (mm) | Crosses | Observed pupation height (mm) | Midparent value (mm) | Comparison |
|---|---|---|---|---|---|
| H1 | 63.62 | ♀ H1 × L1 ♂ | 29.59 | 38.36 | t = 1.62 |
| L1 | 13.10 | ♂ H1 × L1♀ | 28.36 | 38.36 | t = 1.84 |
| H2 | 59.86 | ♀ H2 × L2 ♂ | 30.88 | 35.53 | t = 0.85 |
| L2 | 11.21 | ♂ H2 × L2 ♀ | 22.14 | 35.53 | t = 2.47 (p < 0.05) |

tion[4], although failures of selection in the downward direction were found in the same experiments. Ringo and Wood[5] did not find responses to selection for increased pupation height in *D. simulans*, a fact which led these authors to suggest that, in their recently caught *D. simulans* population, there was no additive genetic variation for the character owing to directional natural selection favoring low pupation sites. They also suggest that the success reported in *D. melanogaster* was due to the use of strains which had been kept for a long time in the laboratory, where natural selection is relaxed. We previously analyzed several isofemale lines from a newly captured *D. simulans* population for pupation height, and a great genetic variation (additive plus dominance) was found[6]. In the present work, we present data from a selection experiment for pupation height carried out with the above *D. simulans* population.

After 27 isofemale lines were examined for pupation height at the third generation in the laboratory, the 4 highest and lowest lines were taken to constitute the base population. Selection was started 4 generations later. Then, 75 newly hatched larvae were seeded in a vial (diameter 18 mm; length 200 mm) with standard bakers' yeast food. After larval pupation and before adult eclosion, the site occupied by the pupae in the vial was registered, and the pupation height in each vial was calculated by the method previously described[6]. Pupae on the medium were classified as being at 0 mm height. Pupae on the vial wall (150 mm length) were classified into one of 15 height classes, with means in height ranging from 5 mm to 145 mm (or touching the vial plug). The highest 8–10 pupae in a vial were taken for the 'high' line. For the 'low' line, the lowest 8–10, located 0–10 mm above the food (1st height class on the wall) were taken, and this number was completed with pupae located on the food only when necessary. Two high lines (H1 and H2) and two low lines (L1 and L2) were started independently. Generations of selection were carried out with 8 vials (600 larvae) per line. The base population was scored for pupation height at selection generations 0,3,5 and 7, with 18,10,10 and 10 vials respectively. The entire experiment was in a chamber at 21.5°C and under 12:12 h light:darkness cycles. A gradient of relative humidity (RH) occurred inside the vials: the high water content of the food caused 100% RH in the sites near the food whereas 40% RH was held

constant outside the vials in the chamber. The interchange of humidity between vials and chamber was controlled by using foam plugs of constant size (25 mm in diameter; 35 mm in length). Under these conditions highly reproducible data on pupation height can be obtained[6].

Mean values of pupation height over the generations are depicted in figure 1. Rapid and consistent responses occurred for the high lines, whereas the low lines and the base population fluctuated without any consistent trend. Figure 2 shows the frequency distributions of pupae for the base population after pooling the data for the generations 3,5, and 7, and the same applies to the two low lines L1 and L2. Also in figure 2 is the distribution of pupae of the two high lines, H1 and H2, (pooled data), for some selected generations, giving a good graphic representation of the selection success. Selection was ended at generation 8. At this point, about 50% pupae in the high lines were at



Figure 2. Frequency distributions of pupae in 16 height classes. In the upper portion, the base population and the two low lines appear after pooling the data from generation numbers 0,3,5 and 7. The remaining distributions illustrate the selection progress in the two high lines (pooled) after some generations of selection.
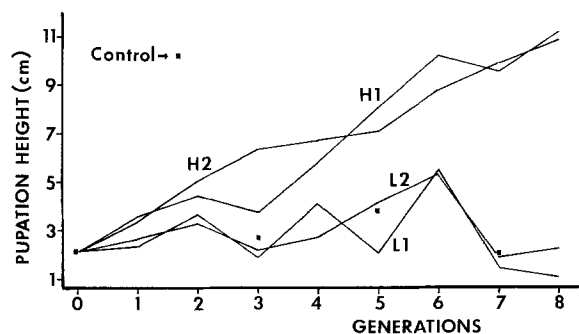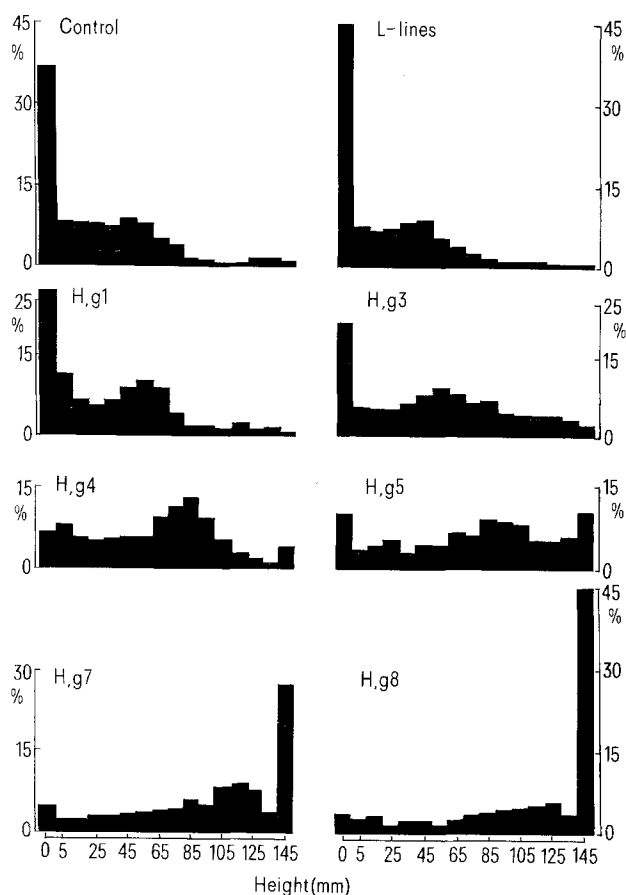


Figure 1. The response to selection for increased (H1 and H2) and decreased (L1 and L2) pupation height. The score of the base population (■) is shown at generation numbers 0,3,5 and 7.

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