expected to be much greater than the 10–17 m observed. Spectral composition, light intensity and the physical size of the light are all factors that could also be important. The light bulbs used by us, which are the same as those used by Sotthibandhu[4], have a horizontal diameter of 7.5 cm and a vertical diameter of 12 cm. As the Moon changes phase its apparent horizontal diameter changes considerably but the vertical diameter is much more constant, subtending to a point on the Earth's surface an angle of 0.518° (diameter = 3,456 km; distance = 382,170 km). The vertical dimension of the light bulb used by us subtends the same angle to a point at a distance of 13.27 m. This is much nearer the distance of response (10–17 m) of a moth near the ground to an elevated (9 m above ground level) light source than is the distance (35–519 m, depending on Moon phase, latitude, and so on[8]) at which the light source has the same level of illumination as the Moon.

We suggest, therefore, that the light-trap response of moths results when the moth ceases to recognise that the artificial light is not the Moon, and that the most important features used in this recognition are first, the elevation, and second, the vertical diameter of the light source. Level of illumination and spectral composition may also be involved[5,8] but are suggested here to be far less important.

On the interpretation of the light-trap response offered here, light traps should catch only those individuals that are in the physiological state in which they would make use of Moon orientation. Most often these will be individuals that are in the process of, or just initiating or terminating, migration. This could explain why light traps do not capture all species of moths in the vicinity[2] (non-migrants not showing the light-trap response) and why males of most species predominate in light-trap catches, males probably being more migratory than females[15]. It could also explain why a better correlation is obtained between light trap catch and volume of migration as determined by radar[3] than between light-trap catch and suction-trap catch[2].

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Received 25 August; accepted 6 November 1978.

1. Williams, C. B. *Phil. Trans.* B **244,** 331–378 (1961).
2. Taylor, L. R. & Carter, C. I. *Trans. R. ent. Soc., Lond.* **113,** 369–386 (1961).
3. Schaefer, G. W. in *Insect flight, Symp. R. ent. Soc. Lond. no. 7* (ed. Rainey, R. C.) 157–197 (Blackwell, London, 1976).
4. Sotthibandhu, S. thesis, Univ. Manchester (1978).
5. Mikkola, K. *Ann. Zool. Fennica* **9,** 225–254 (1972).
6. Hsiao, H. S. *Attraction of moths to light and to infrared radiation* (San Francisco Press, 1972).
7. Taylor, L. R., Kempton, R. A. & Woiwod, J. P. *J. Anim. Ecol.* **45,** 255–272 (1976).
8. Bowden, J. & Morris, M. S. *Bull. ent. Res.* **65,** 303–348 (1975).
9. Sotthibandhu, S. & Baker, R. R. *Anim. Behav.* **27** (in the press).
10. Agee, H. R. *Ann. Ent. Soc. Am.* **65,** 701-705 (1972).
11. Buddenbrock, W. von *Grundriss der vergleichenden Physiologie* (Berlin, 1937).
12. Callahan, P. S. *Nature,* **206,** 1172–1173 (1965).
13. Laithwaite, E. R. *Entomologist* **93,** 133–137 (1960).
14. Roeder, K. D. in *Animal Behavior: Readings from Scient. Am.* (Eds Eisner, T. & Wilson, E. O.) 46–54 (W. H. Freeman, San Francisco, 1975).
15. Baker, R. R. *The Evolutionary Ecology of Animal Migration* (Hodder and Stoughton, London, 1978).
16. Bailey, N. T. J. *J. Anim. Ecol.* **21,** 120–127 (1952).

Male mating experience and competitive courtship success in *Drosophila melanogaster*

MULTIPLE copulations by *Drosophila melanogaster* males reduce their fertility[1], even though these males will continue to court and mate after four or five successive matings. This sterility involves depletion of the accessory glands and not of sperm supply[2] and is only temporary, for when these males are mated 2 or 3 h after the onset of sterility, they once again transfer sperm. A female *Drosophila* would maximise her reproductive fitness by mating with a male which transfers the most sperm; however, virgin females will copulate with temporarily sterile males when placed in a single-pair situation. Although female *Drosophila* are capable of discriminating mates on the basis of genotype differences[3], it is not known whether they will selectively copulate with fertile males in competition with temporarily sterile males of the same strain. In the experiments reported here, we have examined the relative mating success of experienced males with temporarily reduced fertility and virgin males from the Canton-S strain of *D. melanogaster*. The data show that when a virgin female is placed with a virgin and an experienced male, she tends to mate with the virgin male. Examination of some possible factors for increased virgin male success, such as time until initiation of courtship, amount of time spent courting, and overall mating speed, showed that for the courtship parameters measured, virgin and experienced males are equal.

Flies were raised on standard cornmeal–molasses–agar medium at 24 ± 1 °C. Virgin flies were separated by ether anaesthetisation and stored until 3 d old. Virgin females were then placed individually into 8-dram shell vials containing one experienced male and one virgin male. Males were distinguished by wing clipping[3], which was done at the time of collection to avoid the need for a second anaesthetisation. Clipping was alternated between groups to avoid any possible effects on the results. Small clips have not been found to alter mating in the present study (see below) or in previous studies[4]. All subsequent handling of flies was done by aspiration.

Table 1 Number of offspring produced by males mating three successive times

Mating	Mean no. of offspring per mating per male*	No. of males
1	288.0 ± 17.4	33
2	296.1 ± 28.2	31
3*a*	194.7 ± 23.6	30
3*b*	206.0 ± 21.0	29
3*c*	303.2 ± 18.8	35

a, Males mated immediately after the second mating; *b*, males rested 1 h after the second mating; *c*, males rested 24 h after the second mating.
* A Duncan multiple range test places these data in two statistically significantly different subsets ($P < 0.01$) where offspring number from mating 1, 2 and 3*c* are in one subset, and offspring numbers from matings 3*a* and 3*b* are in another subset.

Three series of experiments were carried out. In series 1, 'experienced' males were obtained by placing virgin males in a shell vial containing one virgin female. Immediately after copulation, the male was placed with another virgin female. During the initial phase of the experiments, 97% of the original males had mated the first and second times by the 1-h cut-off period. After the second mating, each experienced male was placed with a virgin male in a clean shell vial, and a virgin female was introduced. Courtship latency, duration of courtship, successful male and duration of copulation were recorded. Vials showing no mating in 1 h were discarded. In series 2, males were handled the same way except that they were stored alone for 1 h between the second and third matings to eliminate any possible effects of postcopulatory preening or inactivity. In series 3, males were stored for 24 h before the third mating and tested with virgin males of the same age.

The number of offspring produced by males mating three times was determined by saving the females from each of the three matings and counting their progeny (Table 1). Fertility is greatly reduced at the third mating when this occurs within minutes of the second mating or when males are rested for an hour. When males are rested for 24 h after the second mating,

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their fertility rises to levels seen in once-mated males. The total number of offspring produced by virgin males is slightly less than reported elsewhere[2]. However, the present study used a different wild-type strain.

Table 2 shows the relative mating success of experienced males. The data for the nine replications ($n = 15–20$ per replication) in series 1 were pooled following testing for homogeneity[5]. The numbers shown for series 2 are pooled values for nine replications, and for series 3 eight replications. In series 1 and 2, virgin males had a distinct mating advantage. In series 3, no advantage existed.

Table 2 Relative mating success of virgin and experienced *D. melanogaster* males

Series	% Mating	Male chosen: Virgin	Male chosen: Experienced	Total	X^2	P
1	95	115	65	180	13.88	<0.01
2	96	104	74	178	5.02	<0.05
3	96	84	91	175	0.28	NS

Overall clipping $x^2 = 0.965$. NS, not significant.

It has been reported that in *Drosophila*, the females 'decide' if and with which male a mating will take place[3,6]. Obviously, these 'decisions' depend on various sensory cues from the males. It is known that males which spend less time courting have a reduced mating success[7]. However, the disadvantage of the males with reduced fertility in the present study could not be explained by any reduction in observable courtship activity. Experienced males from series 1 and 2, whether successful or not, equalled virgin males in (1) being first to begin courtship, and (2) the proportion of time spent not courting. The average courtship times in series 1 and 2 were 6.01 ± 0.29 min for successful virgin males and 5.97 ± 0.33 min for successful experienced males ($t = 0.024$, NS). The duration of copulation was 20.61 ± 0.91 min and 21 ± 1.06 min for virgin and experienced males, respectively ($t = 0.76$, NS).

Although the virgin and experienced males of series 1 and 2 were of the same age and strain, they are in some way perceived as differing from each other by females. As the standard tests of courtship which would reflect differences in male vigour cannot explain the differences in success of the two types of males, the possibility that they are characterised by different olfactory stimuli[8], or patterns of organisation of courtship elements[9] should be investigated. Some stimuli from the males must somehow be influencing the mate selection process of the females. Any mechanism which results in females discriminating the level of fertility of prospective mates would certainly have a selective advantage. Other species should be studied to determine how widespread this phenomenon is.

This work was supported by NIMH grant 30382-01 to T.A.M.

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Received 9 February; accepted 8 November.

1. Kvelland, I. *Hereditas* **53**, 281–305 (1965).
2. Lefevre, G. & Johnsson, U. *Genetics* **47**, 1719–1736 (1962).
3. Ehrman, L. *Evolution* **23**, 59–64 (1969).
4. Averhoff, W. & Richardson, R. *Behav. Genet.* **4**, 207–225 (1973).
5. Woolf, C. *Principles of Biometry* (Van Nostrand, New Jersey, 1968).
6. Manning, A. *Anim. Behav.* **15**, 239–250 (1967).
7. Connolly, K., Burnet, B. & Sewell, D. *Evolution* **23**, 548–559 (1969).
8. Leonard, J., Ehrman, L. & Schorsch, M. *Nature* **250**, 261–262 (1974).
9. Bastock, M. & Manning, A. *Behaviour* **8**, 85–111 (1955).

Co-carcinogenic effects of dietary cholesterol in experimental colon cancer

COLORECTAL CANCER is now the most common internal malignancy in the US (ref. 1), but its aetiology is unknown. Western dietary factors are likely to be implicated[2,3], and high fat diets correlate well with the geographical incidence of colon cancer[4–6]. Patients with colon cancer have high levels of faecal bile acids and cholesterol[7] as do patients with diseases known to be associated with colon cancer, for example, familial polyposis[8] and ulcerative colitis[9], and also other high-risk populations[10]. It is thought that faecal bile acid and cholesterol metabolites may act as promoters, co-carcinogens or carcinogens in large bowel tumorigenesis[11–13]. As cholesterol is the obligatory precursor of the bile acids[14], we have tested the ability of dietary cholesterol to promote the induction of colon cancer by dimethylhydrazine (DMH) in the rat. We report here evidence from an animal study that cholesterol is a potent dietary co-carcinogen.

The experimental method and diets used are detailed in Table 1. The effects of a single dietary variable, cholesterol, was investigated on the induction of colon cancer in two identical groups of rats, both fed on Vivonex, a cholesterol-free, chemically defined liquid diet. One group (V) received unmodified Vivonex, and the other group (VC) received Vivonex with added cholesterol. The third dietary group (S) was included solely for comparison as a carcinogen-injected control group and was fed a standard formula solid diet. By design, all three diets were fibre-free and provided equivalent caloric intakes.

The results were analysed after 56 weeks' observation. During the first 6-month period, animals on all dietary regimens maintained comparable weight gains (Fig. 1). Any observed differences between groups are therefore unlikely to be attributable to the effects of caloric restriction. Comparisons beyond 6 months are inaccurate, because of variations between sick animals in relation to appetite and weight loss due to the induced colon cancers. At 56 weeks, all control animals were alive and well, except for a single rat fed on Vivonex plus cholesterol

Fig. 1 Growth curves showing weight gain of rats on various dietary regimens. Each point represents a mean weight of the 10 rats in each group. Standard deviations have been omitted for clarity. Statistical comparison shows no significant differences between groups at 26 weeks ($F = 0.28$, d.f. = 5,54, $P > 0.10$). Groups: ○, S; ●, V control; △, V; ▲, VC; □, VC control; ■, S control.