

## Deleterious Effects of Copulation in *Drosophila* Females as a Function of Growth Temperature of Both Sexes

Y. A. COHET and J. R. DAVID<sup>1</sup>

Laboratoire d'Entomologie expérimentale et de Génétique, CNRS, 43, boulevard du 11 novembre 1918, F-69621 Villeurbanne (France), 11 Decembre 1975.

**Summary.** In *Drosophila* females, copulation always results in a reduction of longevity but the gravity of the phenomenon varies according to growth temperature. The harmful effect of adult males, or aggressiveness, is maximum when growth took place at a middle temperature. Female sensitivity, on the other hand, is at a maximum when larvae were reared at extreme, low or high, temperatures.

It has been known for a long time that longevity is always reduced in mated *Drosophila* females<sup>2-6</sup> while males are relatively free of such deleterious effects<sup>7</sup>. Recently it was reported<sup>8,9</sup> that females grown at low temperature were highly sensitive to copulation and that males reared at 13°C were much less harmful or aggressive than 25° males. Mating of sensitive females with aggressive males resulted in a spectacular decrease (more than 70%) of

their longevity while, usually, the reduction of lifespan of mated females as compared to virgins is less than 20%.

We decided to study how these physiological adult traits varied according to growth temperature. *Drosophila* were reared, from egg to adult emergence, at 10 different constant temperatures from 12° to 32°C, which are the limits compatible with complete development<sup>10</sup>. Two complementary experiments were done.

For measuring variation in male aggressiveness, sensitive 13°-reared females were crossed with males grown at different temperatures. For measuring copulation sensitivity, females grown at various temperatures were mated to 25° males. In all cases, female longevity was measured at 25° in groups of 10 females and 15 males.

Results for male aggressiveness are presented in Figure 1. In all cases the longevity of mated females was significantly decreased. But the amount of reduction is highly dependent on male growth temperature (female lifespan varies from more than 50 days to less than 20). Male harmfulness increases with growth temperature to a maximum around 25°, then falls off above 25°.

Data for female sensitivity are given in Figure 2. In this case, analysis was more complex because the lifespan of control virgin females varied with temperature. Their longevity was maximum for 17° growth. Mating with 25° males shortened the lives of females raised at all temperatures, but the longevity decrease was greater for females grown either at low or high temperature. In Figure 3, female sensitivity is expressed as difference in lifespan between virgin and mated flies and as relative decrease of longevity induced by copulation. The curves show that sensitivity is at a minimum in 25° reared females. When growth temperature varies from 25°, mating sensitivity increases to maxima at the temperature extremes.

It is interesting to imagine superimposing Figure 1 on Figure 3. The curves have approximately the same form: male aggressiveness and female resistance are both maximum with 25° growth.

Variations in male aggressiveness appear linked to variation in their sexual or locomotor activity<sup>11,12</sup>. It is more difficult however, to understand why females are

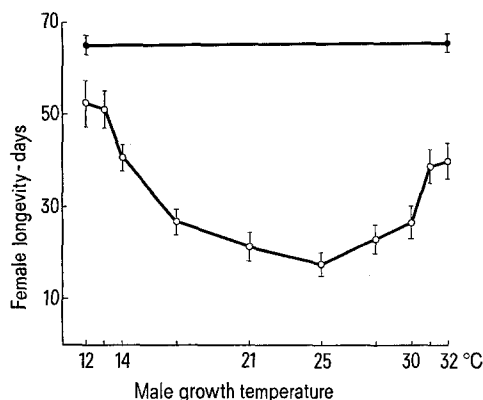


Fig. 1. Study of male aggressiveness: variation of the longevity of sensitive 13° reared females mated with males grown at different temperatures (vertical lines around each point indicate the confidence intervals of means; longevity was measured at 25°C; all values are calculated from 100 females).

●, virgin females; ○, mated females.

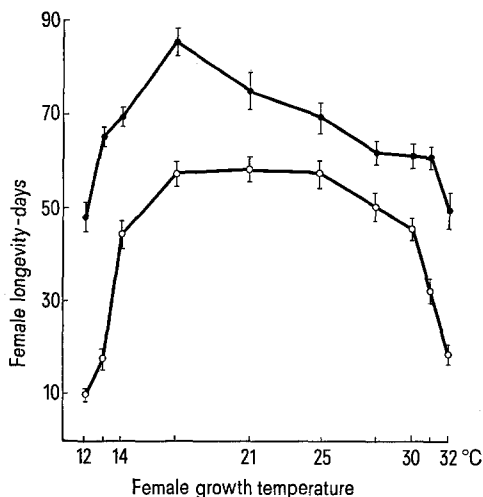


Fig. 2. Study of female sensitivity to copulation: variation of female longevity with growth temperature when mated to aggressive, 25° reared males (other conditions and conventions same as in Figure 1).

●, virgin females; ○, mated females.

<sup>1</sup> We thank R. GRANTHAM for help with the manuscript.

<sup>2</sup> S. BILEWICZ, *Folia biol.*, Kraków 1, 177 (1953).

<sup>3</sup> J. MAYNARD-SMITH, *J. exp. Biol.* 35, 832 (1958).

<sup>4</sup> W. W. DOANE, *J. exp. Zool.* 145, 1 (1960).

<sup>5</sup> H. KUMMER, *Z. vergl. Physiol.* 43, 642 (1960).

<sup>6</sup> J. DAVID and Y. COHET, *C. r. Acad. Sci.*, Paris 273, 1028 (1971).

<sup>7</sup> M. ROCKSTEIN, in *Physiology of Insecta* (Ed. M. ROCKSTEIN; Academic Press, N.Y. 1973), vol. 1, p. 371.

<sup>8</sup> Y. COHET, *C. r. Acad. Sci.*, Paris 273, 2542 (1971).

<sup>9</sup> Y. COHET and J. DAVID, *Experientia* 30, 1266 (1974).

<sup>10</sup> J. DAVID and M. F. CLAVEL, *Naturaliste can.* 94, 209 (1967).

<sup>11</sup> Y. COHET, *Revue comp. Animal* 8, 121 (1974).

<sup>12</sup> Y. COHET, *C. r. Acad. Sci.*, Paris 274, 3102 (1972).

sometimes quickly killed by copulation (see discussion in ref.<sup>9</sup>) and the new finding that sensitivity is also increased by high growth temperature further complicates the interpretation. There is some evidence that sensitive females are sexually more receptive<sup>12</sup>. A recent observation<sup>13</sup> that oogenesis in sensitive female is only slightly stimulated by insemination could also provide a starting point for further analysis.

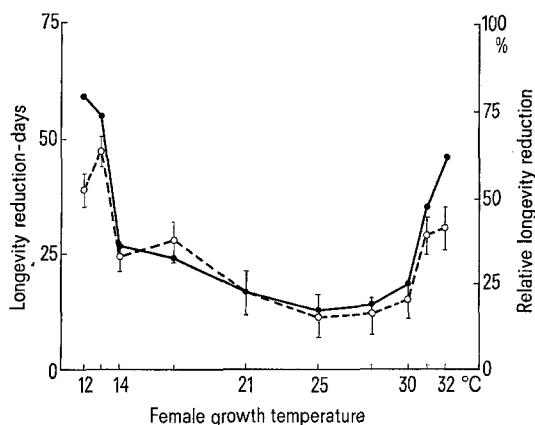


Fig. 3. Variation of female sensitivity to copulation with growth temperature.  
○, reduction in longevity as compared to virgins; ●, relative reduction in % of virgin lifespan.

Behavior studies in *Drosophila*<sup>14</sup> showed that usually, in strains where males were sexually very active, the females had a low sexual receptivity and reciprocally. Our results present some analogies with such observations, although the variations are not genetic but epigenetic and reflect the influence of preimaginal environment upon adult physiology. Moreover, these epigenetic effects are much more extreme than those obtained by genetic factors since we demonstrate that males can be indeed harmful and that females can even be killed by copulation<sup>8</sup>.

When both sexes are grown under the same thermal conditions, mating probably does not result in very harmful effects because the physiological variations are correlated: when males are the most aggressive, females have a maximum resistance. It is probable that the reproductive incompatibility observed when aggressive males are mated to sensitive females rarely occurs under natural conditions. The possible adaptative significance of these variations is still a matter of speculation, although they are probably parameters of the individual fitness and could be important for insect population dynamics. A better knowledge of these variations can be useful in managing pest control experiments, where laboratory reared males are released in nature for competition with wild individuals.

<sup>13</sup> Y. COHET and J. BOULETTEAU-MERLE, C. r. Acad. Sci., Paris 278, 3235 (1974).

<sup>14</sup> P. A. PARSONS, *Behavioral and Ecological Genetics. A Study in Drosophila* (Clarendon Press, Oxford 1973).

## Ultrastructural Changes of the Luminal Plasma Membrane of the Transitional Epithelium of the Rat Urinary Tract in Essential Fatty Acid Deficiency

B. MONIS, A. EYNARD, D. LIS and F. KALINEC<sup>1</sup>

*Instituto de Biología Celular, Facultad de Ciencias Médicas, Universidad Nacional de Córdoba, Casilla Postal 362, Córdoba (Argentina), 2 December 1975.*

**Summary.** Rats fed an essential fatty acid deficient diet (EFAD) showed a statistically significant decrease in the thickness and ultrastructural asymmetry of the luminal membrane and cytoplasmic vesicles of transitional epithelium of the urinary tract, due to a marked thinning of the peculiar thick luminal leaflet. These changes were reversed by adding EFA to the diet. This indicates that the unusual EM appearance of urothelial membrane depends on its content in EFA.

We have been interested in producing in the rat an experimental condition by a deficient diet in certain basic nutrients which should cause changes in cell membranes, expecting that this may contribute to the understanding of their role in membrane organization and function. The most promising model seemed to be the state of deficiency in the essential fatty acids: linoleic, linolenic and arachidonic (EFA)<sup>2</sup>, since they are constituents of phospholipids and cholesterol esters, 2 constant components of biological membranes<sup>3</sup>. It could then be predicted that membrane changes might appear when rats were deprived of EFA. Furthermore, since the condition may occur in man, this could be of further clinical interest<sup>4</sup>.

We wish to report that the characteristic thickness and ultrastructural asymmetry of the unit membrane of the luminal plasmalemma and the cytoplasmic vesicles of transitional epithelium of the ureter and bladder (urothelial membrane) was notably altered by feeding rats on a diet which was deficient in essential fatty acids (EFAD).

In the normal animal, the membrane is distinctly thick, showing an asymmetric unit membrane arranged in plaque zones which are bound by short segments of thinner and symmetric membrane. The luminal (outer) osmiophilic leaflet of the plasmalemma and the luminal (inner) one of the vesicles are about twice as thick as the leaflet adjacent to the cytoplasm (Figure 1). In these laminae or leaflets, subunits, which mainly contain

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<sup>2</sup> G. O. BURR, *Fedn. Proc.* 1, 224 (1942).

<sup>3</sup> A. L. MACMILLAN and H. M. SINCLAIR, in *Essential Fatty Acids* (Ed. H. M. SINCLAIR; Butterworths Scientific Publications, London 1958), p. 208.

<sup>4</sup> A. E. HANSEN, M. E. HAGGARD, A. N. BOELSCHKE, D. J. D. ADAM and H. F. WIESSE, *J. Nutr.* 66, 565 (1958).