Genetic control of dormancy in the potato cyst-nematode

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Summary. Matings of early-hatched parents of the potato cyst-nematode; *H. rostochiensis,* gave F_1 which hatched early - late-hatched parents gave progeny which showed dormancy, the extent of which was in most instances determined by the parents' time of hatching. It is suggested that dormancy is genetically controlled.

When the female of the potato cyst-nematode, *Heterodera* (Globodera) *rostochiensis,* completes its parasitic life, the cuticle hardens to a tough brown cyst wall containing its progeny of several hundred individuals which are already developed to the infective 2nd instar larval stage. Hatching tests of cysts reveal that a) larvae may readily hatch in water, b) show diapause and are stimulated to hatch only by host-root exudate, e) remain dormant, even under optimum hatching conditions, for shorter, longer, or indefinite periods. It is generally agreed that in vitro hatching of field cysts shows seasonal variations; being low or negligible in winter as compared with spring and summer. The causes of dormancy have been a subject of disagreement[2-4]. According to some authors[2,3], there is little or no dormancy if the infested soil is brought indoors in spring or summer, but that dormancy does occur if the soil is collected later in the year. Others[4] showed that in the field loss of the ability to hatch starts long before temperature conditions become unfavourable for hatching and once this happens no treatment is known which stops it.

This study investigates a possible genetic basis for dormancy. Cysts used were of pure pathotype A of *H. rostochiensis* which has been maintained on the potato variety 'Home Guard' in the greenhouse for several years. Collections of exudate made over a period of several weeks were combined in a 2-l flask and stored at 4 °C[5]. Single cyst-progeny tests were used for the study of hatching rate[6].

A large number of greenhouse cysts harvested in April 1975 were soaked in water from 28 May 1975 till mid-September by which time hatching in water appeared to have ceased completely. Hatched larvae were discarded. 3 batches of several hundred cysts each were then soaked in exudate from 16 September to 20 October. Larvae which hatched in the 1st 4 days in diffusate were discarded. From then on, daily hatching and sometimes accumulate hatchings on 2 or 3 successive days were inoculated into pots with well-rooted young potato plants.

Of the 14 populations of cysts harvested by 25 January 1976, only 4 have been studied for F_1 hatching rate. These were cysts containing F_1 of parents which hatched on the 5th; 10th, 11th and 12th; 17th and 18th, and 30th day. Cysts were stored in well aerated glass vials and kept at room temperature.

To study hatching rate of F_1 of parents of different hatching time, a) 8–11 cysts from each of the 4 populations of cysts were soaked individually in water from late January 1976 to mid-April and hatched larvae counted. Exposure of individual cysts to exudate immediately followed and lasted for 26 days, during which a daily count of hatch was made. 2 weeks after hatching had ceased, cysts were opened up and unhatched larvae counted. Results are in the table, upper rows. b) Same treatment of cysts from the same 4 populations repeated 9 months later. Soaking in water was from 5 October 1976 to 11 January 1977 and in exudate from 11 January to 20 February. Count of unhatched larvae made on 2 March. Results are in the table, lower rows. Our results suggest that dormancy is under genetic control and may be partly determined by the parents' hatching time. F_1 of fast-hatching parents hatched early and showed no sign of dormancy as shown by lack of statistical significance between the 2 mean percentages of total F_1 hatched when the parents' hatching time was 5 days. The 30–40% unhatched larvae are believed to be in a state of indefinite dormancy. F_1 of slower-hatching parents of 11 and 17.5 days showed dormancy the extent of which is apparently correlated to the parents' hatching time. On the other hand, the initial and later hatching of F_1 of parents of 30 days were significantly higher than expected and should have been less than 8.76 and 42.24% respectively if the extent of dormancy was correlated to the parents' hatching time.

Pattern of hatching of F_1 of parents of different hatching time, upper rows: January 1976 - lower rows: October 1976

Parents' medium hatching time (days)		No. cysts	Total No. of F_1 larvae	Mean percentage of F_1 hatched in water	Mean percentage of total F_1 hatched (water and exudate)
5	Jan	11	3307	0.2	60.63 ± 8.8 SD 29.25 p > 0.25
	Oct.	14	3484	2.61 ± 0.67 SD 2.53	64.94 ± 5.2 SD 19.56
11		8	4192	0	34.8 ± 7.6 SD 21.7
		9	3292	5.88 ± 1.61 SD 4.84	69.87 ± 5.6 SD 16.82
17.5		9	4617	0	8.76 ± 3.2 SD 9.8
		19	8895	3.87 ± 0.74 SD 3.23	42.24 ± 3.69 SD 16.1
30		11	3864	< 0.1	25.5 ± 5.8 SD 19.3
		11	3506	11.65 ± 3.9 SD 19.3	60.07 ± 5.5 SD 18.5

Work in progress however appears to indicate that very late-hatched larvae are more genetically heterogenous and can be of 2 or more different genotypes and that complementary interaction between 2 late-hatched genotypes may give faster-hatching progeny. In all 4 populations, a proportion of F_1 larvae which would have hatched only in exudate when young, hatched readily in water at an older age. This suggests that the gene or genes which cause hatching in response to exudate are active during diapause and given time will produce enough product to allow hatching to proceed in the absence of the hatching factor. Accordingly, some of the larvae which hatch in water from unselected old populations of *H. rostochiensis* may well belong to this category and this may explain why in earlier work[6], matings of water-hatched parents gave F_1 which largely segregated for exudate-hatched phenotype.

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Repeated mating by female *Drosophila melanogaster:* The adaptive importance

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Summary. Comparisons of productivity, fertility and fecundity between once-mated females of *D. melanogaster* and females given the opportunity to remate reveals that remating sustains high levels of these fitness traits.

Females of many insect species mate numerous times throughout their reproductive lives and often store large numbers of sperm. The storage of sperm would seem to reduce or perhaps eliminate the necessity to remate. However, both laboratory and field studies of *Drosophila*[3-7] reveal that remating is common. But there is still no clear explanation of the adaptive significance of remating for female *Drosophila*. In fact, Ikeda[8] demonstrated that multiple copulation in *D. mercatorum* has a deleterious effect on fitness.

A number of hypotheses have been advanced to explain the origin and maintenance of remating behavior by female *Drosophila*. Remating could result in increasing the genetic heterogeneity of a female's offspring. Richmond and Ehrman[3] postulated that it is advantageous for a female to remate and produce eggs of multiple male parentage since larval competition is reduced in genetically heterogenous culture bottles[9]. Anderson[4] suggested that females need to replenish their sperm supply after its depletion due to egg laying. Remating would also be favored if the first insemination were inadequate or if the energy cost to the female were greater in rejecting a persistant male than in remating[10]. Finally, competition between successive mates for the fertilization of a female's eggs could result in male mating strategies which influence female remating[11-13]. In this paper we explore the relationship between the timing of successive matings by female *D. melanogaster* and their fitness as measured by productivity (the number of progeny produced per female), fecundity (the number of eggs laid per female) and fertility (the proportion of eggs laid which hatched).

Methods and materials. The flies used in this study were taken from a 4-year-old wild-type cage population synthesized from strains of heterogeneous origin[14]. The procedure for obtaining once-mated females used throughout this study is as follows. Virgin females, 3 days old, were put individually into 8 dram food vials with 2 males aged 3-5 days. Vials were examined at 10-min intervals and those containing copulating pairs were gently set aside (copulation in *D. melanogaster* lasts approximately 20 min[15]). Males were removed with an aspirator within 30 min of the completion of copulation.

Single-mated females remained in the yeasted food vials and were treated in one of 2 ways. Females in treatment group 1 (n = 107) were simply transferred without etherization into fresh food vials daily for 14 days and twice more at 4-day intervals. The number of progeny produced per single-mated female per day was recorded. Females in treatment group 2 (n = 70) were subcultured daily as above for 22 days but these females were given the opportunity to remate. 2 males were placed with each female for 2 h each day for 15 days and copulations were scored visually as in the first matings. These group 2 females were transferred into fresh food vials for the last 8 days without the opportunity to remate. The number of progeny produced per female per day was scored and compared to the productivity of single-mated females. Note that group 2 females may include single-mated females as well as those that remated a number of times.

Results and discussion. The productivity of group 2 females was much greater than group 1 females (figure 1). Females from both groups had similar productivity for the first 5 days of testing but thereafter the number of progeny produced by single-mated females per day dropped rapidly approaching 0 at the end of the study, at which time dissection revealed that these females were devoid of sperm. The productivity of group 2 females remained high during the 2 weeks when males were provided, after which their productivity dropped as in group 1 females. The mean number of progeny per female following only 1 mating was 528 and the maximum number of offspring produced by

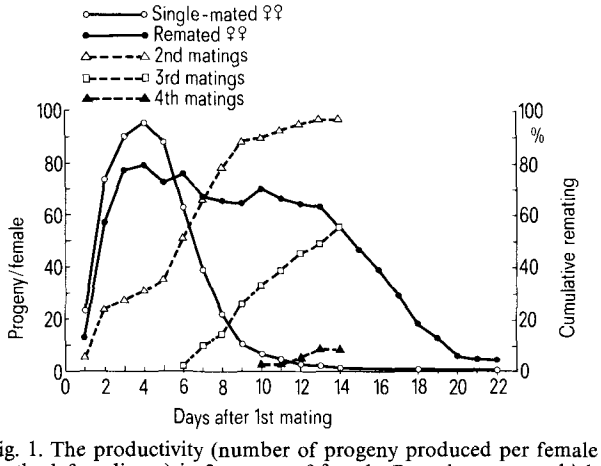

Fig. 1. The productivity (number of progeny produced per female on the left ordinate) in 2 groups of female *D. melanogaster* which are either permitted to mate only once (open circles) or given the opportunity to remate (closed circles) over a period of 22 days (abscissa). The right ordinate shows the cumulative percentage of remating in females given the opportunity to remate (open triangles, double-matings; squares, triple-matings; closed triangles, quadruple-matings).