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Copulation Duration and Its Genetic Control in *Drosophila elegans*

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ABSTRACT—Copulation duration differed between black and brown morphs of *Drosophila elegans*: longer in the former than in the latter. Experiments on copulation between these two morphs revealed that copulation duration was determined by both sexes. The genetic analyses using F_1 hybrids and recombinant inbred lines suggest that two or more loci were responsible for the differences in both of male and female properties for the determination of copulation duration between the black and brown morphs and at least one of the loci governing the male property was probably located on the X chromosome. It also appeared that loci responsible for the difference in copulation duration of males between the brown morph and black morph strains differed from those responsible for the difference in copulation duration of females between them. Genes controlling male copulation duration are at least partly linked with a gene controlling body coloration.

INTRODUCTION

Copulation duration considerably varies in *Drosophila*, from 40 sec in *D. robusta* to 40 min in *D. immigrans* (Grant, 1983). In *D. melanogaster*, *D. pseudoobscura* and *D. athabasca*, copulation duration also varies among geographical or inbred strains (Merrel, 1949; Miller, 1956; Hirdreth, 1962; Hosgood and Parsons, 1965; Kaul and Parsons, 1965; MacBean and Parsons, 1966). To understand how this trait has evolved, it is needed to study its genetic and behavioral control. Patty (1975) carried out hybridization experiments using geographical strains of *D. athabasca* and suggested that loci controlling copulation duration locate on the X-chromosome and autosome(s). In addition, MacBean and Parsons (1967) and Gromko *et al.* (1991) carried out selection for increased and decreased copulation duration in *D. melanogaster* and revealed that copulation duration has a low heritability (about 0.2) and is genetically correlated with courtship vigor or fertility. It has also been suggested in *D. melanogaster*, *D. pseudoobscura* and *D. athabasca* that copulation duration is mainly determined by the male (Kaul and Parsons, 1965; MacBean and Parsons, 1967; Patty, 1975).

Here, we studied the genetic and behavioral control of copulation duration in *D. elegans* Bock and Wheeler as the first step to understand the evolution of copulation duration in this species. In this species, two color morphs, black and brown, are known: the former is distributed in Ryukyu islands and Taiwan, while the latter is distributed in southern China, Philippines and Indonesia (Hirai and Kimura, 1997). Hirai and Kimura (1997) showed that one locus is responsible for the difference of body coloration between these two morphs and F_1 individuals have intermediate coloration.

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MATERIALS AND METHODS

Flies

Experimental strains originated from several females collected from Sukarami (SK: Sumatra, Indonesia), Puncak (PC: Java, Indonesia), Hong Kong (HK: China), Puli (TP: Taiwan), Iriomote (IS: Japan) and Okinawa (OH: Japan). The first three (PC, SK and HK) were the brown morph strains and the last three (TP, IS and OH) were black morph ones. They were maintained for 2-3 years under laboratory conditions before experiments. Experimental individuals were reared on cornmeal-malt medium at 23°C under a long daylength (15 h light: 9 h dark).

Genetical analyses were made using F_1 hybrids and recombinant inbred lines.

Recombinant inbred lines

A number of lines were obtained from F_1 hybrids which were produced by reciprocal crosses between the IS and HK strains, and these lines were maintained independently by full-sib matings (matings between single brother and sister) since the F_2 generation. After twenty generations of full-sib matings, 12 and 14 recombinant lines were obtained from crosses between HK females and IS males, and between IS females and HK males, respectively. In these inbred lines, 97.5% of loci are expected to be homozygous for either of the alleles of the original strains (Falconer, 1960). The number of loci governing copulation duration was estimated from the distribution of mean copulation duration of these inbred lines. If a single autosomal locus is responsible for the difference of this trait between the IS and HK strains, the frequency of lines which show either of the properties of the original strains is expected to be 0.975 (the probability that an allele from one of the original strain becomes homozygous is 0.975/2 = 0.4875). If two unlinked autosomal loci are responsible, the frequency is expected to be 0.475 ($= 2 \times 0.4875^2$). Likewise, if three unlinked loci are responsible, the frequency is expected to be 0.232 ($= 2 \times 0.4875^3$); if

four unlinked loci are responsible, it is expected to be 0.113 (= 2 × 0.4875^4). If the loci governing the trait are linked, the frequency of lines which show either of the properties of the original strains becomes higher than when these loci are not linked. With the increase of responsible loci, the frequency of such lines is expected to decrease.

Measurement of copulation duration

Eight-day-old virgin females and males were introduced into glass vials (35 ml) containing food medium and examined for copulation duration.

For males and females of inbred lines and F_1 hybrids, copulation duration was examined by mating with IS females or males.

RESULTS

Parental strains

Table 1 shows copulation duration in the geographic strains and in some combinations of different strains. Copulation duration was significantly shorter in the brown morph (HK, SK and PC: 11.1–11.2 min) strains than in the black morph (IS, TP and OH: 26.3–34.8 min) strains (*t*-test, $P < 0.01$). Also, copulation duration between the HK and SK strains was short, and that between the TP and IS strains was long.

Mean copulation duration between brown morph females and black morph males was 14.3-14.6 min, significantly different from the duration of the brown and black morph strains (*t*-test, $P < 0.01$). Copulation duration of HK males was significantly longer when they were mated with IS and TP females than when mated with HK females (*t*-test, $P < 0.05$). These results suggest that copulation duration is determined by both sexes. However, copulation duration between OH females and HK males did not significantly differ from that of the HK strain (*t*-test, $P > 0.05$).

F_1 hybrids

Table 2 gives copulation duration when F_1 hybrids (between the HK and IS strains) were mated with males or females of the IS strain. Copulation duration of F_1 males significantly differed by the direction of cross (t-test, P<0.01), longer in F_1 males from a cross between IS females and HK males. In addition, copulation duration of these F_1 hybrid males was significantly (*t*-test, $P < 0.01$) longer than that of a combination of IS females and HK males (mean: 13.6 min) and also significantly (*t*-test, $P < 0.01$) shorter than that of the IS strain (mean: 26.3 min). These results suggest that two or more loci are responsible for the difference of male property for the determination of copulation duration and at least one of the loci is probably located on the X chromosome. A combination of F_1 females and IS males showed intermediate copulation duration between the IS strain (mean: 26.3 min) and a combination of HK females and IS males (mean: 14.3 min).

Table 1. Copulation duration (min) in geographic strains and in some combinations of different strains of *D. elegans*.

Female	Male	N	Mean (SD)
Brown morph strains			
HK	HK	37	11.1 (1.71)
SK	SK	11	11.2 (1.67)
PC	PC	10	11.1 (1.50)
Black morph strains			
IS	IS	37	26.3 (7.38)
TP	TP	12	28.4 (1.98)
OH	OH	13	34.8 (8.41)
Inter-strains			
HK	SK	16	10.9 (1.96)
SK	HK	19	10.4 (2.19)
IS	TP	22	26.5 (4.81)
TP	IS	25	23.2 (6.47)
HK	IS	21	14.3 (3.39)
HK	TP	17	14.6 (4.26)
HK	OH	59	14.6 (3.63)
IS	HK	22	13.6 (3.59)
TP	HK	17	13.5 (3.68)
OH	HK	53	11.4 (2.95)

Table 2. Copulation duration (min) in F_1 females and males (between the HK and IS strains) when they were mated with IS males or females (Copulation duration of these combinations and the IS strains was presented in Table 1).

cross	N	Mean (SD)
F_1 female		
HK♀♀ × IS♂♂	20	19.5 (3.31)
IS♀♀ × HK♂♂	19	20.8 (3.82)
F_1 male		
HK♀♀ × IS♂♂	15	14.9 (3.10)
IS♀♀ × HK♂♂	22	18.5 (4.22)

Recombinant inbred lines

Fig. 1 shows the distribution of mean copulation duration of females of recombinant inbred lines when they were mated with IS males, and Fig. 2 shows that of males when they were mated with IS females. In copulation duration of females, four and nine inbred lines did not significantly differ from the HK and IS strains, respectively (*t*-test, $P > 0.05$). Thus, a half (13/26) lines did not differ from the parental strains, suggesting that two independent loci are responsible for the difference in this property between the HK and IS strain. However, this may be an underestimation, because there is a possibility that the number of strains which do not statistically differ from the parental strains decreases, if sample size increases.

The distribution of mean copulation duration of males was biased: fourteen and one line(s) did not significantly differ from the HK and IS strains, respectively (*t*-test, $P > 0.05$). The cause of this bias is not clear. Selection may worked on male copulation duration or other traits which are closely liked to this trait. Due to this bias, it is difficult to estimate the number of loci responsible for the difference in the male property, but two or more loci seem to be involved.

No correlation ($r = -0.16$, $P > 0.05$) was observed between male and female copulation duration of the inbred lines (Fig. 3), suggesting that loci responsible for the difference in copulation duration of males between the HK and IS strains differed from those responsible for the difference in copulation duration of females between them.

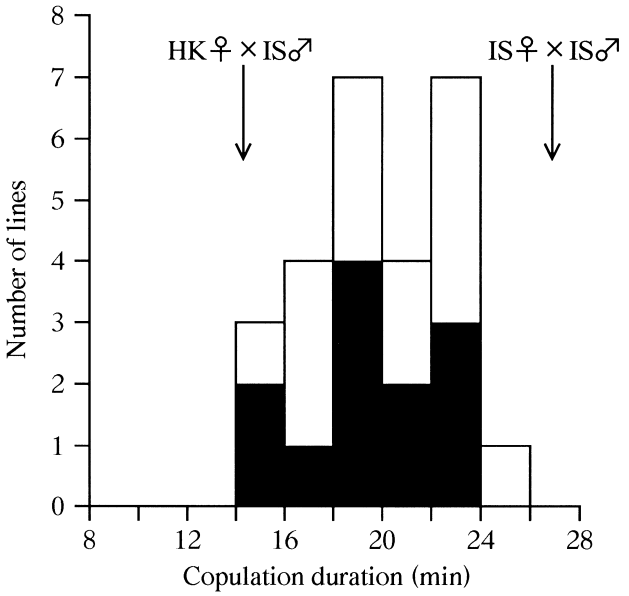

Fig. 1. Distribution of mean copulation duration of females of recombinant inbred lines when they were mated with IS males. Closed bars indicate lines from a cross between HK females and IS males and open bars indicate those from a cross between IS females and HK males. Arrows indicate mean copulation duration of HK and IS females when they were mated with IS males. More than 15 individuals were examined for each line.

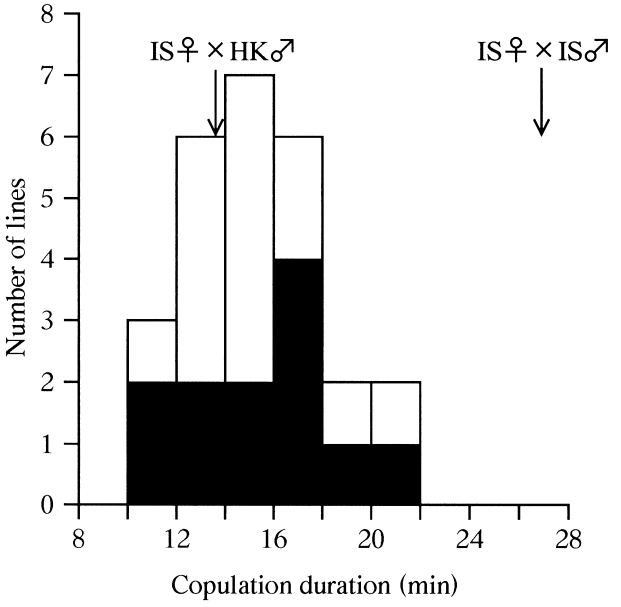

Fig. 2. Distribution of mean copulation duration of males of recombinant inbred lines when they were mated with IS females. Closed bars indicate lines from a cross between HK females and IS males and open bars indicate those from a cross between IS females and HK males. Arrows indicate mean copulation duration of HK and IS males when they were mated with IS females. More than 15 individuals were examined for each line.

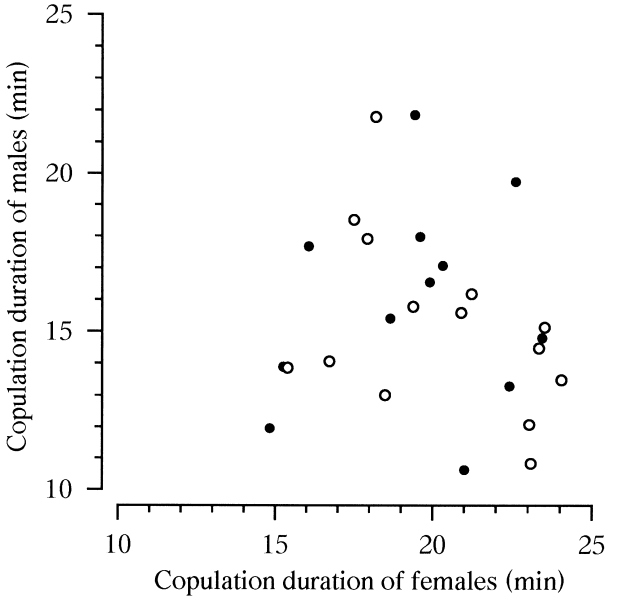

Fig. 3. Correlation between mean copulation duration of females and males from recombinant inbred lines. Closed circles indicate lines from a cross between HK females and IS males and open circles do those from a cross between IS females and HK males.

Body coloration was also examined in recombinant inbred lines: twenty lines were brown (the HK type) and six lines were black (the IS type). Thus, the ratio of HK and IS types was significantly deviated from 1:1 (χ^2-test, $P < 0.01$). These results suggest that a locus or very closely linked loci is (are) responsible for the difference in body coloration between the HK and IS strains and selection may have worked on body coloration during twenty generations of sib-mating.

Male copulation duration was significantly longer in the lines having black coloration than in those with brown one (*t*-test, $P < 0.01$), but female copulation duration did not significantly differ between them (*t*-test, $P > 0.05$) (Fig. 4).

DISCUSSION

Copulation duration was shorter in the brown morph (HK, SK and PC) strains than in the black morph (IS, TP and OH) strains. When HK males were mated with IS or TP females, they copulated longer than when mated with HK females. This indicates that HK males have a higher propensity to prolong copulation over 11.1 min (mean copulation duration between HK males and females) and HK females have a higher propensity to shorten copulation. However, copulation duration of HK males did not differ when they were mated with OH or HK females. This suggests a possibility that OH females have a higher propensity to shorten copulation than IS and TP females. The propensity to shorten copulation duration is assumed to be much high in HK females, because copulation duration between HK females and black morph males was much shorter than that between black morph females and males. This notion is supported by our personal observation

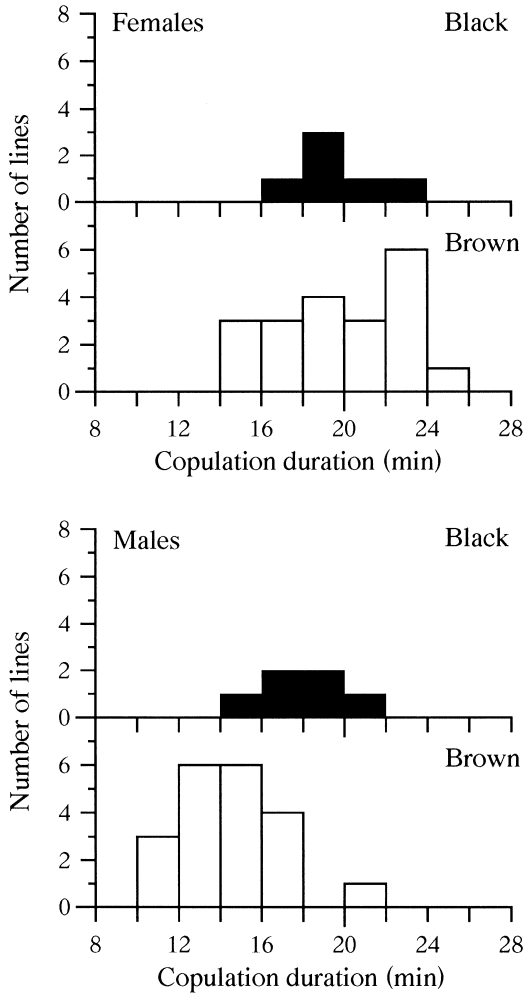

Fig. 4. Distribution of mean copulation duration of females and males of recombinant inbred lines with black coloration and those with brown one.

that HK females violently shivered their bodies and kicked males on their back when copulation was prolonged over 10 min. Females of the OH, IS or TP strains did not show such behavior at least for 25 or 30 min after the start of copulation. On the other hand, IS, TP and OH males have a much higher propensity to prolong copulation than HK males. Thus, copulation duration of *D. elegans* was determined through interactions between females and males. In contrast, Kaul and Parsons (1965), MacBean and Parsons (1967) and Patty (1975) reported that copulation duration of *D. melanogaster*, *D. pseudoobscura* and *D. athabasca* was determined mainly by the male.

The present study suggested that two or more loci were responsible for the differences in the male and female properties for the determination of copulation duration between the HK and IS strains of *D. elegans* and at least one of the loci governing the male property was probably located on the X chromosome. Patty (1975) also reported that the difference in copulation duration between geographic races of *D. athabasca* is due to a small number of genes.

It also appeared in this study that loci responsible for the difference in copulation duration of males between the HK and IS strains differed from those responsible for the difference in copulation duration of females between them. On the other hand, genes controlling male copulation duration are at least partly linked with a gene controlling body coloration.

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