

The Maintenance of an Inversion Polymorphism  
in Coelopa frigida

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## Chapter 8

### Adult Size Variation and its Consequences

#### 8.1 Introduction

Adult Coelopa frigida are very variable in size in natural populations. That this variation is, in part at least, due to variation in levels of larval competition has been demonstrated several times (Mayhew 1939, Burnet and Thompson 1960, Collins 1978). I have repeated the observation that an increase in competition results in smaller adults but my laboratory experiments have also shown a genetic effect on adult size (Chapter 5). It is not clear from these results whether this genetic effect is due to the inversion on chromosome I as a whole or to the Adh locus itself. The sizes of the different genotypes are related to their development times and to their viabilities in laboratory culture. In this chapter I will present evidence that the association between Adh genotype and size can be detected in natural populations and I will examine some possible consequences of size differences.

#### 8.2 Sizes in natural populations

##### a) Methods

Samples of flies were taken from natural populations in one of two ways. Two samples were taken as adults by collecting flies from around wrack beds with an insect aspirator. It is only rarely possible to obtain a large sample in this way because in cold weather they are usually deep in wrack beds or in crevices in cliffs and between pebbles. The remaining samples were taken by the "adult"



collecting method described in Chapter 3. The following samples have been analysed:-

Collected as Adults	St.Mary's Island	12 January 1980
	Morfa Nefyn	5 December 1980
Collected as Larvae	Rustington	14 November 1979
	St.Mary's Island	20 November 1979
	Kampinge	4 December 1980

Precise site locations are given in Chapter 3 for all sites except Kampinge which is in the extreme south-west of Sweden, 20 Km south of Malmö. (This sample was collected by Dr.T.H.Day who kindly allowed me to measure some of the adults.)

Only males from the large St.Mary's Island sample of January 1980 were studied as the females were required for another experiment.

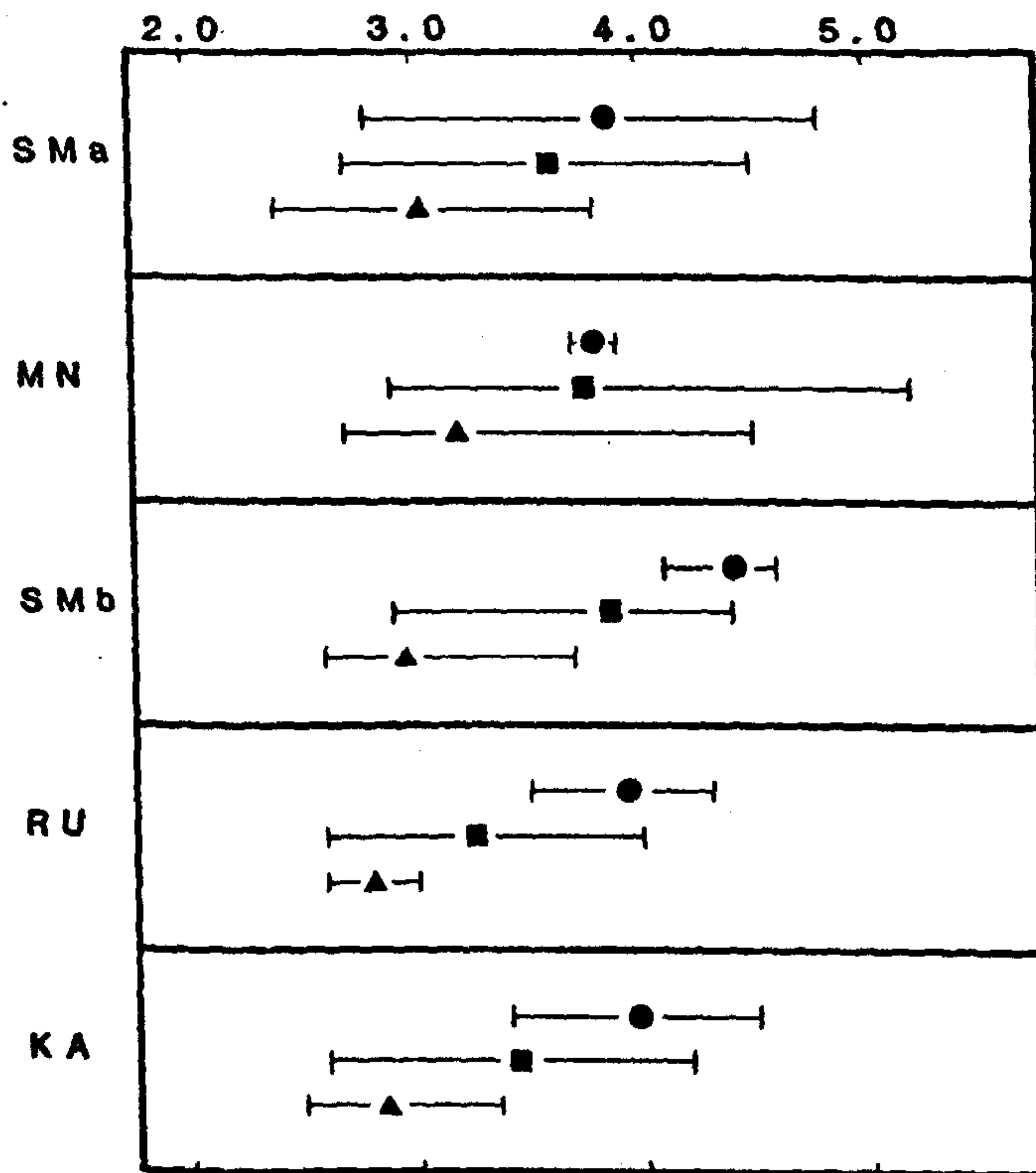
Wing length was used as a measure of adult size. Measurements were made as described in Chapter 2 immediately before electrophoresis.

b) Results

The results are given in full in Appendix 6 and are summarised in Table 8.1 and Figure 8.1. The AdhC allele was rare in the Kampinge sample as in all samples from Scandinavia (Day et al, in prep.).

The relationship between size and genotype for the three common genotypes (BB, BD and DD) is very similar to that observed in the laboratory (Chapter 5). In all cases BB flies are largest on average, DD flies smallest and heterozygotes intermediate. This is true of both males and females but is much more marked in males. The relationship between genotype and size is constant over the four widely separated populations despite differences in

# MALES



# FEMALES

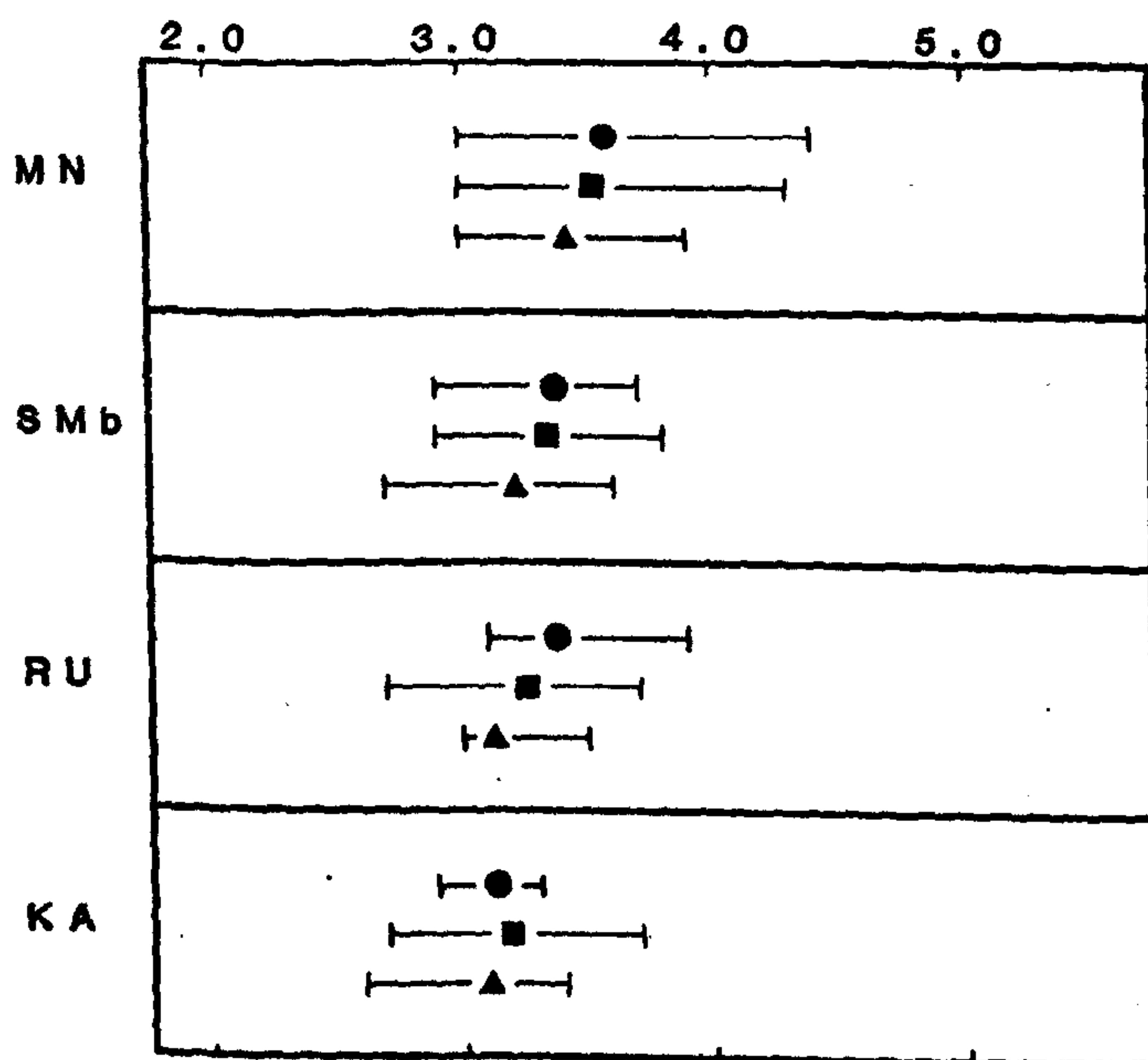


Fig.8.1 Wing lengths and development times of Coelopa frigida

The mean wing lengths, with observed ranges for each genotype are shown for males and females. The units are graticule divisions - see Chapter 2.

Sample collection sites:-

Sm(i) St.Mary's Island, January 1980

Mn Morfa Nefyn

Sm(ii) S.Mary's Island, November 1979

Ru Rustington

Ka Kampinge

Alcohol dehydrogenase genotypes:- ● BB ■ BD ▲ DD

overall mean size which are presumably due to differences in larval density (see Chapter 5). The variance of size within each genotype is much greater than in laboratory cultures. This may be simply the result of more variable conditions of larval density in the natural wrack bed but could also represent greater genetic diversity. In some cases the distributions of sizes appear to be rather skewed but this is not consistent between populations nor between genotypes. It may be an effect of the small sample sizes - there is no suggestion of skewness in the largest sample from St.Mary's Island, 1980 - or it may reflect a patchy distribution of larvae in the natural wrack bed.

There are few BC and CD flies and the variances of size within these genotypes are large. The mean sizes do not fall in consistent positions relative to the three common genotypes but, in males at least, BC flies are larger than CD flies.

If it is assumed that the differences in size between Adh genotypes in natural populations are due to an effect of the chromosome I inversion polymorphism rather than the Adh locus itself, the sizes of flies carrying the Adh-C allele should be predictable. The mean size of the BC flies should fall between that of the BB and BD genotypes because BC flies are a mixture of  $\alpha\alpha$  and  $\alpha\beta$  individuals (Day et al 1982). Similarly the CD flies should be intermediate in size between BD and DD. Both genotypes should have wide size ranges because they are karyotypically heterogeneous.

Of the four male and three female samples containing these genotypes, only the males from St.Mary's Island, 1979, follow the

Table 8.1

Wing lengths and Adh genotypes of flies from natural populations

## a) MALES

<u>Site</u>		BB	BC	<u>Adh Genotype</u>		DD	
				BD	CD		
St.Mary's Island (Jan.'80)	$\bar{x}$	3.86±0.19	3.38±0.13	3.60±0.04	3.25±0.09	3.02±0.03	$F_{4,194}=23.0$
	n	10	13	89	24	59	$P < 0.001$
Morfa Nefyn	$\bar{x}$	3.80±0.99	4.15±0.92	3.74±0.15	3.76±0.23	3.46±0.11	$F_{4,42}=1.19$
	n	2	2	16	5	18	$P > 0.2$
St.Mary's Island (Nov.'79)	$\bar{x}$	4.41±0.07	4.09±0.06	3.83±0.07	3.08±0.18	2.96±0.04	$F_{4,88}=62.1$
	n	7	10	32	6	34	$P < 0.001$
Rustington	$\bar{x}$	3.92±0.15	3.50±0.06	3.25±0.07	3.30±0.15	2.79±0.04	$F_{4,68}=15.0$
	n	6	5	35	6	17	$P < 0.001$
Kampinge	$\bar{x}$	3.96±0.17	-	3.42±0.06	-	2.84±0.03	$F_{2,68}=8.14$
	n	5		40		24	$P < 0.001$

## b) FEMALES

Morfa Nefyn	$\bar{x}$	3.58±0.23	3.67±0.13	3.53±0.10	3.64±0.12	3.42±0.09	$F_{4,46}=0.54$
	n	5	3	16	10	13	$P > 0.2$
St.Mary's Island (Nov.'79)	$\bar{x}$	3.37±0.08	3.13±0.03	3.33±0.04	3.30±0.06	3.21±0.05	$F_{4,93}=1.5$
	n	10	3	43	16	22	$P > 0.2$
Rustington	$\bar{x}$	3.36±0.05	3.19±0.07	3.26±0.03	3.16±0.08	3.11±0.07	$F_{4,70}=2.69$
	n	14	8	34	8	7	$P < 0.05$
Kampinge	$\bar{x}$	3.12±0.07	-	3.17±0.03	-	3.10±0.04	$F_{2,71}=1.11$
	n	5		45		22	$P > 0.2$

$\bar{x}$  mean wing length ± standard error expressed in graticule divisions, where 1 division = 1.45 mm

n sample size

expected order exactly. Although the sample sizes are small and the variances large this inconsistency is still noticeable and is reminiscent of the difficulty of reconciling the observed proportions of these genotypes in field samples with selection acting purely on the inversion as a whole (Chapter 3). It is also likely to be related to the variability in development time of the BC and CD genotypes relative to the others (Chapter 4, Day et al, 1980) especially in view of the relationship between size and development time (Chapter 5).

c) Discussion

These results confirm that the size differences between flies of different Adh genotypes observed in the laboratory also occur in natural populations. While it is not clear whether this is an effect of the Adh locus or of other loci within the inversion, this distinction is probably not important when considering the consequences of size variation because of the very tight linkage caused by the inversion.

In earlier chapters (4 and 5) the relationship between size and development time of flies and viability under competitive conditions has been discussed. In Chapter 4 the possible influence of development time on gene frequencies in the temporally variable wrack bed environment was described. In this and the next chapter some possible direct effects of adult size on fitness will be investigated. In particular, adult size might be expected to influence longevity, fecundity and mating success.

Fecundity has been related to size in many species of insects



(see review by Hinton, 1981), variation in size generally being a result of differences in larval crowding. In some, but not all, insects studied fecundity is correlated with longevity. In Drosophila increase in adult body size is accompanied by an increase in fecundity of females and in longevity of both males and females (Robertson 1957, Roff 1981, Partridge & Farquhar 1981). In Drosophila and in the housefly (Musca domestica) male size has been shown to influence mating success (Ewing 1961, 1964, Monclus & Prevosti 1971, Baldwin & Bryant 1981). If size has similar effects on fitness in Coelopa then the association between the Adh/inversion polymorphism and adult size might have important consequences for the maintenance of the polymorphism.

### 8.3 Fecundity and longevity

The reproductive behaviour of Coelopa frigida has been studied by Thompson (1951), Burnet (1960c, 1961), Dobson (1974a) and Collins (1978). The conclusions can be summarised as follows:-

- 1) Males and females first mate about 20 hours after eclosion at 26°C. Thereafter both sexes mate repeatedly.
- 2) There is little observable preliminary behaviour before mounting and copulation.
- 3) Females lay three or four batches of eggs at one to two day intervals in laboratory conditions laying the first batch about 48 hours after eclosion.
- 4) Batches average 70-80 eggs each but vary from about 20 to 160 eggs. All the eggs in any one batch are fertilised by the last male to mate.

- 5) Fertility is high, usually over 90%.
- 6) Adult longevity at 26°C is about ten days for both males and females. In the field longevity is estimated to be 3-4 weeks.

These observations have not been related to adult size except in the case of number of eggs per batch where Collins (1978) observed that large females laid more eggs. The longevity of Adh-DD homozygotes is higher than that of BB' homozygotes with heterozygotes intermediate but Collins observed no effect of genotype on fecundity or fertility.

The discovery of an association between size and Adh genotype necessitated a reexamination of some of these characteristics taking adult size into consideration. In this section I will consider the effect of size on longevity and fecundity and on some aspects of mating behaviour. As the virginity of females used in these experiments, and in the mating experiments in the next chapter, was important a check on the method of collecting virgins will be described first.

#### 8.3.1 Collection of virgins

Two techniques for collecting virgin females were described in Chapter 2. The first, separation of larvae, cannot fail to produce virgins but is very time consuming. The second, regular collection of all adults from a culture, is much easier but is less reliable. As the second method is the only practical way of collecting large numbers of virgins the frequency of non-virginity in the resulting flies had to be assessed.

Three tank cultures were established from each of the BB(lab)



and DD(lab) lines. Two days after the start of eclosion all adult flies were removed and discarded. From then on the following collection regimes were followed:-

Cage 1 collected twice daily at 9 a.m. and 5 p.m.

Cage 2 collected once daily at 9.30 a.m.

Cage 3 collected every other day at 10 a.m.

During this period the tanks were kept together in the constant temperature room at 26°C. Immediately after collection adults were sexed and the males and females were stored separately at 4°C. On the fifth day after the start of collection some females from each tank were isolated in pots containing fresh culture medium. These females were retained until they had either laid eggs or died. Egg batches were observed daily for hatching.

The results were as follows:-

#### BB(lab) cages

	Twice daily	Daily	Two daily
Died without laying	1	2	11
Infertile egg batches (eggs laid but not hatched)	49	37	10
Fertile egg batches (eggs laid and hatched)	0	7	28
% non-virgin	0%	16%	74%

#### DD(lab) cages

Died without laying	5	4	5
Infertile egg batches (eggs laid but not hatched)	28	28	34
Fertile egg batches (egg laid and hatched)	0	0	3
% non-virgin	0%	0%	8%

Twice daily collection of adults appears to be a reliable method of obtaining virgins and was the method used in most of the experiments to be described here. As expected from Thompson's (1951) observations on time to first mating in Coelopa a few females have been mated within 24 hours and a much higher proportion within 48 hours. A surprising feature of these results is the large and significant difference between the two lines (Daily -  $X_1^2 = 4.87$ ,  $P < 0.05$ ; Two daily -  $X_1^2 = 4.30$ ,  $P < 0.05$ ). This could represent a difference between males, between females, or both in any of several aspects of mating behaviour. However it should not be interpreted as a difference between the Adh genotypes or  $\alpha/\beta$  karyotypes as these lines were inbred and may have differed in many other respects.

### 8.3.2 Longevity and fecundity

a) Method The objective of this experiment was to relate the longevity and fecundity of individual flies to their size. Flies were kept singly in mating pots and supplied daily with fresh culture medium and fresh virgin flies of the opposite sex.

The test flies used were virgins collected twice daily from the SM DD Mixed, S220 BB and S103 DD lines and the F1 of a cross between the S220 BB and S103 DD lines (designated S220B/S103D). A large supply of virgins had to be maintained for mating with the test individuals. This was achieved by collecting twice daily from several stock cages of the above lines and also of the SM B+D and MN B+D lines. After separating the sexes all these flies were mixed and stored at 4°C until required.

On the day on which it was collected each test individual was measured and then placed in a mating pot containing standard culture medium with two virgin flies of the opposite sex. The test individual was at this stage aged from about 1 to 19 hours from eclosion (newly eclosed individuals were not used as their wings were not fully expanded and could not be measured). Each day thereafter the test individuals were moved to new mating pots and supplied with two fresh flies of the opposite sex. Any eggs laid by test females were counted and retained for 24 hours to check for hatching. The two females which had been with each test male were retained in their mating pot for three days and observed daily to check for the presence of larvae which would confirm that the male had mated successfully on that day. This process was continued until all the test flies had died.

b) Results The full results are given in Appendix 7 and are presented graphically in Figures 8.2 to 8.6. Considering the females first, adult size has a significant positive effect on longevity ( $b = 2.55 \pm 0.96$ ,  $P < 0.01$ ), on the number of egg batches laid ( $b = 2.36 \pm 0.41$ ,  $P < 0.001$ ) and on the number of eggs per batch ( $b = 43.05 \pm 4.55$ ,  $P < 0.001$ ). These last two effects combine to give a large increase in total fecundity with increasing size ( $b = 210.65 \pm 22.91$ ,  $P < 0.001$ ). The most common interval between egg batches was two days but occasionally batches were laid on consecutive days or after an interval of three or more days. Very few egg batches failed to hatch (9 out of 133). Most females laid their first egg batch on the second day. This did not appear to vary with female size.

Figs.8.2 to 8.6    Effects of individual size on longevity and  
fecundity

Fig.8.2    Longevity of females

Fig.8.3    Mean number of eggs per.hatch

Fig.8.4    Number of egg batches

Fig.8.5    Minimum number of matings by males

Fig.8.6    Longevity of males

Stock lines:-

▲ S220BB

■ S220B/S103D

● S103DD

○ SM DD Mixed

Fig. 8.2

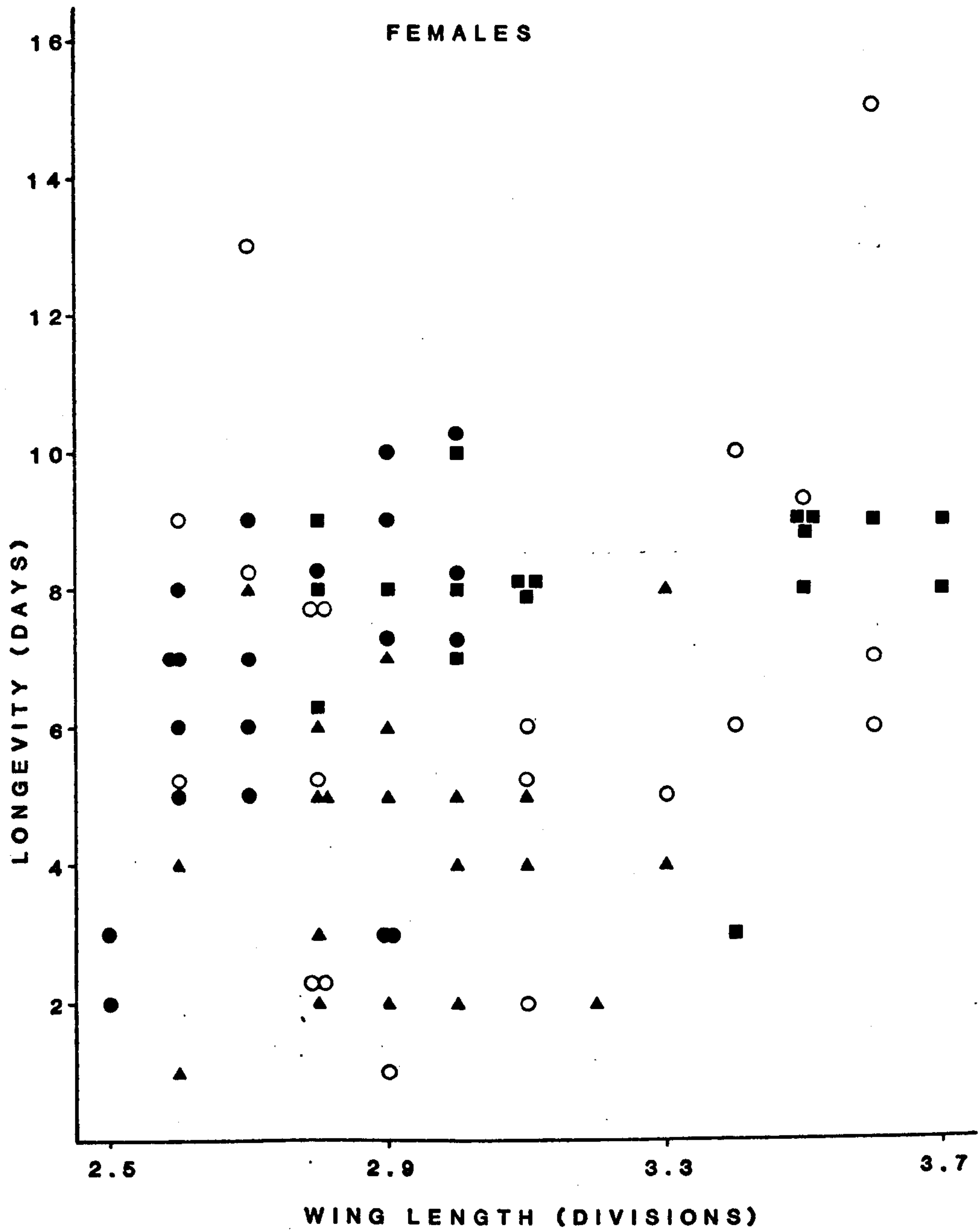


Fig. 8.3

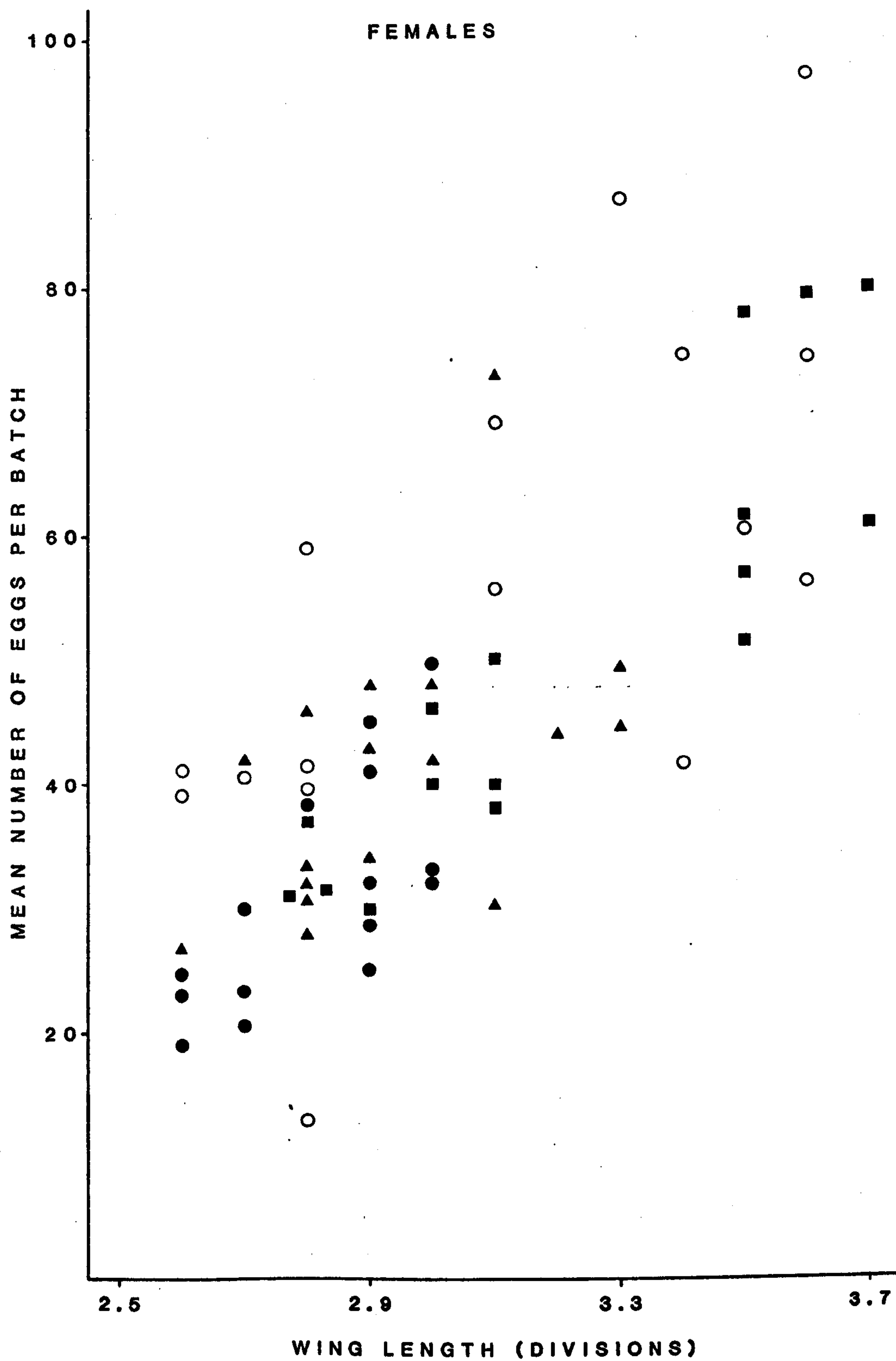


Fig. 8.4

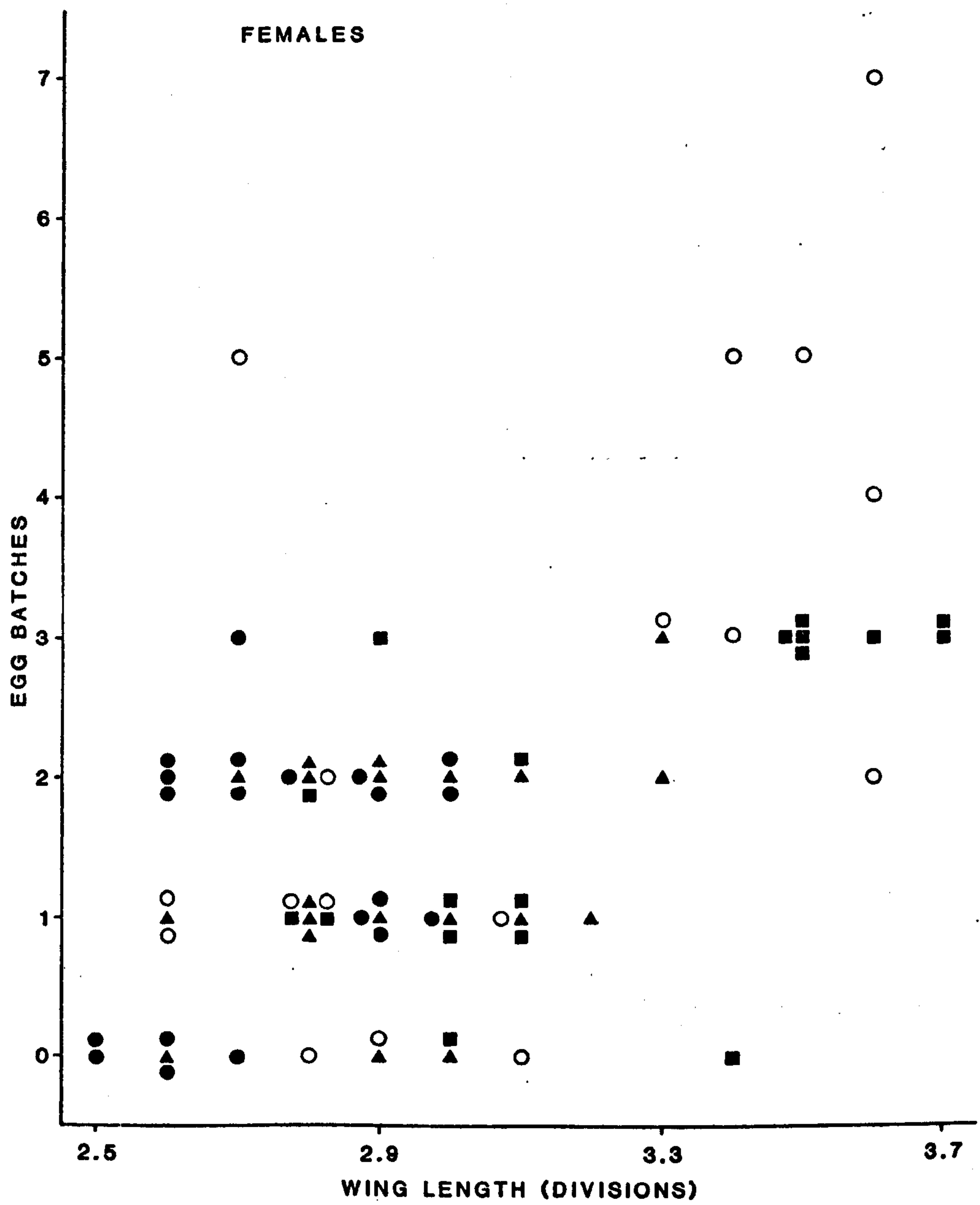


Fig. 8.5

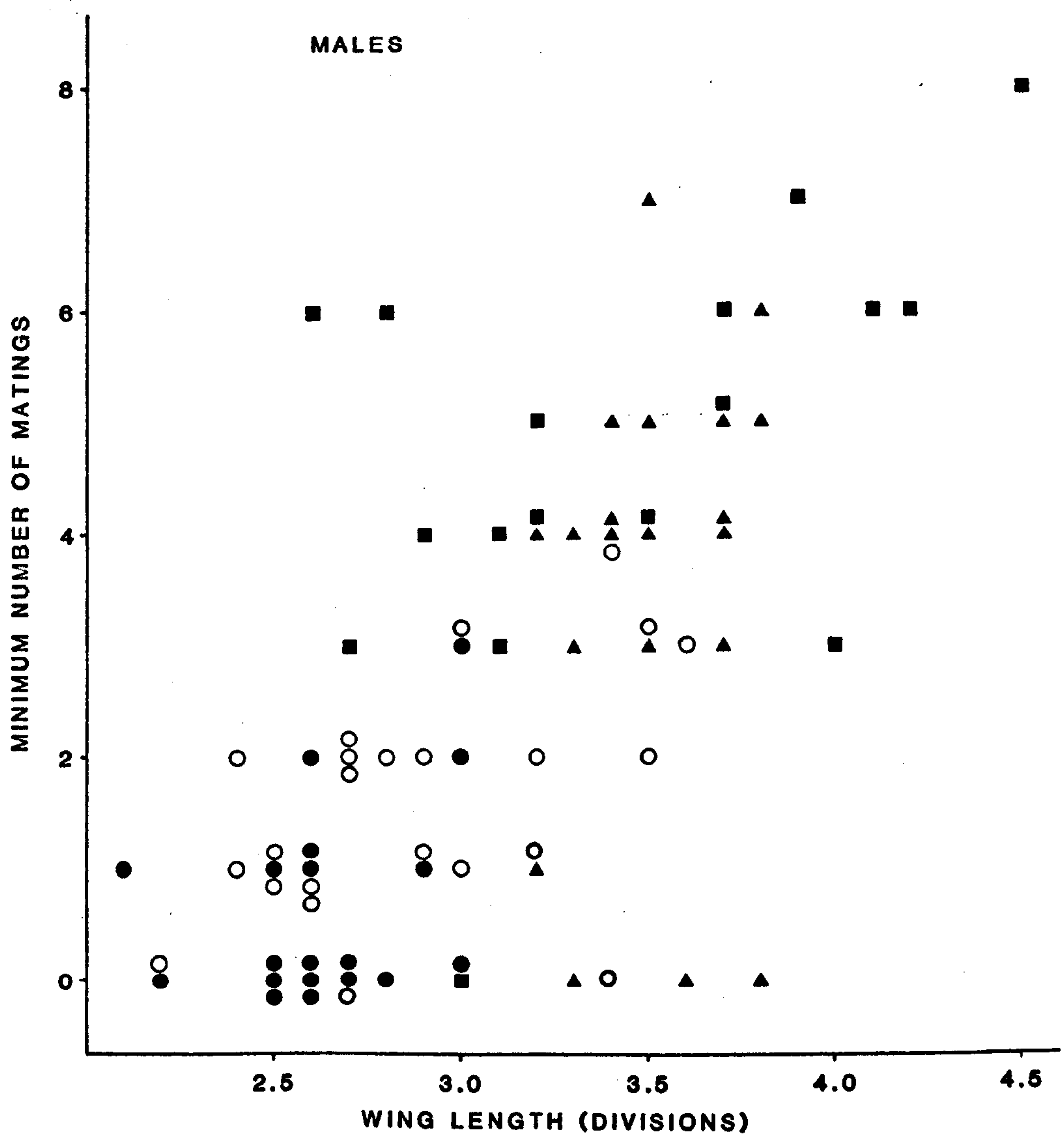
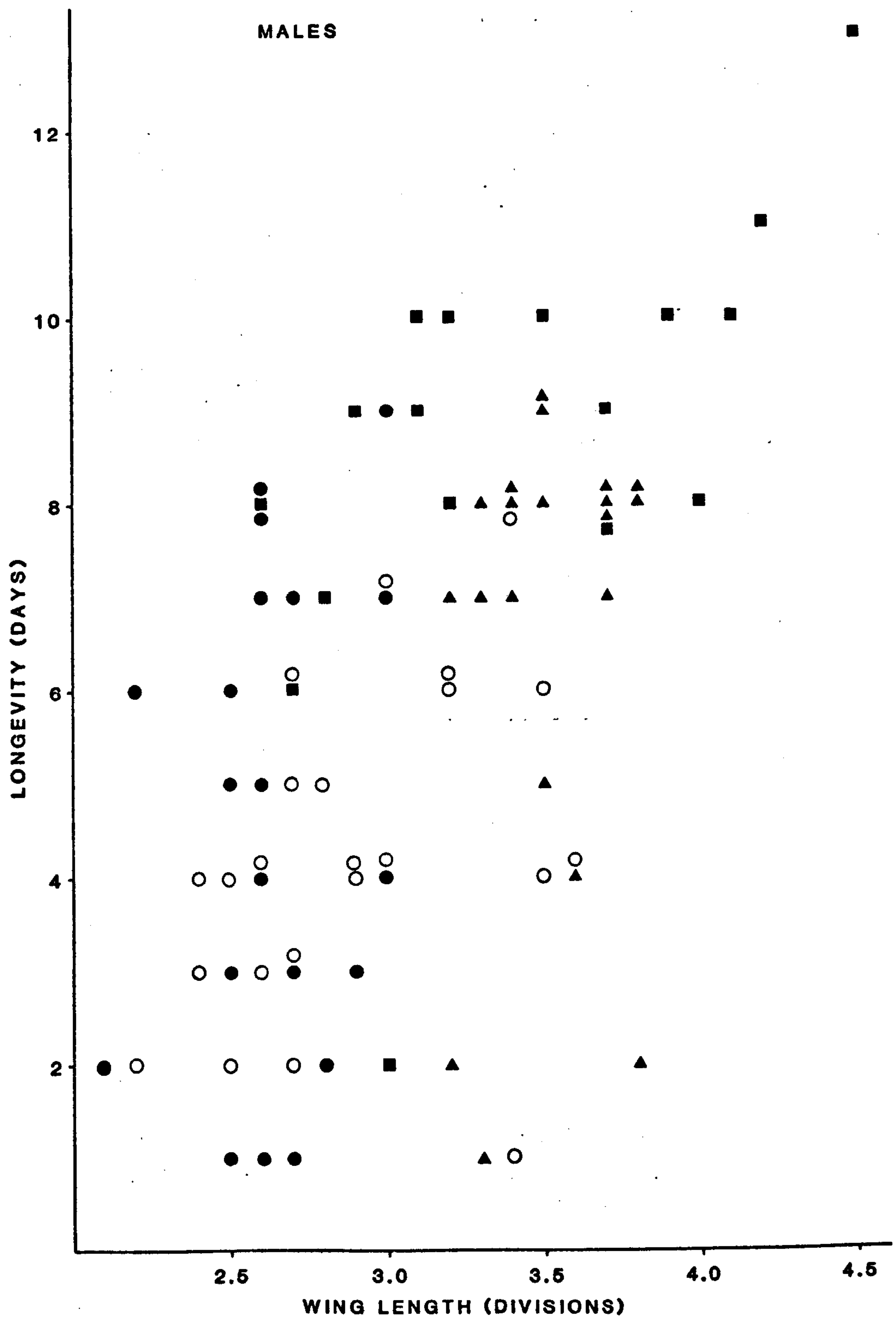




Fig. 8.6



After allowing for the effect of size significant differences remain between the four lines used in longevity and in total fecundity (for longevity  $F_{3,73} = 5.26$ ,  $P < 0.01$ ; for total eggs laid  $F_{3,59} = 7.01$ ,  $P < 0.001$ ). However the orders are different: for longevity  $S220B/S103D > S103DD > SMDD \text{ Mixed} > S220BB$ , and for fecundity  $SMDD \text{ Mixed} > S103DD > S220BB > S220B/S103D$ . The differences between means (after correction for size) are about 3 days between  $S220B/S103D$  and  $S220BB$  for longevity and 75 eggs between  $SMDD \text{ Mixed}$  and  $S220B/S103D$  for fecundity. As the lines were inbred laboratory strains these differences cannot be related to the Adh or inversion polymorphism. It is interesting to note that the relatively outbred  $SMDD \text{ Mixed}$  line was best in terms of overall fecundity.

Turning to males, there was a similar increase in longevity with size ( $b = 3.05 \pm 0.51$ ,  $P < 0.001$ ) and also an increase in number of matings ( $b = 2.75 \pm 0.35$ ,  $P < 0.001$ ). This increase was not simply due to the increase in longevity as the proportion of days on which mating took place also increased with size ( $b = 0.223 \pm 0.049$ ,  $P < 0.001$ ). The estimates of numbers of matings are minimum estimates because they are counts of the number of days on which the male successfully fertilised at least one of the two available females. It would be of interest to know how many females a male could fertilise in one day and whether this too was related to male size.

After removal of the size effect the four strains differed significantly in both longevity and mating frequency: for longevity  $F_{3,75} = 6.99$ ,  $P < 0.001$ , for mating frequency  $F_{3,75} = 6.11$ ,  $P < 0.01$ . In this case there was some similarity between the orders -

for longevity S220B/S103D > S220BB > S103DD > SMDD Mixed and for mating frequency S220B/S103D > S220BB > SMDD Mixed > S103DD. The Adh genotypes were in the same order suggesting an effect of the inversion on male longevity and fecundity. Clearly further experiments with outbred lines or flies from natural populations are needed to confirm this possibility. The mean longevities after allowing for size effects differed by about 3 days and the mating frequencies by about 0.25 matings per day.

As with females there was no evidence for differences in timing of matings between strains or with size. Males usually achieved their first successful fertilisation on the second day.

c) Discussion Both longevity and fecundity in males and in females are strongly influenced by adult size. This is comparable to the effect of adult size on longevity and fecundity of Drosophila pseudoobscura (Tantawy & Vetukhiv 1960) except that in Coelopa there is much more size variation in natural populations. Fecundity is clearly an important element of fitness for a seaweed fly. Longevity may also be important because there are variable periods of time between emergence of adults from one wrack bed and the deposition of a new wrack bed suitable for egg laying. During these periods temperatures will generally be much lower than the 27°C used in these experiments and flies will usually not mate and lay eggs. Mating and egg laying probably shorten a fly's life (Partridge & Farquhar 1981, Lamb 1964) as does high temperature and so there is some question about the extrapolation of these longevity results to natural situations. In the laboratory flies kept at 4°C survive for several weeks and are still capable of

mating and laying eggs. The actual values for longevity are certainly higher in most natural conditions but the relationship with size seems likely to be similar. Further experiments will be necessary to confirm this.

It has been shown that flies of different Adh genotypes differ significantly in size in natural populations. This is particularly true of males but there does also appear to be a small difference in females. The results presented here suggest that size is positively correlated with longevity and fecundity of both males and females and so may be relevant to fitness. A typical mean size for male BB flies in a natural population is about 4.0 divisions (5.8 mm wing length) while for male DD flies it is about 3.0 divisions (4.35 mm). From these laboratory results a 4.0 male lives for about 9-10 days and mates at least 5 times while a 3.0 male lives about 5 days and mates twice. Clearly the size difference between males is potentially a very important selective factor. If large size in males is selected for the Adh-B allele and the  $\alpha$  inversion sequence may be selected on the same basis.

For females the size differences in natural populations are much smaller. Typically BB females have a mean wing length of 3.4 divisions (4.9 mm) and DD females a mean of 3.2 divisions (4.6 mm). Correspondingly they have longevitys of 7.4 and 6.9 days and total egg productions of 180 and 140 eggs respectively. Nevertheless, if fecundity is an important element of fitness, as it may be in a species which lives in a temporally unstable environment, a difference of this order could be important. Both

Collins (1978) and Thompson (1951) found high levels of hatch in Coelopa, ~98%, so it seems likely that the full fecundity will be realised.

Collins (1978) did not find significant differences in fecundity between flies of different chromosome I karyotype and for longevity he found that  $\beta\beta$ , that is Adh-DD, flies lived longer than  $\alpha\beta$  or  $\alpha\alpha$  flies. The discrepancy between his data and mine probably results from the size effect. In retrospect it is unfortunate that Collins did not record the sizes of flies used in his fecundity or longevity experiments.

That these size related effects do indeed occur in natural populations would be very difficult to demonstrate. However it may be possible to examine them in laboratory situations that correspond more closely to natural conditions. Clearly it is also necessary to study the differences between strains that were observed in these experiments. Are these differences in longevity and fecundity associated with Adh genotypes or chromosome I karyotypes independently of size?

Despite the difficulty of interpretation of these results in terms of natural populations it seems reasonable to conclude that larger flies, both male and female, have higher reproductive fitnesses than small ones. The implications of this conclusion will be discussed after the effect of size on mating success has been considered in the next Chapter.



## Chapter 9

### Adult Size and Male Mating Success

#### 9.1 Introduction

In the previous chapter it was shown that male fecundity increases with size. This might represent an increase in fitness but, in natural conditions, the effect on fitness will depend on the ability of males to obtain mates when in competition with other males. It is also important for the fitness of a male that his sperm should be used to fertilise a batch of eggs rather than being displaced by sperm from a later mating (Parker 1970a).

Both in Drosophila (Ewing 1961, 1964, Monclús & Prevosti 1971) and in the house fly (Bryant 1980, Baldwin & Bryant 1981) mating success is associated with male size. Mating success is also affected by inversion polymorphisms in several species of Drosophila (reviewed by Spiess 1970). It therefore seemed necessary to investigate the effect of male size on mating success in Coelopa and, if possible, to separate this from any direct effect of the inversion. The first concern of this project was to identify selective pressures acting on the inversion and so the experiments to be reported here are mainly concerned with identifying which males actually father egg batches rather than the components of mating behaviour that are influenced by size or genotype. However I will start by reporting some observational results.

The courtship and mating behaviour of Drosophila melanogaster has been studied extensively and has turned out to be very complex (Ewing 1977). Elaborate variations on the basic pattern occur in

other species of Drosophila, especially the Hawaiian species (Spieth 1966, 1982). However this complexity does not occur in all groups of Diptera and apparently is not found in Coelopa. Thompson (1951) observed the courtship of Coelopa and could detect no preliminaries to mounting. Once mounted copulation was very brief. An undergraduate project student under my supervision, Isobel Read, observed many pairs of seaweed flies. She concluded that almost any chance encounter between two flies could lead to mounting, even if both flies were male. Frequently the mounted fly immediately rejected the male using leg and wing movements. Otherwise there did appear to be a rapid exchange of information between the flies before copulation took place. In particular the male "tapped" the top of the female's head with his fore-tarsi. It is quite possible that the sequence of behaviour leading to copulation is actually quite complex but is too rapid to be analysed without special techniques such as high speed photography. This type of mating is reminiscent of that found in the Muscidae and Calliphoridae (Ewing 1977) in which pheromonal, tactile and auditory signals are now thought to be involved.

## 9.2 Speed, duration and frequency of mating

The project student, Isobel Read, made some preliminary observations on pairs of flies which she has kindly allowed me to report here. One male and one female from either the BB(lab) or DD(lab) line were placed in a 7.5 x 2.5 cm glass vial with 1 cm of standard culture medium at the bottom, and observed for 30 mins at 27°C in bright white light. The flies were virgins which had been aged 48 hours at 27°C with food before the start of the

experiment. 10 pairs were observed at one time, the activity of each pair being noted at 1 minute intervals. The wing lengths of the flies were measured after completion of the observations.

The results are summarised in Table 9.1. A mounting was counted as successful if it lasted for at least one minute. The BB and DD females were very similar in size (mean wing lengths of  $3.05 \pm 0.05$  and  $3.02 \pm 0.06$  divisions respectively) but the BB males were larger than the DD males ( $3.29 \pm 0.06$  and  $2.88 \pm 0.04$  divisions respectively). The only significant difference between the BB and DD pairs was in the number of successful mountings in the 30 minute period. This was higher for BBs than DDs ( $t_{48} = 2.54$ ,  $P < 0.05$ ) but there was a significant increase in number of successes with male size overall ( $b = 3.54 \pm 0.84$ ,  $P < 0.001$ ) and within DD pairs ( $b = 5.40 \pm 1.63$ ,  $P < 0.01$ ) but not within BB pairs ( $b = -0.28 \pm 2.14$ ,  $P > 0.2$ ). It seems likely that the difference between the genotypes is accounted for by the increased frequency of successful copulations of larger males.

The time to the first successful mounting, which gives an idea of mating speed, was shorter for larger males ( $b = -7.52 \pm 2.61$ ,  $P < 0.01$  for all pairs;  $b = -19.21 \pm 5.62$ ,  $P < 0.01$  for DD pairs;  $b = -5.80 \pm 3.33$ ,  $P < 0.1$  for BB pairs) and for larger females ( $b = -6.17 \pm 3.01$ ,  $P < 0.05$  for all pairs;  $b = -6.69 \pm 5.52$ ,  $P > 0.1$  for DD pairs;  $b = -5.57 \pm 3.78$ ,  $P > 0.1$  for BB pairs). Neither the duration of copulation nor the number of unsuccessful attempts at mounting varied with male or female size or between genotypes.

These observational results tie in with the data on male fecundity in the previous chapter. Larger males mate more frequently within the time scale of these observations and also fertilise



Table 9.1

Observations on mating made by Isobel Read

a) BB(lab) flies

FEMALE WING LENGTH (in divisions)	MALE WING LENGTH	NUMBER OF SUCCESSFUL MOUNTINGS	NUMBER OF UNSUCCESSFUL MOUNTINGS	AVERAGE DURATION OF COPULATION (minutes)	TIME OF FIRST SUCCESSFUL MOUNTING (minutes)
2.7	3.4	4	0	3.25	7
3.2	3.2	5	0	2.2	5
2.9	3.1	3	4	2.3	9
3.0	3.3	4	0	2.25	4
3.4	3.9	6	1	2.4	4
3.0	3.6	6	5	1.0	4
3.3	3.5	0	0	-	-
3.1	3.4	2	4	1.0	5
2.8	3.3	0	4	-	-
3.0	3.3	4	2	3.75	3
2.6	3.3	4	0	3.75	4
2.6	3.2	1	0	5.0	18
3.0	4.0	2	0	1.0	1
3.5	3.2	3	0	2.6	5
3.3	3.2	5	3	2.0	4
3.2	3.4	8	2	2.1	2
3.2	3.0	1	0	22.0	3
3.0	3.1	1	0	7.0	17
2.7	3.1	6	0	2.1	4
3.1	3.4	2	0	5.0	9
3.3	2.7	1	10	1.0	8
3.2	3.3	0	3	-	-
2.8	3.3	4	0	3.25	5
3.2	2.6	0	3	-	-
3.2	3.4	2	2	2.5	2
<u>MEANS ± STANDARD ERROR</u>					
3.05	3.29	2.96	1.72	3.69	5.86
±0.05	±0.06	±0.45	±0.48	±0.97	±0.96

## b) DD(lab) flies

FEMALE WING LENGTH (in divisions)	MALE WING LENGTH	NUMBER OF SUCCESSFUL MOUNTINGS	NUMBER OF UNSUCCESSFUL MOUNTINGS	AVERAGE DURATION OF COPULATION (minutes)	TIME OF FIRST SUCCESSFUL MOUNTING (minutes)
3.0	2.9	6	0	2.5	4
2.9	3.2	4	1	1.5	4
2.7	3.0	0	1	-	-
3.5	3.0	4	7	2.0	7
2.7	3.2	4	1	1.5	2
3.3	3.0	5	1	3.0	3
3.4	2.7	0	2	-	-
3.1	2.8	0	0	-	-
3.0	2.7	0	2	-	-
3.2	2.6	0	4	-	-
3.1	3.1	0	6	-	-
2.8	2.8	0	0	-	-
2.8	2.8	1	0	4.0	21
3.0	2.9	0	1	-	-
3.4	2.6	0	0	-	-
2.6	2.4	1	0	5.0	16
3.2	2.8	0	0	-	-
3.6	3.2	3	2	3.0	3
2.6	2.8	0	0	-	-
3.1	3.2	3	0	4.3	3
2.6	2.9	1	3	3.0	6
2.9	3.0	4	1	2.25	4
2.9	2.8	0	3	-	-
3.0	2.7	0	1	-	-
3.2	2.9	0	1	-	-

MEANS ± STANDARD ERROR

3.02	2.88	1.44	1.48	2.91	6.64
±0.06	±0.04	±0.40	±0.37	±0.34	±1.85

females more often on the longer time scale of the other experiment. The underlying reason for this effect of male size is not known. It could be that small males produce less sperm and cannot, therefore, successfully mate as often as large males but there are other possible explanations. For example, small males may need to spend more time in feeding than large males or they may move about more slowly thus reducing the frequency of contacts with receptive females. Some small males in both experiments failed to achieve any successes which seems difficult to explain simply on the basis of male properties of this type. Possibly the females actively reject small males. There is some evidence that the female rôle is not entirely passive in that female size influences the time to the first successful mounting. In the next section evidence will be presented that also suggests an active part for the female in determining male mating success. In this case she has a "choice" between two males.

### 9.3 "Three-fly" experiments

Up to now the reproductive fitness of individual flies has been examined in isolation. This can give useful information about the specific characteristics in which flies differ but in the natural situation it is much more important to know how flies perform when in competition with other flies for mates. It is likely that most, if not all, females will be fertilised because each male can fertilise several females and so sperm is unlikely to be a limiting resource for them. There is a possible proviso that if a wrack bed is removed early in the emergence time of Coelopa adults there may be considerably more females than males

to start the next generation. In the laboratory this effect is quite noticeable but the data in Chapter 4 (especially Fig.4.4 page 143) suggest that the shortage of males in relatively asynchronous natural populations is small and short lived.

On the other hand competition between males for mates may be intense because each male is capable of fertilising many females - up to eight in the experiments reported in the last chapter and probably many more. Increasing the number of females he fertilises is the main way in which a male seaweed fly can increase his fitness. It has been shown that larger males have a greater reproductive potential and that they mate more frequently in non-competitive conditions but these benefits of large size will increase male fitness only if they generate, or are associated with, an increased ability to obtain mates in competition with other males.

I have conducted a number of experiments aimed at detecting an advantage to large males in competitive situations. These vary in the amount and type of information that they provide and in the closeness of their approximation to natural conditions. In this section I will describe the most extensive series of experiments which involved a single female and two males in each of a large number of trials. In each trial the successful male was determined by examination of the female's offspring. While the conditions used in these trials were very artificial this disadvantage was offset by the large amount of information obtainable - the genotype and size of each of the three flies was known, together with a genetically relevant measure of success.

a) Methods A pilot experiment of 45 trials and the main experiment of 301 trials will be described. About two thirds of the trials in the main experiment were conducted under my supervision by Miss Isobel Read as part of her undergraduate project and I am very grateful for her careful and thoughtful work. The results of this main experiment have been published elsewhere (Butlin, Read & Day, 1982).

For the pilot experiment and trials 1 to 68 of the main experiment virgin males and females were obtained by the method of isolating larvae. In the remaining trials the twice daily collection method was used (see Materials and Methods). As far as possible trials were set up using flies which had emerged on that day but to obtain some of the required size and genotype combinations it was necessary to store flies for up to five days. Storage was at 4°C in bottles with cotton wool wetted with 0.5% mannitol solution.

The flies used in the pilot experiment were from the fourth generation of the Portland line, that is they were from a mixed population recently established from the field and maintained with at least 500 parents in each generation. The difficulties with using a polymorphic line of this type were that 1) a proportion of the trials set up were unusable because the two males were of the same genotype and therefore the successful male could not be distinguished from the genotypes of the offspring, 2) with some combinations of male and female genotypes it was necessary to determine genotypes for 12 or more larvae to be confident of distinguishing between the males, and 3) a very large number of trials would be needed to examine the effects of male and female



genotypes because of the large number of possible combinations of three flies when there were five common genotypes in the population. For these reasons the fixed lines, BB(lab) and DD(lab), were used in the main experiment despite the disadvantage of their narrow genetic base.

For each trial a single virgin female and two virgin males were placed in a glass vial (8 x 2.5 cm) containing about 1 cm depth of culture medium. In all trials the two males were chosen so that one was distinctly larger than the other. In the pilot experiment the two males were otherwise picked at random but in the main experiment one male was taken from the BB(lab) and one from the DD(lab) line. Approximately similar numbers of trials with BB and DD females and with the BB male larger or smaller than the DD male were carried out.

The vials were kept in constant darkness at 27°C and observed daily. When the first egg batch appeared, the three adults were removed and their sizes recorded. In the pilot experiment the measure of size used in the first 31 trials was not wing length but was wet weight. The weight of each fly was recorded to the nearest 0.1 mg on a balance reading in 0.01 mg divisions. After weighing, the adults from the pilot experiment were electrophoresed to determine their Adh genotypes and any trials in which the two males were of the same genotype were discarded. In both experiments vials in which one of the adults had died before the egg batch was laid were also discarded. Larvae hatching in the vials were transferred to round canisters containing culture medium and after about 6 days third instar larvae were collected.

In the main experiment the Adh genotypes of two (trials 1 to 163) or four (trials 164 to 301) larvae were determined by gel electrophoresis. In the pilot experiment the genotypes of four larvae were determined. If these did not distinguish unequivocally between the two males four further larvae were electrophoresed and this was repeated until twelve larvae had been scored. When twelve larvae have been scored from a cross the probability of failing to observe the rarest genotype, which is expected to have a frequency of  $1/4$ , is 0.032. It is, therefore, unlikely using this procedure that any matings were attributed to the wrong male.

b) Results - Pilot Experiment The full results of this series of trials are given in Appendix 8(a). Out of 45 trials the larger of the two males fathered the egg batch in 32 cases and the smaller male in 10 cases. This is a highly significant departure from randomness ( $\chi^2_1 = 12.6$ ,  $P < 0.001$ ). The trials can be grouped by the genotypes and sizes of the three flies although the small number of trials overall means that the numbers in some classes are very low. This analysis is presented in Table 9.2. Only the 31 trials in which sizes were measured as weights are included in the size comparisons.

Neither female size, nor the difference in size between the two males had any effect on the proportion of large males which were successful. There were some differences between the genotypes, especially the male genotypes. These differences suggest that BD males were more likely to be successful than DD males (the two most common genotypes) irrespective of size.

The genotypes of the progeny in the remaining three batches could only be accounted for if both males had fertilised the female.

Table 9.2

Results of pilot "three-fly" experiments grouped according to:-

## a) Genotype of smaller male

<u>Adh</u> Genotype	BB	BC	BD	CC	CD	DD
Number of trials in which larger male was successful	2	-	5	-	7	18
Total number of trials	2	0	11	0	9	20

$$\chi^2_3 = 8.47, P < 0.05$$

## b) Genotype of larger male

<u>Adh</u> Genotype	BB	BC	BD	CC	CD	DD
Number of trials in which larger male was successful	2	3	23	1	3	-
Total number of trials	4	5	27	1	5	0

$$\chi^2_3 = 4.17 \text{ (excluding CC)}$$

## c) Genotype of female

<u>Adh</u> Genotype	BB	BC	BD	CC	CD	DD
Number of trials in which larger male was successful	5	2	21	-	1	3
Total number of trials	6	2	27	0	3	4

$$\chi^2_4 = 3.91$$

## d) Male - male size difference

Difference in size	<2.0 mg	2.0-3.9 mg	>4.0 mg
Number of trials in which larger male was successful	3	13	6
Total number of trials	4	19	8

$$\chi^2_2 = 0.15$$

## e) Female size

Size class	<4.5 mg	4.6-5.5 mg	5.6-6.5 mg	≥6.6 mg
Number of trials in which larger male was successful	6	7	5	4
Total number of trials	8	11	7	5

$$\chi^2_3 = 0.55$$



It may have been that the females in these vials had laid two batches of eggs and that the additional batch was not noticed. Females do sometimes lay egg batches on consecutive days (Chapter 8) but no female has been observed to lay two egg batches within 24 hours. It is likely that in these three cases both males had contributed to the same egg batch. This result was most unexpected in view of earlier work (Thompson 1951, Burnet 1960c) which indicated that when two or more males mated with a female the last male to mate fertilised all the eggs in the subsequent batch. It is difficult to assess from this small set of trials how common mixed fatherhood of batches might be. Although only three mixed batches were detected it is possible that others were also mixed, for example if the two males were BB and BD and the female BD the difference between a mixed and an unmixed batch would only be in the ratio of the progeny. The main "three fly" experiment provides further evidence of mixed fatherhood and later in the chapter some experiments specifically designed to study multiple insemination and batch sharing will be described.

The occurrence of mixed batches introduces a source of error into the determination of the successful male. Some mixed batches may have been scored as successes for one or other of the males. However, unless the proportions of offspring in mixed batches vary with the size of the father, this would be unlikely to affect the ratio of large to small male successes.

c) Results - Main experiment The complete results of this experiment are given in Appendix 8(b). For each of the 301 trials there is essentially just one outcome - either the large male, or

the small male, or both males fathered the egg batch - but there are several factors that might have influenced this result, namely the sizes and genotypes of the three flies. Ideally one would like to examine all these factors together in order to study both their independent effects and their interactions but this would require many more than the 301 trials actually carried out. I have, therefore, examined the factors two or three at a time in order to highlight the principal effects without attempting to identify more complex interactions.

It should be noted that pairs of males were selected to be visibly different in size. Therefore, while the range of male sizes used falls within that observed in natural populations, the distribution of male-male size differences is biased towards higher values.

Out of 257 trials in which only one male contributed to the progeny 200 were fathered by the large male. This is a highly significant departure from randomness ( $\chi^2_1 = 79.6$ ,  $P < 0.001$ ). The effects of several factors on the proportion of trials in which the large male was successful have been examined:

- 1) When the size difference between the two males was less than 0.2 divisions mating was at random (Table 9.3). The advantage to the larger male became apparent when the size difference exceeded 0.2 divisions, increasing until a plateau was reached in the 0.6-0.8 class (approximately a 25% difference in size). At this and greater size differences the larger males fathered over 80% of egg batches.

Table 9.3 Relationship between the success of the larger male and the difference in size between the two males

Difference in size between males	<0.2	0.3-0.5	0.6-0.8	0.9-1.1	>1.2
No. of trials	25	62	79	66	25
% egg batches fathered by larger male	52	71	86	82	84

Sizes are expressed in graticule units (see Chapter 2). The mating in the smallest size difference class is random but in all other classes it departs significantly from randomness (in every case  $\chi^2_1 > 10.9$ ,  $P < 0.001$ ).

2) Considering only trials in which the male-male size difference was greater than 0.6 divisions (i.e. in the plateau region), there was no evidence for an increase in success rate of larger males with size (Table 9.4). Neither was there any indication that males could be so large that their size became disadvantageous.

Table 9.4 Relationship between the success of the larger male and his size for trials where difference in size between males is  $\geq 0.6$ .

Size of the larger male	<3.3	3.4-3.5	3.6-3.7	>3.8
No. of trials	39	46	51	34
% egg batches fathered by larger male	82	91	78	88

Sizes are expressed in graticule units. There is no significant correlation between male success and the size of the larger male ( $b = 0.02$ ,  $P = 0.8$ )

3) The advantage to the larger male increased as the size of the female increased (Table 9.5). This effect was much more pronounced with the DD(lab) females than with the BB(lab) flies. This suggests that the female was not playing an entirely passive role but may

have been exercising some form of choice. If this was so then large females appear to have been showing a greater preference for large males, that is there was assortative mating. However, this was not assortative mating of the type where females chose males close to their own size. Of 237 trials in which only one male was successful, and where the female was not exactly intermediate in size between the males, the male nearer in size to the female was successful 119 times and the one more distant in size 118 times.

Table 9.5 Relationship between the success of the larger male and female size

<u>Female size</u>	<u>% of trials in which the larger male was successful</u>		
	<u>BB females</u>	<u>DD females</u>	<u>(regardless of female genotype)</u>
<2.7	70 (46)	71 (17)	70 (63)
2.8-2.9	67 (27)	81 (21)	73 (48)
3.0-3.1	77 (35)	80 (20)	78 (55)
3.2-3.3	85 (34)	83 (23)	84 (57)
>3.4	71 ( 7)	96 (27)	91 (34)

The number of trials in each size class is given in brackets. Sizes are expressed in graticule units.

There is no significant correlation between success of the larger male and female size with BB females ( $b = 0.05$ ,  $P = 0.6$ ); but there is with DD females ( $b = 0.13$ ,  $P = 0.02$ ), and when the genotype of the female is disregarded ( $b = 0.13$ ,  $P = 0.003$ ).

4) Data for the four different combinations of genotypes are given in Table 9.6. The mean sizes of flies in these combinations are also given because it proved difficult to select DD males as large as the large BB males. Consequently the BB males tended to be larger than the DD males. In addition BB females were smaller on average than DD females. These size differences between the



genotypic combinations make it difficult to separate the effects of size and genotype.

Table 9.6 Interaction between the success of the larger male and genotypes of the males and female

Genotype of larger male and female		% of trials in which the larger male was successful	Mean sizes (st.dev.) of larger males and females		No. of trials
♂	♀		Male size difference <0.6		
BB	BB	74	3.19 (0.26)	2.89 (0.36)	24
BB	DD	92	3.25 (0.29)	3.06 (0.33)	12
DD	BB	54	3.20 (0.13)	2.90 (0.35)	25
DD	DD	56	3.16 (0.22)	3.09 (0.29)	24
			Male size difference >0.6		
BB	BB	81	3.58 (0.33)	2.97 (0.31)	59
BB	DD	97	3.71 (0.31)	3.10 (0.30)	39
DD	BB	76	3.46 (0.24)	2.83 (0.32)	41
DD	DD	84	3.42 (0.20)	3.11 (0.38)	31

The combination of large BB males and DD females had a markedly higher proportion of large male successes than the other combinations. This could be due to the large size of the females, which is known to increase large male advantage, added to the large size of the large males, which may increase their advantage although the evidence does not suggest this. So the exceptional performance of this combination may not be a genotypic effect - it could be entirely due to size differences. Nevertheless it does appear likely that DD females exhibit a preference for BB males irrespective of size. Two observations support this suggestion. When DD females are compared with BB females of similar size (Table 9.5), they show a stronger preference for the larger male.

Also when the males were similar in size (i.e. less than 0.6 divisions size difference, Table 9.6), the DD females still showed a strong preference for large BB males (92%) but not for large DD males (56%).

Although it seems possible that in these trials genotype did influence the outcome this effect was certainly small compared with the importance of male size. However it should be remembered that in natural populations the Adh/inversion genotype is a major determinant of male size and will affect mating success indirectly if not directly.

5) In 44 of the 301 trials both males contributed to the offspring. As in the previous experiment it is possible that two egg batches were laid in these vials before the adults were removed but this is unlikely. The probability is that, contrary to the observations of Thompson (1951) and Burnet (1960c), individual egg batches can be of mixed fatherhood. Thompson and Burnet both presented males one after the other whereas in these trials both males were presented together to the female which may explain the discrepancy between the results.

If mixed batches are common then the small numbers of larvae used to determine fatherhood will have introduced an error into the results. This was the reason for the increase from two to four larvae for the later trials. The real number of mixed batches can be estimated if the assumption is made that all shared batches have the same proportional contributions from the two fathers (Table 9.7(a)). As expected the observed frequency of mixed batches was lower where only two larvae were determined but this deficiency



Table 9.7 Main three fly experiment - batches of mixed fatherhood

a) Estimated frequencies of batch mixing

No. of larvae determined	Total no. of trials	Observed frequency (%)	True frequency (%) assuming mixing was in ratio		
			1:1	1:3	1:9
2	163	4.3	8.5	11.5	23.9
4	138	26.8	30.6	39.4	78.0

b) Effect of male-male size difference

Size difference (divisions)	<0.2	0.3-0.5	0.6-0.8	0.9-1.1	>1.2
No. of trials	31	81	90	74	25
Frequency (%) of mixed batches	19	23	12	11	0

After arcsin transformation of proportions  
 $r = -0.870 \quad 0.10 > P > 0.05$

cannot be explained simply from the proportion of batches missed by chance. There is a suggestion (not statistically significant) that mixed batches were more common where the male-male size difference was smaller (Table 9.7(b)). This trend could result either from a higher frequency of mixed fatherhood at lower male-male differences or from a tendency for mixed batches to be shared equally by males of similar size and unequally by males of widely different size. As the trials for which four larvae were determined by chance contained more low male-male differences than the two larvae trials, this trend may help to explain the different frequencies of batch mixing in these groups.

Mixed fatherhood could have influenced the conclusions about size and genotypic effects on mating success. However this would only happen if one class of males consistently fathered more than half of the offspring in mixed batches. In this case some other aspect of male fecundity has been confounded with the simple measure of male mating success. Indeed if, as suggested above, the share of a mixed batch obtained by a male depended on his size relative to his competitor then batch mixing could account for all of the observed advantage to large males. However this would be no less real an advantage than if large males mated and small males did not.

84% of mixed batches were laid by BB females and only 16% by DD females. This difference is statistically significant ( $\chi^2_1 = 11.1$ ,  $P < 0.01$ ) and implies a genetic difference in reproductive behaviour of females, such as a shorter time to remating in BB females. Pyle and Gromko (1981) have shown that the interval between matings is under genetic control in Drosophila melanogaster.

d) Discussion Both sets of trials clearly demonstrate that, in laboratory conditions, large males have a strong advantage in competing for mates. This observation suggests two lines of further enquiry: first into the behavioural mechanisms underlying this advantage, and second into its consequences in natural populations.

There is a spectrum of possible explanations for the advantage in terms of behaviour from a combat between the two males, the victor of which mates with the passive female, to a choice between the males made by the female. These extremes correspond to Darwin's intra-sexual and intersexual selection respectively but are part of a continuum and not mutually exclusive. Both types of sexual selection can favour large size in insects. For example in dung flies (Parker 1979) and in milkweed beetles (McCauley 1982) large size is an advantage in male-male conflicts for females, although in dung flies there is probably also some element of female choice (Borgia 1981). In Drosophila melanogaster the advantage to large males is thought to lie in their greater wing area which allows them to "sing" more loudly during courtship and increases their chances of stimulating females to mate (Ewing 1961, 1964).

In Coelopa fighting between males has not been observed but females have been observed sometimes to reject males which attempt to mount. These rejections may be associated with a rapid exchange of signals between mounting and copulation. Females could be accepting or rejecting males partly on the basis of their size. The fact that female size, and possibly female genotype, influences the outcome of the three fly trials is evidence for some active role for the females. On the other hand in the observational results

reported above the number of times a male was rejected did not vary with male size.

An alternative possibility is that the greater success of the larger male is due to a generally higher level of activity. This would mean that he encountered females more often and thus mated more often, or when he encountered a female was more likely to mount or less likely to be kicked off once mounted. This type of explanation is consistent with the observational work where the total number of mountings and the proportion of successful mountings increase with male size under non-competitive conditions. It also fits in with the greater fecundity of larger males and their greater longevity which suggest that large size is associated with a general increase in "vigour".

A further possibility is raised by the occurrence of multiple insemination of females resulting in batches of mixed fatherhood. Multiple insemination occurs in many insects (Parker, 1970a, Boorman & Parker, 1976) and has important consequences for reproductive behaviour (Parker 1974) and population genetics (Prout & Bundgaard 1977). In this case the advantage to large males could be explained if sperm displacement ability was associated with large size - a larger ejaculate might possibly displace an earlier ejaculate more completely - or if large males were more likely to be the last to mate with a female before she laid an egg batch. Some further results pertaining to sperm displacement are reported below.

At present it is not possible to distinguish these various explanations for the advantage of larger males. It may well be that some combination of these possibilities is involved. The

investigation of courtship behaviour in Coelopa would be a fertile area for future research.

There are several reasons for caution in extrapolating these laboratory results to natural populations. The conditions used in the trials were at best a simplification of natural conditions. The flies were in constant darkness at a steady 27°C and although food was present it was unnatural. In the field mating probably takes place in the small spaces within wrack beds where conditions are rather similar to this but mating may also take place at the surface in daylight and at lower temperatures. In the trials the type of choice available involved just one female and two males. It is not clear whether encounters in the field usually involve more or less flies than this. Some experiments to be described later in this chapter attempt to examine mating in more natural conditions.

The principal effect uncovered by this experiment is the advantage to large males. In the field large male size is associated both with the Adh/inversion genotype and with development time. When adult flies first start to emerge from a wrack bed the only males available for mating will be small, fast developing Adh-DD males. Later, males of all genotypes will be available to mate but they will vary in size and, therefore, presumably in mating success. The consequences for gene frequencies in natural populations of sexual selection for large male size will depend on the length of life of the wrack bed. A short lived wrack bed will favour the Adh-D allele and  $\beta$  sequence because the males which father the next generation will be mainly DD( $\beta\beta$ ) individuals. A long lived wrack bed will favour the Adh-B allele and  $\alpha$  sequence



because the larger BD( $\alpha\beta$ ) and BB( $\alpha\alpha$ ) males will obtain a disproportionate number of mates.

This pattern is complicated by the possibility that the male and female genotypes directly affect mating success. The flies used in the main series of trials were from inbred laboratory stocks so the indication of differences between genotypes in these trials cannot be extrapolated to natural populations. However the pilot experiment, which used a recently established outbred stock, also indicated genotypic effects but in this case the number of trials was too small to separate reliably genotypic from size effects. A large scale experiment with flies taken, if possible, directly from the field would be required to confirm a direct effect of genotype but it seems unlikely that this would be important relative to the size effects.

In the following sections I will describe attempts to confirm the existence of non-random mating with respect to size in more natural conditions and some further results concerning multiple fatherhood of egg batches.

#### 9.4 Mass choice experiment

The experiment was essentially a repeat of the main three-fly experiment except that matings took place in a larger space and with more flies present. This was intended to overcome the objection that the one female - two male "choice" was unnatural.

a) Method Virgin males and females were obtained from the BB(lab) and DD(lab) stocks by the twice daily collection method and stored at 4°C until sufficient males and females were available.



At the start of the experiment the oldest flies used had been stored for 4 days. The males from each line were divided into large and small groups by eye.

Four tanks containing standard culture medium were set up with 80 females, 40 large males and 40 small males in the four possible genotype combinations. After 18 hours in darkness at 27°C the adult flies were moved to another set of four tanks for a further 18 hours. Egg batches laid in the tanks were moved into round canisters immediately after the adults had been removed. These canisters were retained until the larvae were large enough for electrophoresis when four larvae from each egg batch were collected and their genotypes determined. After the second laying period the remaining adults were counted and the males electrophoresed in order to determine the mortality of the different genotypes over the period of the experiment. Twenty flies from each group were measured.

b) Results The results are given in Table 9.8. There was differential mortality over the 36 hours of the experiment but this has been allowed for in calculating the expected proportion of egg batches fathered by the larger male assuming random mating using the average of the proportion of large males at the start (0.5) and the proportion at the end. In all combinations the larger males were successful more frequently than expected ( $\chi^2_1 > 18.0$ ,  $P < 0.001$  in all except the BB female, large DD male combination where  $\chi^2_1 = 5.27$ ,  $P < 0.05$ ). This result is in complete agreement with the three-fly experiments, indeed if anything the large male advantage is even more marked. This is true despite the fact that the male

to female ratio was 1:1 in this case and 2:1 in the other experiments  
 - a change which might have been expected to reduce competition  
 between males and allow smaller males more matings.

Table 9.8 Results of mass choice experiment

a) Sizes of flies

<u>Line</u>	<u>Large Males</u>	<u>Small Males</u>	<u>Females</u>
BB(1ab)	3.65	2.48	3.04
DD(1ab)	3.39	2.76	3.32

mean wing length (divisions) of 20 flies

b) Fatherhood of egg batches

Line and no. surviving for				Total batches	Observed proportion fathered by large male	Expected proportion fathered by large male	No. of mixed batches
Female	Large male	Small male					
BB 64	BB 31	DD 39		46	0.83	0.48	10
DD 62	BB 36	DD 33		52	0.96	0.51	0
BB 52	DD 24	BB 39		36	0.77	0.58	1
DD 73	DD 24	BB 37		51	0.96	0.57	2

The excess of large male fathers was greater where the female was from the DD(1ab) line. This could be due to a genotypic effect or to the larger size of these females. In either case it is consistent with the three-fly experiments in which larger females and DD females both showed greater preferences for large males.

Once again mixed batches occurred and were laid more commonly by BB females than by DD females. In fact they were almost entirely restricted to the BB female, large BB male combination.

c) Discussion There are two important aspects of this experiment that make it significantly closer to natural conditions than the three-fly experiment. Firstly encounters between individuals were much less restricted both in terms of the physical space available and in terms of the number of individuals available. Secondly the ratio of males to females was 1:1 which is likely to be similar to the sex ratio in the field. The major advantage to large males observed in the three-fly experiment was undiminished by these changes and it was encouraging to find that other trends in the data were also similar.

#### 9.5 Isolated female experiments

On the strength of these laboratory observations of a pronounced large male advantage I decided to attempt to demonstrate the effect directly in a natural population. The technique chosen was to sample adult flies from the beach, to determine the sizes and genotypes of the available males and the genotypes of males which had successfully inseminated females. This last could be achieved by isolating females and determining their genotypes and the genotype of any progeny they produced. If, as expected, males of BB, BC and BD genotypes were larger on average than CD and DD males then they should be overrepresented amongst the fathers when compared with their frequencies in the male population as a whole.

Three experiments have been conducted along these lines. The first was a pilot experiment in the laboratory to test the feasibility of the technique, the second a field trial and the third in the laboratory again.

a) Methods

(i) St.Mary's Island, November 1979 - a subsample was taken from the field sample collected at St.Mary's Island during November 1979 (Chapter 3) and kept in the laboratory until about the time of peak adult emergence. At this time a sample of males was collected, measured and electrophoresed. At the same time 48 females were collected and placed individually in mating pots containing medium. These were observed daily until an egg batch appeared when the female was removed and electrophoresed. Egg batches that hatched were transferred to round canisters and third instar larvae were collected from these after about six days. These larvae were electrophoresed in lots of four until either the genotype of the male parent could be determined unambiguously or twelve larvae had been used (as in the pilot three-fly experiment).

(ii) St.Mary's Island, 12 January 1980 - adult flies were collected on the beach using an insect aspirator. At the time of collection the weather was very cold (air temperature 1-2°C) but dry and still. There was no wrack bed in the vicinity of St.Mary's Island but large numbers of adult Coelopa frigida and Coelopa pilipes were present on the sandy beach of the south bay (see map, Chapter 4, page 130) under scattered patches of seaweed. These conditions proved to be ideal for collecting adults as they were easy to find and relatively sluggish. The flies were sexed on site and the females placed individually in mating pots with a short strip of split Laminaria stipe and a piece of cellosene wadding soaked in seawater to maintain humidity. The males were kept in bulk in bottles for return to the laboratory where they were stored

at  $-20^{\circ}\text{C}$  for subsequent measurement and electrophoresis. The females and their progeny were treated exactly as in (i).

(iii) St.Mary's laboratory stock - flies of the first laboratory generation of this outbred stock were used to start a tank culture which was maintained in the laboratory, that is with fluctuating light and temperature (about  $16-18^{\circ}\text{C}$  on average). Flies were collected from this tank on six occasions spanning the emergence period of the adults. On each occasion the sexes were separated and treated as in (i).

#### b) Results

(i) St.Mary's Island, November 1979 - Of the 48 females isolated in this pilot experiment 39 laid egg batches and 20 of these batches hatched. The genotypes of the male parents inferred from these batches (Table 9.9) differed significantly from the distribution of genotypes in the males which were available for mating. By far the greatest contribution to this deviation is from the excess of CD male parents despite the fact that the CD genotype was the second smallest group in terms of wing length.

Table 9.9 Results of St.Mary's Island (November 1979) isolated female experiment

<u>Adh</u> Genotype	BB	BC	BD	CD	DD	Total
No. of males in sample of available males	7	10	32	6	34	89
Mean size of males (1)	4.41	4.09	3.83	3.08	2.96	
No. of male parents -observed	0	1	9	6	4	20
-expected	1.6	2.2	7.2	1.3	7.6	

$$\chi_4^2 = 21.4 \quad P < 0.001$$

(1) Analysis of these size differences has been presented in Chapter 8



(ii) St.Mary's Island, January 1980 - 320 females were isolated at the start of this experiment. Of these 210 laid egg batches and 38 egg batches hatched. Two egg batches were laid before the females were raised to 27°C in the laboratory (48 hours after collection). More than 60% of batches were laid within 24 hours of the rise in temperature but laying continued until the fourth day. The last fertile egg batch was laid on the third day after transfer. Of the fertile egg batches five produced insufficient progeny for determination of the male parent. In two cases the resulting progeny could not be accounted for in terms of a single male parent and must have resulted from multiple insemination. It is possible that other egg batches were of mixed fatherhood but that this was not detected because it resulted only in a shift in progeny genotype frequency. The two cases of mixing which were identified both involved the rare Adh-A allele and were therefore determined unequivocally.

The female parents of the remaining 31 egg batches were a random sample of the females which laid eggs (Table 9.10). The distribution of genotypes in the male parents was significantly different from expectation. There was an excess of CD and DD male parents and a deficiency of BD males. Once again this was despite the significant size differences between those genotypic classes with BD males larger on average than both CD and DD males.

The most likely explanation for the unexpected excess of small male parents both in this experiment and the previous one lies in the development time differences between genotypes. The majority of males do not mate successfully until 24 to 48 hours



Table 9.10 Results of St.Mary's Island (January 1980) isolated female experiment

a) Males

<u>Adh</u> Genotype	BB	BC	BD	CC	CD	DD	Total
Nos. in sample of available males	10	13	89	4	24	59	199
Mean size <sup>+</sup>	3.86	3.38	3.60	3.07	3.25	3.02	
No.of male parents-observed*	1	1	6	0	8	14	30
-expected	1.5	2.0	13.4	0.6	3.6	8.9	

$$\chi_4^2(\text{omitting } \underline{\text{Adh}}\text{-CC}) = 13.1, P < 0.05$$

<sup>+</sup>Analysis of these size differences has been presented in Chapter 8

\*In addition one egg batch was fathered by an Adh-DE male and there were two egg batches which were apparently of mixed fatherhood

b) Females

<u>Adh</u> Genotype	BB	BC	BD	CD	DD	Others	Total
All females which laid eggs	19	12	81	27	44	11	194
Females which laid eggs which hatched†	5	2	13	5	6	0	31

†This is not significantly different from the expectation assuming a random sample of all females which laid eggs

$$\chi_5^2 = 3.29, P > 0.2$$

after eclosion. In the laboratory experiment a higher proportion of the larger males (BB, BC, BD) amongst those counted as available for mating will have been within this period than of the smaller males (CD, DD) because these genotypes eclose later. So the distribution of males actually able to fertilise females was shifted toward the smaller males as was the distribution of males which were successful (although it is surprising that CD males were much more successful than DD males).

The position with the field experiment was slightly different because the sample was not taken during the adult emergence period but after removal of the wrack bed from which the flies emerged. Here the explanation probably lies in the low ambient temperature. Coelopa frigida are reluctant to mate at temperatures below about 20°C (I.L.Read, pers.comm.) and so it is likely that few females had been inseminated in this population since the removal of the wrack bed. The females which had been fertilised must have mated before the removal and probably during the emergence period. The same explanation for the excess of smaller, faster developing male parents can, therefore, apply.

(iii) St.Mary's laboratory stock - In this experiment samples of males and females were taken at six points during the emergence of adults to test the possibility that differences in timing of emergence were generating the unexpected distributions of male parents. In all, 491 females were isolated and 257 of these laid eggs. 56 egg batches hatched and produced sufficient progeny for determination of the male parent genotype. There was no significant deviation from the expected distribution of male parents overall (Table 9.11) - indeed the numbers were very close to expectation

for all genotypes except that no BB male parents were observed.

Table 9.11 Results of St.Mary's (laboratory stock line) isolated female experiment

<u>Adh</u> Genotype	BB	BC	BD	CC	CD	DD	TOTAL
<u>Date</u>							
4/6 Male parents			1			2	3
Males available		1	7			14	22
6/6 Male parents			4		1	3	8
Males available	1	2	28		5	14	50
9/6 Male parents		1	24	1	3	5	34
Males available	5	6	56	2	7	18	94
11/6 Male parents			3		1	1	5
Males available	11	8	37		4	10	70
13/6 Male parents			1				1
Males available	3	2	19				24
16/6 Male parents		4	1				5
Males available	10		12	1		1	24
TOTAL Male parents <sup>(i)</sup>	0	5	34	1	5	11	56
Males available	30	19	159	3	16	57	284
Mean sizes <sup>(ii)</sup> (divisions)	2.90	2.82	2.71	2.87	2.60	2.53	

(i) The overall numbers of male parents do not differ from the random mating expectation  $\chi^2_5 = 7.0$ ,  $P > 0.10$

(ii) There are significant differences between mean sizes  $F_{4,280} = 5.49$ ,  $P < 0.001$  (excluding the small number of CC males)

The effect of development time can most easily be studied using the Adh-B allele frequencies in the available and successful males (Figure 9.1). As expected the B frequency increases steadily through the emergence period in the available males. The Adh-B frequency amongst the male parents is consistently lower than in the available males but also rises. If the explanation for the excess of small, early emerging male parents is the lag between

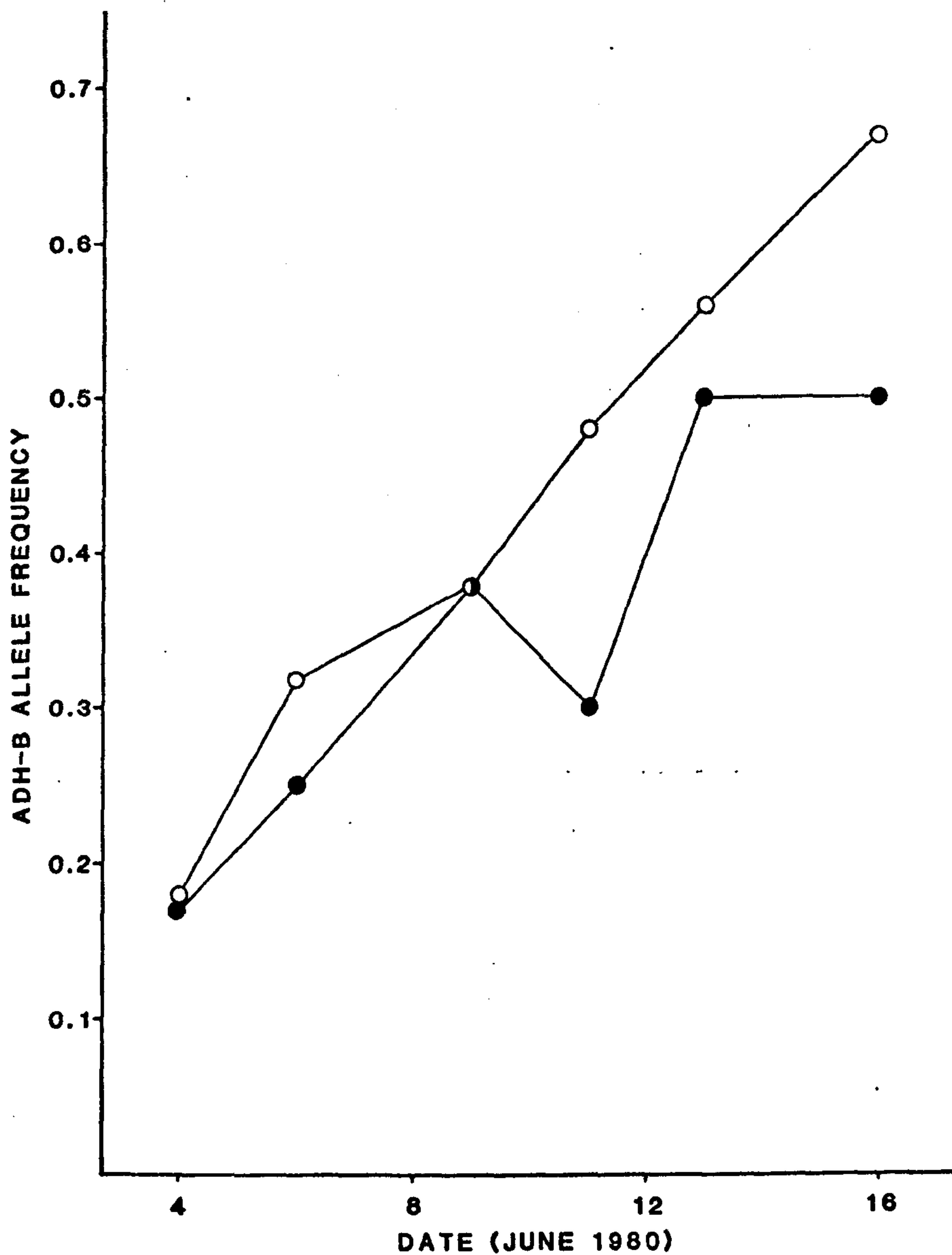


Fig.9.1 Comparison of Adh-B allele frequencies in the males available for mating and those which actually fathered egg batches in the St.Mary's (laboratory line) isolated female experiment

X  
which  
is  
which

emergence and the start of mating then these lines might be expected to converge in the later samples which were at the very end of the emergence period. In fact they tend to diverge but this result carries only limited weight considering the small numbers involved.

The flies used in this last experiment were noticeably smaller than in the previous experiments, probably because larval density was high in the tank culture. The size differences between male genotypes were significant (Table 9.11) but nevertheless they were small - less than 0.4 divisions separating the means for BB and DD compared with 0.8 divisions in the St.Mary's Island, January 1980 sample. This might have reduced the chances of detecting sexual selection for large male size.

c) Discussion The "isolated female" experimental design has allowed me to extend my study of non-random mating into conditions much more similar to those in nature and in one case actually into a field population. The major difficulty with the technique is that a large investment of effort in the early stages of the experiment is rewarded by only a small amount of data at the end. This was because only a small percentage of females were fertilised. Nevertheless a large male advantage of the order observed in the laboratory should have been detectable, at least in the first two experiments where the male size range was large. In fact there was no excess of large male parents but instead there was an excess of the smaller genotypes, especially CD. Dr.T.H.Day (pers.comm.) has since repeated my last experiment - with several time points - on a larger scale and using flies from a natural population brought into the laboratory as larvae. His results also show an excess of CD males amongst the parents.



Clearly this discrepancy requires an explanation and further experiments will be necessary before the correct interpretation is known. Several possibilities deserve attention:-

- 1) The combined effects of development time differences and a short lag between eclosion of males and their reproductive maturity have been mentioned above. If this was the correct explanation then the earliest emerging males should show the greatest excess. In the laboratory CD males emerge after DD males (Day et al 1980) but in the field my results (Chapter 4) showed that CD males emerged first. This explanation can fit the results of the first two experiments and, although the results of the last experiment do not agree, it could well be at least a part of the explanation. A further experiment examining mating success under conditions of changing gene frequencies is reported in the next section.
- 2) The very different conditions in which mating took place in the laboratory experiments and these isolated female experiments could explain the different outcomes. The mass mating experiment suggests that the number of flies was not an important factor. In the second and third isolated female experiments, mating probably took place at a lower temperature and may have taken place in daylight. The first experiment was carried out in the constant temperature room in the same conditions as the choice experiments. A potentially important distinction is that in the isolated female tests there was no handling of the flies until after mating whereas in the other experiments flies had to be sorted under CO<sub>2</sub> anaesthetic before the trials began. Perhaps large males are more resistant to CO<sub>2</sub> than small males. Also in the three fly and mass choice experiments the sexes were kept



separate for up to 4 days before testing. This sex starvation could have affected the outcome of competition for mates.

3) The main three fly and the mass choice experiments used highly inbred laboratory lines. It is unlikely that a preference for large males has become genetically fixed in these two independent lines but on the other hand they are not representative of the range of genotypes in natural populations. However the flies from the Portland line used in the pilot three fly experiment included all the common Adh genotypes from a broadly based population recently brought into the laboratory. In these trials there was a marked excess of large male successes and what indication there was of a genotypic effect favoured BD males and not CD males. It seems unlikely that differences in the genetic constitution of the flies used has caused the distinction between the experiments.

4) In the isolated female experiments there was scope for frequency dependent effects which was not present in the previous experiments. The apparent advantage to CD males could be a "rare male effect" (see Spiess 1982 for a review) although the BC and BB genotypes were present at similar frequencies without apparently experiencing an advantage. This possibility is clearly amenable to experimental investigation - at present there is no evidence to support or deny it.

5) The success of the larger males in the laboratory experiments could have been due to some attribute other than their size which is not necessarily correlated with size in different circumstances. For example the larger males, especially the large DD males, tended to come from lower density cultures and may have been used younger or older than the smaller males because of development time

differences. Effects of this type might influence general male activity and thus mating success. The design of the three fly experiments was intended to minimise male-male differences other than size and genotype but it is possible that other differences did occur.

6) The differences between the results obtained with the two techniques could be a result of their measuring different things. The three fly and mass choice experiments ask which male(s) successfully fathered the first egg batch. The isolated female technique asks which male(s) fertilised the female before the time of sampling. The distinction is important because females are known to mate repeatedly before laying an egg batch (Chapter 8) and the last male to mate may fertilise a disproportionate number of eggs. Indeed in Burnet's (1960c) and Thompson's (1951) experiments where males were mated to females in sequence the last male fathered all the offspring. In more natural conditions where a variety of males are available at all times there is likely to be a high proportion of mixed egg batches but the last male could still have an advantage. In the dung fly, Scatophaga stercoraria, each subsequent male to mate displaces about 80% of the sperm deposited by previous males, placing a high premium on mating last before egg laying (Parker 1970b).

If the large males' advantage in Coelopa was a result of their mating with females last before each egg batch was laid then this advantage would be detected by the three fly and mass choice experiments but not by the isolated female experiments.

How could large males achieve this end? In dung flies males guard females after insemination, fighting off other males which

attempt to mount (Parker 1970d,e). This confers an advantage on larger males which can dislodge, but cannot be dislodged by, smaller males. The observational evidence available for Coelopa does not give any suggestion of this type of behaviour. However there are other ways of being last: a) if females become less receptive as they approach egg laying a larger male capable of producing a stronger stimulatory signal would be able to mate later; b) if larger males have larger ejaculates they may be more efficient displacers of previous ejaculates and less susceptible to displacement themselves; c) females may be less likely to remate after mating with a large male as in houseflies (Baldwin & Bryant 1981), or d) if larger males mate more frequently they will be more likely to be the last in any sequence of matings. There is evidence (Chapter 8) that larger males mate more frequently but this possibility alone does not explain the difference between the experimental designs as large males would more often be last in sequences ending with female isolation as well as with egg laying.

An important area for future research in Coelopa will be the question of male mating strategies in relation to multiple insemination and mixed fatherhood of egg batches. Some very preliminary observations will be reported in section 9.7.

The conclusion from the experiments reported so far on male mating success must be an open one. The evidence for a considerable large male advantage from laboratory experiments is strong but it is contradicted by the isolated female results. There are various ways in which these results can be reconciled, and distinguishing these possibilities is likely to be a fertile area for future research.

## 9.6 Mating success in undisturbed laboratory cultures

This experiment was intended to combine the advantage of looking at mating success in terms of fatherhood of egg batches laid by unsegregated females with the need to study mating success under conditions of changing genotype frequencies while flies are eclosing. This was achieved by establishing pairs of laboratory cages as nearly identical as possible and using one to determine the sizes and genotypes of flies emerging on each day and the other to collect egg batches laid by a similar population of flies.

a) Method Ideally this experiment should have been conducted with flies taken directly from a natural population but this would generate a large number of possible mating combinations and a large number of egg batches would be needed to get useful results. The experiment was, therefore, started with flies from the St.Mary's B + D line which combines a broad genetic base with only two Adh alleles, B and D.

About 1000 adults from the tenth laboratory generation of the St.Mary's B + D stock were placed in each of two culture tanks. In place of the usual layer of medium each of these tanks had two plastic boxes (17.5 x 11.5 x 6 cm) in the bottom completely filled with standard medium. After a 24 hour egg laying period all the adult flies were removed from the tanks. Six days later, before pupation began, one box of medium was removed from each tank and placed in a fresh tank (without any new medium). The pairs of tanks were kept together in the constant temperature room at 27°C. The original tanks were designated MC1 and MC2 and the two extra tanks MC1A and MC2A respectively.



All flies emerging from tanks MC1A and MC2A were collected daily until no flies emerged for 3 consecutive days. These flies were stored at  $-20^{\circ}\text{C}$  for subsequent measurement and electrophoresis-

From the appearance of the first adults until ten days after the appearance of the last, a round canister containing fresh medium was placed each day in tanks MC1 and MC2. After 24 hours the canisters were removed and these tanks were not disturbed in any other way. Although a few egg batches were laid on the old medium in the plastic boxes most egg batches were laid on the fresh medium in the round canisters. These batches were moved into separate round canisters with fresh medium and left in the constant temperature room for about 6 days. Larvae were then removed and stored for electrophoresis.

Wherever possible the genotypes of 12 larvae were determined in order to establish the parenthood of an egg batch. Where fewer than 10 larvae reached a sufficient size for electrophoresis the batch was discarded. The criteria for assignment of a batch to a particular type of cross were:

<u>Type of cross</u>	<u>Expected Offspring</u>	<u>Criterion for assignment</u>
BB x BB	all BB	all BB larvae
BB x BD	1BB:1BD	BB and BD larvae only present unless ratio is $(n-1)\text{BD}:1\text{BB}$
BB x DD	all BD	all BD larvae
BD x BD	1BB:2BD:1DD	all three genotypes present
BD x DD	1BD:1DD	BD and DD larvae only present unless ratio is $(n-1)\text{BD}:1\text{DD}$
DD x DD	all DD	all DD larvae

where n is the number of larvae determined.

Batches in which just one larva was either BB or DD and the remainder were BD were equally likely to be BD x BD or BD x BB or DD crosses and so these cases were excluded. Where two or more similar homozygotes were found the parents were more likely to be homozygote versus heterozygote than both heterozygote and they were scored accordingly. No attempt was made to detect mixed parenthood, i.e. more than two parents, and clearly male and female parents could not be distinguished.

b) Results Appendix 9 gives the full results of this experiment. The two cages, MC1A and MC2A, from which flies were collected daily started to produce flies on the same day and completed emergence just one day apart. The distributions of genotypes from the two cages were similar ( $\chi^2_2 = 4.96$ ,  $P > 0.05$ ) as were the total numbers of flies produced (404 and 416). These observations confirm that the two cages from which flies were collected were good models for the egg laying cages, MC1 and MC2. They were expected to be more similar to their respective models than the models were to one another because they were started with the same flies.

(i) SIZE AND DEVELOPMENT TIME

The development times and adult sizes of the three genotypes showed the expected distributions, that is there was little difference between females but in males BBs were the largest and latest to emerge, DDs the smallest and earliest and BDs were intermediate (Tables 9.13 and 9.14). The flies from MC2A were overall slightly larger than from MC1A.

The flies from these two cages represent the largest sets of individuals which have developed together and for which the sizes and development times of all adults are known. Therefore it is



worthwhile studying the relationship between size and development time within genotypes and sexes in view of the results presented in Chapter 5 which suggested a negative correlation.

In eight out of the twelve comparisons (Table 9.12) a linear regression gave a negative slope which was significantly different from zero in four cases (all in MC2A). DD females from MC1A gave

Table 9.12 Coefficients for linear and quadratic regression of size on development time

<u>MC1A</u>				<u>MC2A</u>		
	x	x <sup>2</sup>	% variance accounted for	x	x <sup>2</sup>	% variance accounted for
<u>Males</u>						
BB 1	0.055	-	22	-0.023	-	9
q	-0.359	0.015	50	-0.120	0.004	34
BD 1	0.016	-	1	-0.018 <sup>*</sup>	-	3
q	-0.235 <sup>***</sup>	0.010 <sup>***</sup>	21	-0.230 <sup>***</sup>	0.011 <sup>***</sup>	20
DD 1	-0.007	-	0	-0.028 <sup>***</sup>	-	28
q	-0.021	0.001	1	-0.112 <sup>***</sup>	0.006 <sup>***</sup>	40
<u>Females</u>						
BB 1	-0.002	-	10	0.015	-	8
q	0.164	-0.010	2	-0.045	0.003	12
BD 1	-0.004 <sup>*</sup>	-	0	-0.019 <sup>***</sup>	-	12
q	-0.067 <sup>*</sup>	0.003 <sup>*</sup>	3	-0.149 <sup>***</sup>	0.007 <sup>***</sup>	38
DD 1	0.021 <sup>**</sup>	-	10	-0.016 <sup>*</sup>	-	7
q	-0.044	0.003 <sup>*</sup>	16	-0.093 <sup>**</sup>	0.002 <sup>**</sup>	15

l = linear, q = quadratic

Significance levels for differences from zero:

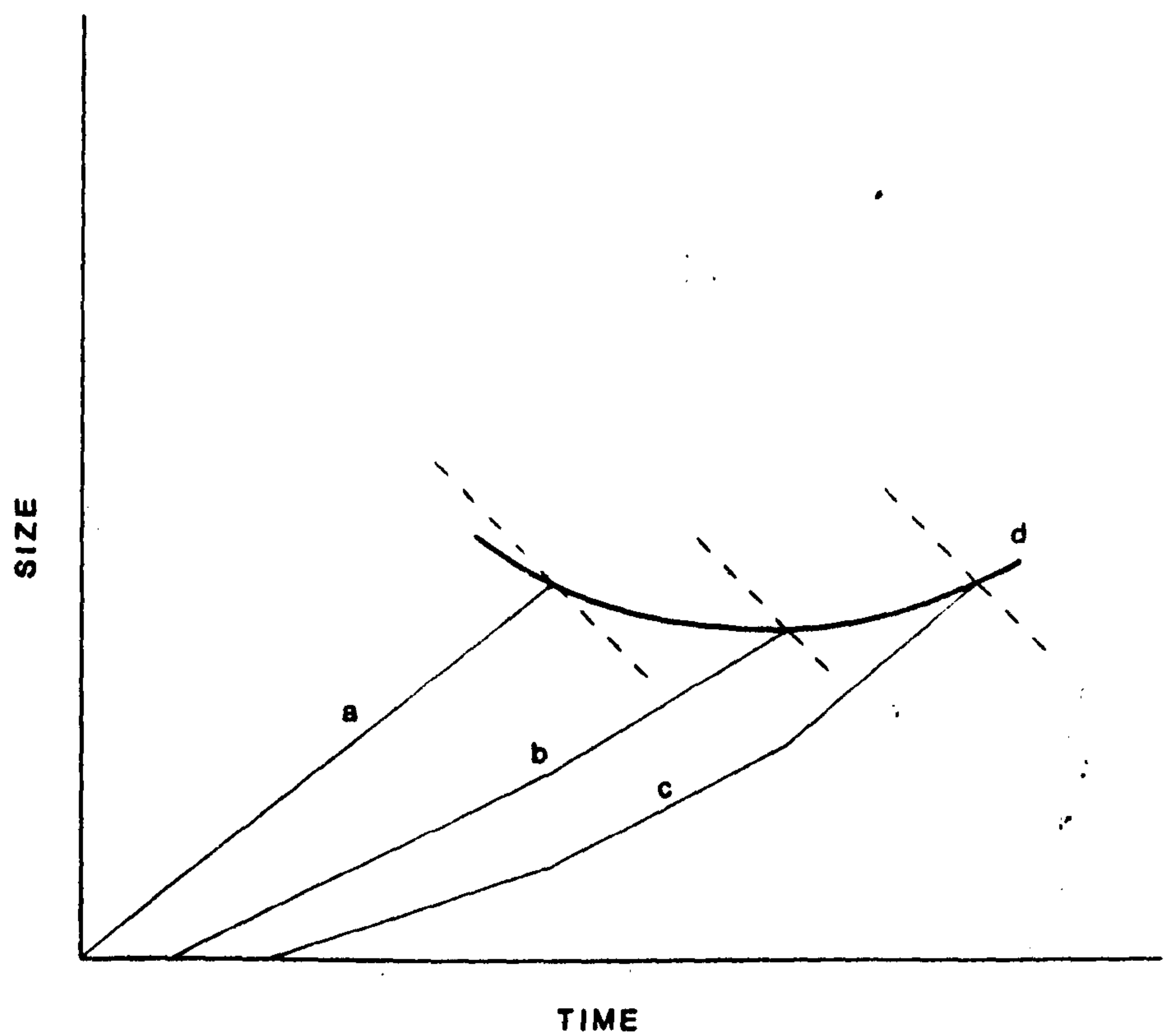
- \* P < 0.05
- \*\* P < 0.01
- \*\*\* P < 0.001

gave a significant positive slope. Examination of the data showed that in several cases the last few flies to emerge were unusually large and so a quadratic regression model was applied. In all but

one case (BB females from MC1A of which there were only 12) this model explained a greater proportion of the variance than the linear model and the coefficients for development time and the square of development time were negative and positive respectively. This says that at first size decreases with development time but towards the end of emergence it increases again. There was no evidence for such a relationship in the data from the density experiment reported in Chapter 5. This could simply be due to the relatively small numbers used in that case but it may be a genuine difference resulting from the relative scales of the experiments, the densities, or the methods of establishment. The flies used were from the same SM B + D line.

Can this observation be reconciled with the explanation put forward in Chapter 5 for the relationship between size and development time? I believe it can - in one of two ways. A locus or loci independent of the chromosome I inversion could be segregating in the SM B + D line which also affects size and development time. It is, in fact, highly probable that this line is segregating for other inversions (Philip 1958, 1966). The large late emerging flies would then be explicable in the same way as the BB males are large and late emerging. Clearly this hypothesis could easily be tested - for example by looking at size and development time in highly inbred lines. The second possibility depends on the assumption made in Chapter 5 and supported in Chapter 6 that growth rate depends on the level of competition between larvae. If this is so, then as more and more fast developing larvae pupate the growth rate of the remaining larvae will increase. The eggs for this experiment were laid over a 24 hour period and,

Fig.9.2 Hypothetical relationship between time and size in Coelopa larvae - see text for explanation.



therefore, the larvae hatched over a similar period. Early hatching larvae probably grow faster than late hatching larvae because of their "head start" and a small initial difference can be magnified if growth rate is dependent on size as proposed for Drosophila by Bakker (1961). The small difference in hatch time could give a large difference in the position of the pupation line (Chapter 5) if this is determined by an event such as the moult to third instar. The result of combining the effects of such differences in timing with the effect of density on growth rate is illustrated in Fig.9.2. Straight lines in place of curves have been used for simplicity and the differences exaggerated. Line (a) represents the rapid growth of the first larvae to hatch. These larvae have an early pupation line. Later hatching larvae (b) grow more slowly at first but faster when the earliest larvae start to pupate. Their pupation line is shifted to the right. These effects are much more marked for the last larvae to hatch (c). Line (d) shows the resulting size/time relationship for pupation which would be paralleled by adult emergence. Clearly it is possible to generate the quadratic relationship observed but it should be emphasised that this is not the only possible result. It depends on the particular combination of growth rates and displacements of the pupation line.

This hypothesis rests on the idea that growth rate depends on density. This is equivalent to postulating interference competition of some sort. It could result from interactions between larvae - either physical or chemical - or from a limitation of the rate of nutrient supply. The latter possibility seems the more likely, as discussed in Chapter 6 as Coelopa larvae are known to depend on microorganisms in the decaying seaweed (Rowell 1969).

Table 9.13 Mating success in tank cultures - overall results

MC1A

<u>Adh</u> genotype	BB	BD	DD	Total
Total no. of males	7	100	82	189
Mean size of males ( $\pm$ s.e.)	3.23 $\pm$ 0.15	3.12 $\pm$ 0.04	2.78 $\pm$ 0.03	
Total no. of females	12	123	80	215
Mean size of females ( $\pm$ s.e.)	2.87 $\pm$ 0.07	2.98 $\pm$ 0.03	2.94 $\pm$ 0.04	

MC1

Mating type	BBxBB	BBxBD	BBxDD	BDxBD	BDxDD	DDxDD	Total
Overall observed number	0	8	1	26	21	1	57
Expected number	0.1	2.9	2.2	17.3	25.4	9.2	

$$\chi^2_5 = 22.2, P < 0.001$$

Table 9.14 Mating success in tank cultures - overall results

MC2A

<u>Adh</u> genotype	BB	BD	DD	Total
Total no. of males	7	101	70	178
Mean size of males ( $\pm$ s.e.)	3.44 $\pm$ 0.09	3.07 $\pm$ 0.06	2.84 $\pm$ 0.03	
Total no. of females	17	155	66	238
Mean size of females ( $\pm$ s.e.)	3.01 $\pm$ 0.06	3.09 $\pm$ 0.02	2.98 $\pm$ 0.03	

MC2

Mating type	BBxBB	BBxBD	BBxDD	BDxBD	BDxDD	DDxDD	Total
Overall observed number	0	0	3	35	23	3	64
Expected number	0.2	4.2	2.5	23.7	26.5	7.0	

$$\chi^2_5 = 12.6, P < 0.05$$



Hughes (1980) attributed a very similar quadratic relationship between adult size and development time in Drosophila melanogaster to the effects of interference competition. He also proposed that the slower developing larvae were able to grow rapidly once the majority of larvae had pupated.

In the field it is unlikely that this sort of size/development time relationship would be important because eggs are laid over a much longer period. Wrack beds would generally either be removed or become too cold or dry for larvae before slow growing individuals could gain any benefit from decreasing density. Otherwise a second generation of larvae would probably overlap the tail of the first generation.

#### (ii) MATING AND EGG LAYING

88 egg batches were collected from MC1 of which the parenthood of 57 was determined. For MC2 64 out of 100 batches were satisfactorily determined. The matings generating these batches are given in Tables 9.13 and 9.14 and are compared with expectations based simply on the total numbers of males and of females of each genotype in the model cages (MC1A and MC2A). In both cases there are significant differences. These differences include a deficiency of DD x DD and BD x DD matings and an excess of BD x BD matings in both cages but in MC1 there was an excess of BB x BD matings whereas there was a deficiency of this type in MC2.

A similar picture emerges if the numbers of flies of each genotype which succeeded in contributing to egg batches are considered (Tables 9.15(a) and 9.16(a)). In MC1 both BB and BD flies were more common than expected amongst the parents while DD

flies were less common than expected. In MC2 only BD flies were more common than the expectation and this excess was somewhat less than in MC1. For the two genotypes (BD and DD) which make up the great majority of the available flies in these cages (and which are also the most common genotypes in natural populations) the results from the two pairs of cages are very similar. BD flies apparently have an advantage over DD flies in the period from emergence to egg laying.

Is this advantage due to the fact that BD males tend to be larger than DD males? This question cannot be answered directly from the results of this experiment because it could not distinguish between male and female parents and because of the unavoidable association between size and genotype. However some indications can be obtained. In the previous chapter an effect of adult size on longevity and fecundity of both males and females was demonstrated in laboratory conditions similar to those of this experiment. These effects can be built in to a model to predict the parents of egg batches in MC1 and MC2 both overall and day by day. If the discrepancies cannot be accounted for by longevity and fecundity differences then sexual selection is likely to be involved.

Tables 9.15 and 9.16 (b) and (c) show the expected parents in MC1 and MC2 after allowing for the effect of size on longevity and longevity plus fecundity respectively and the predicted time courses are presented in Figures 9.4 to 9.7 for the BD and DD genotypes. To allow for longevity the expected life span of each male was obtained from the formula:

$$\text{Lifespan} = (-3.58 + 3.05 \times \text{winglength}) \text{ days}$$

**Table 9.15** Expected and observed proportions of genotypes amongst parents (MC1 and MC1A)

a) Equal contributions from all flies

	BB	BD	DD	Total
Males	7	100	82	189
Females	12	123	80	215
Expected parents	5.29	62.77	45.94	
Observed parents	9	81	24	114

$$\chi^2_2 = 18.37 \quad P < 0.001$$

b) Allowing for size related differences in longevity (figures are flies x days)

	BB	BD	DD	Total
Males	50	688	485	1223
Females	84	903	582	1569
Expected parents	5.38	64.87	43.75	
Observed parents	9	81	24	114

$$\chi^2_2 = 15.36 \quad P < 0.001$$

c) Allowing for size related differences in longevity and fecundity (flies x matings for males, flies x egg batches for females)

	BB	BD	DD	Total
Males	20.06	265.56	145.34	430.96
Females	8.92	105.77	65.11	179.80
Expected parents	5.48	68.65	39.86	
Observed parents	9	81	24	114

$$\chi^2_2 = 10.79 \quad P < 0.01$$

Table 9.16 Expected and observed proportions of genotypes amongst parents (MC2 and MC2A)

a) Equal contributions from all flies

	BB	BD	DD	Total
Males	7	101	70	178
Females	17	155	66	238
Expected parents	7.09	78.00	42.92	
Observed parents	3	93	32	128

$$\chi_2^2 = 8.02 \quad P < 0.05$$

b) Allowing for size related differences in longevity (flies x days)

	BB	BD	DD	Total
Males	56	717	426	1199
Females	123	1194	48.5	1802
Expected parents	7.36	80.68	39.96	
Observed parents	3	93	32	128

$$\chi_2^2 = 6.05 \quad P < 0.05$$

c) Allowing for size related differences in longevity and fecundity (flies x matings for males, flies x egg batches for females)

	BB	BD	DD	Total
Males	24.74	280.92	132.54	438.20
Females	15.85	179.33	63.42	258.60
Expected parents	7.54	85.41	35.05	
Observed parents	3	93	32	128

$$\chi_2^2 = 3.67 \quad P > 0.10$$

and for females:

$$\text{Lifespan} = (-1.28 + 2.55 \times \text{winglength}) \text{ days}$$

taken from the regression equations in Chapter 8 (in both cases rounding to the nearest integer). The numbers of males and females of each genotypes and sex available on each day could then be calculated from the known emergence time and estimated lifespan of each individual.

The expected daily contribution of each individual was then calculated for males from:

$$\text{Contribution} = (-0.32 + 0.22 \times \text{winglength}) \text{ matings per day}$$

and for females from:

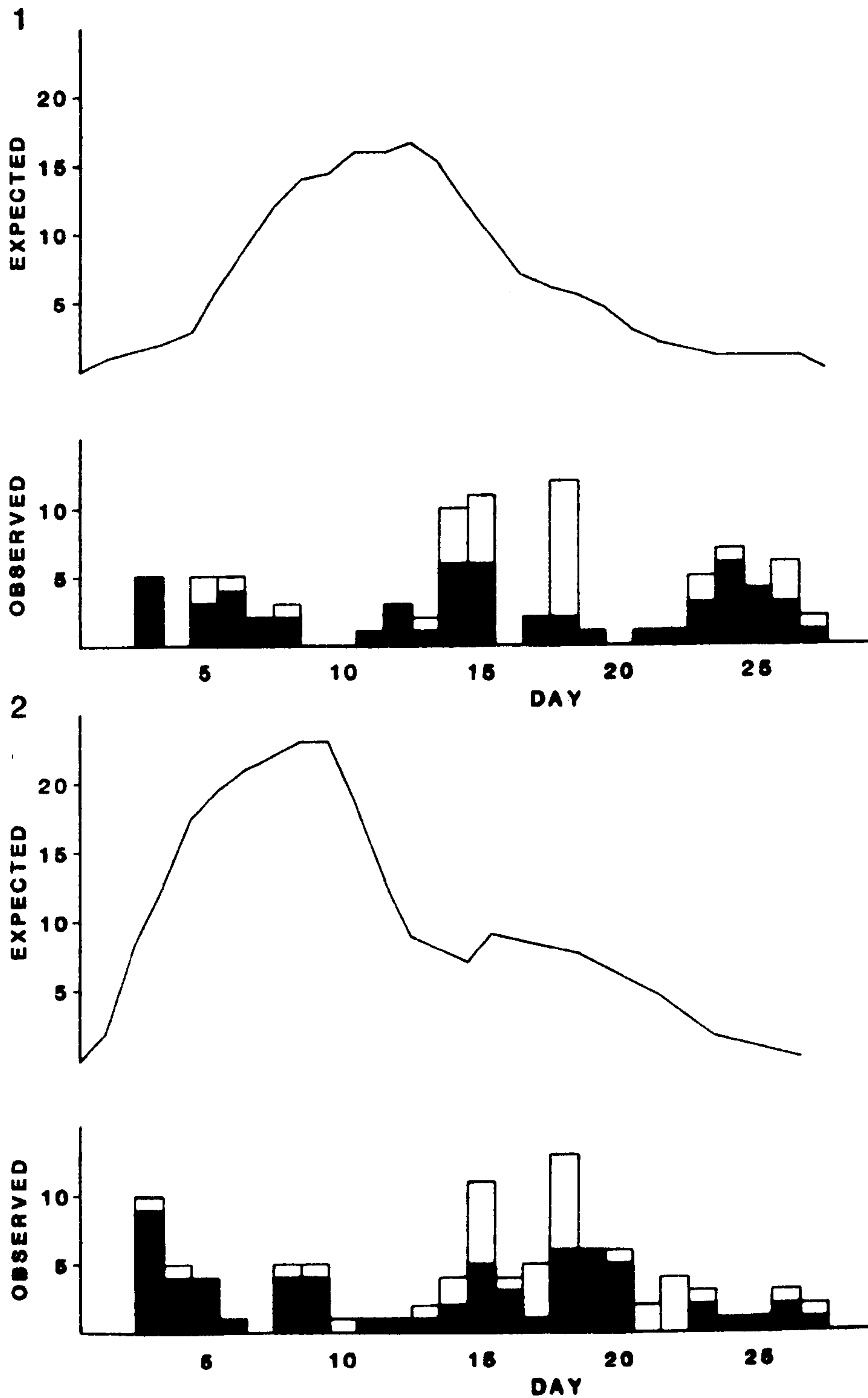
$$\text{Contribution} = \frac{(-5.35 + 2.36 \times \text{winglength})}{\text{lifespan}} \text{ egg batches per day}$$

again using the regression equations in Chapter 8 (negative values were replaced with zeros). The daily contribution of each genotype and sex was then calculated as the sum of the contributions of all flies alive on that day.

In Figures 9.4 to 9.7 these predictions are presented as proportions of the total daily expectations and in Tables 9.15 and 9.16 (b) and (c) as the totals over the whole egg laying period. In addition the total numbers of egg batches each day are compared with the numbers of egg batches actually collected in Figure 9.3.

Considerably fewer egg batches were laid than were predicted for either MC1 or MC2. It seems unlikely that this was because fewer flies were present than in MC1A and MC2A. A more likely reason is that some egg batches were laid on the old medium from which the flies had emerged. It is also possible that conditions were not so conducive to egg laying in the cages as in the regularly

Fig.9.3 Observed and expected numbers of egg batches in cages MC1 and MC2. See text for derivation of expected numbers of batches. Shaded sections of the histograms of observed numbers represent those batches for which parenthood was successfully determined.





Figs.9.4 to 9.7 Observed and expected daily contributions of the two most common Adh genotypes to egg batches in cages MC1 and MC2. Each figure has four sections:

Emergence      the frequency of the genotype amongst flies emerging on each day

Available      predicted frequency of the genotype amongst flies alive on each day

Contribution   predicted frequency of the genotype amongst the parents of egg batches laid on each day

Parents        observed frequency of the genotype amongst parents

Fig.9.4        Adh-BD   Cage MC1

Fig.9.5        Adh-DD   Cage MC1

Fig.9.6        Adh-BD   Cage MC2

Fig.9.7        Adh-DD   Cage MC2

Fig. 9.4 Adh-BD Cage MC1

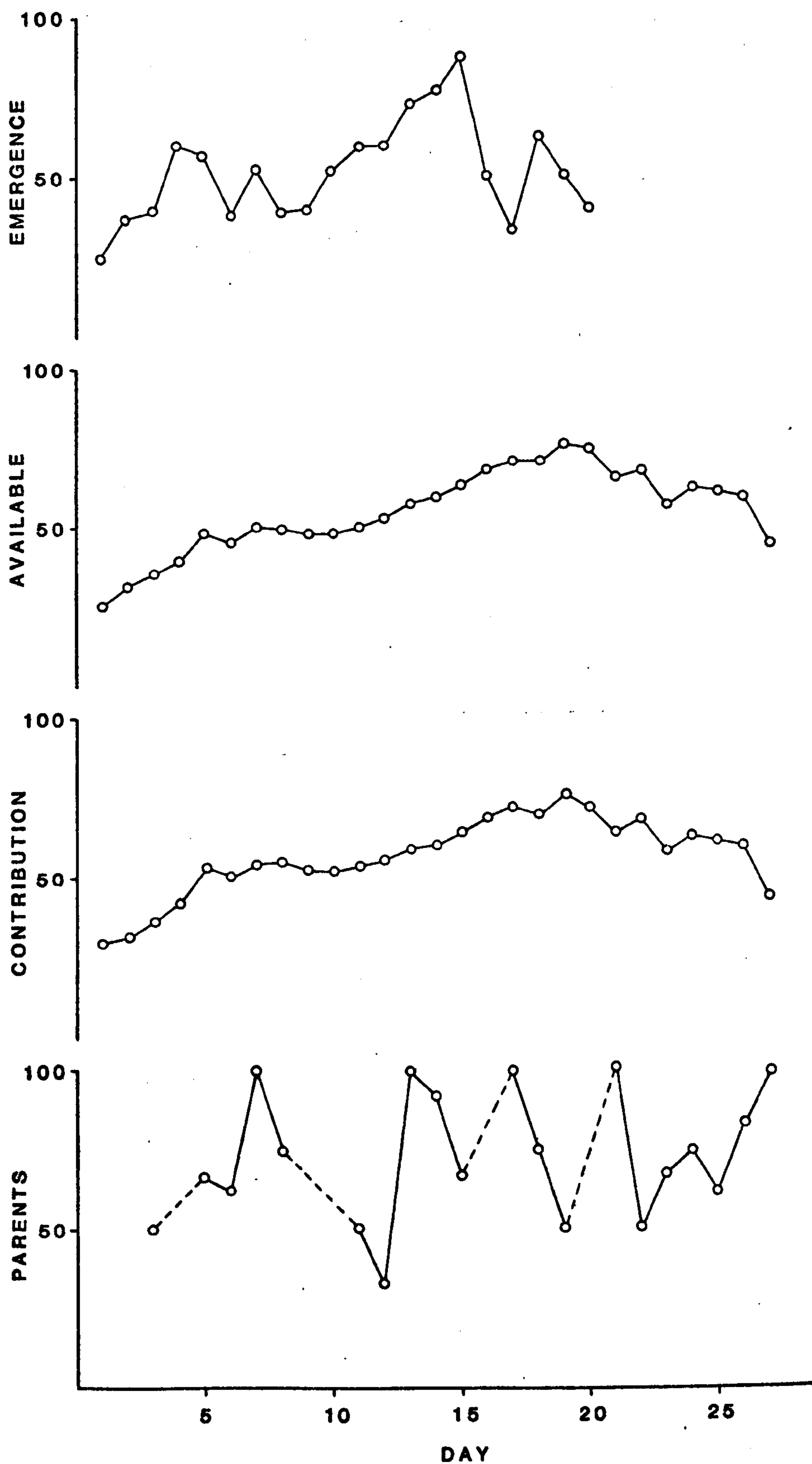


Fig. 9.5 Adh-DD Cage MC1

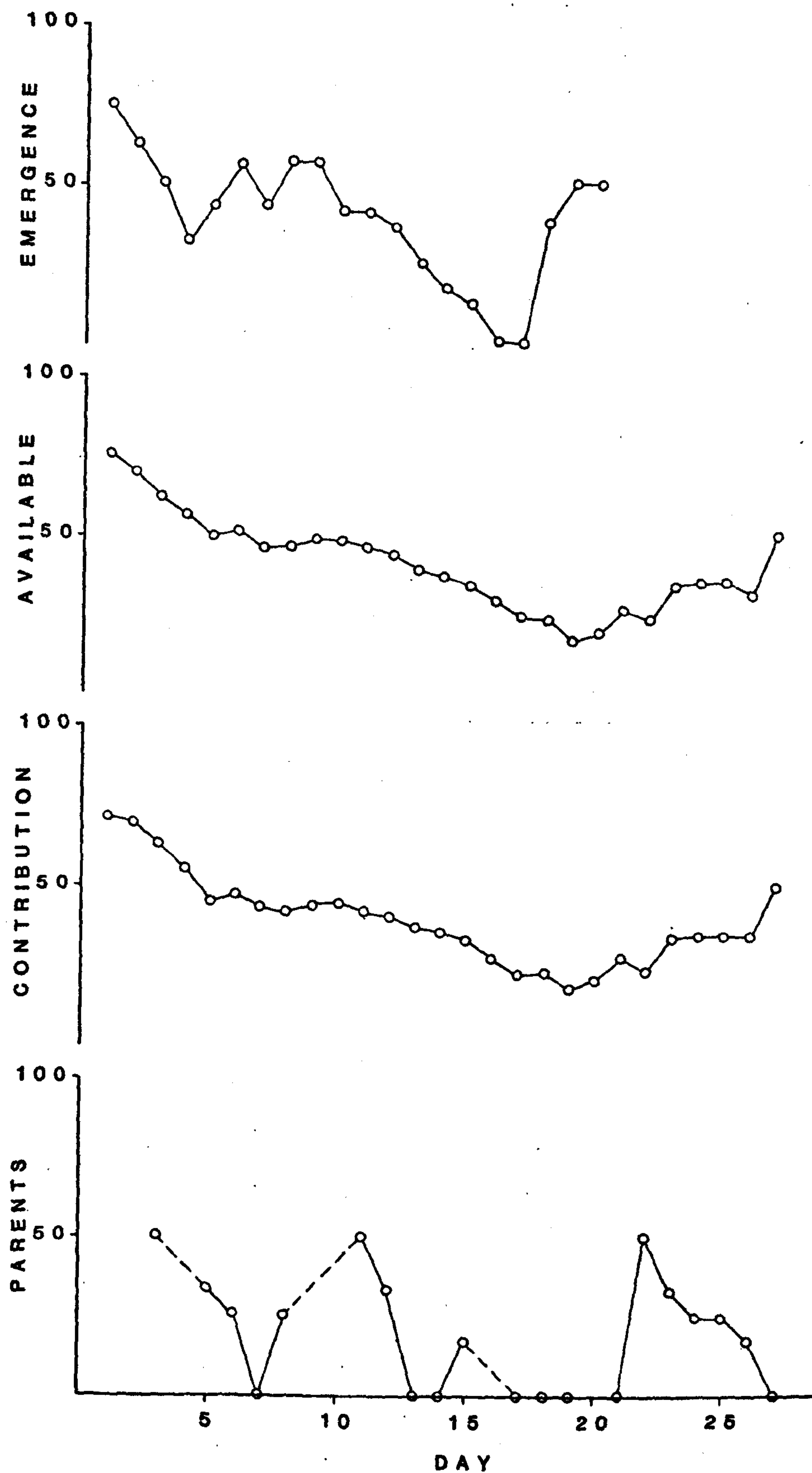


Fig. 9.6 Adh-BD Cage MC2

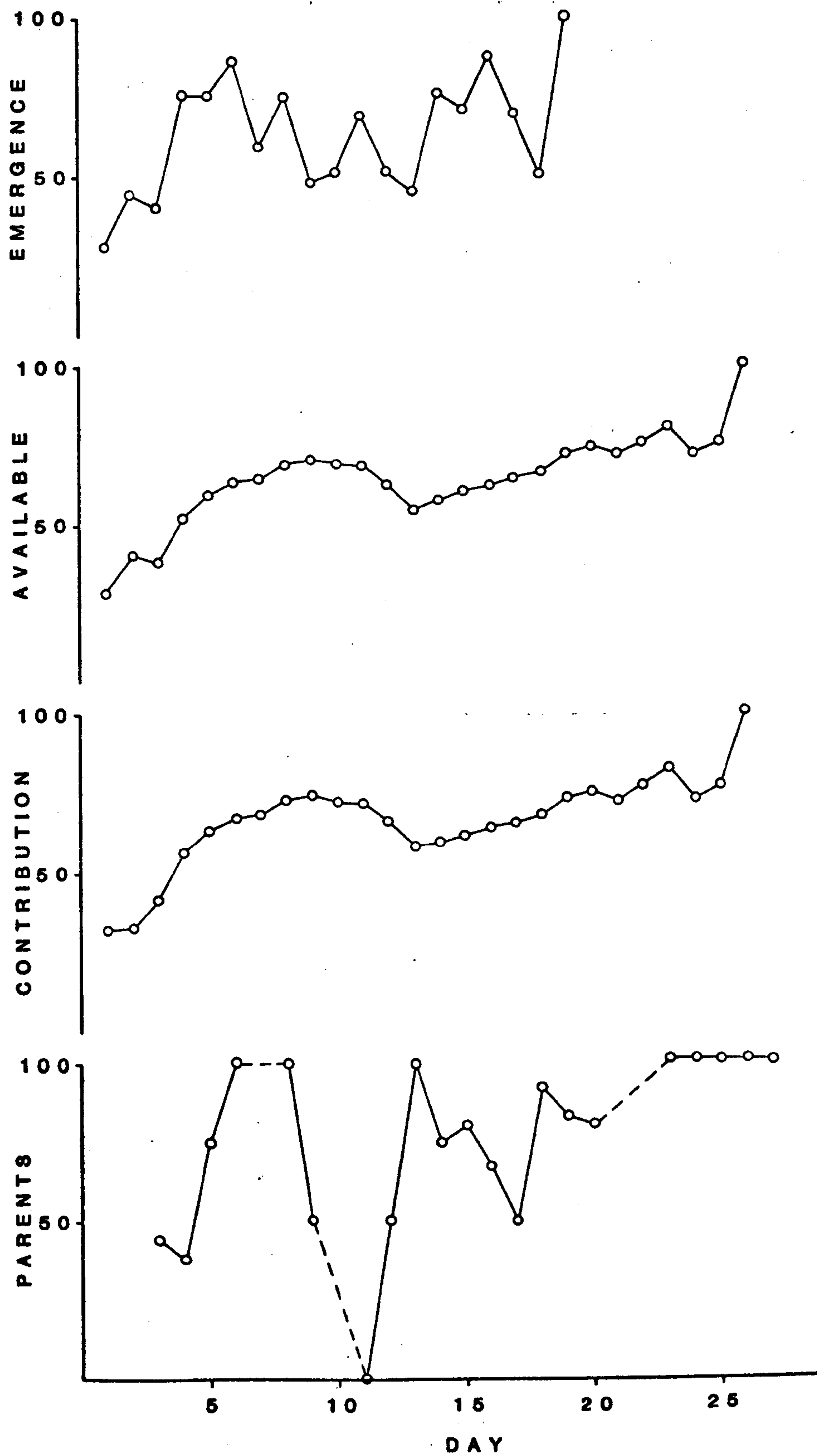
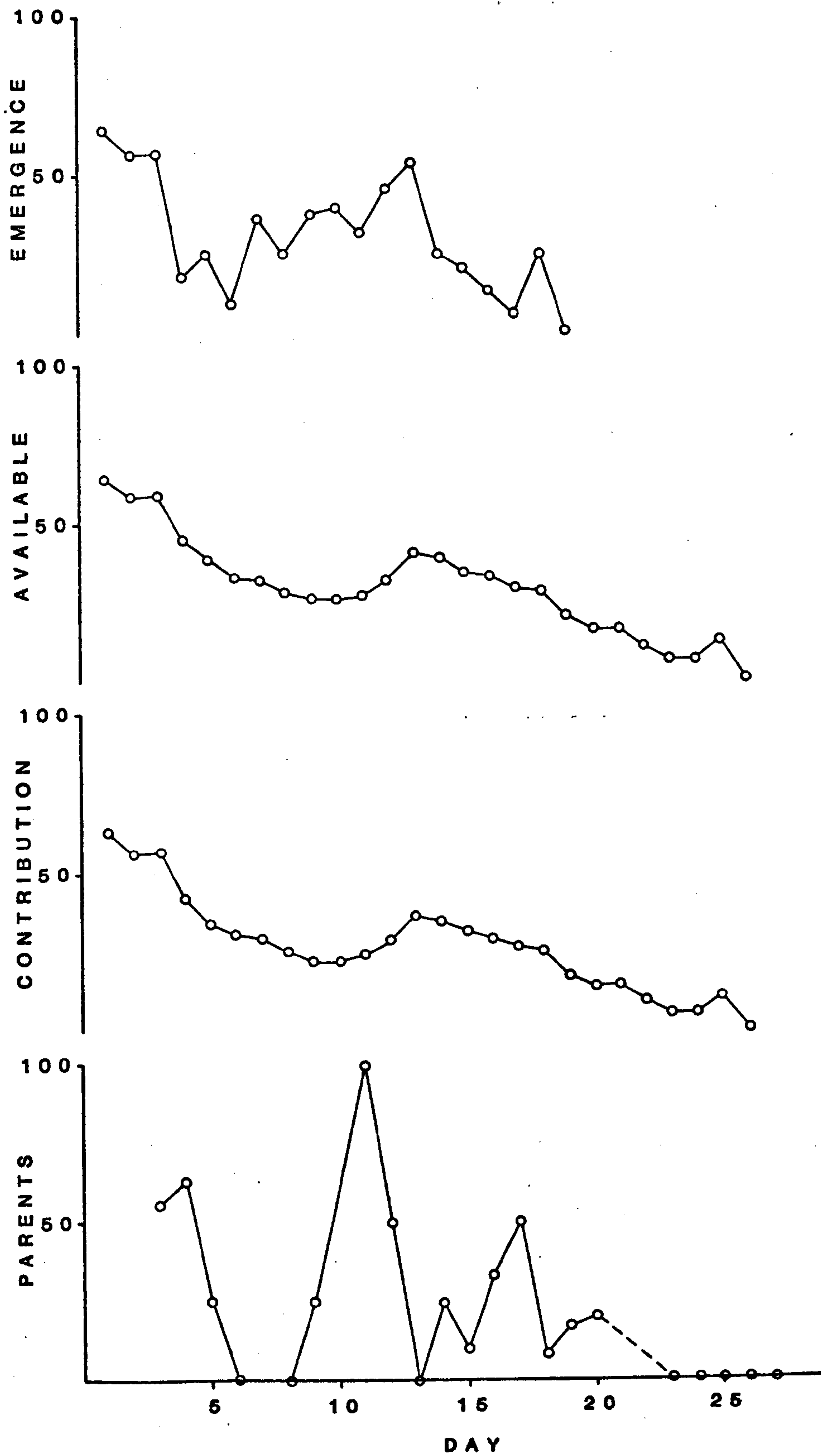


Fig. 9.7 Adh-DD Cage MC2





changed mating pots of the longevity and fecundity experiments on which the predictions are based. The fact that some females apparently did not lay as many batches as they were capable of laying means that there is the possibility of differences between females contributing to the observed discrepancies between observed and predicted proportions of genotypes amongst the parents. On the other hand the total daily expected number of matings for males was consistently higher than the number of egg batches expected, and much higher than the number observed. There is, therefore, much scope for sexual selection to act on males and produce the observed discrepancies.

The peak of egg laying was later than the predicted peak and egg laying was spread over a longer period than expected in both cages. The artificiality of assuming in the calculation of expectations that egg laying is spread evenly through the life of a female may have contributed to this difference. Also if conditions were in some way less suitable for egg laying as suggested above one might expect it to be delayed and thus spread over a longer period. Nevertheless it is encouraging to note that the predicted times of first and last egg laying are very close to those observed.

Allowing for longevity increases the expected proportion of larger flies amongst the parents, whether male or female. This does not alter the proportions of the genotypes amongst the expected female parents because the mean size differences are small. Amongst males the expected contributions of BB and BD genotypes are increased and that of DD decreased. This change is not very significant for the BB genotype because the numbers are so small but for the other genotypes it represents a swing away from

DD and to BD males of about 3% in both MC1 and MC2. The resulting alteration in the predicted parents brings them closer to the observed parents but significant differences remain (Tables 9.15 (b) and 9.16 (b)).

When the effect of size on the frequency of mating or of egg laying is also taken into account the result is similar. There is little if any effect on the genotypic distribution of female parents but amongst males there is a further increase in the predicted proportion of BD parents at the expense of DD males. The swing in this case is a further 5%. Overall, allowing for longevity and fecundity increases the expected proportion of BD male parents from 53% to 62% in MC1 and from 57% to 64% in MC2. This reduces the difference between the observed and predicted (male plus female) parents still further (Tables 9.15 (c) and 9.16 (c)). Nevertheless BD parents are still in excess of, and DD parents below, expectation in both cages (although the differences are no longer significant in MC2).

The expected and observed proportions of parental genotypes can be studied day by day during the emergence period (Figures 9.4 to 9.7) although the numbers of batches on individual days are generally small. As predicted from known development time differences the availability (taking into account longevity) and the contribution (taking into account longevity and fecundity) of the BD genotype increases with time and the DD genotype decreases. Despite large fluctuations due to small numbers trends can also be seen in the proportions of observed parents in the same directions. There is no evidence for differences in timing of the contributions of the different genotypes - the observed contribution of BD flies is

consistently above expectation and that of DD flies below.

c) Discussion The analysis of these results has demonstrated how differences in adult size between Adh genotypes can affect their reproductive success favouring the larger flies. Because females differ little in size the advantage is restricted mainly to males but it can occur without implicating any form of sexual selection such as fighting between males or female choice. However the most important feature of the results is that the effect of size via longevity and fecundity cannot fully account for the observed excess of BD and deficiency of DD. Possible explanations for the residual differences fall into two groups: either they were due to genotypic effects on egg laying by females, or they were due to competition for mates between males.

In the previous chapter significant differences between females of different strains were reported in overall fecundity after allowance was made for the effect of size. However the main difference was a higher fecundity for the outbred SM DD mixed strain than for the three inbred strains. It would be wrong to extrapolate from these laboratory strains to the Adh genotypes in the segregating population used in this experiment. Although it is possible that BD females lay more egg batches than DD females there is no evidence to support this possibility.

On the other hand there is very good evidence from the three fly and mass choice experiments that larger males are more successful in competition for mates than small males. The effect of size was much greater than any effect of genotype in these experiments but again inbred flies were used and it is, therefore,

dangerous to extrapolate genotypic effects to the current experiment.

In MC1A the difference between the mean sizes of BD and DD males was 0.34 divisions. From the results of the three fly experiment this male-male difference would be expected to produce a 10-20% excess of BD male parents over expectation. If the observed excess of BD parents in MC1 is to be accounted for solely by male parents then an excess of BD males of 21% is needed over the expectation allowing for longevity and fecundity differences. For MC2A the mean size difference was 0.23 divisions suggesting an excess of BD males of less than 10% while the required excess to explain the observations in MC2 is 12%.

These results are in very good agreement. A large male advantage would also be expected to produce an excess of BB parents. This occurs, and indeed is very marked, in MC1 but in MC2 there was a deficiency of BB parents. This discrepancy may simply be a result of the small numbers of BB flies involved.

Although this experiment has not provided direct evidence for a large male advantage in competition for mates the results are in very good agreement with predictions on that basis. The experiment was conducted with a broadly based segregating population of flies recently brought in from the field. There was a minimum of disturbance during mating which took place under conditions of changing genotype and size distributions in both males and females. Conditions were unnatural in that the food was artificial and the cultures were maintained at constant temperature and in constant darkness. Nevertheless conditions were nearer to those in natural populations than in any except the isolated female experiments and were, in fact, rather similar to those in the two laboratory



experiments with isolated females. If large males were favoured under these conditions the results of the isolated female experiments appear even more anomalous than before. In these experiments small CD and DD males were apparently at an advantage, especially the rare CDs. Several ways in which these results could be reconciled with the three fly and mass choice results were discussed at the end of the last section. Some of these explanations now appear less likely:-

- 1) The explanation in terms of development time is unlikely because in this experiment there was an excess of BD and deficiency of DD parents throughout the eclosion period.
- 2) The conditions in this experiment were rather similar to those in the isolated females experiments and yet the results agree with the three fly experiments. The differences in conditions are, therefore, unlikely to account for the discrepancy.
- 3) The argument that large male advantage was a feature of the inbred laboratory stocks does not account for the results of this experiment with the St. Mary's B + D line. However the C allele was again excluded and it could possibly be associated with male mating success independent of size.
- 4) Frequency dependence, rare male advantage, remains a possible explanation for the advantage of the CD males in the isolated females experiments but in addition to the lack of any excess of the equally rare BC males in those experiments must be added the rare BB males of this experiment. This possibility effectively reduces to a specific advantage to CD males as in (3).
- 5) The possibility remains that size was not the important factor but was merely correlated with some other important feature of the

successful males. That this correlation must have applied in the very different circumstances of this experiment and the three fly experiment makes it difficult to imagine a suitable character. For example density differences may have been involved in the three fly experiment but could not have been involved here.

6) This experiment and the three fly and mass choice experiments used the same criterion for mating success i.e. parenthood of egg batches. The isolated females experiment did not; instead it assessed which male or males had mated before the females were isolated. This distinction seems most likely to be the key to the differences in results. As discussed in the previous section the discrepancies can be explained if large males gain an advantage by being last to mate with females before they lay their egg batches or in some other way fathering the largest proportion of their offspring. The proposal depends on the way in which fatherhood of egg batches is shared between males when a female mates more than once. Some very preliminary observations on batch sharing will be presented in the next section.

### 9.7 Mixed fatherhood of egg batches

The three fly and mass choice experiments demonstrated clearly that multiple insemination of females leading to egg batches of mixed paternity is common in Coelopa frigida. The small numbers of progeny examined for each batch made an accurate assessment of the frequency of shared batches impossible but a reasonable minimum estimate is that 30% of batches were mixed under the conditions of these experiments. Observational work reported at the beginning of the chapter suggests that most, if not all, females mate repeatedly before egg laying.



The three fly and mass choice experiments both involved the simultaneous presentation of distinguishable males to females whereas in earlier work by Thompson (1951) and Burnet (1960c) males were presented in sequence. In these experiments the last male to mate was invariably successful. On this basis I have suggested that large males might gain an advantage by mating with females last before they lay egg batches or by having a greater ability to displace the sperm of preceding males.

In the three fly experiment there was a suggestion that batch sharing was more common where there was only a small difference in size between the two males. This appearance could have resulted from a more even "share-out" between close males than between males one of which was much larger than the other.

In addition there was a striking excess of shared batches where the female parent was Adh-BB compared to Adh-DD females. There are probably differences between these strains in some female characteristic, such as willingness to remate, but as the strains used were highly inbred this may not be associated with the Adh locus or the  $\alpha/\beta$  inversion.

I have carried out two small experiments to investigate batch sharing further. In the first males were presented sequentially as in Thompson's (1951) and Burnet's (1960c) experiments and in the second males were presented together and their sizes were compared with their representation in the offspring.

a) Males presented sequentially About 150 virgin females were collected by the twice daily removal method from the BB(1ab) and from the DD(1ab) stock lines. They were aged for 24 hrs with

standard culture medium to feed on at 27°C and then mixed with a similar number of males from their own line. Each group of males and females was then kept at 27°C for a further 24 hrs to allow mating to take place. During this time medium was present to encourage mating but flies were excluded from it by a gauze screen to prevent egg laying. At the end of this period a sample of 48 BB and 48 DD females was taken to ascertain the proportions which had mated. The remaining flies were sexed and then placed in standard culture tanks - the DD females with the BB males and vice versa. Egg batches laid in these tanks were removed after 18 hours to round canisters and the resulting larvae were electrophoresed. 24 larvae were determined from each egg batch in order to have a very good chance of detecting all mixed batches.

In the samples taken to ascertain the proportions of mated females, 13 out of 45 egg batches (29%) laid by BB females hatched and 11 out of 45 (24%) laid by DD females hatched. All 51 of the egg batches laid by DD females that had had the opportunity to mate a second time (with BB males) were fathered by the second male alone (i.e. all progeny were BD). Amongst the batches laid by BB females 1 was fathered by the first, BB, male alone, 27 were fathered by the second, DD, male alone and 8 batches were of mixed fatherhood. In total 25% (9 out of 36) egg batches laid by BB females contained some eggs fertilised by the first group of males compared with the expected 29% of females which had mated with those males. By contrast where the females were DD none of the expected 24% mated by the first group of males laid egg batches in which these males were represented.

In 7 of the 8 mixed batches laid by BB females more than half

the progeny were fathered by the second, DD male. Indeed in five cases there was only 1 BB larva in the 24 progeny determined.

These results confirm the precedence of the last male to mate in a sequence but this precedence is not absolute as suggested by Thompson and Burnet. There may be mixed fatherhood with the later male taking the larger share of the progeny. It is not known how many times females might have mated during this experiment but they had similar lengths of time with the two groups of males and all flies were sexually mature at the start of the experiment. More closely controlled experiments are clearly desirable to quantify the replacement of sperm at succeeding copulations.

A striking feature of the results is the difference between the two groups. Replacement in the DD females group was apparently much more complete than in the BB females group. This could either be because DD females remate more readily than BB females or because BB males are more efficient at replacing sperm from earlier matings than are DD males. In the three fly experiments BB females laid more mixed batches than DD females as they did here but in that case with two different males available simultaneously one would expect the opposite result. Frequent remating with two types of males available throughout should give many mixed batches, whereas frequent remating with males available sequentially should give few mixed batches. This paradox may be solved by differences in male replacement ability which would not have shown up clearly in the three fly experiments. It is possible that BB males were larger than DD males in this experiment (sizes were not recorded) and so a greater replacement ability for BB males could be either a size effect or a genotypic effect.

b) Male-Male size differences and batch sharing Virgin flies collected by the twice daily removal method were set up for this experiment exactly as for the three fly experiments, that is one female and two males in each mating pot with medium. The flies used were from the SM/MN BB Mixed, SM/MN CC Mixed and SM DD Mixed lines and were used in the three combinations: BB female with CC and DD males, CC ♀ with BB and DD males, DD ♀ with BB and CC males. This design provided an important internal check for virginity. All flies were measured at the beginning of the experiment. Adults were removed when the first egg batch appeared in each pot and larvae were transferred to round canisters. Up to 24 larvae from each batch were determined by electrophoresis. Batches which produced less than 10 larvae were discarded. Unfortunately this experiment suffered from an unidentified infection which destroyed many batches around the time of hatching. Overall 68 pots were established but only 34 produced enough larvae to be of use.

Of the 34 successful batches 18 were fathered by the larger male only, 4 by the smaller male and in two cases where there was only one father the two males were of equal size (Table 9.17(a)). This overall excess of large males was significant ( $\chi^2_1 = 8.91$ ,  $P < 0.01$ ) and consistent over the three genotypic combinations ( $\chi^2_2 = 1.97$ ,  $P > 0.2$ ). The remaining 10 egg batches were of mixed paternity. Seven of these had BB female parents, 3 had CC and none DD female parents (Table 9.17 (b)). These values are not statistically heterogeneous ( $\chi^2_2 = 4.7$ ,  $0.05 < P < 0.10$ ) but this could be simply due to the small numbers involved. It is interesting that the completely independent BB and DD strains used here gave similar results to the BB(lab) and DD(lab) strains of the three fly experiments.

Table 9.17 Results of batch sharing experiment

a) Egg batches with only one male parent

Female genotype	Large male successful	Small male successful	Males equal in size
BB	6	0	2
CC	8	3	0
DD	4	1	0
TOTAL	18	4	2

b) Egg batches with two male parents

Female genotype	Shared batches	Total number of batches
BB	7	15
CC	3	14
DD	0	5
TOTAL	10	34

c) Male-male size differences and distribution of larvae

Size difference (divisions)	Proportion of larvae fathered by larger male	Number of larvae determined
BB♀ 0.4	0.70	23
0.3	0.78	18
0.4	0.83	24
0.3	0.83	24
0.3	0.58	19
0.1	0.21	24
0.4	0.79	24
CC♀ 0.3	0.65	17
1.0	0.96	25
1.0	0.96	24



Also the CC females, which like the DDs were karyotypically  $\beta\beta$ , gave a low frequency of shared batches.

Looking at the distribution of larvae within the shared batches (Table 9.17(c)) the proportion fathered by the larger male increases with increasing male-male size difference ( $b = 0.88 \pm 0.20$ ,  $P < 0.05$ , after arcsin transformation). In nine out of ten cases the larger male had the larger share of the offspring and in the one exceptional case the size difference between the males was only 0.1 divisions. This relationship clearly needs to be investigated further but if it turns out to be confirmed it will strongly support the hypothesis that the larger male's advantage resides either in an ability to mate last or in a greater ability to displace sperm from previous ejaculates.

### 9.8. Discussion

In natural populations, as well as in the laboratory, variation in adult size of Coelopa frigida is associated with alcohol dehydrogenase genotype. The differences are much more pronounced in males than in females. Larger females live longer and lay more eggs. Larger males also live longer and they mate more often - both on a lifetime scale and during a 30 minute observation period. In addition larger males are more successful in competition for mates, at least in a variety of conditions in the laboratory. Some experimental results at first sight suggest that this last advantage does not occur in natural conditions (the isolated female experiments) but the results can be reconciled by assuming that the large male advantage lies in an ability to gain precedence for his sperm. This



may be achieved either by a greater sperm displacement efficiency or an ability to be the last male to mate before egg laying. There is some independent evidence that larger males can gain an advantage in this way. Wade and Arnold (1980) have pointed out that mixed fatherhood of batches reduces the intensity of sexual selection on males but this depends on the relative contributions of males in the sequence of matings.

There are several indications in the results of direct genotypic effects on elements of reproductive behaviour. Perhaps the most striking and important of these is the tendency for Adh-BB females to lay more egg batches of mixed fatherhood than Adh-DD females. If this represents a difference in the females' willingness to remate then it may account for some of the other observed genotypic effects such as the unusually high proportion of large male successes with Adh-DD females in the three fly experiments. Genotypic effects on remating frequency have been observed in Drosophila (Pyle and Gromko 1981). On the whole though, the direct genotypic effects are small in comparison with the influence of adult size and so it is the size differences between adults of different genotypes that are likely to have the most important influence on gene frequencies in natural populations.

As in previous sections of this thesis the results of the observations and experiments on adult size and reproductive success have been recorded in terms of alcohol dehydrogenase genotypes because this is the way in which the results were obtained. But the association between the Adh locus and the  $\alpha/\beta$  inversion system must be taken into consideration. Are the observed relationships effects of the inversion, the Adh locus, or both? In most of the

experiments there is no way of distinguishing the two because the strains used were fixed for Adh-B and the  $\alpha$  sequence of Adh-D and the  $\beta$  sequence. Other laboratory strains were segregating for the Adh-B and D alleles but these were probably completely associated with the  $\alpha$  and  $\beta$  sequences respectively. Only where the Adh-C allele occurred was there any possibility of detecting effects of the Adh locus independent of the inversion. The sizes of flies carrying the C allele are very variable within and between populations and, although they do not fit with expectations on the assumption that the Adh locus has no effect on size, the numbers of these genotypes are always too small for detailed analysis.

Examples are known in other insects where inversion polymorphisms affect adult size (Prevosti 1966, White et al 1963, and see Introduction) and many cases where they affect components of reproductive behaviour (see review by Spiess 1970 and Introduction). Indeed in Drosophila subobscura inversion polymorphisms are associated with adult size and adult size affects mating speed (Monclus & Prevosti 1971, Krimbas & Loukas 1979). It is, therefore, entirely plausible that the  $\alpha/\beta$  inversion in Coelopa could affect adult size and hence mating success or could affect mating success directly. Adult size is likely to be polygenically determined and an inversion could hold together a set of genes having effects in the same direction.

On the other hand an effect of a single enzyme locus on adult size or directly on mating behaviour is more difficult to imagine. In Drosophila melanogaster links between Adh genotype and adult size (Pieragostini et al 1979) and mating success (Knoppien et al 1980) have been suggested but, especially in the case of size, these

effects may well be due to other genes in linkage disequilibrium.

In many species of insects larger females lay more eggs (Hinton 1981) and this is often associated with a longer life span. Several examples have been studied in which large males have increased mating success including Drosophila melanogaster (Ewing 1961, 1964), Drosophila subobscura (Monclus & Prevosti 1971), Musca domestica (Bryant 1980, Baldwin & Bryant 1981), Scatophaga stercoraria (Parker 1970f, Borgia 1981), Tetraopes tetraophthalmus (McCauley 1979, 1982), soldier beetles (Mason 1980) and weevils (Johnson 1982). However the mechanisms by which the advantage is gained may be different. In the Drosophila species the advantage is probably in the greater ability of large males to stimulate females and this may well be true in Musca also. In the others the advantage is in conflicts between males either before mating or while guarding mates after mating.

The situation in Scatophaga has been particularly well studied and is relevant here because of the involvement of multiple insemination of females and sharing of egg batches between males (Parker 1970b,c,d,e,f). After copulation males stay in the mounted position for a "passive" or "guarding" phase. During this time other males may attempt to dislodge them and if they succeed will mate with the female. As each subsequent male to mate displaces some 80% of sperm already present from previous matings there is a clear advantage to a male in guarding a female between mating and egg laying, which occurs in bouts comparable to the laying of Coelopa egg batches. Large males are at an advantage because they are better at displacing guarding males and are themselves less easily displaced. However even in this male controlled system females show a preference

for large males when in a position to choose (Borgia 1981).

This is just one possible way of ensuring last mating. In some butterflies a plug or sphragis is inserted by the male after copulation to prevent further matings (Eltringham 1925) and in some diptera the male accessory gland secretion induces non-receptivity in females after mating (Craig 1967). Nevertheless multiple insemination is common (Boorman & Parker 1976, Richmond 1976, Gromko et al 1980, Cobbs 1977, Milkman & Zeitler 1974).

Usually the male ejaculate is larger than is necessary to fill the female storage organs and there is probably a "flushing out" effect which tends to mean that the latest male to mate fertilises the majority of subsequent offspring (Parker 1970a, Boorman & Parker 1976). In some cases the male might actually "clean out" the spermathecae (Waage 1979). It is clearly possible that the size of the male ejaculate could affect the extent of sperm displacement. If ejaculate size is related to body size this could confer an advantage on larger males.

Parker (1974) has considered the factors affecting a female's propensity to remate. One factor may be depletion of the store of sperm in the spermathecae. This seems to be the case in Drosophila (Manning 1967, Pyle & Gromko 1981), although in D. melanogaster remating occurs after as little as 2 hours (Fuerst et al 1973), apparently when sperm supply is depleted but not necessarily exhausted (Gromko & Pyle 1978). Baldwin and Bryant (1981) suggest that the titre of male accessory gland fluid, effectively the volume of the ejaculate, affects the propensity of female houseflies to remate and that this explains the more frequent rematings observed when the first male to mate is of small body size. In Coelopa this



sort of thing could contribute to large male advantage. If small males have small ejaculates, and females are therefore more likely to remate after mating with a small male, then large males will be the last to mate in more cases than expected. This type of explanation of the large male advantage in Coelopa is probably the most plausible on the available evidence. It can explain the superficially conflicting evidence of the various mating experiments and is consistent with the observations of mixed paternity. At the same time it does not involve behaviours such as male guarding which have not been observed in Coelopa. It allows for an element of female choice because once a female's spermathecae are full she may reject further males and it can accommodate greater selection for large males by large females, as seen in the three fly experiments, if they need more matings to maintain a supply of sperm. Parker (1974) also suggests that females might remate because to do so wastes less time than continually to reject persistent male courtship. If larger males court more persistently then a female may be more likely to remate with a large than with a small male and large males may gain the advantage of being last in this way.

The question of non-random mating in Coelopa needs to be approached on two fronts. It is important to establish unequivocally that there is an advantage to large males in natural conditions and that multiple insemination is common. This would require sampling in the field from an adult population and from the egg batches they laid. This type of experiment is feasible but very much dependent on finding a suitable field situation where adults are sufficiently numerous for the collection of large samples and also young enough



for reliable electrophoresis. Searching for egg batches in natural wrack beds is tedious but if the wrack bed was in a suitable condition it would be possible to obtain a reasonable sample size.

In the laboratory the type of question which needs to be answered is: do larger males have larger ejaculates? is a single copulation sufficient to fertilise an egg batch? when do females become unreceptive? are females less likely to remate after mating with a large male? how is the fatherhood of larvae shared between males mated in a sequence of different sizes and genotypes? All of these questions would be susceptible to simple experiments.

If there is a large male advantage in natural conditions then it is important to consider its implications for the maintenance of the Adh and inversion polymorphism. In the experiment with undisturbed cages in the laboratory the Adh-B frequencies amongst adults emerging in MC1A and MC2A were 32.3% and 36.5% respectively while amongst the offspring in cages MC1 and MC2 the frequencies were 43.4% and 38.7%. These increases in B frequency are comparable to the differences between parents and offspring observed in the viability experiments of Chapters 5 and 6. They indicate a substantial selective advantage for the Adh-B allele or  $\alpha$  sequence which must be balanced by some advantage to the  $\beta$  sequence (or Adh-D allele) in order to maintain the stable polymorphism observed in natural populations. Indeed in natural populations the frequency of the D allele is almost always higher than that of the B allele, and similarly the  $\beta$  sequence is more common than the  $\alpha$  sequence. In Chapter 3 it was proposed that the interaction between development time and wrack bed duration could favour the faster developing

Adh-DD and  $\beta\beta$  individuals. In the following chapter I will examine the way in which size, development time and viability differences between genotypes might interact to produce the pattern of gene frequencies observed in natural populations.

## Chapter 10

### Discussion

#### 10.1 Synthesis

The Chromosome I inversion polymorphism in Coelopa frigida had been under study for several years before the start of this project. The frequency of the  $\alpha$  arrangement in samples from natural populations was almost always between 0.4 and 0.5 and heterozygotes were in excess. In the laboratory effects of the inversion on egg to adult viability and on development time had been demonstrated. Electrophoretically detectable alleles at the Adh, Est-2 and Pep-1 loci showed associations with the inversion, that for the Adh-B and Adh-D alleles probably being complete (Collins 1978, Day et al 1980, 1982). This project has added the following observations:-

- 1) An extensive programme of sampling from natural populations has confirmed the observation of very stable inversion frequencies both geographically and temporally but with the addition of a seasonal cycle. The  $\alpha$  frequency has a peak in late summer and a trough in mid-winter. There is also a correlation between the  $\alpha$  frequency and the frequency of Coelopa pilipes.
- 2) This set of samples also confirms the existence of a consistent excess of heterozygotes in natural populations.
- 3) Development time differences between karyotypes have been confirmed in conditions close to those of natural populations.
- 4) The effect of larval density on viability differences has been examined both in the laboratory and in the field. High density does seem to increase mortality of homozygotes relative to heterozygotes but the effect is much less marked than suggested by Collins (1978).

Selective mortality appears to be concentrated mainly in the first two days of larval life.

5) The karyotypes differ in adult size both in the laboratory and in the field. Larval density affects both adult size and development time - the interrelationships of these three variables have been examined.

6) Adult size is correlated with longevity and fecundity in both males and females, and large males enjoy greater mating success than small males.

7) There is a lack of evidence for coadaptation in crosses between flies from different geographic populations. Results suggest that viability differences between karyotypes are due to genic rather than karyotypic effects.

To what extent is the information now available about this polymorphism sufficient to explain the observed frequencies in natural populations?

Collins (1978) produced a computer simulation of a Coelopa population incorporating the selective effects then known, that is viability, development time and longevity differences. The simulation produced an equilibrium frequency of  $\alpha$  in the region 0.40 to 0.45. Collins took this good fit to the observed  $\alpha$  frequencies in natural populations as an indication that the principal selective effects on the inversion had all been identified, although he was clearly aware of the possibility that the fit was coincidental. The equilibrium in his model population was effectively maintained by heterokaryotype advantage in viability and was biased in favour of the  $\beta$  sequence because the  $\beta\beta$  homozygote had the shortest development time and greatest longevity.

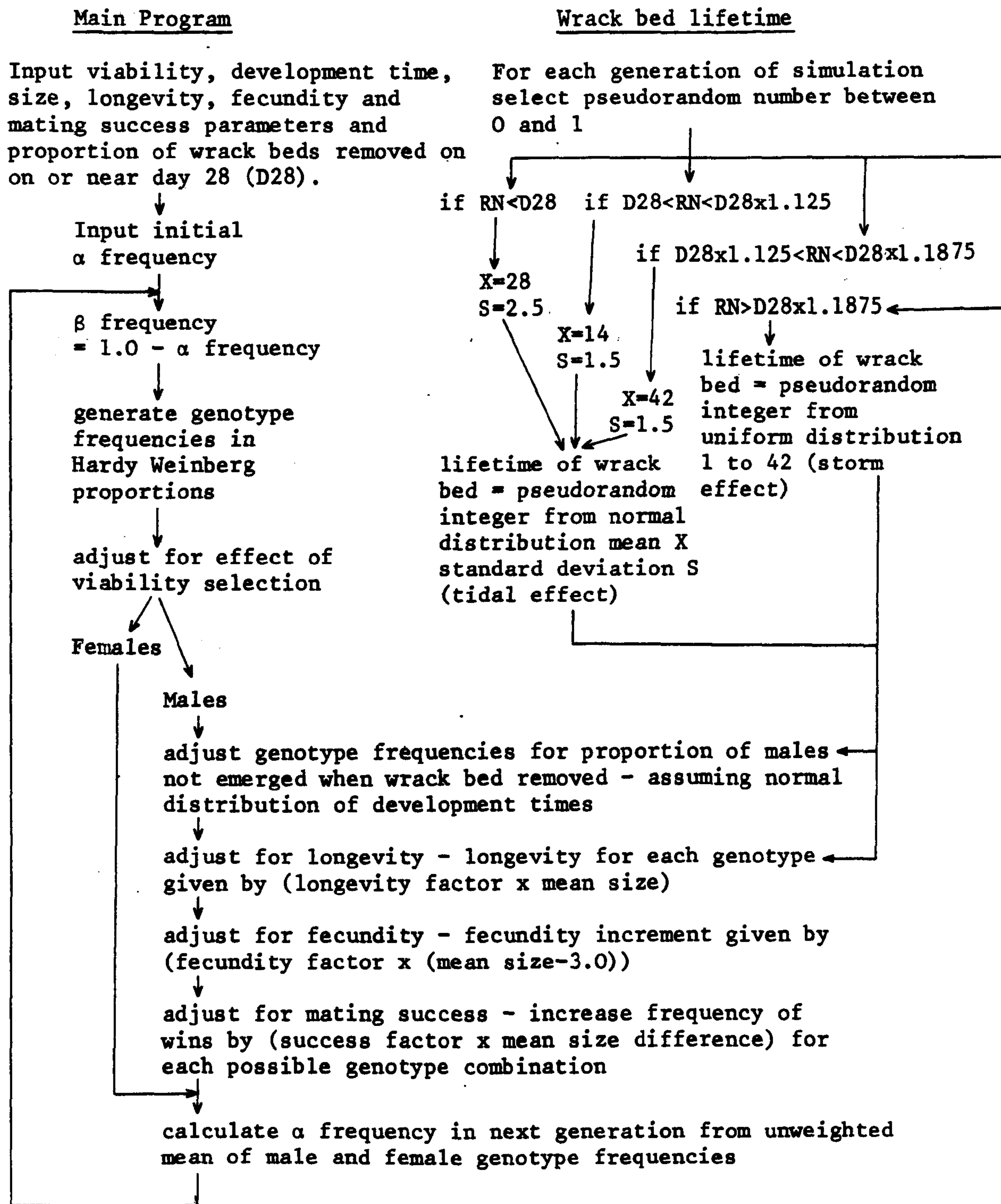


Fig.10.1 Flow diagram of simulation. For details of the procedures see the program listing in Appendix 10.



It is now clear that this simulation was inadequate for two reasons:-

- 1) It did not include the size differences between karyotypes and their potentially important effects on longevity, fecundity and mating success.
- 2) The data on natural populations were insufficient to provide a good test of the model. In particular Collins was not aware of the existence of a season cycle in inversion frequencies and therefore could not attempt to reproduce such a cycle in the model population.

However Collins' model did show how development time differences were likely to interact with wrack bed life times and with viability selection. This is the type of information that should be sought from simulation studies rather than attempting to produce fits to observed frequencies. It is often possible to produce a given equilibrium frequency from a variety of different sets of parameters.

The set of possible selective influences on the inversion polymorphism is now even larger and so a simulation study is potentially more useful. I have constructed a simple deterministic simulation in FORTRAN with the aim of examining the likely effects of individual selection pressures and combinations of pressures, and of simulating the seasonal cycle in inversion frequencies. An outline of the program is given in Fig.10.1 and the full listing is in Appendix 10. The important assumptions are:-

- 1) The relative frequencies of wrack bed removal by the spring tides (day 28) and inter-spring tides (days 14 and 42) are taken from Collins (1978). The proportion of removals due to storms is set at 5% in most program runs but can be varied.
- 2) The distributions of development times are taken as normal with standard deviations of 7.50 days and means set for each genotype

in each program run.

- 3) Adult size is assumed not to be related to development time.
- 4) Differences between karyotypes in development time and size are restricted to males.
- 5) There are no size independent differences between karyotypes in longevity, fecundity or mating success.
- 6) Effects of larval density are not included in the model for two reasons: firstly there is no objective way in which to assign densities in each generation and secondly although the effect of density on size and development time is reasonably well characterised its effect on relative viabilities is still uncertain.
- 7) The model includes no element of genetic drift, the only variable effect included being the wrack bed lifetime.

A run of the simulation program with a set of parameters chosen as best approximations to the effects in natural populations estimated from my results gives an equilibrium  $\alpha$  frequency of about 0.48 with variation from about 0.40 to 0.55 (Fig.10.2). This is encouragingly close to the frequencies observed in natural populations (average about 0.44). Although the fit is not perfect the simulation appears to be a valid working model.

The observed selective effects are certainly sufficient to explain the average frequencies found in nature, but the estimates of parameters may be inaccurate. The fit does not mean that there are not other selective effects still to be discovered or, indeed, that the effects included are necessary to explain the observed frequencies. Clearly it would be possible to obtain a similar equilibrium frequency with viability selection alone given suitable values for the selection against  $\alpha\alpha$  and  $\beta\beta$  homokaryotypes.

Figs.10.2-10.7 Results of simulation runs. Each figure shows the results of 15 runs of 100 generations; 5 runs each with starting  $\alpha$  frequencies of 0.1, 0.5 and 0.9. The settings of the parameters are given on each figure:-

SBB	Viability selection against $\alpha\alpha$
SDD	Viability selection against $\beta\beta$
BBDM	Mean development time of $\alpha\alpha$ males
BDDM	Mean development time of $\alpha\beta$ males
DDDM	Mean development time of $\beta\beta$ males
BBS	Mean size of $\alpha\alpha$ males
BDS	Mean size of $\alpha\beta$ males
DDS	Mean size of $\beta\beta$ males
F	Fecundity coefficient
S	Mating success coefficient
Q	Longevity coefficient
D28	Proportion of wrack beds removed on or about day 28

Fig. 10.2

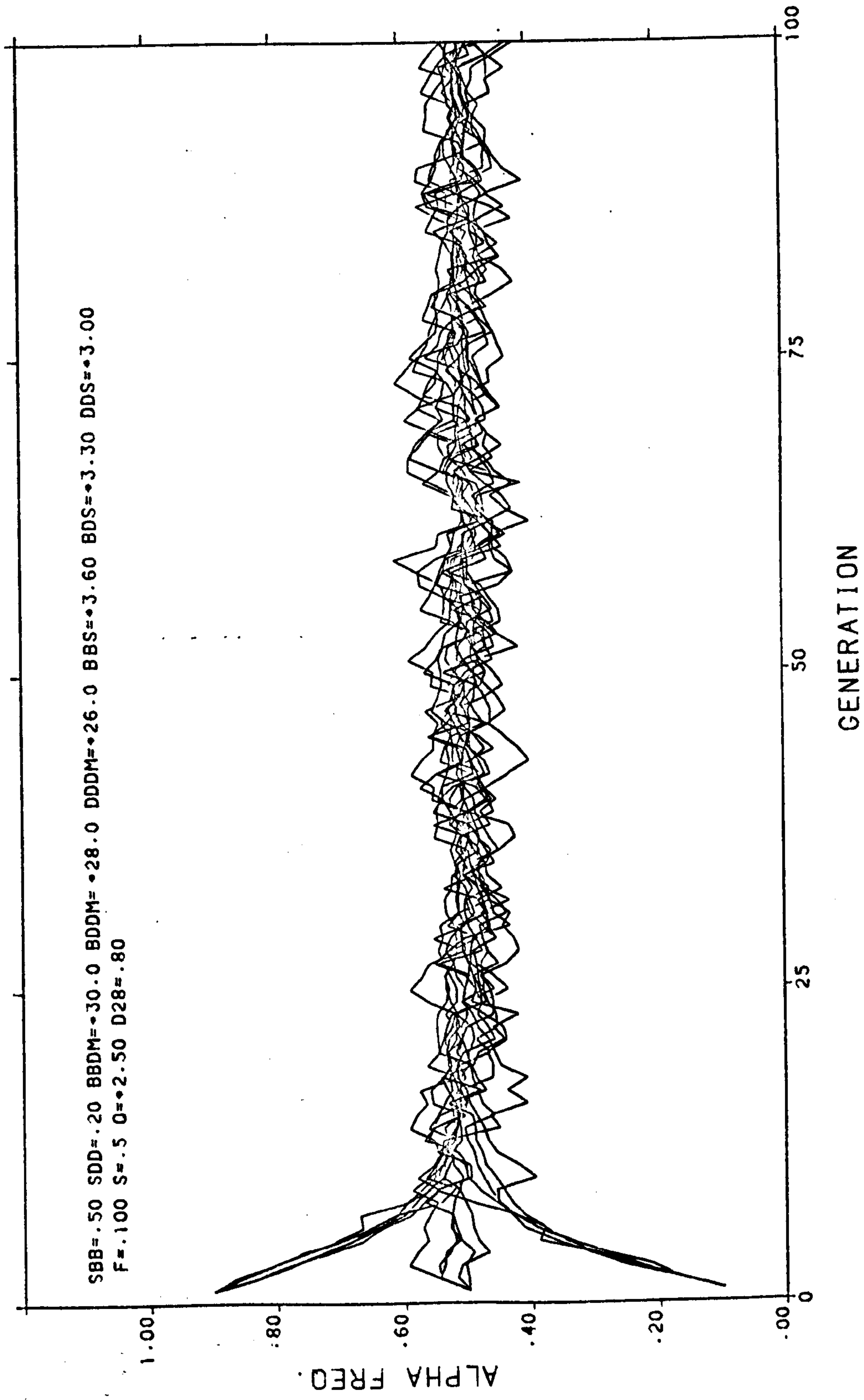


Fig. 10.3

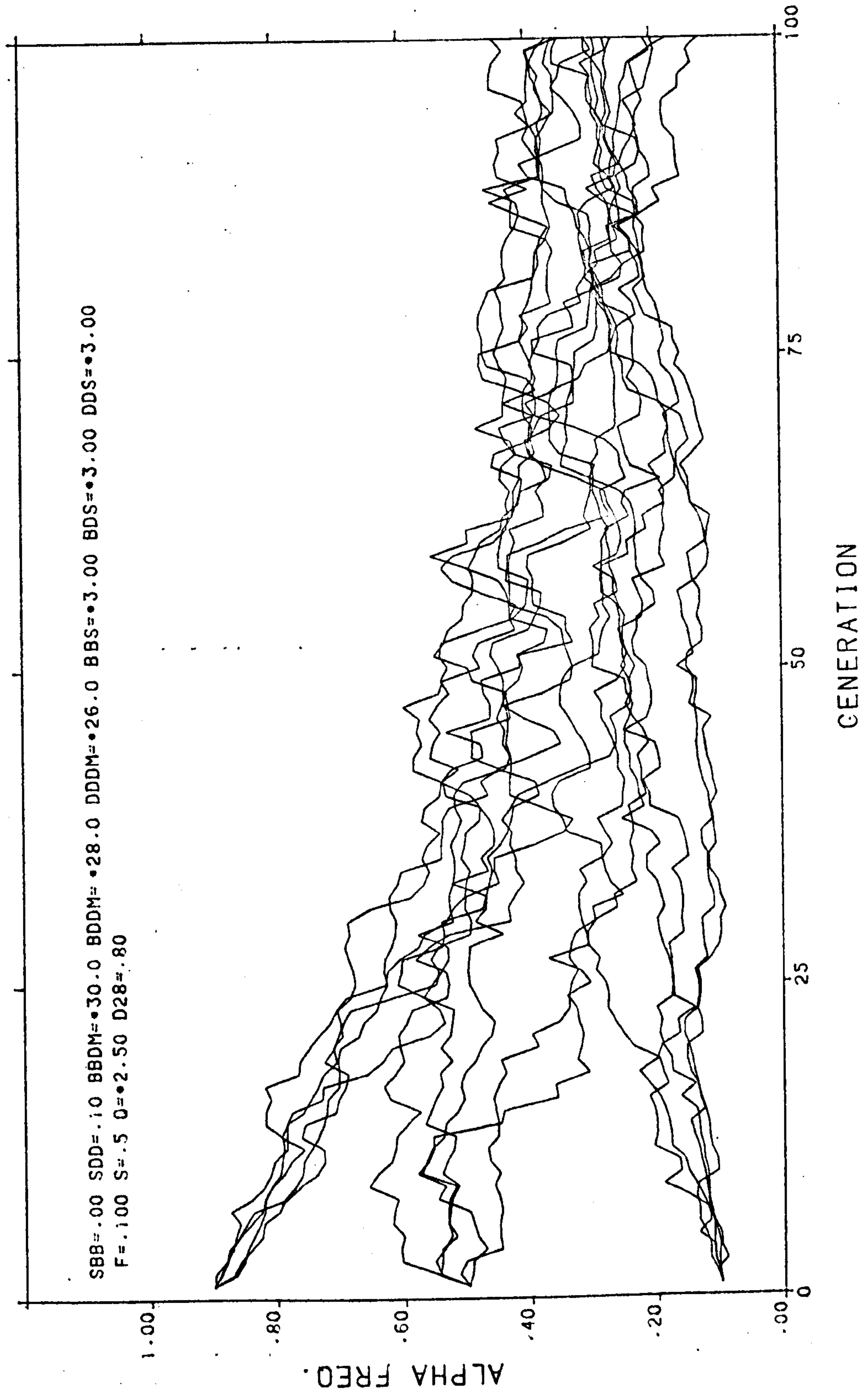




Fig. 10.4

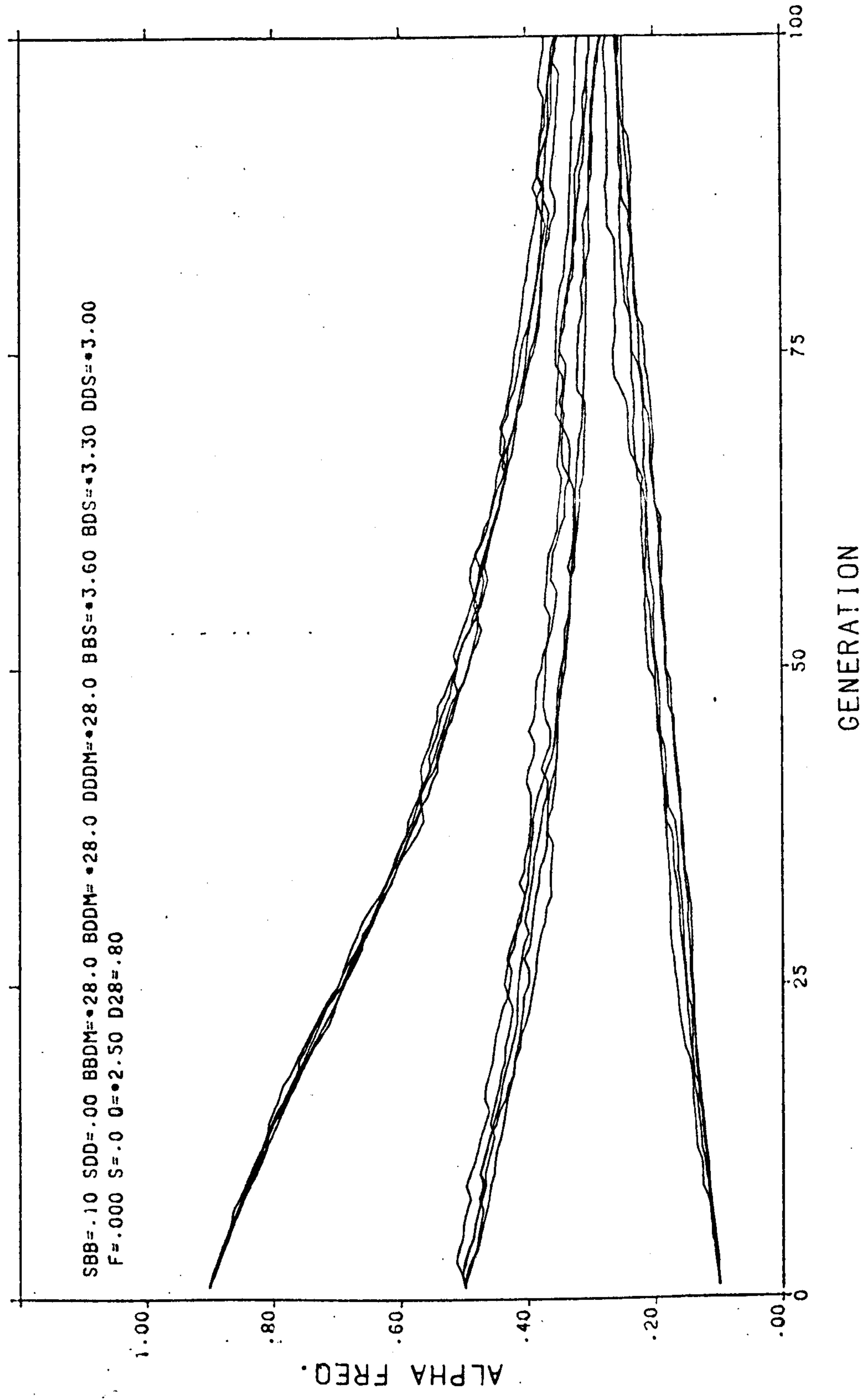


Fig. 10.5

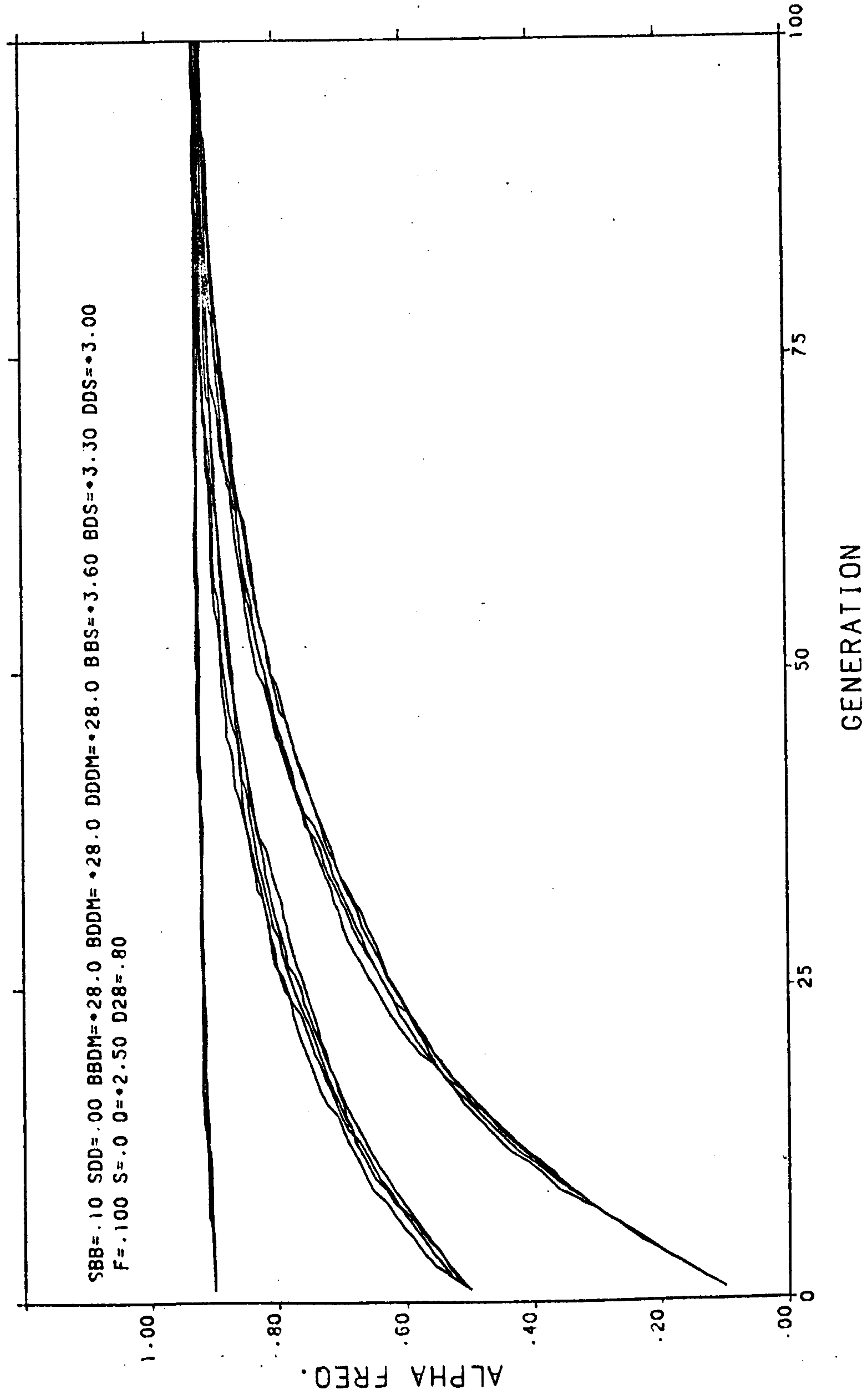


Fig. 10.6

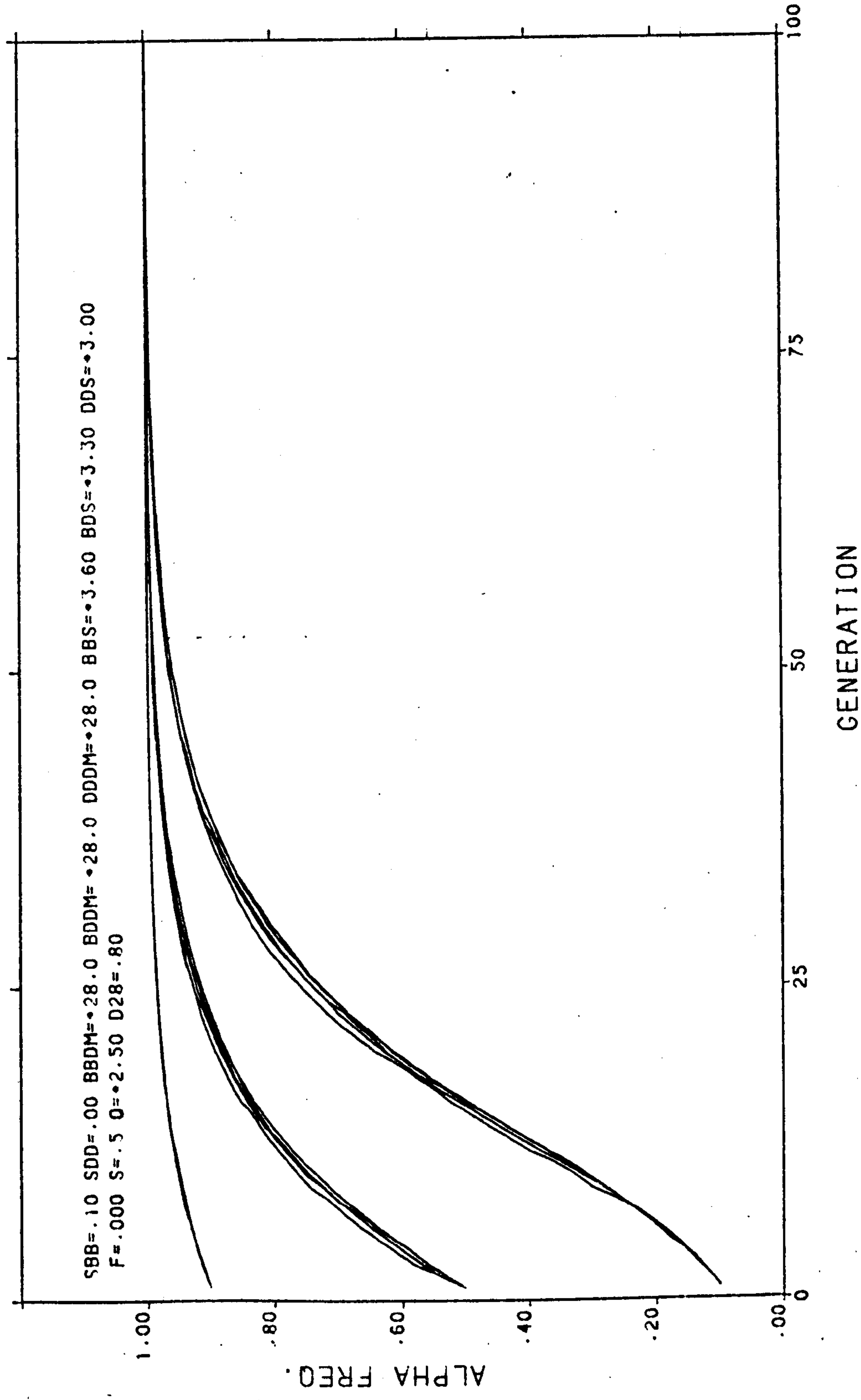
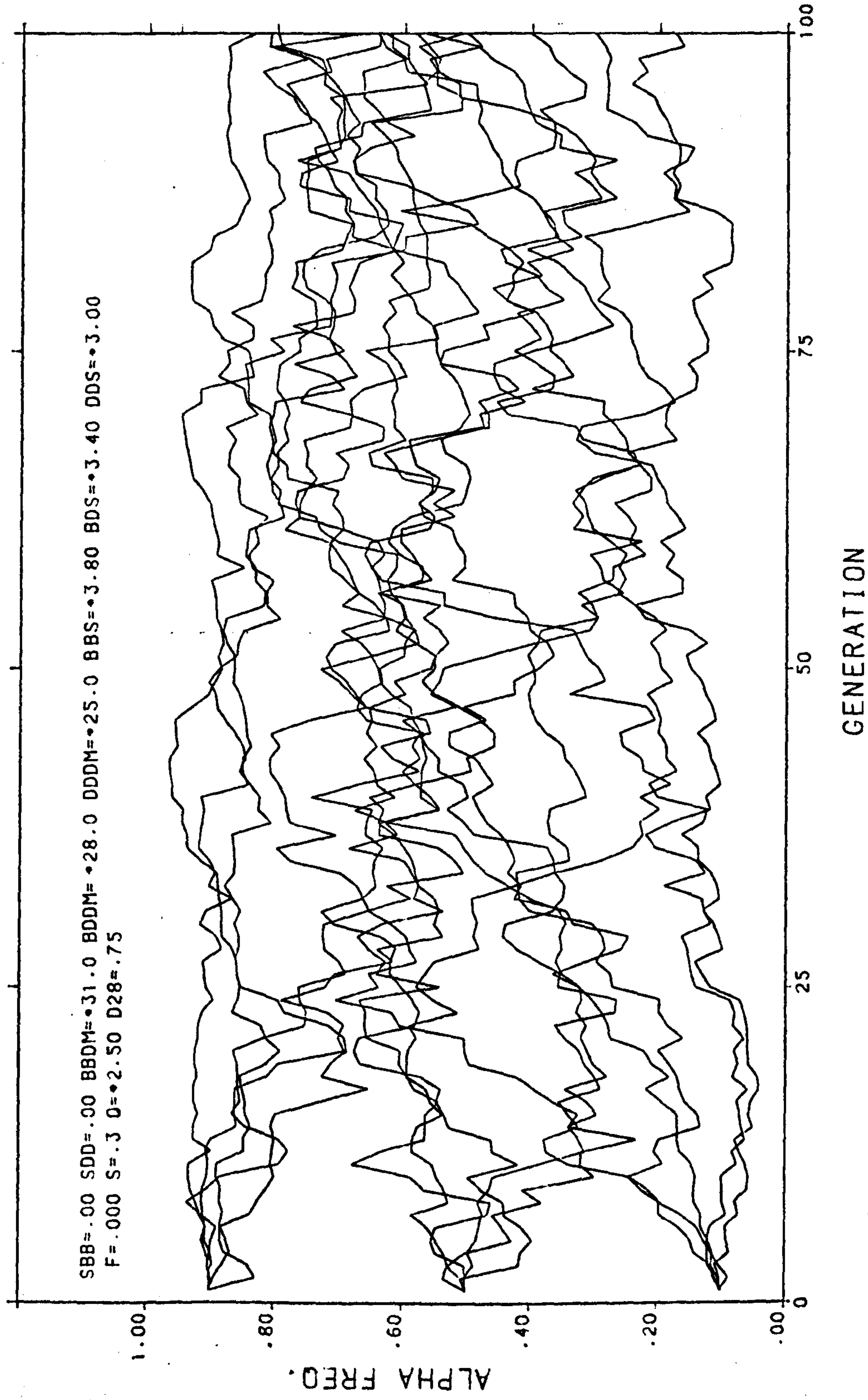


Fig. 10.7



With the viability selection coefficients used in the simulation in Fig.10.2 alone ( $S_{\alpha\alpha} = 0.5$ ,  $S_{\beta\beta} = 0.2$ ) the equilibrium  $\alpha$  frequency would be 0.29. How do the other types of selection included contribute to the shift in equilibrium to an  $\alpha$  frequency of 0.48? The simulation can be used to answer this question by examining the effects of the other selection pressures one or two at a time.

The observed differences in development time favour the  $\beta$  arrangement. This can be seen in a simulation run with no size differences but with realistic development time differences set against a viability selection coefficient of 0.1 for  $\beta\beta$  (Fig.10.3). The system moves slowly towards an equilibrium at about 30%  $\alpha$ . There is still a wide spread of values amongst 15 runs at generation 100 and the frequency changes within single generations can be quite large (5% or more). Clearly a combination of viability and development time effects alone would produce an equilibrium below 30%  $\alpha$ . There must be some balancing advantage to the  $\alpha$  arrangement and this presumably lies in the size related effects.

Runs of the simulation including size differences but not development time differences are shown in Figs.10.4 to 10.6. In Fig.10.4 size has no effect on fecundity or mating success but is correlated with longevity. The result is an equilibrium at about 30%  $\alpha$  against a 10% viability disadvantage for  $\alpha\alpha$ , so the selective effect of longevity differences favours the  $\alpha$  arrangement as expected but is only weak by comparison with development time selection. Including the effect of size on fecundity (Fig.10.5) gives much stronger selection in favour of the  $\alpha$  arrangement. The equilibrium in the region of 90%  $\alpha$  indicates an effect at least as strong as that of development time. Replacing the fecundity effect with a mating



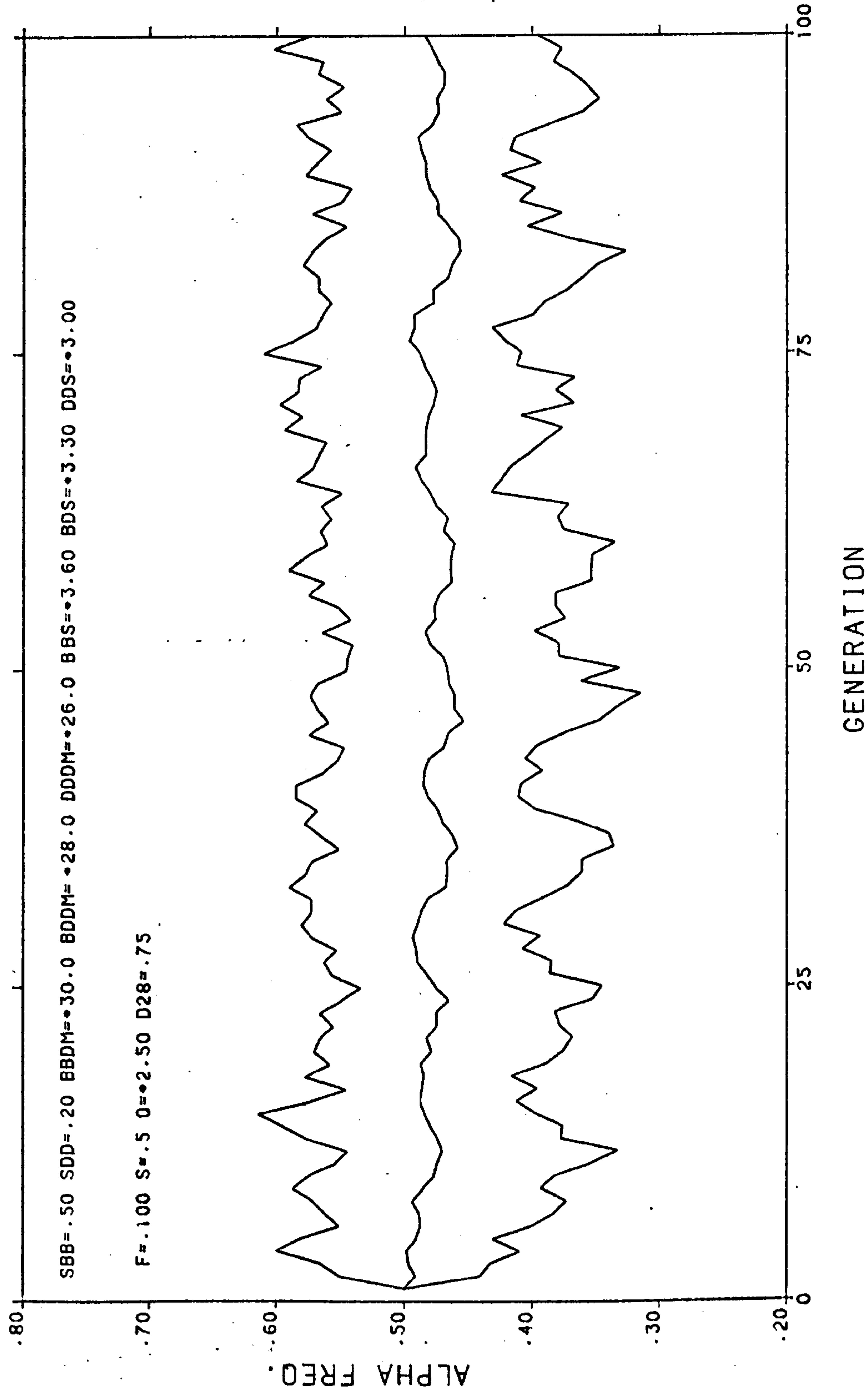
advantage to large males (Fig.10.6) gives effective fixation for the  $\alpha$  arrangement despite the viability disadvantage to the  $\alpha\alpha$  karyotype. The combined effects of size differences are, therefore, much stronger than the effect of development time and explain the bias in favour of the  $\alpha$  sequence away from the equilibrium due to viability differences alone. Selection due to size differences is much less variable from generation to generation because the simulation assumes that individual size is not related to development time within karyotypes. This is probably a reasonable assumption (Chapters 5 and 9).

Is it possible for the opposing influences of size and development time to maintain a stable equilibrium in the absence of heterosis in viability? The simulation run in Fig.10.7 indicates that this is possible although the approach to equilibrium is slow and inversion frequencies vary widely from generation to generation. If population sizes were small so that drift became a significant effect the majority of populations would probably fix for one arrangement or the other. Notice that the size and development time differences have been increased in this run but the fecundity effect has been removed and the mating effect reduced. This is only one of a variety of sets of parameters which produce similar results.

Can a cycle of  $\alpha$  frequencies be detected in the simulation with a realistic set of parameters? Fig.10.8 shows the result of a simulation run with all parameters identical to the run in Fig.10.2, i.e. the most reasonable estimates available, except that the proportion of wrack beds removed by storms as opposed to tides, instead of being fixed at 5%, varies cyclically between 10% and 70% with a period of 12 generations. 12 generations of Coelopa take about one year in nature so this is intended to simulate a seasonal

Fig.10.8 Results of the simulation runs using variable effects of storms. Parameter values are given as in Figs.10.2-10.7 except that D28 varies sinusoidally between 0.25 and 0.75 with a period of 12 generations. The three lines are the maximum, mean and minimum  $\alpha$  frequencies in each generation over 50 simulation runs. (Note that the  $\alpha$  frequency scale is expanded relative to the scale in Figs.10.2-10.7.)

Fig. 10.8



variation in weather conditions. Storms of sufficient ferocity to remove wrack beds are supposed to occur about every 20 weeks in the summer and every 4 weeks in the winter. The result is a clear cycle in  $\alpha$  frequency with an amplitude of about 4% imposed on a mean frequency of about 47%. The data currently available on the cycle in natural populations suggest an amplitude of more like 8% about a mean 44% which is a reasonable if not precise, agreement. However the important conclusion from this simulated cycle is that the known selection pressures are sufficient to produce a cycle in combination with a very plausible seasonal fluctuation of environment conditions. Clearly it is desirable to have observations of actual wrack bed durations and storm versus tide removals and it is still necessary to investigate the other suggested causes of the cycle such as changes in seaweed composition and temperature (Butlin et al 1982a).

The correlation between  $\alpha$  frequency and the frequency of Coelopa pilipes in natural populations may also have an explanation in terms of wrack bed duration. Because C. pilipes develops more slowly than C. frigida it may be favoured in conditions which also favour the  $\alpha$  arrangement (Day et al, in prep). However the two species are likely to differ in many respects besides development time such as low temperature tolerance and seaweed species preference (Dobson 1974b).

The stable equilibrium frequency with superimposed annual cycle of the  $\alpha/\beta$  inversion system is thus potentially explicable in terms of known selection pressures. What, then, of the other major features of the natural populations - the geographic uniformity and the associations with enzyme loci? Although there are some suggestions of consistent frequency differences between coasts the

similarity of samples from sites all round the British Isles remains striking (Chapter 3). There are essentially two possible explanations: either there is sufficient gene flow between populations to prevent their divergence or the populations are subjected to similar selection pressures. Observations of Coelopa dispersal are limited but suggest that, although there may be gene flow between adjacent populations, there is unlikely to be significant exchange between groups of populations isolated by stretches of unsuitable coastline. This point of view is supported by the distribution of frequencies of the rare alleles at the Adh locus (Adh-C, -A; and -E, Chapter 3) and by the observed population differences in development time in the "coadaptation" experiments (Chapter 7) although there was no indication of divergence from the viability results.

On the other hand there is evidence that viability, development time and size differences between karyotypes are similar in widely separated populations. Of the major environmental influences, the tidal cycle is broadly consistent throughout the British Isles and the effect of storms is likely to vary as much over a short distance (for example with aspect and beach profile) as it does between say the South coast and North East coast. Therefore it is not unreasonable to envisage selection maintaining the observed geographic uniformity.

The association between the Adh locus and the  $\alpha/\beta$  inversion also has two possible explanations: it may be a chance association generated at the time of origin of the inversion polymorphism or at a subsequent population bottleneck, which has decayed slowly because of the restriction of recombination (Ishii & Charlesworth 1977,



Nei & Li 1980); or the association may be due to selection acting on the Adh locus which is part of the coadapted gene complex held together by the inversion. There is, of course, the intermediate possibility that the Adh locus is closely linked to another locus (or loci) which is under selection. It is difficult to envisage a chance sequence of events which could have led to the complete association of the Adh-B allele with one sequence and the Adh-D allele with the other while the Adh-C allele was present on both sequences. It is possible that the electrophoretically designated Adh-C alleles are actually a heterogeneous class which may show further associations with the inversion. Adh-C frequencies are fairly stable in the British Isles (5-15%) but the allele is rare or absent in Scandinavia. If the association is purely a chance one these consistencies in the frequencies of the Adh-C allele would not be expected. In addition the frequencies of the BC, CD and CC genotypes in samples from natural populations do not fit expectations based on inversion effects alone (Chapter 3), there are suggestions of Adh genotype effects on development times (Chapters 4 and 7) and the CD genotype enjoys unexpectedly high mating success in some experiments (Chapter 9). All of these observations are suggestive of selection acting either on the Adh locus or a nearby locus. Further studies involving the Adh-C allele in association with both arrangements are needed.

So far I have concentrated on the maintenance of the  $\alpha/\beta$  inversion polymorphism but is it possible to say anything about its origin? Any conclusions about a unique event of this sort in the past must be speculative but they may help in formulating questions about the present polymorphism. A number of factors must be taken into

account: 1) theoretical studies on the origin of inversion polymorphism suggest that epistasis is a necessary condition for the initial spread of a new inversion (Charlesworth & Charlesworth 1973), 2) the lack of evidence for coadaptation from studies of viability, 3) the geographically consistent association between karyotype and both development time and adult size.

It seems to me that the most likely sequence of events which accommodates these three points is for the initial inversion to have held together a combination of alleles determining both long development time and large size in a population of small, rapid developing flies (or vice versa). The simulation has shown that a stable equilibrium is possible with these characteristics alone. A small fly which was not fast developing would have low fitness in a population of large flies and similarly a slow developing fly which was not large would not survive in a population of rapid developing flies. There is, therefore, a fitness interaction between genes for size and genes for development time - in other words, epistasis. (It is necessary to assume that a large, rapid developing fly is not possible.) The present day viability differences would then be a secondary consequence of two processes: the accumulation of deleterious recessive alleles in the two arrangements, and selection favouring alleles increasing the fitness of the heterokaryotype, because this is the most common karyotype. The accumulation of such alleles would increase the stability of the polymorphism but, as viability selection would be at the genic level, would not produce divergent coadaptation in isolated populations.

The fact that the  $\alpha$  and  $\beta$  arrangements differ by three over-

lapping inversions does not affect this general outline of events. Presumably the second and third inversions conferred an advantage either by incorporating extra loci in the area of restricted recombination or by reducing gene exchange due to double recombination.

## 10.2 Implications

There is now a considerable amount of information available about the  $\alpha/\beta$  inversion system on Chromosome I in the seaweed fly, Coelopa frigida. The system is interesting in its own right but it also has implications for the study of the genetics of natural populations in general.

Research on inversion polymorphisms has been dominated by the classic work of Dobzhansky on Drosophila pseudoobscura (see Introduction). His demonstration of the maintenance of this polymorphism by large selective differentials was a milestone in the development of evolutionary genetics. However it is still not clear just what form this selection takes, mainly because of a lack of knowledge of the natural ecology of the flies. It is likely that a variety of selection pressures acts on any inversion because it holds together a large number of alleles with effects on many phenotypic characteristics. This has been demonstrated in Coelopa where the inversion covers 5-10% of the genome and influences at least three complex and important characters - survival, development time and adult size. It is essential that studies of inversion polymorphism should take into account this multiplicity of selective effects and avoid concentration on the more obvious characteristics such as larval survival. This conclusion also applies to studies of polymorphism at single loci. Lewontin (1974) maintains that the web of relationships between genotype and phenotype is so complex

that every gene potentially affects every character of an organism. This may be an extreme view but the general point is valid - any locus under study may have many effects on the phenotype and any number of these may alter the fitness of the individual. The effects may be apparently unrelated at the phenotypic level and thus may easily be overlooked. This may be especially true when a polymorphism is identified as a difference in mobility of a particular enzyme in an extract of a whole organism.

In the past there was a tendency to concentrate on the viability component of selection because this is expected to produce greater departures from Hardy-Weinberg equilibrium than reproductive selection. However when research workers started to look for evidence of selection in the reproductive phase, especially differential mating success, many examples were quickly discovered (e.g. Petit & Ehrman 1969, Spiess 1970, Spiess 1982), and in some cases found to be more important than viability selection (Anderson & Watanabe 1974, Prout 1971). Interest in other components of fitness is even more recent, such as selection on aspects of life history (Lande 1982), of which development time in Coelopa is an example. It is difficult to find individual polymorphisms in which a variety of selective effects have been investigated. The best examples are the inversion polymorphisms in D. pseudoobscura and D. persimilis which have been studied from the point of view of viability, longevity, fecundity and mating success (e.g. Moss 1955, Spiess 1970). This approach needs to be applied to other polymorphisms.

None of the selective effects demonstrated in Coelopa is independent of the environment. Larval density, itself the product of a complex interaction between the fly population and the environment,



influences the relative viabilities of the karyotypes, their development times and sizes. The length of life of a wrack bed determines the selection in each generation due to development time differences. The selective importance of longevity depends on wrack bed life time and also the interval between successive wrack beds. The outcome of competition between males for mates is influenced by larval density, which determines size, and wrack bed lifetime, which determines the numbers of different genotypes available. In short it is impossible to assign any constant fitness values to the karyotypes. The realised fitness in each generation depends on a complex interaction between the several selective pressures and various components of the environment. This situation is certainly not unique. In some circumstances variable selection pressures can be responsible for the maintenance of a polymorphism. The case of frequency dependent selection has gained much attention recently (Kojima 1971, Clarke 1979) because of its potential for explaining the high level of genetic variation found in populations. Spatially variable selection pressures have also received attention (Levene 1953, Maynard Smith 1966, Udovic 1980), for the different reason that they may promote speciation. However temporally variable selection pressures are also capable of maintaining polymorphism and have been studied less (Haldane & Jayakar 1962, Felsenstein 1976). Coelopa provides an excellent case study in this last category because its generations are largely discrete and each generation experiences a different combination of selection pressures. It seems likely that temporally variable selection pressures are the norm rather than the exception, at least for short lived animals like insects, if only because environmental factors such



weather are so variable from day to day and from year to year. Longer lived animals may experience such fluctuations as "fine grained" but there may well be other less obvious fluctuations over longer periods. A greater awareness of the variability of selection pressures is needed for a full understanding of the maintenance of genetic variability.

The rationale behind this study of Coelopa frigida was to investigate the strong selection pressures associated with an inversion polymorphism in a species in which selection pressures observed in the laboratory could be related to the animals' natural ecology. I believe the results justify this approach and reveal a complex and fascinating set of interactions between an organism and its environment.

They told him it couldn't be done.,

Smiling, he went right to it,

He tackled the thing that couldn't be done -

And couldn't do it.

Anon.

### Acknowledgements

I am very grateful for the advice and support I have received throughout this project from my wife, Alison, and from my supervisor, Tom Day.

My thanks also go to Dr P.M.Collins, Sally Skevington, Isobel Read, Sue Miles, Pam Goody, Steve Berry, and Carol Buckman for allowing me to use their data and for practical assistance. I benefited from useful discussions with many members of the Department of Genetics. Mrs Janet Crook typed the thesis carefully and efficiently.

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## Appendix 1

### Genotype frequencies in samples from natural populations

#### Explanation of tables:-

- (i) Sites are referred to by the following codes:-

BE	Beer
PO	Portland
FL	Flamborough
RH	Robin Hood's Bay
SM	St.Mary's Island
RU	Rustington
BN	Barn's Ness
MN	Morfa Nefyn
WH	Whitburn
LU	Lulworth

Full details of locations are given in Chapter 3,  
Tables 3.1-3.4

- (ii) For 1980 samples P = Preadult sampling method  
                                   A = Adult sampling method  
 $\chi^2$  AD/PRE =  $\chi^2$  test for comparison of  
                                   sampling methods with 5 degrees  
                                   of freedom
- (iii) For 1981 samples  $\chi^2$  m/f =  $\chi^2$  test for comparison of  
                                   sampling methods with 5 degrees  
                                   of freedom unless the CC geno-  
                                   type was absent then 4 degrees  
                                   of freedom (number in parentheses  
                                   after  $\chi^2$  value)
- (iv)  $\chi^2$  HWE =  $\chi^2$  test for comparison with the Hardy-Weinberg  
                                   expectations. The six most common genotypes were  
                                   included giving 3 degrees of freedom unless the  
                                   expectation for the CC genotype was below 1.0.  
                                   In this case the test has 2 degrees of freedom  
                                   (number in parentheses after  $\chi^2$  value)

SITE	DATE	ALCOHOL DEHYDROGENASE GENOTYPE										T	$\chi^2$ AD/PRE	$\chi^2$ HWE
		AB	AC	AD	BB	BC	BD	CC	CD	DD	BE	CE	DE	
BE	10.74				12	9	64	9	17	35				18.60***
PO	11.74				10	5	50	4	16	30				7.60
FL	2.75				23	10	69	3	20	52				1.39
RH	3.75				25	11	97	4	23	56				6.04
SM	10.75				42	13	188	8	16	87				48.32***
RU	1.76				48	9	206	8	31	127				34.39***
BE	10.79			1	25	17	160	3	17	59	1	-	2	30.37***
PO	8.79			1	33	15	119	-	28	58	-	-	-	8.31*
FL	8.79	2	-	-	44	30	96	11	33	51	-	-	1	3.66
RH	10.79	-	-	2	35	47	117	7	25	42	-	-	-	15.17**
SM	11.79	-	-	-	21	19	118	6	42	62	-	-	-	12.31**
RU	10.79	-	-	-	35	18	147	1	23	57	1	-	-	14.16**
BN	4.80	-	2	7	92	31	286	15	44	98	1	1	-	46.71***
		A	1	2	95	37	244	11	36	92	-	-	-	19.67***
SM	6.4.80	P	2	2	48	23	143	9	35	57	1	0	1	12.86**
		A	7	10	150	104	424	18	129	198	2	1	4	8.57*
PO	7.80	P	2	1	41	18	172	8	23	92	1	-	-	24.67***
		A	1	-	104	36	334	12	50	110	-	-	-	42.00***
SM	9.80	4	2	4	81	54	311	15	80	171	-	1	2	14.69**
MN	26.10.80	3	1	-	57	28	178	4	50	87	3	-	-	7.30
MN	4.12.80	-	-	2	52	38	201	4	61	102	1	-	-	10.44*



SITE	DATE	ALCOHOL DEHYDROGENASE GENOTYPE											T	COELOPA PILIPES	$\chi^2$ m/f	$\chi^2$ HWE
		AB	AC	AD	BB	BC	BD	CC	CD	DD	BE	CE	DE			
WH	18.3.81	1	-	-	32	15	84	3	15	25	-	-	-	175		
		-	-	1	26	12	39	-	18	14	1	-	1	112		
		1	-	1	58	27	123	3	33	39	1	-	1	287	586	5.58
SM	18.3.81	-	-	1	5	10	56	2	17	35	-	-	-	126		
		1	-	-	21	11	62	-	23	41	1	1	1	162		
		1	-	1	26	21	118	2	40	76	1	1	1	288	-	5.43
SM	15.4.81	2	-	-	8	8	45	2	22	39	-	-	-	126		
		1	-	2	9	5	71	3	18	50	-	-	-	159		
		3	-	2	17	13	116	5	40	89	-	-	-	285	3	9.08*
BN	15.4.81	-	-	-	-	-	13	1	2	7	-	-	1	24		
		-	-	-	2	2	12	1	2	9	-	-	-	28		
		-	-	-	2	2	25	2	4	16	-	-	1	52	8	5.28(2)
RU	20.4.81	-	-	-	13	9	59	2	14	40	-	-	-	137		
		-	-	-	14	11	61	2	19	42	1	-	-	150		
		-	-	-	27	20	120	4	33	82	1	-	-	287	-	3.19
SM(N)	14.5.81	-	-	2	19	13	51	6	12	30	1	-	-	134		
		-	-	2	10	9	63	1	18	36	-	-	-	139		
		-	-	4	29	22	114	7	30	66	1	-	-	273	-	6.33
SM(S)	14.5.81	1	-	-	15	14	67	2	13	27	-	-	1	140		
		-	1	-	8	6	71	-	11	42	-	-	1	140		
		1	1	-	23	20	138	2	24	69	-	-	2	280	-	14.67**
WH	14.5.81	-	-	-	5	6	12	-	1	4	1	-	-	29		
		-	-	-	2	1	6	-	1	2	-	-	-	12		
		-	-	-	7	7	18	-	2	6	1	-	-	41	728	3.32(2)
RU	17.5.81	-	-	-	-	1	6	1	-	4	-	-	-	12		
		-	-	-	1	-	8	-	-	4	-	-	-	13		
		-	-	-	1	1	14	1	-	8	-	-	-	25	-	4.57(2)
SM	18.6.81	1	-	2	10	9	40	3	14	34	-	-	-	113		
		-	-	1	7	4	53	-	11	27	1	-	-	104		
		1	-	3	17	13	93	3	25	61	1	-	-	217	37	5.13

SITE	DATE	ALCOHOL DEHYDROGENASE GENOTYPE										T	COELOPA PILIPES	$\chi^2$ m/f	$\chi^2$ HWE
		AB	AC	AD	BB	BC	BD	CC	CD	DD	BE	CE			
WH	18.6.81	m	-	1	2	4	41	-	9	15	-	-	-	-	72
		f	-	1	3	9	30	-	6	23	-	-	-	-	72
		T	-	2	5	13	71	-	15	38	-	-	34	6.1(4)	16.96***
LU	24.6.81	m	-	7	8	2	36	-	8	15	1	-	1	-	71
		f	-	-	11	7	30	-	8	11	-	-	-	-	67
		T	-	-	19	9	66	-	16	26	1	-	1	4.4(4)	6.74
PO	26.6.81	m	-	-	9	12	83	-	14	36	-	-	-	-	154
		f	-	-	24	13	68	1	14	35	-	-	-	-	155
		T	-	-	33	25	151	1	28	71	-	-	-	9.4	12.77**
SM	8.7.81	m	-	1	7	5	66	1	6	39	1	-	-	-	128
		f	-	4	24	16	58	1	13	32	-	-	1	-	149
		T	-	5	31	21	124	2	19	71	1	-	5	17.47**	5.93
WH	8.7.81	m	-	1	12	9	35	-	7	10	-	-	-	-	75
		f	-	1	12	9	25	-	7	14	-	-	1	-	69
		T	-	2	24	18	60	-	14	24	-	-	28	2.1(4)	4.28
RH	8.7.81	m	-	-	14	8	24	1	8	8	-	-	-	-	63
		f	-	2	6	4	27	1	14	8	-	-	-	-	63
		T	-	2	20	12	51	2	22	16	-	-	-	6.3	6.49
RU	13.7.81	m	-	-	4	5	38	1	4	18	-	-	-	-	70
		f	-	-	5	3	36	1	9	15	1	-	1	-	71
		T	-	-	9	8	74	2	13	33	1	-	1	2.9	13.81**
SM	30.7.81	m	-	1	17	17	84	4	15	33	2	1	1	-	175
		f	-	2	22	11	60	1	13	34	-	-	-	-	144
		T	-	3	39	28	144	5	28	67	2	1	1	5.2	8.42*
WH	30.7.81	m	-	-	3	3	10	1	4	24	-	-	-	-	45
		f	-	-	11	8	47	4	7	20	1	-	-	-	99
		T	-	-	14	11	57	5	11	44	1	-	1	17.1**	9.41*
PO	19.8.81	m	-	-	6	6	31	-	6	19	-	-	-	-	68
		f	-	-	9	5	40	2	5	11	1	-	-	-	73
		T	-	-	15	11	71	2	11	30	1	-	1	5.9	8.16*

SITE	DATE	ALCOHOL DEHYDROGENASE GENOTYPE											T	COELOPA PILIPES	$\chi^2$ m/f	$\chi^2$ HWE
		AB	AC	AD	BB	BC	BD	CC	CD	DD	BE	CE	DE			
SM	27.8.81	m	-	1	-	13	12	74	2	15	31	-	-	-	148	
		f	1	-	1	13	9	72	-	8	31	-	-	-	135	
		T	1	1	1	26	21	146	2	23	62	-	-	-	283	18.51***
WH	27.8.81	m	1	-	1	10	2	25	-	4	7	-	1	-	51	
		f	1	-	1	10	8	46	2	8	16	-	-	-	92	
		T	2	-	2	20	10	71	2	12	23	-	1	-	143	7.62
BE	9.9.81	m	-	-	-	7	4	33	1	4	16	1	-	-	66	
		f	-	-	-	16	4	27	1	5	21	1	-	-	75	
		T	-	-	-	23	8	60	2	9	37	2	-	-	141	0.16(2)
SM	25.9.81	m	-	-	1	9	18	73	2	18	20	-	-	-	141	
		f	-	-	-	21	12	72	1	19	20	1	-	-	146	
		T	-	-	1	30	30	145	3	37	40	1	-	-	287	27.33***
WH	25.9.81	m	2	-	1	26	6	31	-	8	8	-	-	-	82	
		f	-	-	1	11	6	28	-	5	13	-	-	-	64	
		T	2	-	2	37	12	59	-	13	21	-	-	-	146	6.4(4) 0.95
WH	11.10.81	m	2	1	1	29	16	53	-	8	9	-	-	-	119	
		f	3	1	1	12	6	29	-	4	13	1	-	-	70	
		T	5	2	2	41	22	82	-	12	22	1	-	-	189	6.7 6.12
FL	25.10.81	m	1	-	-	16	10	23	1	13	6	-	-	-	70	
		f	-	-	-	9	5	34	2	9	12	-	-	-	71	
		T	1	-	-	25	15	57	3	22	18	-	-	-	141	8.8 4.28
SM	4.11.81	m	-	1	1	30	13	66	2	12	17	-	-	-	142	
		f	1	-	-	27	15	68	1	13	20	-	1	-	146	
		T	1	1	1	57	28	134	3	25	37	-	1	-	288	7 0.9 7.85*
WH	4.11.81	m	-	-	-	2	7	35	1	6	8	-	-	-	59	
		f	-	1	-	12	5	36	-	9	13	-	-	-	76	
		T	-	1	-	14	12	71	1	15	21	-	-	-	135	8.5 13.18**

Appendix 2

Adh genotypes of flies emerging on each day from the collection made at St.Mary's Island on 6 April 1980.

## MALES

DATE OF EMERGENCE (1980)	GENOTYPES OF					FLIES EMERGING EACH DAY								TOTAL FLIES EMERGING EACH DAY
	AB	AC	AD	BB	BC	BD	BE	CC	CD	CE	DD	DE		
12.4									4		6		10	
13.4	1			3	6	22		2	11		13		58	
15.4	1		3	19	14	60		3	21		17	1	139	
16.4	1	1	1	3	7	11		1	2		2		29	
17.4				8	5	27					5		45	
18.4						7					2		9	
19.4				4	3	10		1	6		2		26	
20.4				3	3	6					2		14	
22.4	1			3		12			3		5		24	
23.4	1		1	1	2	11			2		2		20	
24.4				1	4	13	1		2		3		24	
25.4				3	2	12			1		2		20	
26.4				3		11		2	2		3		21	
28.4				5	2	6			4		1		18	
29.4				1		5			1		1		8	
30.4				2	1	4			1		1		9	
2.5				6	2	9					3		20	
4.5				1	1	8			1		4		15	
5.5				1	2	1			1				5	
6.5				1	1	2			1		4		9	
7.5					1	2					3		6	
8.5				4		1			2		2		9	
9.5				3	1						1		5	
12.5				2		1					1		4	
TOTAL GENOTYPES	5	1	5	77	57	241	1	9	65	0	85	1	547	



FEMALES

DATE OF EMERGENCE (1980)	GENOTYPES OF					FLIES EMERGING EACH DAY								TOTAL	FLIES
	AB	AC	AD	BB	BC	BD	BE	CC	CD	CE	DD	DE	EMERGING EACH DAY	EMERGING EACH DAY	
12.4			2	12	2	19		1	5		12	1		54	
13.4			1	12	10	35		2	12	1	12	1		86	
15.4			1	15	11	37		1	11		17			93	
16.4				2		8			2		1			13	
17.4				2	3	4			1		5			15	
18.4				1		4		1	1		2			9	
19.4				4	5	8	1	1	3		6			28	
20.4				3		3			2		1			9	
22.4				1	2	6		1	2		7			19	
23.4				3	3	11					9			26	
24.4			1			4		1	4		2			12	
25.4		1		2	2	1			3		1			10	
26.4	1			3	3	8			1		3			19	
28.4				2	1	8			2		6	1		20	
29.4				3	1	1			1					6	
30.4				1		4			2		3			10	
2.5				1		6			2	1	8			17	
4.5					1	7			3		7			18	
5.5				1		1					1			3	
6.5				1	1	3			3		2			10	
7.5				1	1				2		2			6	
8.5					1	3		1	1		3			9	
9.5				2							1			3	
10.5						1			1		1			3	
12.5				1		1					1			3	
13.5	1													1	
TOTAL GENOTYPES	2	1	5	73	47	183	1	9	64	2	113	3		502	

### Appendix 3

Development times (days) and sizes (graticule divisions) of all flies emerging in the larva to adult density experiment. An asterisk indicates that the fly had damaged wings so that no size measurement was available. 1 graticule division = 1.45 mm (Chapter 2).

MALES						FEMALES					
BB		BD		DD		BB		BD		DD	
DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE
DENSITY - 100; REPL. - 1											
18.5	4.8	17.5	3.9	15.5	3.5	15.5	3.9	16.5	3.7	16.5	3.7
		18.5	4.6	17.5	3.4	16.5	3.8	16.5	3.8	16.5	4.0
		18.5	4.8	17.5	3.7	16.5	3.9	16.5	3.8	16.5	4.0
		19.5	4.7	18.5	2.9	18.5	3.3	16.5	3.8	17.5	3.8
		19.5	4.6					16.5	3.9	17.5	3.7
		20.5	4.3					16.5	3.9	18.5	3.6
		20.5	4.9					17.5	3.4		
		22.5	4.0					17.5	3.8		
								18.5	3.8		
								18.5	3.7		
								22.5	3.7		
18.50	4.80	19.63	4.47	17.25	3.37	16.75	3.73	17.59	3.75	17.17	3.80 M
		2.41	0.14	1.58	0.12	1.58	0.08	3.29	0.02	0.67	0.03 V
DENSITY - 100; REPL. -- 2											
19.5	4.4	18.5	4.5	14.5	3.7	16.5	3.7	14.5	*	15.5	3.8
20.5	3.7	18.5	4.4	15.5	4.1	16.5	3.7	14.5	4.1	16.5	3.9
20.5	4.7	20.5	4.9	16.5	3.6	17.5	3.7	15.5	3.9	16.5	3.7
24.5	5.3	20.5	4.6	17.5	4.1	17.5	3.5	16.5	3.5	18.5	3.7
		21.5	4.1	17.5	3.4			16.5	3.8		
		21.5	4.1	21.5	3.4			16.5	3.6		
		23.5	4.1					17.5	3.6		
		23.5	3.9					18.5	3.7		
								18.5	3.4		
								18.5	3.7		
								19.5	3.5		
								19.5	3.8		
								20.5	3.2		
21.25	4.49	21.00	4.33	17.17	3.72	17.00	3.65	17.42	3.65	16.75	3.77 M
4.92	0.44	3.71	0.11	5.87	0.10	0.33	0.01	3.74	0.06	1.58	0.01 V
DENSITY - 100; REPL. - 3											
24.5	4.0	19.5	4.5	17.5	3.6	16.5	3.7	14.5	4.0	16.5	3.8
25.5	5.1	20.5	4.6	17.5	3.7	17.5	4.0	16.5	3.7	19.5	3.6
25.5	4.6	20.5	3.7	18.5	3.3	22.5	3.6	16.5	4.1	19.5	3.3
		22.5	4.4	23.5	2.9			17.5	3.5	20.5	3.8
		22.5	4.8					18.5	4.0	22.5	3.6
		23.5	4.7					19.5	3.6	23.5	3.2
		23.5	4.5								
25.17	4.57	21.79	4.46	19.25	3.37	18.83	3.77	17.17	3.82	20.33	3.55 M
0.33	0.30	2.57	0.13	8.25	0.13	10.33	0.04	3.07	0.06	6.17	0.06 V

M = Mean; V = Variance

MALES						FEMALES					
BB		BD		DD		BB		BD		DD	
DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE

DENSITY - 200; REPL. - 1

21.5	3.6	17.5	4.1	18.5	3.1	16.5	3.5	14.5	3.7	16.5	3.6
21.5	4.4	19.5	4.5	19.5	2.7	17.5	3.9	16.5	3.8	16.5	3.6
22.5	4.4	20.5	3.9	21.5	3.2	17.5	3.2	16.5	3.5	17.5	3.9
22.5	4.0	20.5	4.2			17.5	3.7	16.5	3.7	18.5	3.3
		21.5	3.8			18.7	3.6	16.5	3.7	18.5	3.6
		21.5	4.5			19.5	3.5	16.5	3.8	19.5	3.8
		21.5	3.7			20.5	3.0	16.5	3.7	20.5	3.5
		21.5	4.1					17.5	3.6	20.5	3.8
		22.5	3.8					17.5	3.9	21.5	2.7
		22.5	3.5					17.5	3.5	23.5	3.1
		22.5	4.1					18.5	3.7		
		23.5	3.1					18.5	3.5		
		23.5	4.6					18.5	3.7		
		23.5	4.3					19.5	3.8		
		24.5	4.3					19.5	3.7		
		24.5	3.8					20.5	3.6		
		27.5	3.5					20.5	3.2		
								20.5	3.4		
								20.5	3.4		
								20.5	3.0		
								21.5	3.6		
								21.5	3.1		
								21.5	3.3		

22.00	4.10	22.27	3.99	19.83	3.00	18.21	3.49	18.59	3.56	19.30	3.49	M
0.33	0.15	5.07	0.16	2.33	0.07	1.91	0.09	4.17	0.06	5.07	0.13	V

MALES						FEMALES					
BB		BD		DD		BB		BD		DD	
DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE

DENSITY - 200; REPL. - 2

21.5	4.1	19.5	3.9	16.5	3.6	15.5	3.7	14.5	3.8	17.5	3.4
21.5	4.5	19.5	3.2	16.5	3.2	16.5	3.3	14.5	3.7	18.5	3.1
22.5	3.3	20.5	3.4	18.5	3.2	19.5	3.5	14.5	3.5	18.5	3.2
22.5	4.5	20.5	3.0	18.5	3.7	20.5	3.1	15.5	3.3	21.5	3.2
22.5	4.1	21.5	3.8	19.5	3.0	21.5	3.4	16.5	3.5		
23.5	4.0	21.5	4.0	22.5	2.9	21.5	2.6	18.5	3.5		
		22.5	3.4			21.5	3.6	18.5	3.5		
		23.5	3.6			22.5	3.4	18.5	3.3		
		23.5	4.0			23.5	3.1	19.5	3.0		
		23.5	3.4					19.5	3.5		
		24.5	3.3					19.5	3.7		
		24.5	3.2					19.5	3.5		
		24.5	4.0					20.5	3.1		
		24.5	4.0					20.5	3.6		
		25.5	3.5					20.5	3.5		
		26.5	3.6					20.5	3.0		
								21.5	3.1		
								21.5	3.3		
								23.5	3.2		
								23.5	2.9		
								24.5	2.9		

22.33	4.08	22.88	3.58	18.67	3.27	20.28	3.30	19.31	3.35	19.00	3.23	M
0.57	0.19	4.65	0.11	4.97	0.10	7.19	0.11	8.56	0.07	3.00	0.02	V



MALES						FEMALES					
BB		BD		DD		BB		BD		DD	
DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE
DENSITY - 200; REPL. - 3											
20.5	3.8	19.5	4.2	16.5	3.4	16.5	3.6	14.5	3.6	17.5	3.4
21.5	4.5	20.5	4.0	18.5	3.8	17.5	3.5	16.5	3.8	18.5	3.4
22.5	4.3	20.5	4.4	18.5	3.2	17.5	4.0	16.5	3.7	18.5	3.7
24.5	4.0	21.5	4.5	18.5	3.3	17.5	3.5	16.5	3.8	23.5	3.2
25.5	3.3	21.5	4.1	21.5	2.8	19.5	3.3	17.5	3.7		
25.5	3.1	21.5	3.7	22.5	2.9	23.5	3.2	17.5	3.7		
		22.5	3.3					17.5	3.5		
		23.5	3.9					18.5	3.5		
		24.5	3.0					19.5	3.3		
		24.5	3.3					19.5	3.5		
		25.5	4.0					19.5	3.4		
		25.5	4.2					20.5	3.5		
		25.5	3.1					21.5	3.6		
		25.5	3.7					21.5	3.0		
		26.5	3.7					22.5	3.4		
		27.5	4.5					22.5	3.3		
		28.5	3.5					22.5	3.5		
								23.5	3.1		
								24.5	2.6		
23.33	3.83	23.79	3.83	19.33	3.23	18.67	3.52	19.61	3.45	19.50	3.43 M
4.57	0.30	7.10	0.22	4.97	0.13	6.57	0.08	7.88	0.09	7.33	0.04 V

MALES						FEMALES					
BB		BD		DD		BB		BD		DD	
DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE
DENSITY - 400; REPL. - 1											
25.5	*	19.5	*	14.5	3.3	14.5	3.7	14.5	3.8	21.5	3.2
25.5	3.8	22.5	3.5	16.5	2.9	16.5	2.7	15.5	3.7	22.5	3.0
32.5	3.7	22.5	3.4	17.5	2.8	17.5	3.1	16.5	3.5	22.5	2.9
36.0	3.3	23.5	2.5	17.5	3.3	19.5	3.0	16.5	3.6	24.5	3.1
		23.5	3.2	17.5	2.9	20.5	2.9	17.5	3.4	25.5	2.8
		25.5	3.0	20.5	3.1	23.5	3.1	18.5	3.3	26.5	3.0
		26.5	3.0	21.5	2.9	25.5	*	18.5	3.1	26.5	2.6
		26.5	3.1	21.5	2.6	25.5	3.1	18.5	3.4	27.5	2.8
		26.5	3.6	21.5	*	26.5	2.9	20.5	2.9		
		26.5	3.3	22.5	2.8	26.5	2.9	20.5	3.1		
		26.5	3.6	22.5	2.6	26.5	3.0	20.5	3.2		
		26.5	4.3	26.5	2.4	34.5	2.6	20.5	3.5		
		26.5	3.5					21.5	3.4		
		26.5	3.4					21.5	3.3		
		27.5	3.7					21.5	3.0		
		27.5	2.3					21.5	3.5		
		27.5	3.9					21.5	3.1		
		27.5	3.4					22.5	3.1		
		27.5	3.8					22.5	3.0		
		27.5	2.5					23.5	3.6		
		27.5	2.5					23.5	3.3		
		27.5	2.9					24.5	3.0		
		27.5	3.2					24.5	3.2		
		28.5	2.7					24.5	3.4		
		28.5	4.0					25.5	2.8		
		33.5	2.5					26.5	3.2		
								26.5	2.6		
								26.5	2.8		
								26.5	2.4		
								27.5	2.9		
								29.5	3.1		
								34.5	2.8		
29.88	3.60	26.42	3.23	20.00	2.87	23.08	3.00	22.31	3.19	24.63	2.93 M
27.56	0.07	6.63	0.28	11.18	0.08	31.36	0.08	18.80	0.10	4.98	0.04 V

MALES						FEMALES					
BB		BD		DD		BB		BD		DD	
DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE
DENSITY - 400; REPL. - 2											
24.5	3.1	20.5	3.5	16.5	3.4	16.5	3.7	15.5	4.1	16.5	3.1
25.5	3.5	20.5	4.2	18.5	2.5	16.5	3.4	16.5	3.4	19.5	2.7
26.5	3.5	20.5	3.3	19.5	2.9	19.5	3.1	16.5	3.1	20.5	3.4
28.5	3.3	20.5	3.5	19.5	3.3	19.5	3.4	16.5	3.4	20.5	3.0
		21.5	3.4	19.5	3.4	19.5	3.0	17.5	3.2	20.5	3.1
		23.5	4.0	20.5	3.5	20.5	3.5	17.5	3.3	21.5	3.4
		23.5	3.7	20.5	3.0	20.5	2.8	18.5	3.3	21.5	3.0
		24.5	3.3	20.5	3.1	24.5	3.0	19.5	3.1	21.5	3.7
		25.5	2.6	23.5	3.0	24.5	3.0	20.5	3.6	22.5	3.2
		25.5	2.6			24.5	2.6	20.5	3.6	23.5	3.2
		25.5	3.4			25.5	2.5	20.5	3.7	23.5	2.8
		26.5	3.5			25.5	3.0	20.5	3.8	23.5	3.3
		26.5	3.6			26.5	3.0	21.5	3.3	34.5	3.1
		26.5	2.4					21.5	3.5		
		26.5	3.3					21.5	3.5		
		26.5	3.5					22.5	3.2		
		26.5	2.5					22.5	2.8		
		27.5	3.0					22.5	2.9		
		27.5	3.2					22.5	3.1		
		31.0	3.7					23.5	3.1		
		31.0	3.8					23.5	2.3		
		32.5	2.8					23.5	3.3		
		36.0	3.4					23.5	3.3		
								24.5	2.6		
								24.5	3.1		
								24.5	2.9		
								24.5	3.3		
								25.5	2.4		
								25.5	3.0		
								25.5	2.9		
								26.5	3.3		
								26.5	2.9		
								27.5	2.6		
26.25	3.35	25.91	3.31	19.83	3.11	21.81	3.08	21.92	3.18	22.27	3.15 M
2.92	0.04	16.13	0.22	3.50	0.10	12.23	0.12	10.75	0.15	17.19	0.07 V

MALES						FEMALES					
BB		BD		DD		BB		BD		DD	
DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE
DENSITY - 800; REPL. - 1											
25.5	3.6	23.5	2.9	20.5	3.4	22.5	2.9	19.5	3.3	15.5	3.8
28.5	2.7	23.5	2.4	22.5	2.6	26.5	2.9	21.5	2.6	18.5	3.4
29.5	3.5	24.5	3.7			27.5	2.9	22.5	3.4	20.5	3.0
29.5	3.0	25.5	3.0			27.5	2.7	23.5	2.5	21.5	2.9
29.5	3.1	25.5	*			28.5	2.4	23.5	2.8	22.5	2.6
31.0	3.2	25.5	2.2			28.5	2.9	23.5	3.0	23.5	3.1
31.0	3.6	26.5	3.2					23.5	3.0	23.5	2.4
31.0	3.6	26.5	3.2					23.5	2.3	24.5	2.7
31.0	*	26.5	2.9					23.5	3.4	24.5	2.8
32.5	4.0	27.5	3.2					23.5	2.7	26.5	2.7
38.5	2.4	27.5	2.4					24.5	2.9	26.5	2.7
		27.5	3.8					26.5	2.6	28.5	2.0
		27.5	2.4					27.5	3.0	28.5	2.5
		27.5	3.4					27.5	2.5	34.5	2.9
		28.5	3.0					28.5	2.6	37.5	3.4
		28.5	2.8					28.5	2.6	37.5	3.2
		28.5	2.9					28.5	2.3		
		28.5	2.5					29.5	2.2		
		29.5	2.8					29.5	2.9		
		29.5	2.8					31.0	2.6		
		29.5	2.3					33.5	3.0		
		29.5	3.4					36.0	3.4		
		29.5	3.2					36.0	2.7		
		31.0	3.2					37.5	2.9		
		31.0	2.7								
		31.0	3.8								
		31.0	3.0								
		32.5	3.3								
		37.5	2.6								
		37.5	3.9								
		37.5	2.8								
30.68	3.27	28.89	2.99	21.50	3.00	26.83	2.78	27.19	2.80	25.88	2.88 M
10.06	0.23	13.15	0.21	2.00	0.32	5.07	0.04	23.84	0.12	39.72	0.19 V

MALES						FEMALES					
BB		BD		DD		BB		BD		DD	
DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE	DEV. TIME	SIZE
DENSITY - 800; REPL. - 2											
23.5	3.0	23.5	3.4	19.5	2.6	23.5	3.2	16.5	3.0	17.5	3.2
24.5	4.1	23.5	3.8	21.5	2.6	23.5	3.0	16.5	3.1	17.5	2.9
26.5	3.8	25.5	2.5	21.5	2.3	23.5	2.2	17.5	2.6	19.5	2.9
26.5	3.2	26.5	2.9	23.5	2.3	23.5	3.2	20.5	2.6	20.5	3.1
26.5	2.8	27.5	2.8	23.5	2.5	24.5	3.2	21.5	3.3	21.5	2.4
27.5	2.7	27.5	2.1	23.5	2.4	24.5	3.0	23.5	3.2	23.5	3.3
27.5	3.2	27.5	2.6	23.5	2.6	24.5	3.2	23.5	3.0	23.5	2.7
28.5	2.4	27.5	3.6	25.5	2.7	25.5	2.7	23.5	3.4	23.5	3.0
34.5	3.4	27.5	3.1	25.5	2.9	25.5	2.5	23.5	2.7	24.5	2.6
		27.5	2.8	25.5	2.7	26.5	3.3	23.5	3.1	24.5	2.8
		28.5	3.0	27.5	2.3	26.5	3.1	24.5	2.7	24.5	3.0
		29.5	3.7	31.0	2.8	27.5	*	24.5	2.6	24.5	2.9
		31.0	2.3	34.5	2.8	27.5	2.8	24.5	2.8	25.5	2.7
		31.0	2.7	36.0	2.8	27.5	3.1	24.5	3.0	25.5	2.3
		36.0	3.0			29.5	3.0	24.5	3.0	25.5	2.8
						36.0	2.8	24.5	2.9	25.5	2.4
								25.5	3.3	25.5	2.4
								25.5	3.3	25.5	2.3
								25.5	2.4	26.5	3.0
								25.5	2.7	26.5	2.6
								25.5	2.9	28.5	2.5
								25.5	2.9	28.5	2.8
								25.5	2.5	36.0	3.0
								25.5	3.1		
								26.5	2.8		
								26.5	2.3		
								26.5	2.6		
								26.5	2.8		
								26.5	3.1		
								27.5	2.7		
								27.5	2.6		
								28.5	2.8		
								31.0	3.5		
								36.0	3.2		
								37.5	2.9		
								37.5	3.3		
								37.5	3.1		
27.28	3.18	28.00	2.95	25.86	2.59	26.22	2.95	25.85	2.91	24.52	2.77 M
9.69	0.29	9.64	0.25	23.67	0.04	10.07	0.09	24.53	0.09	14.97	0.08 V



Appendix 4

Results of electrophoresis of large larvae and pupae collected in the core series from the experimental wrack bed at St.Mary's Island, Tyne & Wear, and of adults resulting from collections of small larvae from the cores.

(Genotypes AX and EX include all Adh-A or Adh-E bearing genotypes)

LARGE LARVAE

DATE	CORE	ADH GENOTYPES								TOTAL COLLECTED	NON-FRIGIDA
		AX	BB	BC	BD	CC	CD	DD	EX		
6 APRIL	1	2	16	4	36	3	7	28	1	102	3
	2	2	17	1	18	0	4	9	0	45	4
	3	0	4	3	13	2	10	11	0	49	3
	4	1	11	6	33	2	13	15	0	83	1
	5	0	3	2	16	1	1	6	0	31	0
	6	1	4	4	28	0	8	12	1	61	3
	7	1	9	2	19	0	5	20	0	58	0
	8	0	8	10	25	1	14	23	0	84	2
	9	1	32	8	73	2	21	36	2	180	3
	10	2	5	3	15	0	5	6	1	41	1
10 APRIL	1	1	7	7	60	4	13	22	0	117	1
	2	1	11	9	40	3	9	14	0	87	0
	3	1	12	11	51	2	11	45	3	142	1
	4	2	8	0	14	0	1	9	0	38	3
	5	0	7	10	48	2	20	48	1	144	3
	6	1	12	5	17	1	7	12	1	60	0
	7	1	12	6	52	0	13	33	1	123	0
	8	5	22	14	82	2	20	55	0	213	1
	9	1	14	6	60	1	7	18	1	108	0
	10	1	15	5	49	1	17	33	1	124	1
14 APRIL	1	0	3	3	11	0	4	8	0	27	0
	2	2	4	2	11	0	2	3	0	26	0
	3	2	7	7	18	0	7	12	1	59	1
	4	0	0	4	12	0	2	7	0	25	0
	5	2	5	4	12	0	4	11	1	42	0
	6	1	10	1	20	0	7	7	0	48	0
	7	3	11	8	23	1	5	12	0	63	0
	8	1	9	5	27	2	9	11	0	63	0
	9	2	15	4	28	0	8	11	0	75	0
	10	0	14	7	20	0	16	14	2	72	0
17 APRIL	1	0	3	3	7	1	4	3	1	23	1
	2	0	4	1	7	0	4	1	0	17	0
	3	2	17	6	29	0	12	9	2	79	0
	4	2	4	2	23	0	7	9	0	47	0
	5	1	14	3	17	1	5	5	0	48	1
	6	0	5	4	18	0	0	13	0	44	0
	7	1	6	5	19	1	1	8	1	42	0
	8	2	14	8	39	1	15	12	1	96	1
	9	0	13	7	21	2	4	10	0	57	0
	10	0	8	4	24	1	3	11	0	53	0

PUPAE

DATE	CORE	ADH GENOTYPE							TOTAL	
		AX	BB	BC	BD	CC	CD	DD	EX	COLLECTED
6 APRIL	1	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0	0
	4	0	0	0	0	0	0	0	0	0
	5	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0	0	0	0	0
	7	0	0	0	1	0	1	1	0	3
	8	0	0	0	1	0	0	0	0	1
	9	0	0	0	0	0	0	0	0	1
	10	0	1	0	2	0	1	0	0	4
10 APRIL	1	0	0	0	0	0	1	4	0	5
	2	0	0	0	1	0	1	0	0	2
	3	0	0	0	1	0	3	10	0	15
	4	0	0	0	0	0	0	1	0	1
	5	0	3	1	8	1	4	8	0	27
	6	0	0	0	0	0	2	1	0	3
	7	0	2	4	1	0	3	7	1	18
	8	0	2	1	9	0	2	7	0	21
	9	0	1	0	1	0	0	1	0	3
	10	0	1	1	1	0	0	1	0	4
14 APRIL	1	0	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0	0
	3	0	2	0	0	0	0	0	0	3
	4	0	0	0	3	0	3	2	0	8
	5	2	9	8	19	1	7	21	0	70
	6	0	2	1	20	0	3	6	1	34
	7	2	7	12	42	4	17	72	3	161
	8	0	1	0	6	0	0	4	0	11
	9	0	0	2	1	0	0	1	0	5
	10	2	1	0	8	1	4	4	0	20
17 APRIL	1	0	1	0	1	0	0	1	0	3
	2	0	0	0	0	0	0	1	0	1
	3	0	3	2	4	0	3	5	0	17
	4	0	1	0	5	0	0	3	0	9
	5	1	7	7	8	1	2	10	0	39
	6	1	7	2	27	1	5	25	0	71
	7	0	2	2	7	0	5	10	1	28
	8	0	11	7	35	2	19	35	0	112
	9	0	0	0	2	0	1	1	0	4
	10	0	1	0	3	0	0	2	0	6

## SMALL LARVAE (MALES)

DATE	CORE	ADH GENOTYPE								TOTAL	TOTAL	NON-
		AX	BB	BC	BD	CC	CD	DD	EX	COLLECTED (MALE + FEMALE)	EMERGED (MALE + FEMALE)	FRIGIDA (NOT SEXED)
6 APRIL	1	0	2	2	17	2	4	11	0	170	65	4
	2	1	3	0	3	0	0	0	0	53	18	20
	3	0	3	1	4	0	2	1	0	97	25	25
	4	2	7	3	10	0	5	5	0	167	48	3
	5	0	0	0	7	0	2	6	0	62	37	6
	6	0	1	2	8	0	1	6	0	85	40	7
	7	0	0	0	5	0	1	6	0	140	34	62
	8	0	1	0	10	0	3	10	0	143	59	23
	9	1	6	6	11	0	5	9	0	191	80	10
	10	1	1	2	1	0	3	3	0	54	17	13
10 APRIL	1	0	8	4	23	1	4	14	0	381	103	11
	2	0	4	5	14	0	7	16	0	185	76	48
	3	0	0	1	3	0	2	4	0	93	19	3
	4	0	2	2	5	0	1	4	0	75	25	28
	5	1	1	3	21	0	6	7	1	195	85	5
	6	0	1	0	6	0	1	4	0	127	24	43
	7	1	10	9	27	2	7	15	0	378	122	1
	8	2	8	6	37	2	9	21	0	348	161	5
	9	1	6	4	18	0	4	12	0	139	74	2
	10	1	1	2	13	0	5	7	1	83	50	14
14 APRIL	1	0	2	1	7	0	0	7	0	93	26	44
	2	0	1	0	7	0	4	4	0	142	34	21
	3	0	0	0	4	1	1	5	0	73	22	30
	4	0	0	1	13	0	2	8	0	89	47	2
	5	0	2	2	9	1	4	13	0	113	53	11
	6	0	2	6	18	1	2	6	0	165	61	22
	7	0	4	2	16	0	5	9	0	192	60	13
	8	0	2	2	10	0	3	3	0	69	37	10
	9	2	1	1	16	0	4	7	0	80	55	2
	10	2	14	7	50	1	6	24	0	490	199	0
17 APRIL	1	0	5	1	12	0	2	6	0	144	54	25
	2	1	0	0	2	1	0	2	0	87	14	29
	3	1	0	2	7	0	1	7	0	170	41	16
	4	2	1	1	4	0	1	6	0	95	37	10
	5	1	1	0	4	0	2	3	0	58	19	15
	6	0	1	2	2	0	6	7	0	91	37	16
	7	0	1	0	14	1	3	9	0	170	54	28
	8	2	8	1	21	0	4	19	0	357	104	10
	9	2	5	3	19	0	6	14	0	153	91	4
	10	0	2	0	9	1	3	11	0	121	57	9

SMALL LARVAE (FEMALES)

DATE	CORE	ADH GENOTYPE							
		AX	BB	BC	BD	CC	CD	DD	EX
6 APRIL	1	1	4	0	10	0	2	10	0
	2	1	3	0	4	0	0	1	0
	3	0	2	1	3	1	0	6	0
	4	0	2	1	6	0	1	4	2
	5	0	2	2	11	1	1	4	0
	6	0	0	1	10	0	5	5	0
	7	0	3	4	10	0	2	3	0
	8	0	4	2	14	0	5	8	0
	9	0	7	4	16	0	3	12	0
	10	0	2	0	3	0	0	2	0
10 APRIL	1	2	9	1	14	7	2	12	0
	2	0	3	0	12	0	6	7	1
	3	0	0	2	2	1	1	3	0
	4	1	1	0	2	0	1	6	0
	5	2	4	1	21	0	7	10	0
	6	0	1	1	4	0	1	3	1
	7	0	7	5	22	0	4	10	0
	8	0	6	6	34	2	11	17	0
	9	1	3	0	11	1	5	8	0
	10	0	2	4	6	0	3	5	0
14 APRIL	1	0	1	1	3	1	2	1	0
	2	0	1	0	10	1	3	3	0
	3	0	1	0	5	0	0	4	0
	4	0	0	2	10	0	3	8	0
	5	0	1	0	11	0	2	12	0
	6	1	3	3	8	1	3	5	0
	7	0	0	1	12	0	3	8	0
	8	0	1	2	9	0	0	5	0
	9	1	2	1	13	0	3	2	1
	10	2	6	5	44	0	8	21	0
17 APRIL	1	1	7	0	6	0	6	7	0
	2	0	1	1	2	0	1	3	0
	3	2	1	3	8	0	1	5	0
	4	1	1	0	9	0	5	4	0
	5	0	2	0	1	0	1	2	0
	6	1	3	0	10	1	0	6	0
	7	2	2	1	10	0	2	9	0
	8	1	3	3	24	1	4	12	0
	9	1	3	4	19	0	7	8	0
	10	1	2	5	10	0	1	12	0



## Appendix 5

Numbers of eggs and sexes, Adh genotypes and development times of offspring in the crosses described in Chapter 7

- a) Parental Generation
- b) F1 Generation
- c) F2 Generation
  - (i) Replicates in which all offspring were gelled
  - (ii) Replicates in which only a sample of the offspring was gelled. For each cross the sample genotypes are given in the last three columns. Hom 1 is the first alphabetically of the two possible homozygotes in each case.
- d) FX Generation
  - (i) Replicates in which all offspring were gelled
  - (ii) Replicates in which only a sample of the offspring was gelled. The last four columns give the sample genotypes as in 5(c)(ii). Het 1 is the first alphabetically of the two possible heterozygotes in each case.

a) Parental Generation

Line No.	Rep.	No. Eggs	S	Nos. of flies emerging on day n (from egg-laying)																															T	Mean Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
S111AA	1	39	m f							1	2	7																			10	14.60	0.70				
	2	58	m f			2	8						1																		10	11.80	0.42				
			m																												0	-	-				
			f																												1	15	-				
	3	148	m f													2	8	8	3												21	18.57	0.87				
			f										3	2	1																6	14.67	0.82				
S39BB	1	273	m f																													14	20.64	1.55			
			f													1		3	2	4	2	2									6	18.33	1.37				
S220BB	1	59	m f																													31	18.32	1.33			
			f									1	16	8																	25	13.28	0.54				
	2	229	m f																													34	21.57	1.29			
			f													2	1	1	2	1	1	1									9	16.33	2.55				
	3	53	m f																													16	16.13	0.96			
			f																												15	12.13	0.35				
	4	209	m f																													52	25.13	1.91			
			f																												25	19.60	3.73				
	5	97	m f																													4	14.50	0.58			
			f																												2	12	0				
	6	73	m f																													5	14.00	2.45			
			f																												15	10.47	0.83				
S249BB	1	251	m f																													6	12.50	0.55			
			f																												6	12	0				
	2	67	m f																													2	12.50	0.71			
			f																												0	-	-				
	3	85	m f																													0	-	-			
			f																												3	9	0				

Line No.	Rep.	No. Eggs	S	Nos. of flies emerging on day n (from egg-laying)																															T	Mean Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
M115BB	1	49	m											4	6	4	1															13	16.00	0.91			
			f					5	8	1																						14	11.71	0.61			
	2	212	m														1	1	6	10	10	3	4	3	2	2						42	22.21	2.12			
			f							3	2	1	2	3	4	3	3	2	1	1													25	17.64	2.87		
	3	125	m														1	4	9	1	4											19	21.16	1.17			
			f									3	5	2	3	5	1															19	16.26	1.63			
	4	306	m														1	1	1	6	7	2	2	1								21	22.71	1.62			
			f									2	1	1	1	2	3	1	4	4	2	2										23	19.78	3.03			
M179BB	5	112	m													1	4	2														7	17.00	1.00			
			f							14	4	2	1																			21	12.52	0.87			
	6	106	m													1	3	2														9	16.00	1.87			
			f							8	6	5	1			1	3	2														20	12.95	0.94			
	7	83	m													1	1	3	3	1	1											11	17.18	1.72			
			f				1		2	2	3	3	4	4																		19	14.68	2.00			
	8	164	m																													0	-	-			
			f						1	1																						2	12.50	0.71			
M179BB	1	46	m																													0	-	-			
			f									1	1	4																		6	14.50	0.84			
	2	170	m																													2	24.00	1.41			
			f														1	3	1												35	17.71	1.36				
	3	208	m														1															1	18	-			
			f																													1	21	-			
	4	131	m																													3	13.67	0.58			
			f							2																						2	12	0			
M179BB	5	51	m																													1	13	-			
			f																													7	12	0			
M179BB	6	340	m																													1	17	-			
			f																													14	12.95	1.07			

Line No.	Rep.	No. Eggs	S	Nos. of flies emerging on day n (from egg-laying)																															T	Mean Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
M179BB contd.	7	325	m																																		
			f				1	1	1				1	3	4	1																					
S2CC	1	171	m																																		
			f																																		
	2	66	m																																		
			f																																		
	3	358	m																																		
			f																																		
	4	91	m																																		
			f																																		
	5	90	m																																		
			f																																		
S15CC	1	33	m																																		
			f																																		
	2	167	m																																		
			f																																		
	3	43	m																																		
			f																																		
	4	320	m																																		
			f																																		
	5	133	m																																		
			f																																		
	6	156	m																																		
			f																																		
	7	40	m																																		
			f																																		
	8	51	m																																		
			f																																		

Line No.	Rep.	No. Eggs	S	Nos. of flies emerging on day n (from egg-laying)																															T	Mean Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
S176CC	1	37	m					11																						11	12	0					
			f					4	3																					7	12.43	0.53					
	2	152	m																																		
			f																																		
	3	59	m																																		
			f																																		
4	257	m																																			
		f																																			
5	143	m																																			
		f																																			
6	247	m																																			
		f																																			
7	307	m																																			
		f																																			
S39CC	1	85	m																																		
			f																																		
	2	80	m																																		
			f																																		
	3	120	m																																		
			f																																		
	4	101	m																																		
			f																																		
	5	93	m																																		
			f																																		
	6	108	m																																		
			f																																		

Line No. Rep.		No. Eggs	S	Nos. of flies emerging on day n (from egg-laying)																															T	Mean Dev.	S.D. Dev.
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35		Time	Time			
M114CC	1	40	m					2	7	11	5	3																			28	14	1.09				
			f				1	10	7	6	1																				25	13.84	0.99				
	2	198	m								2	11	14	22	6	8	3														66	17.83	1.46				
			f									2	14	32	14	10	2	2	2												78	18.51	1.42				
	3	64	m																												19	15	0.58				
			f					1				16	2																		27	15.11	0.64				
											3	19	4	1																							
	4	181	m																													16	16.94	1.06			
			f																													32	16.78	1.04			
S8DD	5	101	m																													3	12.67	0.58			
			f																													6	12.50	0.55			
	6	160	m																													21	12.29	0.46			
			f																													16	12.44	0.51			
	7	53	m																													11	11.27	0.90			
			f																													7	11.57	0.53			
	8	60	m																													5	12.00	0.71			
			f																													3	12.00	1.00			
	1	58	m																													2	11	0			
			f																													3	11	0			
	2	134	m																													3	14.33	1.53			
			f																													2	14	2.83			
	3	40	m																													11	12.91	0.54			
			f																													12	12.83	0.58			
	4	274	m																													32	18.06	1.16			
			f																													48	18.13	1.09			
	5	219	m																													4	14.00	0.82			
			f																													0	-	-			
	6	37	m																													1	11	-			
			f																													4	11.75	0.50			



Line No.	Rep.	No. S Eggs	Nos. of flies emerging on day n (from egg-laying)																												T	Mean Dev. Time	S.D. Dev. Time
			8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35			
S8DD contd	7	74	m				6	9	1																					16	11.69	0.60	
			f				5	4	1																					10	11.60	0.70	
S9DD	1	85	m				1																							1	11	-	
			f				3																							3	11	0	
	2	179	m				2																							2	11	0	
			f																											0	-	-	
	3	73	m					11	2																					13	12.15	0.38	
			f					9	3	2																				14	12.50	0.76	
	4	269	m						7	5	4																			16	13.81	0.83	
			f						8	16	9																			33	14.03	0.73	
	5	37	m					1																						1	12	-	
			f					3	2																					5	12.40	0.55	
	6	130	m					8	15	1	1																			25	12.84	0.85	
			f					11	26	3	1																			41	12.85	0.65	
	7	123	m					3																						3	12	0	
			f				1	2	1																					4	11	0.82	
	8	147	m				3	4	8	2																				17	11.53	0.94	
			f					1	12	3																				16	12.13	0.50	
S11DD	1	31	m					1	6	2																				9	13.11	0.60	
			f					1	7	3	2																			13	13.46	0.88	
	2	91	m						3	2	7	9	2																	23	15.22	1.17	
			f						2	4	8	12	3																	29	15.34	1.08	
	3	47	m						3	1																				4	12.25	0.50	
			f																											0	-	-	
	4	57	m					3	8	5																				16	13.13	0.72	
			f					1	4	3																				8	13.25	0.71	
	5	112	m																											1	13	-	
			f																											2	13	0	

Line No.	Rep.	No. Eggs	S	Nos. of flies emerging on day n (from egg-laying)																															T	Mean Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
S11DD contd	6	110	m								1	1																		2	13.50	0.71					
			f							1	2																			3	13.67	0.58					
	7	290	m							1		7	2	3	2	2	2													21	16	2.30					
			f								2	4	4	5	10	5	7	1		1										39	16.85	2.02					
S15DD	8	243	m																											11	11.64	0.81					
			f											2	4	3	1	1												20	17.60	1.67					
	1	38	m							6	3	2																		11	11.64	0.81					
			f							7	3																			10	11.30	0.48					
	2	147	m								1	18	14	6	1															40	13.70	0.85					
			f								1	20	23	5	1	1														51	13.76	0.89					
	3	61	m								5	19	6																	30	13.03	0.61					
			f								2	17	7																	26	13.19	0.57					
	4	165	m																											31	16.16	0.97					
			f											2	4	14	9	2												48	16.48	1.30					
	5	60	m																											5	13.20	0.45					
			f								1	3	1																	5	13	0.71					
	6	165	m								1	1																		2	12.50	0.71					
			f								5	1																		6	12.17	0.41					
	7	88	m							2	2	2																		6	12	0.89					
			f							2	1	2																		5	12	1.00					
S82DD	8	61	m							2	4	2																		8	11	0.76					
			f																											16	11.25	1.06					
	1	28	m																											14	12.50	0.52					
			f																											7	12.71	0.76					
	2	141	m								5	11	1																	17	12.76	0.56					
			f								1	6	8	1																16	13.56	0.73					
	3	37	m								1	4	6	5																17	14.12	1.17					
			f									1	2	3	1	1														8	14.88	1.25					

Line No.	Rep.	No. Eggs	S	Nos. of flies emerging on day n (from egg-laying)																															T	Mean Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
S82DD contd	4	64	m													4	2	2													8	15.75	0.89				
			f													3	2	5													10	16.20	0.92				
	5	182	m							1						1	1	3	1												7	15.14	1.68				
			f														6	5													11	16.45	0.52				
	6	245	m													1				2	4										7	17.14	1.46				
			f																3	10	4	3								20	18.35	0.93					
	7	205	m																												6	18.67	0.82				
			f																	3	2	1								9	19	0.87					
S103DD	1	34	m				6	4	1																							11	11.55	0.69			
			f				7	2	1																						10	11.40	0.70				
	2	189	m							4	15	7				1	1														28	13.36	1.10				
			f								4	19	3	2																	28	14.11	0.74				
	3	24	m				1										1	1													3	14.33	2.08				
			f				2	4																							6	12.67	0.52				
	4	229	m				4	12	14	2	1																				33	13.52	0.91				
			f							4	16	10	2																		32	14.31	0.78				
	5	63	m				5																								5	12	0				
			f				2																								2	12	0				
	6	78	m				3	6	2	1																					12	11.08	0.90				
			f				3	4	2																						9	10.89	0.78				
	7	58	m				5				1																				6	10.33	0.82				
			f				1	5																							6	9.83	0.41				
	1	31	m				6	9	1																						16	11.69	0.60				
			f				3	7	1																						11	11.82	0.60				
S176DD	2	94	m																												35	14.54	0.82				
			f																												28	14.36	0.95				
	3	46	m																												14	13.57	0.85				
			f																												21	13.62	0.67				

Line No.	Rep.	No. Eggs	S	Nos. of flies emerging on day n (from egg-laying)																												T	Mean Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35			
S176DD contd	4	194	m									1	13	17	11	3															45	16.04	0.95	
			f										10	17	24	5	2														58	16.52	1.00	
	5	105	m								5	5																			10	12.50	0.53	
			f								7	15																			22	12.68	0.48	
SMEE	6	126	m								14	1																			15	12.07	0.26	
			f								17	7																			24	12.29	0.46	
	7	110	m			9	5																								14	10.36	0.50	
			f			6	2	1																							9	10.44	0.73	
	8	35	m			2	8																								10	10.80	0.42	
			f			4	1																								5	10.20	0.45	
	1	75	m							11	20	5	1	1																	38	12	0.99	
			f							6	18	16	3	2																	45	12.49	0.97	
	2	293	m							2	4	12	16	25	17	15	4	4	2	2												103	16.36	2.02
			f							2	6	11	18	31	26	11	12	6	3													126	16.45	1.94
3	130	m																													43	14.09	0.81	
		f																													35	14.63	1.00	
4	370	m																													32	18.16	1.92	
		f																													40	19.28	2.04	
5	106	m																													27	12.33	0.55	
		f																													25	12.44	0.51	
6	78	m																													25	12.25	0.59	
		f																													34	12.76	0.70	
7	171	m																													22	12.91	1.27	
		f																													23	13.78	1.73	
8	159	m																													10	12.60	0.70	
		f																													23	12.22	0.85	

Line No.	No. Eggs	Rep.	S	Nos. of flies emerging on day n (from egg-laying)																															T	Mean S.D.	
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	Dev.	Time				
PORT.EE	56	1	m						7	9	8																				24	13.04	0.81				
			f					2	8	14	4																				28	13.71	0.81				
	147	2	m																												52	15.73	1.27				
			f								1	7	16	14	11	1	2														57	16.35	1.40				
	31	3	m					2	4	1																					7	11.86	0.69				
			f					9	6																						15	12.40	0.51				
	286	4	m																												42	22.95	2.84				
			f											1	2	2	7	1	2	8	5	6	2	2	6					48	23.17	3.47					
	143	5	m																												4	16.25	0.50				
			f												3	1														7	15.43	1.27					
	114	6	m																												14	13.36	0.74				
			f						2	5	7																			12	14.33	1.30					
	75	7	m																												1	13	-				
			f																											0	-	-					
	61	8	m																												5	12.60	0.55				
			f																											3	12.67	0.58					

b) F1 Generation

Line No.	Rep.	No. Eggs	S	8	9	10	11	12	13	Nos. of flies emerging on day n (from egg-laying)																T	Mean. Dev.	S.D. Time					
S111AAf	1	252	m										2	8	12	14	22	14	11	7		1		91	19.91	1.86							
xS15DDm			f									1	14	26	21	7	5	1	1				76	17.57	1.31								
	2	253	m												21	40	39	12	4				116	19.47	1.02								
			f									2	8	24	38	19	4	2					97	17.87	1.14								
S220BBf	1	228	m												1	1	3	5	11	22	8	2	2	55	22.67	1.52							
xM115BBm			f									2	2	7	7	10	8	4	8	2	2	1	53	18.55	2.33								
S220BBf	1	103	m												1	5	2	7	2	13	6	4	3	1	44	19.52	2.26						
xS2CCm			f							2	5			3	2	2	5	8	4	6	3	1	41	18.98	3.10								
S2CCf	1	230	m														11	30	35	13	4	2	95	19.74	1.10								
xS220BBm			f										2	14	36	22	12						86	18.33	0.99								
S220BBf	1	75	m					1	7	6													14	12.36	0.63								
xS15CCm			f			9			1														10	11.46	1.47								
S220BBf	1	127	m														3	13	34	16	8		75	20.24	1.13								
xM114CCm			f								2	2	8	20	17	9	1	1				1	60	17.40	1.32								
M114CCf	1	116	m												15	3	1						19	15.26	0.56								
xS220BBm			f								14												14	13	0								
	2	98	m																				12	14.83	0.94								
			f								2		8	2									10	13	0								
	3	217	m																				62	18.02	0.97								
			f														2	16	28	12	3	1	58	16.34	0.91								
															11	21	22	3	1														
S220BBf	1	74	m																				2	11	0								
x S8DDm			f																				2	11	0								
	2	78	m																				59	19.49	0.95								
			f																				56	17.14	0.98								



Line No.	Rep.	No. Eggs	S	Nos. of flies emerging on day n (from egg-laying)																															T	Mean Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
S220BBf	1	51	m									1	1	6	7		1															16	16.44	1.09			
			f					9	11																							20	12.55	0.51			
M115BBf	2	43	m								1				4	20	28	17	7	1	1											79	19.05	1.35			
			f									2	28	18	12	3	1															64	16.83	1.03			
xS15CCm	1	150	m							14			9																			23	-	-			
			f						31																							31	-	-			
	2	51	m							10			7																			17	-	-			
			f							23																						23	-	-			
	3	104	m							16			2																			18	-	-			
			f							15																						15	-	-			
S15CCf	1	184	m										1	1	12	25	9	6	1	1	4											60	17.52	1.68			
			f							1	5	21	11	3	4	2		1														48	15.75	1.52			
M115BBf	1	230	m										1	2	3	7	9	9	7	4												42	19.29	1.73			
			f								1	2	4	6	3	10	10	3	4													43	17.72	2.04			
M115BBf	1	65	m										3	18	6		1															28	16.25	0.93			
			f							4	10			1																		15	14.67	1.29			
xS8DDm	2	117	m											29	20	6	1															56	16.64	0.82			
			f							1	24	9	1																			35	15.26	0.66			
S8DDf	1	86	m													2	10	26	3	1												42	18.81	0.83			
			f												7	11	9	4														31	17.32	0.98			
M115BBf	1	307	m												7	17	1	1														26	16.85	0.67			
			f							4	21	4																				29	14.00	0.53			
xS103DDm	2	180	m																													26	17.77	1.73			
			f																													18	13.22	1.80			

Line No.	Rep.	No. Eggs	S	Nos. of flies emerging on day n (from egg-laying)																												T	Mean S.D.	
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35		Dev. Time	Dev. Time
M115BBf	1	253	m										3	14	20	33	38	11														119	19.03	1.25
			f									3	8	14	15	36	17	4														97	18.44	1.42
M179BBf	2	206	m										2	13	39	37	14	8	3	2	1											119	18.84	1.41
			f									1	6	9	13	35	19	9	7	1	1	1										102	18.21	1.79
M179BBf	1	165	m												1	2	4	5	12	5	3	1	8	5	10	16						72	24.85	3.67
			f									1	2	2	4	6	5	4	2	2	2	5	5	4	8							57	23.33	4.52
xS9DDm	2	51	m																													29	19.00	1.28
			f									22	15	4	5	12	4	3	1													37	15.41	0.50
M179BBf	3	111	m											2	5	17	8	1														33	17.03	0.88
			f						4				5	3	1																	13	14.77	1.02
M179BBf	4	68	m											3	17	3																23	16.00	0.52
			f									3	12	1																		16	14.69	0.87
M179BBf	5	128	m											1	2	8	11	5	1													28	18.71	1.08
			f									3	12	7	2	1																25	15.36	1.29
xS11DDm	1	181	m													1	2	1	14	11	6	6	8	6	8	5						68	24.69	2.73
			f													1	3	6	5	4	4	9	4	5	5							46	25.17	2.77
M179BBf	2	58	m													3	8	7	6	2	1											27	21.00	1.39
			f										1	3	5	3	5															17	17.47	1.28
M179BBf	3	105	m													1	14	14	3													32	19.59	0.71
			f										1	1	5	2	1															10	17.10	1.10
M179BBf	4	124	m													4	1															5	16.20	0.45
			f									1	5	1	2																	9	15.33	1.22
M179BBf	5	132	m													1	1	9	20	1	1											33	20.67	0.85
			f													4	8	14	6	1												33	19.76	1.00

Line No.	Rep.	No. Eggs	S	Nos. of flies emerging on day n (from egg-laying)																														T	Mean S.D.	
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	Dev. Time	Dev. Time			
M179BBf xS82DDm	1	139	m											1			1	4	6	4	12	10	8	6	5						57	24.44	2.29			
			f							1	2	1		7	3	9	9	7	3	5	1										48	21.42	2.50			
	2	78	m														4	14	14	4	1										37	20.57	0.93			
			f							4	6	13	6	2	1																32	17.97	1.20			
S2CCf xS176CCm	1	68	m									7	16	6																	29	14.97	0.68			
			f							3	17	7																			27	15.15	0.60			
	2	193	m											2	10	16	14	15	2	2	1										62	18.79	1.45			
			f											3	11	32	32	8	1												87	19.39	0.98			
S2CCf xM114CCm	1	106	m											20	8	5	1		1												35	16.74	1.12			
			f											17	14	7	2														40	16.85	0.89			
S2CCf xS9DDm	1	220	m								3	7	12	10	3																35	15.09	1.09			
			f									5	20	13	1	2	1														42	15.50	1.15			
S2CCf xS103DDm	1	152	m								1	11	10	1																	23	14.48	0.59			
			f									7	4																		11	14.36	0.50			
	2	163	m									1	4	35	5	1															46	16.02	0.61			
			f										4	28	11	1															44	16.20	0.63			
S2CCf xS176DDm	1	374	m									1	3	9	28	17	4		1												63	18.17	1.12			
			f											1	5	23	40	2	2												73	18.62	0.83			
S15CCf xM114CCm	1	112	m							1	1	22	14	10	2	1															51	14.80	1.10			
			f									5	14	23	13	1	1														57	14.89	1.03			
S176CCf xS220BBm	1	170	m												1	2	5	12	2											22	19.55	0.96				
			f									3	1	2	7	1															14	15.21	1.48			
S39CCf xM114CCm	1	90	m										1	2	7	13	3													26	17.58	0.95				
			f									1	7	2	1																11	15.18	0.98			

Line No.	Rep.	No. Eggs	S	Nos. of flies emerging on day n (from egg-laying)																														T	Mean S.D.	
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	Dev. Time	Dev. Time			
S39CCf	2	120	m												3	22	18	16	3	1												63	16.95	1.07		
			f									7				24	12	1	1	1												46	15.15	1.23		
	3	100	m												8	25	10	2															45	16.13	0.76	
			f									21				35																	56	14.25	0.98	
S39CCf	1	96	m												5	8	12	3	1														29	16.59	1.12	
			f									11				17	6	1															35	14.60	1.19	
M114CCf	1	132	m												2	2	9	6	1														20	18.10	1.02	
			f									1	3	2	2	1																	9	14.89	1.27	
M114CCf	1	189	m												3	16	13	9	7														48	17.02	1.18	
			f													16	29	5	1	1													52	15.88	0.81	
	2	202	m												3	2	6	12	11	2	1													37	18.97	1.38
			f													13	5	1	2	3													27	15.70	1.68	
	3	124	m												1	4	15	9	3															32	17.28	0.92
			f													2	17	7	3	1													30	15.40	1.04	
M114CCf	1	77	m						1	4	4																							9	12.33	0.71
			f							2	2																							4	12.50	0.58
M114CCf	1	178	m												1	1	2	11	11	7	13	5	2											53	17.64	1.74
			f																4	9	24	18	19	6									80	18.71	1.29	
	2	65	m												3	15	8																	26	14.19	0.63
			f													4	5	10	2														21	14.48	0.93	
M114CCf	1	97	m												3	3	15	6	1															28	14.96	0.96
			f																9	11	15	3											38	15.32	0.93	
xS176DDm	2	129	m												2	9	39	8	1															59	14.95	0.71
			f																															73	15.52	0.75



Line No.	Rep.	No. Eggs	S	Nos. of flies emerging on day n (from egg-laying)																															T	Mean Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
S11DDf xS2CCm	2	130	m								6	10	10	32	16	1																75	17.60	1.23			
			f								4	14	27	22	7																	74	18.19	1.03			
S11DDf xS15CCm	1	167	m								1	5	10	7	22	38	24	2														109	18.42	1.49			
			f								1	13	9	10	29	43	11	2	1													119	19.03	1.59			
	2	178	m							3	5	19	18	19	1																	65	14.74	1.15			
			f								7	35	16	11	6																	75	15.65	1.10			
S11DDf xSMEEm	1	125	m								3	3	14	13	15	14	9	7	2	3	1	3										87	18.47	2.48			
			f									7	11	23	16	11	2	2	4	1	2	1										80	18.94	2.18			
	2	56	m							5	9	8	2	14	14																	52	15.02	1.77			
			f								1	4	10	29	5																	49	16.37	1.27			
S15DDf xM115BBm	1	189	m													20	13	19	30	20	9	5	1									117	18.59	1.73			
			f									4	8	28	14	24	17	4	3	1												103	17.30	1.68			
	2	24	m																													0	-	-			
			f																													3	11	0			
S15DDf xS11DDm	1	23	m								44	3																				47	14.06	0.25			
			f								25	4																				29	14.14	0.35			
	2	147	m								1	3	19	27	9	9																68	16.99	1.13			
			f										1	14	37	23	21															96	17.51	1.03			
S15DDf xS176DDm	1	61	m								16	24	2																			42	13.67	0.57			
			f								1	25	4																			30	14.10	0.40			
	2	44	m								2	9	4	1																		16	13.25	0.77			
			f									13	7	2																		22	13.50	0.67			
S15DDf xSMEEm	1	78	m								2	7	14	21	4	1																49	15.43	1.04			
			f									10	10	9	25	12	1															67	15.33	1.37			



Line No.	Rep.	No. S Eggs	Nos. of flies emerging on day n (from egg-laying)																										T	Mean Dev. Time	S.D. Dev. Time
			8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	
S15DDf	2	77	m					2	6	36	19																		65	14.14	0.72
xSMEEm			f					1	22	36																			59	14.59	0.53
S82DDf	1	91	m									7	11	7	1														26	17.08	0.84
xS22OBBm			f					1	13	11	2	2																	29	14.69	0.93
	2	205	m									3	3	6	12	13	3	1	1										42	21.14	1.59
			f								3	6	6	4	1	4		1											25	17.88	2.39
S82DDf	1	94	m									7	14	24	11														56	15.70	0.93
xS2CCm			f									6	20	25															51	16.37	0.69
	2	60	m				5	3																					8	11.38	0.52
			f				2	1																					3	11.33	0.58
S82DDf	1	92	m									5	2	7	2														16	15.38	1.09
xS176DDm			f									1	7	13	3														24	15.75	0.74
	2	170	m									4	23	5	1														33	16.09	0.63
			f									1	27	13	2														43	16.37	0.62
S103DDf	1	121	m									3	4	14	9	8	4	3											45	16.87	1.56
xS176CCm			f									1	9	10	10	9	6	8											53	18.26	1.73
	2	208	m									2	12	31	38	26	13	1				2							125	19.08	1.58
			f									4	25	41	42	19	2	8	1	1									143	19.67	1.46
S103DDf	1	261	m									5	20	26	24	9	4	1											89	17.31	1.28
xS176DDm			f									9	31	2	14	9	7	1											93	18.10	1.49
	2	127	m									1	20	46	3														70	15.73	0.56
			f									1	56	11	1	1													70	16.26	0.77
S176DDf	1	233	m																										123	20.83	2.37
xS111AAm			f									1																	137	19.11	1.87

Line No.	Rep.	No. Eggs	S	Nos. of flies emerging on day n (from egg-laying)																															T	Mean Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
S176DDf	2	164	m											1	11	27	29	12	13	2	1	2									98	19.06	1.53				
			f												1	10	9	28	23	7	1	1	1								81	17.20	1.43				
S176DDf	1	289	m																	2	8	11	24	35	31	11	6				128	24.95	1.54				
			f														1	4	11	8	31	18	31	19	8	1				132	22.97	1.84					
xS22OBBm	2	74	m												2	1	1														4	16.75	0.96				
			f																											6	13.50	0.84					
S176DDf	1	179	m																												108	16.37	1.46				
			f														37	30	22	10	4	2	3							99	15.32	1.24					
xM115BBm	2	164	m																												60	16.77	1.08				
			f															2	29	15	11	2	1							29	16.14	1.06					
	3	150	m																												38	16.37	1.46				
			f															12	13	7	2	1	3							23	15.70	1.84					
S176DDf	1	23	m																												27	12.67	0.62				
			f																											25	12.76	0.60					
xS15DDm	2	92	m																												35	16.57	0.65				
			f																											43	16.88	0.70					
M122DDf	1	94	m																												13	14.62	0.51				
			f																											4	12.50	1.00					
xS22OBBm	2	43	m																												1	12	0				
			f																											2	12	0					
	3	73	m																												1	13	0				
			f																											0	-	-					
M122DDf	1	86	m																												9	12.11	0.93				
			f																											18	10.06	0.73					











Line No.	Rep.	No. Eggs	S	Geno- type	Nos. of flies emerging on day n (from egg-laying)																															T	Mean Dev. Time	S.D. Dev. Time
					8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
M115BBf xM114CCm	1	122	m	BB											1	2	2	2	3	1										11	17.64	1.57						
				BC												1	2	4	3	5	2											18	17.61	1.82				
				CC												2	4	2														8	14.75	1.16				
				BB												2	9	2														13	14.50	0.87				
				BC												9	13	6														28	14.34	1.11				
				CC													8	1	1													10	14.90	0.88				
	2	85	m	BB												1	1													2	15.50	0.71						
				BC													1	3	1													5	16	0.71				
				CC																											0	-	-					
				BB															1												4	14.50	1.91					
				BC															2												9	14.17	0.66					
				CC															2												9	14.83	0.66					
M115BBf xS8DDm	1	51	f	BB																										0	-	-						
				BD																											2	13.50	2.12					
				DD																											4	11.75	0.50					
				BB																											2	9	-					
				BD																											5	10	-					
				DD																											3	12	-					
			m	BB																										3	12.67	0.58						
				BD																											3	12.67	1.15					
				DD																											2	11.50	0.71					
				BB																											2	9	-					
				BD																											5	10.40	0.55					
				DD																											0	-	-					

Line No.	Rep.	No. S Eggs	Geno- type	Nos. of flies emerging on day n (from egg-laying)																																Mean T Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
M115BBf xS8DDm	3	67	BB							3	1																						4	12.25	0.50		
			m BD				4	9	2	1																							16	12.00	0.82		
			DD		1	1																											3	11.67	2.08		
			BB			7																											7	10	-		
S8DDf xM115BBm	2	185	f BD		3	2																											5	10.40	0.55		
			DD		1																											1	11	-			
			BB																														3	23.33	0.58		
			m BD																														21	20.24	1.22		
M115BBf xS103DDm	3	205	DD																														11	18.18	1.66		
			BB																														8	17.63	1.19		
			f BD																														14	18.29	1.44		
			DD																														8	19.00	1.51		
M115BBf xSMEEm	1	103	BB																														5	19.80	2.17		
			m BD																														31	17.84	0.64		
			DD																														18	16.28	0.75		
			BB																														16	16.56	0.81		
M115BBf xSMEEm	1	103	f BD																														43	16.65	0.61		
			DD																														22	16.45	0.86		
			BB																														12	17.92	1.00		
			m BE																														28	17.14	0.76		
M115BBf xSMEEm	1	103	EE																														6	14.50	1.05		
			BB																														3	15.67	0.58		
			f BE																														16	15.38	1.31		
			EE																														5	16.00	1.00		







Line No.	Rep.	No. S Eggs	Geno- type	Nos. of flies emerging on day n (from egg-laying)																																Mean Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	T					
M179BBf xS82DDm	2	51	BB															1	2												3	23.33	1.15				
			m													3	3	1														7	20.71	0.76			
			DD								1	3																					4	17.75	0.50		
			BB											1	1																		3	18.67	1.53		
S2CCf xS9DDm	1	82	BD																	2	2										6	19.00	2.37				
			DD																	1	3											4	17.75	0.50			
			CC								3		3	1																			7	13.07	1.13		
			m							2		17	2	1																			22	13.61	0.84		
S2CCf xS9DDm	2	175	DD																													8	13.50	0.80			
			CC																														12	14.04	1.20		
			f																															24	14.58	0.83	
			DD																															15	14.67	1.13	
S2CCf xS103DDm	3	180	CC																													0	-	-			
			m																															2	15	-	
			f																															0	-	-	
			DD																															1	16	-	
S2CCf xS103DDm	3	180	CC																													4	16.00	0.82			
			m																															1	16	-	
			f																																		
			DD																																		
S2CCf xS103DDm	3	180	CC																													9	14.44	0.88			
			m																															26	13.85	1.16	
			f																															14	14.29	0.73	
			DD																															10	14.30	0.67	
S2CCf xS103DDm	3	180	CC																													22	14.77	0.81			
			f																															14	14.86	0.77	





Line No.	Rep.	No. S Eggs	Geno- type	Nos. of flies emerging on day n (from egg-laying)																																T	Mean Dev.	S.D. Dev.
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35							
S39CCf	1	96	CC																													0	-	-				
			m CD				2	3																								6	12.33	1.86				
			DD				1	1																								2	11.50	0.71				
			CC																														0	-	-			
xS15DDm			f CD			1	2																									3	10.67	0.58				
			DD								2																					2	13	-				
			CC																														3	15.33	0.58			
			m CD																														7	15.29	0.95			
	2	86	DD							1																						1	12	-				
			CC																														5	11.60	0.55			
			f CD					2	3																							9	13.44	1.59				
			DD																														1	12	-			
	3	55	CC																													3	13.67	1.15				
			m CD																														5	14.20	0.45			
			DD																														3	11.33	1.53			
			CC																														2	11	-			
			f CD																													3	11	-				
			DD																														3	11.00	1.00			
			AA																														7	19.57	2.03			
			m AC																														17	18.88	1.95			
M114CCf	1	115	CC																													2	17.00	1.03				
			AA																														4	15.00	0.82			
			f AC																														25	15.64	1.19			
			CC																														8	15.75	1.16			







Line No.	Rep.	No. Eggs	S	Geno- type	Nos. of flies emerging on day n (from egg-laying)																															T	Mean Dev. Time	S.D. Dev. Time
					8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
S8DDf	1	45	m	CC						4																												
				CD								15																										
				DD								2																										
				CC								6																										
				f	CD							9																										
				DD						5																												
				CC								2	5			1	1																					
				CD								5	3	4	6		2		1																			
				DD							1		3	2			1																					
				CC								2	3	3	3		2																					
	2	165	f	CD																																		
				DD																																		
				CC																																		
				CD																																		
				DD																																		
S9DDf	2	132	m	BB																																		
				BD																																		
				DD																																		
				BB																																		
				f	BD																																	
				DD																																		
				BB																																		
				BD																																		
				DD																																		
				AA																																		
S11DDf	2	89	f	AA																																		
				AD																																		
				DD																																		
				AA																																		
				f	AD																																	
				DD																																		
				AA																																		
				AD																																		
				DD																																		
				AA																																		





Line No.	Rep.	No. Eggs	No. S	Geno- type	Nos. of flies emerging on day n (from egg-laying)																															T	Mean Dev. Time	S.D. Dev. Time
					8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
S11DDf xS2CCm	2	79	m	CC																											0	-	-					
				CD																												1	13	-				
				DD																												0	-	-				
				CC																												1	13	-				
				f CD																												0	-	-				
				DD																											0	-	-					
				CC																												13	15.46	1.05				
				CD																												26	14.23	1.18				
				DD																												13	14.54	0.88				
				CC																												11	15.82	0.87				
	3	95	f	CD																											24	14.58	0.93					
				DD																												8	15.00	0.76				
				CC																												8	17.25	1.04				
				CD																												12	16.00	1.48				
				DD																												13	17.77	0.93				
S11DDf xS15CCm	1	123	f	CC																											10	17.30	2.16					
				CD																												25	16.64	1.32				
				DD																												11	17.00	1.34				
				CC																												5	12.80	0.45				
				CD																												12	12.33	0.49				
	3	50	f	DD																											8	12.50	0.53					
				CC																												8	13.13	0.35				
				CD																												13	12.62	0.65				
				DD																												9	12.56	0.53				

Line No.	Rep.	No. Eggs	S	Geno- type	Nos. of flies emerging on day n (from egg-laying)																															T	Mean Dev. Time	S.D. Dev. Time
					8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
S11DDf xM114CCm	2	146	m	CC											1		1	1	1	1	1	1	1	1							8	22.38	2.67					
													1	1	2		1	2	3	1	2	2											15	21.20	2.88			
															2		2	2	2		2	1											10	21.30	2.75			
																3	1	1	1	1	2	1		2									13	22.00	3.29			
														1	2	1	2	2	1	3	1	5	5	3	1									27	22.44	3.18		
S15DDf xM115BBm	2	51	f	CD											1	2	1														9	18.11	3.44					
S82DDf xS220BBm	1	225	f	DD																																		
S15DDf xM115BBm	2	51	f	DD																																		
S15DDf xM115BBm	2	51	f	DD																																		
S15DDf xM115BBm	2	51	f	DD																																		
S15DDf xM115BBm	2	51	f	DD																																		
S15DDf xM115BBm	2	51	f	DD																																		
																		</																				

Line No.	No. Rep.	No. S Eggs	Geno- type	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	T	Mean Dev. Time	S.D. Dev. Time
S82DDf xS220BBm	2	177	BB															1		1	2	3	1	1	2	1					12	26.42	2.31	
			m BD											1	3	1	4	5	2	1	1										18	21.33	1.85	
			DD				1	1	1	2	5	1	1																			12	17.33	1.67
			BB											1	1	1	1	1	1				1								6	20.83	3.71	
			f BD											1	8	3	1	1	1	1	1	2									18	19.67	2.50	
DD											1	1	2	3															7	18.00	1.15			
S82DDf xS2CCm	2	115	CC						1	3	2			1																	7	15.57	1.27	
			m CD							1	6	1																			8	16.00	0.53	
			DD								7																				7	16	-	
			CC									2	2		2	1															7	17.71	1.60	
			f CD				1	1	4	1	2	1																				10	16.50	1.51
DD								1	2	1	2																		6	16.67	1.21			
S103DDf xS176CCm	1	62	CC						2		3	2																			7	14.71	1.25	
			m CD						2	5	6		1																		14	14.50	1.02	
			DD							1	2																				3	14.67	0.58	
			CC							1	5			1																	7	15.29	1.25	
			f CD							3	5	1	1																		10	15.00	0.94	
DD									2	1	1		1															4	16.25	1.89				
			CC						1																						1	13	-	
			m CD								3	4		1																	8	15.88	0.99	
			DD									3	2																		5	16.40	0.55	
			CC																												5	15.00	1.00	
			f CD										2	1	2																13	16.46	0.97	
DD																													5	16.20	0.45			



Line No.	Rep.	No. S Eggs	Geno- type	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	T	Mean Dev. Time	S.D. Dev. Time
S176DDf	2	84	BB																												0	-	-	
			m																												1	19	-	
			DD																												2	18.50	0.71	
			BB																												2	18.50	2.12	
			f																												2	18.50	0.71	
xS220BBm			DD																												2	17	-	
			BB																												1	15	-	
			m																												7	15.14	1.07	
			DD																												2	11.50	0.71	
			BB																												3	10.33	0.58	
S176DDf	1	41	f																												13	11.38	0.87	
			DD																												4	12.50	1.73	
			BB																												2	20	-	
			m																												5	18.20	3.11	
			DD																												2	16.00	1.41	
xM115BBm	2	86	BB																												2	14.50	0.71	
			f																												2	14	-	
			DD																												2	14	-	
			BB																												2	16	-	
			m																												10	15.70	2.00	
S176DDf	3	48	DD																												4	12.50	1.73	
			BB																												2	11.00	1.41	
			f																												10	12.40	0.97	
			DD																												2	12.	-	
			BB																												2	12.	-	







c) (ii) F2 Generation: offspring sample gelled

Line No.	R e P	No. S Eggs	Nos. of flies emerging on day n (from egg-laying)																																			T	Mean Dev. Time	S.D. Dev. Time	Hom 1	Het 2	Hom 2
			8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35													
S220BBf xM114CCm	3	46	m	1	2	1	7	8	6	16	8	5	6	1	3	2	2													68	17.26	2.84	4	16	13								
			f	3	3	2	5	13	9	12	8	5	2																	62	15.92	2.20	6	17	5								
S220BBf xS15DDm	1	295	m				1	2	2		2	7	6	11	12	6	6	5	1	2	1	3	5	1	2	2	2			79	23.16	4.79	4	16	3								
			f					1	6		6	10	5	9	16	6	10	8	4	5	1		3	1	3	1			95	23.59	4.00	4	21	4									
S8DDf xM115BBm	1	319	m							1	2	2	2	5	5	5	4	4	5	7	4	6	4	2	1				59	25.03	3.79	13	9	8									
			f								1	2	9	8	8	5	2	5	3	3	2	4	1		1			55	23.20	3.50	5	17	7										
	3	157	m							2	3	10	9	13	2	6													45	16.29	1.59	6	15	6									
			f								1	3	17	17	7	6		2											53	15.06	1.51	7	15	8									
M115BBf xS103DDm	1	463	m								1	1	1	6	5	5	6	4	6	3	5	6	3	2	6	2	1	1	68	24.67	4.43	2	19	11									
			f							1	1			5	10	5	5	7	4	3	5	1	3	4	3		3	2	67	23.37	4.58	5	16	7									
	2	290	m								1	1	2	5	7	7	5	3	3	2	4	2	5	4	2	5	1	1	67	25.10	5.16	3	21	8									
			f								1		4	12	7	5	6	4	1	1	3	3	5	6	1	1	2	2	70	23.71	4.85	2	16	10									
M179BBf xS9DDm	2	189	m											1	3	9	7	4	3	6	4	5	2	3	6	3		59	24.36	4.07	1	23	8										
			f												1	11	11	6	12	5	4	3	2	3		1	1	60	21.95	2.81	3	20	5										
M179BBf xS11DDm	1	168	m											1	3	6	2	10	7	4	8	1		2	2	1	1	51	21.94	3.97	5	19	6										
			f												1	2	3	14	10	4	3	3	1	1	3			47	20.28	2.53	5	18	7										
M179BBf xS82DDm	3	102	m																										42	18.76	2.68	3	19	12									
			f																										45	16.87	1.42	6	14	6									
S2CCf xS103DDm	1	419	m											2	1	2	2	11	3	2	4	3	4	3	5	1	1	44	22.36	3.40	10	16	3										
			f																										54	23.67	4.04	8	21	4									
	2	219	m																										38	22.16	3.92	6	8	7									
			f																										58	24.53	3.97	12	23	4									
S176CCf xS220BBm	1	241	m																										35	21.86	3.22	5	17	5									
			f																										47	20.87	3.08	4	16	14									



[illegible]





Line No.	R No. p Eggs	S type	Geno-	Nos. of flies emerging on day n (from egg-laying)																																T	Mean Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35							
M179BB/S9DD	x	m	BB										2	1	2	4		1															10	16.20	1.55			
			BD						4	2	1	5																					12	15.58	1.38			
			BC			2	1		3	2		3		1																			12	14.67	2.53			
			CD			1	1	1		1		1																					5	13.60	2.41			
M114CC/S220BB 1 128		f	BB		1	1	1	1	1	3	5																						12	13.58	1.73			
			BD					2		2	2	2																					8	15.25	1.58			
			BC		2	1	3	2																									8	11.63	1.19			
			CD			1			4	3	1	1																					10	13.60	1.35			
		m	BB													1	2		4	5	2	1	1	2	1							19	20.32	2.45				
			BD										1		2	3		7	1													14	17.61	1.72				
			BC									1		3	1		5																10	17.15	1.60			
			CD								1	1	2																				4	15.25	0.96			
2 115		f	BB						1	1	1	6																					9	15.33	1.12			
			BD							1	2	1	1																				5	15.40	1.14			
			BC							1	3	1	2					1															8	15.06	1.89			
			DD					1	1		1	2	5	1																			11	14.91	1.87			
S15CC/M115BB	x	m	AB																														2	19	-			
			AC								1	2	1	2	1																		7	17.00	1.41			
			BC									1	1	2	1																		5	17.60	1.14			
			CC									5	2																				9	14.50	1.13			
M114CC/S111AA 1 69		f	AB																														7	15.00	1.78			
			AC																														6	14.25	1.25			
			BC																														5	14.20	0.67			
			CC																														3	14.50	1.50			

Line No.	R. No. p Eggs	S	Geno- type	Nos. of flies emerging on day n (from egg-laying)																																T	Mean Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35							
S15CC/M115BB	x	m	AB																													3	15.00	-				
			AC																													1	14.50	-				
			BC																													1	14.50	-				
			CC																													2	13.75	-				
M114CC/S111AA 2 46 contd.		f	AB																													1	14.50	-				
			AC																													3	13	-				
			BC																													1	13	-				
			CC																													2	13	-				
M114CC/S111AA	x	m	AB																													5	14.50	-				
			AC																													3	14.50	-				
			BC																													6	14.25	-				
			CC																													1	13	-				
S15CC/M115BB 2 98		f	AB																													3	13	-				
			AC																													6	13.25	-				
			BC																													1	13	-				
			CC																													5	13.30	-				

Line No.	R No. p Eggs	S type	Geno-	Nos. of flies emerging on day n (from egg-laying)																															T	Mean Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35						
M114CC/S220BB	x		BB											2	3	2															7	16.00	0.82				
			BD								1	4	1	2																	8	14.50	1.07				
		m	BC																												4	13.75	2.63				
			CD																												6	10.83	0.75				
M115BB/S8DD	1		BB																												9	11.11	1.05				
			BD																												11	11.36	0.92				
		f	BC																												9	11.22	1.64				
			CD																												3	14.67	1.15				
			BB																												6	17.92	1.36				
			BD																												6	16.75	2.07				
		m	BC																												5	16.70	1.15				
			CD																												4	13.00	1.41				
	2		BB																												6	16.25	1.51				
			BD																												9	15.61	1.92				
		f	BC																												7	15.79	2.66				
			CD																												4	16.00	-				
			BB																												10	13.70	0.67				
			BD																												6	12.00	0.89				
		m	BC																												4	13.25	0.50				
			CD																												5	10.20	0.45				
	3		BB																												7	9.71	0.76				
			BD																												7	10.14	0.69				
		f	BC																												5	9.80	0.45				
			CD																												4	10.75	0.50				

Line No.	R No. Eggs	S	Geno- type	Nos. of flies emerging on day n (from egg-laying)																												T	Mean Dev. Time	S.D. Dev. Time
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35			
M114CC/S220BB			BB				1																								1	11	-	
			BD				2																								2	11	-	
			BC				1																								1	11	-	
			CD				1	3	1																						4	9.75	0.50	
S11DD/M115BB	1	60		BB			3																								3	9	-	
				BD			3																								3	9	-	
			f	BC			1																								1	9	-	
				CD			2																								2	9	-	
	2	64		BB								6	2	1																	9	13.44	0.73	
				BD							1	1		1																	3	13.33	1.53	
		m	BC								1	1																			2	12.50	0.71	
			CD				2	4																							6	10.67	0.52	
			BB				4																								4	10	-	
			BD				8																								8	10	-	
		f	BC				2	1	3																						6	11.17	0.98	
			CD				4	4																							8	10.50	0.53	
			BB																												7	16.57	0.53	
			BD																												7	15.71	0.95	
		m	BC																												6	14.83	1.33	
			CD				2	2																							8	12.38	1.06	
	3	144		BB			2																								7	13.29	1.89	
			BD																												7	13.57	1.81	
		f	BC																												7	13.57	1.27	
			CD																												5	14.20	1.64	



Line No.	R No. p Eggs	S type	Geno-	Nos. of flies emerging on day n (from egg-laying)																															T	Mean S.D.	
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	Dev. Time	Dev. Time				
M114CC/S249BB			BB																											0	-	-					
			BD				3	1																					4	11.25	0.50						
	x		BC				3																						3	11.00	-						
			CD				1	1	1																				3	10.00	1.00						
S176DD/M115BB 1 140			BB			2																							2	9	-						
			BD			3																							3	9	-						
	f		BC			2																							2	9	-						
			CD			4	1																						5	9.20	0.45						
			BB									2		1	4	1													8	15.25	1.56						
			BD								2		2		1														5	14.40	1.34						
	m		BC									1	1	3	3	1													11	14.36	2.11						
			CD					3	5																				8	10.63	0.52						
			BB									1																	6	11.33	0.82						
			BD								1																		8	11.63	1.60						
	5		BC								1	5																	10	10.80	0.63						
			CD								3	6	1																11	12.00	2.00						



Line No.	R No. e p	S Eggs	Geno- type	Nos. of flies emerging on day n (from egg-laying)																											T	Mean Dev. Time	S.D. Dev. Time		
				8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35				
S11DD/M115BB			BB						1	1	2	2																			6	14.83	1.17		
			BD					2	3																						5	12.60	0.55		
		m	BC						2	1	2																				5	14.00	1.00		
			CD			4	1																								5	10.20	0.45		
M114CC/S249BB			BB		2	6																									8	9.87	0.48		
			BD			4	2																								6	10.33	0.52		
		f	BC			3	4	1																							8	10.75	0.71		
			CD			1	5	1																							7	11.00	0.58		
			BB						1																							1	12	-	
			BD				4	2																								6	11.33	0.52	
		m	BC				4	3																							7	11.43	0.53		
		CD		4	3																											7	9.43	0.53	
	2	58	BB			4	2																									6	10.33	0.52	
		f	BD		2																											2	9	-	
		BC																														0	-	-	
		CD		1	1																											2	9.50	0.71	
			BB										2	2		4	2	1														11	18.27	1.71	
		m	BD											2	2	1																8	16.06	1.55	
		BC												1	2	2																12	16.63	1.80	
		CD					5	3					1	1	1	5																9	11.67	1.00	
	3	143	BB				1	3	4	4	2																						14	13.21	1.19
		f	BD				1	2	1	4	2					1																	11	13.73	1.68
		BC						2	5	3																							10	13.10	0.74
		CD																															1	15	-



d) (ii) FX Generation: offspring sample gelled

Line R No. No. p Eggs	S	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	T	Mean		S.D.		Hom		Het		Hom																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																					
																															Dev.	Time	Dev.	Time	1	2	1	2	1	2																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																				
A	3 175	m	4	3	1	1	5	14	10	16	2	2	2	2	3	2	2	2	2	1	1	1	1							68	17.10	3.10	4	12	16	5																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																								
		f	1	2	5	5	10	7	4	4	3					1			2	2	1								45	16.13	3.25	5	7	6	5																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																									
B	1 168	m	2	2	10	7	7	12	6	10	4	3																		61	16.82	2.25	9	11	6	7																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																								

- Line No.    A    =   M179BB/S9DD x M114CC/S220BB  
              B    =   M114CC/S111AA x S15CC/M115BB  
              C    =   M114CC/S249BB x S176DD/M115BB

Appendix 6

Wing lengths of flies from natural populations. Lengths are in graticule divisions where 1 division = 1.45 mm.

For rare genotypes each individual genotype is given in the row appropriate to its wing length.

ST.MARY'S ISLAND      12.1.80

WING	MALES						
LENGTH	BB	BC	BD	CD	DD	OTHERS	
2.4					1		
2.5							
2.6		1			1		
2.7			1	2	4	CC	
2.8	1		4	1	3		
2.9		1	1	2	11		
3.0	1	2	4	4	18	CC	
3.1		1	2	5	6	AD	
3.2		2	6	1	6	CC	
3.3			8	3	6		
3.4			6	1	1	CC	
3.5		2	6		1		
3.6	1		9	1			
3.7			5			AB	
3.8	2	1	11		1		
3.9			11	1			
4.0	1	2	6	2			
4.1		1	2				
4.2	1		1				
4.3	2		2			AA	
4.4			1	1			
4.5			3				
4.6							
4.7							
4.8	1						

KAMPINGE      4.12.80

WING	MALES			FEMALES			
LENGTH	BB	BD	DD	BB	BD	DD	
2.4							
2.5			1				
2.6		1	2			1	
2.7			5		1		
2.8		1	3		4	2	
2.9		1	7	1	1		
3.0		5	3		8	5	
3.1			3	2	4	4	
3.2		6		1	9	5	
3.3		3		1	9	4	
3.4	1	2			6	1	
3.5		5			2		
3.6		7					
3.7		2			1		
3.8		3					
3.9	1	1					
4.0	2	1					
4.1		1					
4.2		1					
4.3							
4.4							
4.5	1						
4.6							
4.7							
4.8							









Appendix 7

Longevity and fecundity of individual flies from laboratory lines

Sizes are expressed as wing lengths in graticule divisions where  
1 division = 1.45 mm.

- a) Males - the number of each day, counting from the day on which the male eclosed, on which the male successfully fertilised at least one of the two females with which it was confined and the number of the day on which the male died.
- b) Females - the number of the day, counting as for males, on which each egg batch was laid, the number of eggs in each batch and the day on which the female died.



b) FEMALES

	WING LENGTH	EGG BATCHES			DAY DIED
<u>S220BB</u>	2.8	day	3		6
		no.	46		
	3.0	day			2
		no.			
	2.8	day	2		2
		no.	32		
	2.9	day			2
		no.			
	2.9	day	2	4	7
		no.	45	51	
	2.8	day	2	5	5
		no.	39	28	
	3.3	day	2	4	8
		no.	54	67	27
	3.0	day	2	3	5
		no.	28	68	
	3.2	day	2		2
		no.	44		
	2.9	day	2	4	5
		no.	33	53	
	2.8	day	2		3
		no.	31		
	2.7	day	2	6	8
		no.	48*	36	
	2.9	day	6		6
		no.	34		
	3.0	day	2		4
		no.	42*		
	2.8	day	2	5	5
		no.	35	21	
	2.6	day			1
		no.			
	3.3	day	2	4	4
		no.	60	29	
	3.1	day	1	4	5
		no.	37	24	
	2.6	day	2		4
		no.	27		
	3.1	day	1		4
		no.	73		

\* Unhatched  
batches

	WING LENGTH	EGG BATCHES			DAY DIED
S220B/S103D	3.1	day 2			8
		no. 50			
	3.5	day 4	6	8	8
		no. 66	61	27	
	3.6	day 3	5	7	9
		no. 90	90	79	
	3.5	day 3	5	7	9
		no. 51	69	51	
	3.7	day 2	3	5	8
		no. 85	78	76	
	3.4	day			3
		no.			
	2.8	day 3			8
		no. 37			
	3.5	day 2	4	9	9
		no. 80	70	35	
	3.0	day 4			8
		no. 46			
	2.8	day 4	8		9
		no. 33	32		
	3.1	day 6			8
		no. 38			
	3.7	day 2	6	8	9
		no. 50	68	64	
	3.0	day 4			10
		no. 40			
	2.8	day 3			6
		no. 32			
	3.5	day 2	4	8	9
		no. 85	77	72	
	2.9	day 3	6	8	8
		no. 36	28	26	
	3.1	day 2	5		8
		no. 39	40		
	3.0	day			7
		no.			



	WING LENGTH	EGG BATCHES			DAY DIED
<u>S103DD</u>	2.6	day no.	3 22	5 24	8
	2.7	day no.	3 21	5 27* 22*	9
	2.5	day no.			2
	2.5	day no.			3
	3.0	day no.	2 33		8
	2.9	day no.	1 41		9
	2.6	day no.	2 23	5 26	5
	2.7	day no.	3 27	7 33	7
	2.9	day no.	2 45		3
	2.9	day no.	2 25		3
	2.7	day no.	2 26	5 15	5
	3.0	day no.	3 43	4 56	7
	2.6	day no.			7
	2.6	day no.	2 22*	5 16	6
	2.8	day no.	2 38	5 39	8
	3.0	day no.	3 25	5 41	10
	2.9	day no.	3 40	6 24	10
	2.6	day no.			7
	2.9	day no.	2 40*	6 17	7
	2.7	day no.			6
* Unhatched batches					



Appendix 8

## Results of the three-fly mating experiments

- a) Pilot experiment
- b) Main experiment

(Note that in the pilot experiment the sizes of flies for the first 33 replicates are weights whereas for the last 12 replicates they are wing lengths. All sizes in the main experiment are wing lengths.)

a) PILOT EXPERIMENT

LARGE MALE		SMALL MALE		FEMALE		SUCCESSFUL
GENOTYPE	SIZE (Weight in mg)	GENOTYPE	SIZE (Weight in mg)	GENOTYPE	SIZE (Weight in mg)	*MALE
BB	6.4	DD	1.6	BD	3.1	BOTH
BD	6.4	DD	1.9	BD	3.8	L
BB	4.2	BD	2.2	DD	2.5	L
CD	5.9	BD	4.7	BB	5.4	S
BD	5.1	CD	3.3	BB	4.7	L
BD	6.2	CD	4.1	BD	5.0	S
BB	7.0	BD	4.5	BD	5.1	S
BD	8.2	DD	3.8	BD	4.7	L
BD	7.0	CD	4.9	BD	6.6	S
BD	7.0	CD	5.1	BD	6.9	L
BD	6.0	DD	3.7	BD	5.9	L
BD	5.5	CD	4.5	BB	5.3	BOTH
BD	7.3	CD	3.9	BB	6.7	L
BD	6.2	CD	3.5	BD	6.4	L
CD	5.7	DD	3.2	BD	4.4	L
BD	6.1	DD	3.7	BD	6.4	S
BD	6.2	BB	4.5	CD	5.2	L
CD	5.7	DD	3.3	BD	6.2	L
BD	7.2	DD	3.7	BB	4.1	L
BD	5.9	DD	3.9	BB	5.4	L
BD	4.2	DD	2.1	BD	6.0	L
BD	6.6	DD	2.1	BD	5.7	L
CD	7.6	BD	5.4	BD	3.8	S
BC	7.9	BD	4.7	DD	4.5	S
BC	9.0	BD	3.3	DD	6.9	L
BD	8.1	DD	3.6	BD	5.1	L
BD	6.3	DD	3.2	BC	5.4	L
CC	7.5	CD	5.0	BD	4.4	L
BC	10.6	BD	2.3	BD	8.2	L
BD	9.4	CD	6.0	DD	5.3	L
BC	7.3	BD	3.6	BB	4.1	L
BC	7.4	BD	2.9	CD	5.9	S
BB	7.7	BD	3.6	CD	4.6	S

\*L - LARGE MALE  
S - SMALL MALE

a) PILOT EXPERIMENT

LARGE MALE		SMALL MALE		FEMALE		SUCCESSFUL *MALE
GENOTYPE	SIZE (Wing length in divs)	GENOTYPE	SIZE (Wing length in divs)	GENOTYPE	SIZE (Wing length in divs)	
BB	3.4	BD	2.5	BD	2.7	L
BD	3.0	CD	2.5	BD	3.1	L
CD	3.3	DD	2.5	BD	3.0	L
BD	3.2	DD	2.4	BD	2.9	S
BD	3.1	DD	2.5	BD	2.8	L
BD	3.6	DD	2.6	BD	2.6	L
BD	3.0	DD	2.2	BD	2.6	L
CD	2.8	BD	2.2	BB	2.5	BOTH
BD	3.4	BB	2.8	BD	2.5	L
BD	3.6	DD	2.5	BD	2.6	L
BD	2.5	DD	2.1	BD	2.7	L
BD	3.0	DD	2.3	BC	2.5	L

\*L - LARGE MALE  
S - SMALL MALE

## b) MAIN EXPERIMENT

i) Trials with Large Male BB, Small Male DD, Female BB

SIZES (wing length in divisions)				SIZES (wing length in divisions)			
LARGE	SMALL	FEMALE	SUCCESSFUL	LARGE	SMALL	FEMALE	SUCCESSFUL
♂ BB	♂ DD	BB	*MALE	♂ BB	♂ DD	BB	*MALE
3.3	2.6	3.1	L	3.3	2.8	2.7	L
3.4	2.9	3.0	BOTH	3.5	2.9	3.2	L
3.6	2.8	3.2	L	3.1	2.7	3.1	L
3.7	2.6	2.8	BOTH	3.0	2.5	3.0	L
3.6	2.9	2.8	L	3.3	2.8	2.4	S
3.7	2.7	3.3	L	3.3	3.0	2.0	S
3.6	3.1	3.1	BOTH	2.6	2.2	2.4	L
3.7	3.0	2.9	L	3.2	2.5	2.4	L
3.7	2.7	2.8	BOTH	3.0	2.4	2.1	S
3.8	3.0	3.1	S	2.9	2.5	2.4	L
3.4	2.9	3.4	L	2.4	1.9	2.9	L
3.4	3.0	3.1	L	2.5	1.6	2.4	L
3.3	2.7	3.0	L	2.7	2.0	2.2	L
3.6	3.1	2.7	BOTH	3.3	3.1	3.0	L
3.6	2.7	3.2	BOTH	4.2	2.8	2.8	L
3.7	2.8	3.0	L	3.6	2.5	3.2	L
3.1	2.8	3.2	S	4.1	2.5	3.1	L
3.6	2.9	2.8	BOTH	3.8	2.9	3.1	BOTH
3.1	2.8	2.8	BOTH	3.5	3.0	3.4	BOTH
3.2	2.8	2.9	S	3.2	2.5	2.7	S
3.4	2.5	3.4	BOTH	3.7	3.0	3.1	L
3.6	2.4	2.9	L	3.5	2.6	3.1	L
3.3	2.8	2.7	L	3.3	2.6	3.2	BOTH
4.1	2.5	2.6	S	4.2	2.6	3.2	S
3.7	2.5	2.8	L	3.6	2.7	3.0	S
3.4	2.5	2.6	L	4.0	2.9	3.3	L
3.2	2.8	2.7	L	4.0	2.8	3.1	L
3.4	2.7	2.8	L	3.9	2.8	3.3	L
3.6	2.7	2.4	L	3.6	2.7	2.9	L
3.5	2.4	2.6	L	3.6	2.7	2.4	S
3.8	2.7	2.6	L	3.5	3.0	2.7	BOTH
3.2	2.5	3.4	L	3.8	2.7	3.1	BOTH
3.2	2.5	3.3	L	3.7	3.1	3.3	L
3.2	2.4	3.1	L	3.1	2.9	2.6	BOTH
3.1	2.6	3.3	L	3.3	3.2	3.1	S
3.2	2.6	3.2	L	3.7	2.9	3.2	BOTH
3.4	2.8	3.1	L	3.5	2.6	3.1	L
3.8	2.5	3.3	L	3.3	2.8	3.1	L
3.5	2.4	3.1	L	3.9	2.6	2.8	L
3.7	2.8	3.2	BOTH	3.1	2.9	3.2	L
3.6	2.6	3.1	L	3.7	2.4	3.2	L
3.9	2.4	3.2	L	3.6	2.6	2.8	S
4.1	3.1	3.4	L	3.5	3.2	2.8	L
4.0	3.0	2.9	L	3.6	2.8	2.9	S

\*L - LARGE MALE S- SMALL MALE



## b) MAIN EXPERIMENT

i) Trials with Large Male BB, Small Male DD, Female BB contd.

SIZES (wing length in divisions)				SIZES (wing length in divisions)			
LARGE	SMALL	FEMALE	SUCCESSFUL	LARGE	SMALL	FEMALE	SUCCESSFUL
♂BB	♂DD	BB	*MALE	♂BB	♂DD	BB	*MALE
3.5	2.9	2.7	BOTH	3.7	2.7	3.2	L
3.7	3.0	2.8	BOTH	3.4	2.9	3.2	L
3.5	3.0	2.2	BOTH	3.5	3.2	3.2	BOTH
3.5	2.9	2.8	BOTH	3.3	3.0	3.2	S
3.6	2.6	2.7	L	3.5	2.9	3.2	L
3.6	3.0	2.7	L	3.5	3.1	3.2	L
3.7	2.8	3.1	S	3.5	2.6	3.2	L
3.5	2.8	3.3	L	3.4	2.8	3.3	L

ii) Trials with Large Male BB, Small Male DD, Female DD

SIZES (wing length in divisions)				SIZES (wing length in divisions)			
LARGE	SMALL	FEMALE	SUCCESSFUL	LARGE	SMALL	FEMALE	SUCCESSFUL
♂BB	♂DD	DD	*MALE	♂BB	♂DD	DD	*MALE
3.6	3.0	2.6	L	3.6	2.3	2.5	L
3.5	2.6	3.5	L	3.6	2.5	2.9	L
3.4	2.7	3.0	L	3.5	2.6	2.8	L
3.6	2.9	3.4	L	3.2	2.5	2.8	L
3.4	2.6	2.9	L	3.5	3.0	3.7	L
3.7	2.8	3.3	L	3.5	2.8	3.5	L
3.6	3.0	2.9	L	3.1	2.7	3.4	L
3.6	2.5	2.9	S	3.4	2.7	3.5	L
3.2	2.5	2.8	L	3.3	2.8	3.2	L
3.9	2.6	3.2	L	3.1	2.9	3.3	S
3.3	2.7	2.9	BOTH	3.4	2.5	3.6	L
3.4	3.0	2.9	L	3.6	2.4	2.7	L
3.6	2.5	3.1	L	3.1	2.9	3.0	L
4.1	2.9	3.5	L	4.2	2.6	3.3	L
4.0	2.9	3.3	L	4.5	3.0	3.3	L
3.4	2.9	3.1	L	4.3	2.7	3.5	L
3.5	3.0	2.7	L	4.1	2.7	3.3	L
3.6	2.9	2.6	L	3.9	2.9	3.5	L
3.5	3.1	3.1	L	4.1	3.1	3.2	L
3.7	2.6	3.0	L	3.9	3.0	3.0	L
3.8	2.8	3.2	L	3.7	3.0	2.8	L
3.5	2.7	3.1	L	4.0	3.0	2.9	L
3.5	2.7	3.2	L	3.9	3.2	2.7	L
3.6	2.7	3.5	L	3.4	2.9	3.2	L
4.0	2.7	3.0	L	2.6	2.2	2.6	L
3.4	2.9	2.7	L	2.8	2.6	2.8	L
3.9	2.9	3.1	BOTH	3.2	2.6	3.2	L

\*L - LARGE MALE S - SMALL MALE

iii) Trials with Large Male DD, Small Male BB, Female BB

SIZES (wing length in divisions)				SIZES (wing length in divisions)			
LARGE	SMALL	FEMALE	SUCCESSFUL	LARGE	SMALL	FEMALE	SUCCESSFUL
♂ DD	♂ BB	BB	*MALE	♂ DD	♂ BB	BB	*MALE
3.3	2.3	3.0	L	3.2	2.8	3.1	BOTH
3.4	2.8	2.3	L	3.3	3.1	2.7	L
3.2	2.2	2.5	S	3.0	2.8	2.9	S
3.4	2.7	2.4	S	2.9	2.8	2.9	BOTH
3.0	2.6	3.0	L	3.1	2.4	2.8	BOTH
3.5	2.8	2.3	L	3.5	2.5	2.5	L
3.0	2.8	1.9	L	3.7	2.6	2.6	S
3.2	2.5	3.3	L	3.6	2.7	2.6	L
3.1	2.6	2.6	BOTH	3.1	2.3	2.5	L
3.4	3.0	3.1	BOTH	3.2	2.7	2.9	L
3.6	2.5	3.1	L	3.2	2.4	2.5	S
3.8	3.0	3.0	BOTH	3.2	2.6	2.5	L
3.0	2.6	2.5	S	3.4	2.5	2.3	L
3.2	3.0	2.9	BOTH	3.5	2.5	2.4	L
3.2	2.7	3.4	L	3.7	2.6	2.7	L
3.0	2.7	3.1	BOTH	3.6	2.6	3.1	S
3.0	2.6	2.8	BOTH	3.2	2.5	3.2	L
3.2	3.1	2.8	S	4.2	2.8	3.3	L
3.2	3.0	2.6	BOTH	3.8	2.5	3.0	S
3.2	2.8	2.8	L	3.3	2.8	3.4	S
3.3	2.7	2.6	L	3.8	2.6	3.1	L
3.7	3.0	2.6	S	3.1	2.5	3.2	L
3.2	3.0	3.1	L	3.6	2.8	3.2	L
3.4	2.9	2.9	L	3.4	2.7	3.1	S
3.2	2.9	3.3	L	3.2	2.5	3.0	L
3.3	2.9	2.5	S	3.4	2.8	2.7	BOTH
3.3	2.5	3.3	BOTH	3.5	3.1	2.7	L
3.2	2.5	3.0	L	3.5	2.6	2.7	L
3.2	3.0	2.9	L	3.5	2.5	2.7	L
3.0	2.9	2.8	BOTH	3.7	2.9	2.7	L
3.1	2.9	2.9	L	3.6	2.4	2.7	L
3.2	3.0	3.4	S	3.3	2.6	3.1	L
3.1	2.8	3.0	BOTH	3.4	2.8	3.1	L
3.0	2.8	2.8	S	3.3	2.8	3.2	S
3.3	2.5	2.8	S	3.2	2.8	3.1	S
3.3	3.2	2.8	S	3.9	2.8	3.2	L
3.0	2.7	2.6	S	3.8	2.8	3.2	L
3.1	3.0	3.1	L	3.3	2.7	3.5	L
3.3	3.0	3.0	BOTH	3.3	2.5	2.9	L
3.2	3.0	3.3	S	3.4	2.6	2.8	L
3.3	3.0	2.7	L	3.4	2.5	2.9	S

\*L - LARGE MALE    S - SMALL MALE

iv) Trials with Large Male DD, Small Male BB, Female DD

SIZES (wing length in divisions)				SIZES (wing length in divisions)			
LARGE	SMALL	FEMALE	SUCCESSFUL	LARGE	SMALL	FEMALE	SUCCESSFUL
♂DD	♂BB	DD	*MALE	♂DD	♂BB	DD	*MALE
3.5	2.4	3.5	L	3.4	3.0	2.8	S
3.6	2.5	3.1	L	3.3	3.0	3.1	S
2.6	2.2	2.8	S	3.1	2.7	3.2	BOTH
3.5	2.9	2.8	S	3.1	2.7	3.4	L
3.2	2.0	2.6	S	3.1	3.0	3.0	L
3.2	2.4	2.5	S	3.4	2.3	3.2	L
3.0	2.6	2.5	S	3.2	2.9	2.9	L
3.0	2.8	3.2	S	3.5	2.9	2.6	L
3.2	2.5	2.6	L	3.4	2.8	2.8	L
3.0	2.1	3.4	L	3.7	2.8	2.8	L
3.7	3.2	2.6	S	3.3	2.9	3.4	L
3.1	3.0	3.0	BOTH	3.2	3.0	3.4	L
3.3	2.4	3.2	L	3.4	2.6	3.4	L
3.2	2.5	2.5	L	3.3	2.8	3.2	L
3.3	3.0	2.9	BOTH	3.5	2.8	3.3	L
3.1	2.9	3.1	S	3.5	2.7	3.6	L
3.6	2.6	3.1	S	3.6	3.0	3.5	L
3.1	2.8	3.0	BOTH	3.6	2.9	3.4	L
2.9	2.6	2.9	L	3.6	2.8	3.5	L
3.2	2.8	2.8	L	3.4	2.9	3.3	L
3.1	2.5	3.1	L	3.7	2.8	3.0	S
2.9	2.6	3.0	L	3.4	2.6	2.8	L
3.2	2.8	3.0	BOTH	3.2	2.2	3.7	L
3.4	2.8	2.7	L	3.9	2.7	3.2	L
3.1	3.0	2.7	S	3.4	2.3	3.6	L
3.3	3.0	3.4	L	3.2	2.3	3.0	L
3.5	2.9	2.8	L	3.3	2.6	3.7	L
3.0	2.7	3.3	S	3.0	2.6	3.7	S
3.2	2.9	3.1	L	3.4	2.8	3.4	L
3.1	2.9	3.2	S	3.2	2.7	3.2	L
3.3	3.1	3.1	L				

\*L - LARGE MALE    S - SMALL MALE

## Appendix 9

Results of the mating cage experiment.

For mating cages 1 and 2 the results of electrophoresis of progeny larvae and the inferred parenthood of egg batches are given.

For mating cages 1A and 2A the sizes and days of emergence of adult flies are recorded for each genotype.

MATING CAGE 1 - PROGENY

DATE BATCH LAID (1981)	BATCH NO.	GELLED PROGENY			INFERRED MATING*
		BB	BD	DD	
2.5	1		6	5	HD
	2		7	5	HD
	3		2	10	HD
	4		7	5	HD
	5		5	7	HD
4.5	1		7	5	HD
	2		7	5	HD
	3	2	4	6	HH
5.5	1	2	10		BH
	2	2	8	2	HH
	3		7	5	HD
	4		1	11	?
	5		7	5	HD
6.5	1	2	6	4	HH
	2	2	7	3	HH
7.5	1	1	9	2	HH
	2		7	4	HD
10.5	1		5	7	HD
11.5	1			12	DD
	2	3	9		BH
	3	6	6		BH
12.5	1	1	3	6	HH
13.5	1	1	6	5	HH
	2	3	7	2	HH
	3	1	4	7	HH
	4	2	7	3	HH
	5	2	8	2	HH
	6	3	7		BH
14.5	1		6	6	HD
	2	2	4	6	HH
	3	4	8		BH
	4	1	6	5	HH
	5		12		BD
	6	3	6	3	HH
	7		11	1	?
16.5	1	2	7	3	HH
	2	5	3	4	HH
17.5	1	4	4	4	HH
	2	6	6		BH
18.5	1	1	4	8	HH
20.5	1	3	8	1	HH
21.5	1		6	6	HD
22.5	1		9	3	HD

DATE BATCH LAID (1981)	BATCH NO.	GELLED PROGENY			INFERRED MATING*
		BB	BD	DD	
22.5	2	3	5	4	HH
	3		7	5	HD
23.5	1	2	6	4	HH
	2		6	6	HD
	3		8	4	HD
	4	1	9	2	HH
	5		7	5	HD
	6	2	7	3	HH
24.5	1		8	4	HD
	2	4	7	1	HH
	3	3	9		BH
	4		3	9	HD
25.5	1	3	8	1	HH
	2		7	5	HD
	3	2	6	4	HH
26.5	1	1	7	4	HH

\* Inferred matings

DD - DDxDD

HD - DDxBD

HH - BDxBD

HB - BDxBB

BB - BBxBB

BD - BBxDD

\* Inferred matings  
DD - DDxDD  
HD - DDxBD  
HH - BDxBD  
HB - BDxBB  
BB - BBxBB  
BD - BBxDD

MATING CAGE 9 - PROGENY

DATE BATCH LAID (1981)	BATCH NO.	GELLED PROGENY			INFERRED MATING*
		BB	BD	DD	
2.5	1			12	DD
	2		8	4	HD
	3		3	9	HD
	4		9	3	HD
	5		4	8	HD
	6		4	8	HD
	7		7	5	HD
	8		5	7	HD
	9		7	5	HD
3.5	1		8	4	HD
	2		5	7	HD
	3		9	3	HD
	4			12	DD
4.5	1		5	7	HD
	2	4	3	6	HH
	3	3	5	2	HH
	4		9	3	HD
5.5	1	1	7	4	HH
7.5	1	2	6	4	HH
	2	2	7	3	HH
	3	3	7	2	HH
	4	1	10	1	HH
8.5	1	1	7	4	HH
	2		12		BD
	3	2	8	2	HH
	4		12		BD
10.5	1			12	DD
11.5	1		9	3	HD
12.5	1	1	11		?
	2	2	8	2	HH
13.5	1		9	3	HD
	2	3	4	5	HH
	3	1	11		?
14.5	1	2	7	3	HH
	2	2	7	1	HH
	3	2	6	4	HH
	4	1	5	6	HH
	5		11	1	?
	6		12		BD
15.5	1		5	7	HD
	2		4	8	HD
	3	3	6	1	HH
16.5	1		6	6	HD

DATE BATCH LAID (1981)	BATCH NO.	GELLED PROGENY			INFERRED MATING*
		BB	BD	DD	
17.5	1	1	8	3	HH
	2		10	2	HD
	3	3	8	1	HH
	4	1	8	3	HH
	5	2	6	4	HH
	6		1	11	?
	7	2	5	3	HH
18.5	1	3	7	2	HH
	2		8	4	HD
	3	3	7	1	HH
	4	1	6	5	HH
	5		8	4	HD
	6	1	6	4	HH
19.5	1		6	6	HD
	2		7	5	HD
	3	2	6	4	HH
	4	4	4	4	HH
	5	3	7	2	HH
21.5	1		1	11	?
22.5	1	3	6	3	HH
	2	4	5	3	HH
23.5	1	3	6	3	HH
24.5	1	3	7	2	HH
25.5	1	3	6	3	HH
	2	2	5	3	HH
26.5	1	1	7	4	HH

\* Inferred matings  
 DD - DDxDD  
 HD - DDxBD  
 HH - BDxBD  
 HB - BDxBB  
 BB - BBxBB  
 BD - BBxDD



## MATING CAGE 1A - FEMALES

DATE OF EMERGENCE (1981)	WING LENGTH (MEASURED IN DIVISIONS)		
	BB	BD	DD
30.4		2.9,3.1	3.0,2.5
1.5		2.5,2.7,2.8	2.8
2.5	2.4	2.5,2.6,3.3,3.2	
3.5	3.2	3.1,3.5,2.7,2.3, 3.3	3.0
4.5		3.5,3.4,3.3,3.3, 2.8,3.5,3.3,3.2, 3.3,3.4,3.0,3.5	3.1,2.8,2.8,3.1, 3.1
5.5	2.9,2.8	3.2,3.2,3.1,3.2, 3.1,3.2,2.7	3.0,3.1,3.0,3.3, 2.7,3.4,2.8,2.6, 3.0,2.9
6.5	2.8,3.3	3.1,2.9,2.6,3.4, 2.7,3.1,2.9,3.2, 3.1,2.7,2.8,2.8, 3.1,3.1,2.7,3.3, 2.8	2.9,3.1,2.9,3.0, 3.1,3.0
7.5	2.9	2.9,3.0,2.8,3.2, 3.0	2.5,2.9,3.1,3.1, 2.5,2.6,3.0,3.2, 2.9,3.2,2.9,2.9, 3.2,3.2,3.1,3.0, 2.7,2.8
8.5	2.9	2.8,2.8,3.0,3.0, 3.0,2.8,2.0	3.1,3.2,3.0,2.8, 3.0,2.6,2.9
9.5	2.8	3.0,3.1,2.8,3.0, 2.9,3.0,2.7,2.7, 3.1	3.0,3.0,2.8,2.8
10.5		3.0,3.3,2.9,2.5	2.8,2.8,2.7,3.1
11.5	3.0,2.6	2.3,2.9,3.0,2.9, 2.5,3.1,2.7,3.4, 2.7,3.1,2.7,2.6, 2.5,2.8,2.9,3.0	2.9,2.5,2.9,2.8, 3.0,3.1,2.7,2.4
12.5	2.8	3.2,2.8,3.1,3.1, 3.0,3.2,3.0,2.8, 2.9,3.0,2.9,3.2, 2.6,2.6,3.1,2.6, 2.7	3.2,2.9,2.9,2.8
13.5		2.7,2.9,2.7,3.5, 2.9,2.8	3.0,3.2,3.2
14.5		2.8,2.8,3.1,3.2, 2.8,3.2	3.0,2.9
17.5		3.3,3.6,3.6	3.6,3.7,3.7
18.5			3.2
19.5			3.2

## MATING CAGE 1A - MALES

DATE OF EMERGENCE (1981)	WING LENGTH (MEASURED IN DIVISIONS)		
	BB	BD	DD
30.4			2.7,3.3,3.1,2.7, 2.9,2.9
1.5			2.4,2.5,2.3,2.3
2.5			2.7
3.5		3.5	3.2
4.5		3.3,3.5,3.5,3.1 2.6,3.6	2.8,3.2,2.5,3.2, 3.0,3.3,2.9,3.0
5.5		3.6,3.5,2.8,3.0	2.9,2.5,2.9,3.1, 3.1,2.6
6.5		3.5,3.7,3.1,3.1, 3.0	3.0,2.6,2.9,2.8, 2.9,2.7,3.1,2.7
7.5	3.2	3.2,2.9,3.3,3.1, 3.4,3.7,3.3,2.8, 2.6,3.5,3.1,2.9	2.7,3.2,2.7,2.9, 3.0,2.9,2.4,2.8
8.5		3.4,3.9,3.3,3.0, 2.9	2.9,2.7,2.5,2.9, 2.9,2.6,2.5,2.9, 2.9,2.7
9.5	2.8	3.1,3.0,2.5,2.3, 2.8,2.7,2.6,3.0	2.5,2.8,2.9,2.8, 2.8,2.8,2.7,3.0, 2.7,2.4
10.5		2.9,3.8,2.5,3.0, 3.4,2.8,2.9,2.6, 2.7	2.6,2.8,2.9,2.4
11.5		3.1,3.3,2.8,2.7, 3.2,2.9,2.6,2.8, 3.4,2.8,2.8	2.8,2.7,2.5,2.6, 3.0,2.6,2.5,2.7
12.5		3.3,3.2,2.8,2.3, 2.8,3.3,3.6,3.2, 3.2,2.7,2.6,2.8, 3.0,2.5,2.9	2.5,2.8,2.8,2.8, 2.3,2.9,2.7
13.5	2.9	3.3,3.1,3.1,3.3, 3.3,2.6,2.3	
14.5		3.5	
15.5	3.6	3.1	
16.5	3.1,3.1	2.5	
17.5		3.3,3.7,3.3	3.4
18.5		4.4,3.8,3.8,4.3, 3.3,2.4,3.0	
19.5	3.9	3.5,3.8,4.5,2.9	

## MATING CAGE 2A - FEMALES

DATE OF EMERGENCE (1981)	WING LENGTH (MEASURED IN DIVISIONS)		
	BB	BD	DD
30.4	2.9	3.7,3.5,3.5,3.2	3.2,3.1
1.5		3.5,3.6,3.4,3.3, 3.4,3.2,2.8,3.3, 3.1,3.5,3.3,3.4, 3.3,3.4,3.1,3.5	2.7,3.4
2.5	3.2,2.9	3.3,3.5,3.4,3.2, 3.2,3.3,3.0,2.9, 3.4,3.2,3.5,3.3, 3.2,3.3,3.3	3.3,2.5,2.9,3.2, 3.7,3.4,3.5,3.0, 3.0
3.5	3.0,3.0,2.9	3.6,3.2,3.4,2.6, 2.9,3.2,3.4,3.2, 3.2,3.0,3.3,3.1, 3.6,3.1,3.3,3.4, 3.1	3.3,3.5,3.2,2.9
4.5		3.2,2.8,3.1,3.0, 3.4,2.8,2.7,3.1	3.0,2.9,3.0,3.2, 2.7,3.1
5.5	3.0	3.4,3.2,2.8,3.1, 3.0,3.0,2.7,3.1	2.7,3.1
6.5	3.0	3.0,2.7,3.3,3.3	2.8,2.9,3.0,3.0, 2.4
7.5		3.3,2.8,3.1,2.8	3.2,2.9,3.1,3.1
8.5	2.6,2.6	2.8,2.8,3.1,3.1, 3.1,2.7	3.0,2.9
9.5	3.0	2.8,3.0,3.0,2.7, 2.6,2.9,2.9,3.0	2.7,2.6,2.7,2.8
10.5		2.7,3.0,2.7,2.5, 2.8	2.8,3.2
11.5	3.2	2.3,2.8,3.1,2.8, 2.7,2.8,2.9,2.7	2.8,2.8,2.9,3.0, 2.8
12.5		3.0,2.8,2.6,3.0, 2.9,3.4,3.4,2.9, 2.6,3.0	2.8,2.7,2.8,2.8, 2.7,3.1,2.9,2.9
13.5		3.4,3.0,3.1,3.1, 2.8,2.9,2.4,3.0, 2.9	3.1,2.4,3.4
14.5	3.3,3.2	2.5,3.2,3.2,3.1, 3.1,3.0,3.0,3.0, 3.2,3.1,3.0,3.1, 3.1,3.2,3.3,3.3, 3.1,2.8,2.7,2.8	2.9,2.9,3.0,3.2, 3.2,2.9
15.5		3.2,3.3,3.2,3.1, 3.3,3.4,3.1	
16.5	3.3,2.7	3.5,3.2,3.1,3.3, 3.0	3.0
17.5	3.4		3.1
18.5		3.4	

## MATING CAGE 2A - MALES

DATE OF EMERGENCE (1981)	WING LENGTH (MEASURED IN DIVISIONS)		
	BB	BD	DD
30.4			3.3,3.2,2.9,3.0, 3.0,2.8,3.1,3.3, 2.7,3.3
1.5			3.0,2.9,3.2,3.1, 3.3,3.0
2.5		3.4,3.4	3.0,3.5,3.3,2.8, 2.5,3.0,3.1
3.5		3.7,3.9,3.5,3.7, 3.0,2.8,3.0,3.4, 4.0,3.5,3.4,3.5	2.9,3.3,2.8
4.5		3.1,3.6,3.6,3.6, 2.8,3.5,3.8,3.4, 3.1,3.3,3.6,3.3, 2.5	2.4
5.5		3.2,3.0,2.9,2.7, 3.0,3.2,3.4,3.9, 3.4,3.1,3.5	
6.5		3.4,3.5,3.8,3.0, 3.6,2.7,2.5,	2.8,3.0
7.5		3.1,3.0	
8.5	3.8	3.2,2.7,2.7,2.8	2.7,2.6,2.9,2.6, 2.6,2.8
9.5	3.4,3.2	3.1,2.7,2.9,3.1, 2.7,2.8	2.6,2.6,2.6,3.0, 2.7,2.5,2.7
10.5		3.2,2.7,2.9,3.5	2.7,2.7
11.5		3.6,3.3,2.3,3.2, 2.9	2.6,2.5,2.8,2.8, 2.4,2.6
12.5	3.7	2.6,3.1,3.4,3.9, 2.8,3.1,2.8,3.0	2.9,2.5,2.5,2.5, 2.7,2.8,2.9,2.7, 2.7,2.8,2.2,2.9, 2.7,2.8
13.5		2.4,2.9,2.7,3.3, 2.9,3.2,2.6	2.7,2.9
14.5	3.2,3.4	3.0,3.2,2.5,2.9, 3.2,3.0,2.8,2.8, 3.1,3.6,3.6,3.3	2.9,3.0,3.0
15.5		3.4,3.5,3.5	3.0
16.5	3.4	3.5,2.9,3.4	
17.5		3.6,3.8	

APPENDIX 10 Listing of the simulation program used in Chapter 10.  
 The program is in FORTRAN IV and used the NAG library routines GO5DYF, SI5ABF, GO5CAF and GO5DDF. It was run on the University of East Anglia ICL1906A Computer.

```

0018      MASTER
0019      C
0020      C      INPUT THE FOLLOWING DATA:
0021      C      SBB      VIABILITY SELECTION ON BB
0022      C      SDD      SAME FOR DD
0023      C      BBDM     MEAN D.T. FOR BB
0024      C      BBDS     S.D. OF D.T. FOR BB
0025      C      BDDM,BBDS,DDDM,DDDS SAME FOR OTHER GENOTYPES
0026      C      BBS,BDS,DDS - MEAN SIZES OF MALES
0027      C      F - SIZE/FECUNDITY RELATIONSHIP
0028      C      S - MATING SUCCESS FACTOR
0029      C
0030      C      Q - LIFE EXPECTANCY FACTOR
0031      C      D28 - PROP. OF BEDS REMOVED ON OR NEAR DAY 28
0032      C
0033      READ(5,100) SBB,SDD
0034      READ(5,101) BBDM,BBDS,BDDM,BBDS,DDDM,DDDS
0035      READ(5,102) BBS,BDS,DDS
0036      READ(5,103) F,S,Q,D28
0037      100  FORMAT(2F2.2)
0038      101  FORMAT(F3.1,F3.2)
0039      102  FORMAT(3F3.2)
0040      103  FORMAT(F3.3,2F2.1,F2.2)
0041      C
0042      C      DIMENSION ARRAYS AND INITIATE FB LOOPS
0043      C
0044      DIMENSION FB(3,5,100)
0045      INTEGER GO5DYF,NIN(3,5)
0046      REAL SI5ABF,GO5CAF,GO5DDF
0047
0048
0049
0050
0051      IFAIL=0
0052      DO 20 I=1,5
0053      FB(1,I,1)=0.1
0054      FB(2,I,1)=0.5
0055      FB(3,I,1)=0.9
0056      20  CONTINUE
0057      DO 21 I=1,3
0058      DO 22 J=1,5
0059      DO 23 K=1,99
0060      B=FB(I,J,K)
0061      C
0062      C      GENOTYPE FREQUENCIES IN ADULTS AFTER VIAB EFFECTS
0063      C
0064      C      FIRST SETTING UP LWB
0065      C
0066      RN=GO5CAF(X)

```



```

0067      IF(RN.GT.D28) GOTO 50
0068      LWB=GO5DDF(28.0,2.5)
0069      GOTO 53
0070  50    IF(RN.GT.(D28*1.125)) GOTO 51
0071      LWB=GO5DDF(14.0,1.5)
0072      GOTO 53
0073  51    IF(RN.GT.(D28*1.1875)) GOTO 52
0074      LWB=GO5DDF(42.0,1.5)
0075      GOTO 53
0076  52    LWB=GO5DYF(1,42)
0077  53    D=1.0-B
0078      FBB=B**2*((1-SBB)/(1-SBB*B**2-SDD*D**2))
0079      FBD=B*D*2/(1-SBB*B**2-SDD*D**2)
0080      FDD=1.0-(FBB+FBD)
0081  C
0082  C      MALE DEV. TIME AND LONGEVITY EFFECTS
0083  C
0084      XBB=(LWB-BBDM)/BBDS
0085      X1BB=(LWB-(Q*BBS)-BBDM)/BBDS
0086      PBB=S15ABF(XBB,IFAIL)-S15ABF(X1BB,IFAIL)
0087      XBD=(LWB-BDDM)/BDDS
0088      X1BD=(LWB-(Q*BDS)-BDDM)/BDDS
0089      PBD=S15ABF(XBD,IFAIL)-S15ABF(X1BD,IFAIL)
0090      XDD=(LWB-DDDM)/DDDS
0091      X1DD=(LWB-(Q*DDS)-DDDM)/DDDS
0092      PDD=S15ABF(XDD,IFAIL)-S15ABF(X1DD,IFAIL)
0093      IF((PDD+PBD+PBB):NE:0:0) GOTO 54
0094      NIN(I,J)=K
0095      GOTO 22
0096  54    FBBM=(FBB*PBB)/((FBB*PBB)+(FBD*PBD)+(FDD*PDD))
0097      FBDM=(FBD*PBD)/((FBB*PBB)+(FBD*PBD)+(FDD*PDD))
0098      FDDM=1.0-(FBBM+FBDM)
0099  C
0100  C      ALLOWANCE FOR SIZE EFFECTS ON FECUNDITY AND MATING SUCCESS
0101  C
0102      FBBM=FBBM+F*(BBS-3.0)
0103      FBDM=FBDM+F*(BDS-3.0)
0104      FDDM=FDDM+F*(DDS-3.0)
0105      FBBM=FBBM/(FBBM+FBDM+FDDM)
0106      FBDM=FBDM/(FBBM+FBDM+FDDM)
0107      FDDM=FDDM/(FBBM+FBDM+FDDM)
0108      CBB=FBBM**2+2*FBBM*FBDM*(0.5+S*(BBS-BDS))
0109      CBB=CBB+2*FBBM*FDDM*(0.5+S*(BBS-DDS))
0110      CBD=FBDM**2+2*FBDM*FBBM*(0.5+S*(BDS-BBS))
0111      CBD=CBD+2*FBDM*FDDM*(0.5+S*(BDS-DDS))
0112      CDD=FDDM**2+2*FDDM*FBDM*(0.5+S*(DDS-BDS))
0113      CDD=CDD+2*FDDM*FBBM*(0.5+S*(DDS-BBS))
0114  C
0115  C      GENE FREQUENCY CHANGE
0116  C
0117      L=K+1
0118      FB(I,J,L)=((FBB+FBD/2)+(CBB+CBD/2))/2
0119      NIN(I,J)=L
0120  23    CONTINUE
0121  22    CONTINUE
0122  21    CONTINUE

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