The effect of larval competition on development time and adult size in the seaweed fly, *Coelopa frigida*

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**Summary.** The effect of larval competition on adult size and egg to adult development time has been investigated in laboratory populations of the seaweed fly, *Coelopa frigida*. Increased larval density results in longer development times and smaller adults, suggesting a strong interference element to the competition. This may be due to a limiting rate of food supply rather than interactions between larvae. The relationship between development time and size suggests that both these characters are involved in control of the onset of pupation. *C. frigida* is polymorphic for an inversion on chromosome I. Differences in relative viability between the karyotypes are not related to the development time or size differences.

**Introduction**

The Darwinian fitness of a particular genotype is not constant but depends on its interaction with the environment (Kojima 1971; Clarke 1979). The melanic morph of *Biston betularia*, for example, has a higher fitness than the nonmelanic in urban, but not in rural areas, and the fitnesses of the alcohol dehydrogenase genotypes in *Drosophila melanogaster* depend on the amount of alcohol in the food medium. An important component of the environment for many organisms is the presence of other individuals of the same species with which they must almost inevitably compete for essential resources. A number of cases are known where increasing intraspecific competition alters the adaptive values of segregating genotypes in polymorphic populations. Both Dobzhansky (1947) and Birch (1955) found that crowding of *Drosophila pseudoobscura* larvae affected the relative fitnesses of third chromosome arrangements.

To understand how natural selection is operating in such situations it is necessary to analyse the competitive interactions within and between genotypes, and to identify the phenotypic characters underlying differential competitive success. Bakker (1961) attempted to do this in a pioneering study with *D. melanogaster*. He was able to show that under the conditions of his experiments, competition resulted entirely from depletion of the limiting resource, food. In Park's (1954) terminology, competition was "exploitative" — it contained no "interference" element due to physical or chemical interactions between individuals. Bakker also demonstrated that the difference in competitive success between his two strains was a result of a difference in their hatching times — the early hatching strains showing the greater survival. Other experiments with *D. melanogaster* in different conditions have clearly indicated an interference component to larval competition (Hughes 1980).

We report here an investigation into the nature of intraspecific competition in another Dipteran insect, the seaweed fly, *Coelopa frigida*. This species is polymorphic for two arrangements of the first chromosome, $\alpha$ and $\beta$. The $\alpha\beta$ karyotype is in excess of Hardy-Weinberg expectations in all samples from natural populations (Butlin et al. 1982; Day et al. 1983). It has higher viability than either homokaryotype and this effect increases with increasing larval density, both in the laboratory and in the field (Butlin et al. 1984). We have made observations on the effect that larval density has on egg to adult development time and adult size, and on the relationship between these two variables. The results are interpreted in terms of the exploitative and interference elements of competition, and we discuss how this competition might affect the selective advantage of chromosomal heterokaryotypes.

**Materials and methods**

A stock line, designated SMB + D was established using 168 pairs of flies from a natural population at St. Mary's Island, Tyne and Wear, U.K. (Ordnance Survey grid reference: NZ 350753) in September 1980. It was maintained by transfer of at least 500 adults each generation.

The SMB + D line contained only the $B$ and $D$ alleles at the alcohol dehydrogenase locus. (Details of the derivation of this line are given by Butlin 1983). These alleles are known to be associated with the $\alpha\beta$ inversion on chromosome I such that $\alpha$ chromosomes carry the $Adh-B$ allele, and $\beta$ chromosomes the $Adh-D$ allele (Day et al. 1982). It was therefore possible to identify the karyotypes of flies using starch gel electrophoresis. (For technical details, see Butlin et al. 1982 *)

In the main experiment larvae were cultured at various densities to determine how density affected development time and adult size. A second experiment was carried out at a single density (and on a much larger scale) so that the relationship between development time and adult size could be examined independently of density.

For the main experiment about 5,000 flies from the third
laboratory generation of the SMB + D line were allowed to lay eggs for 24 h on a seaweed based culture medium in a large cage (30 × 20 × 20 cm) (Butlin et al. 1982). 48 h after removal of the adults, larvae were counted into plastic canisters (7.5 diam. × 6.5 cm) containing 3 cm depth of medium. Three replicate cultures were established using 100 larvae, three using 200 larvae and two each with 400 larvae and 800 larvae. These densities are equivalent to 0.8–6.7 larvae per gram of medium and are comparable with the upper part of the range found in natural populations (Butlin et al. 1984). The canisters were maintained in constant darkness at 27°C, and adult flies were collected daily until no flies emerged for three consecutive days. The development time of each fly was taken as the estimated mean time from hatching to eclosion. Wing length was used as a measure of adult size and was assessed by the method of Butlin et al. (1982). The karyotype of each fly was inferred from its Adh genotype (Butlin et al. 1982).

The second experiment was carried out with flies from the tenth laboratory generation of the SMB + D line. For each of two replicates, approximately 1000 flies were allowed to lay eggs for 24 h on a tray of medium (17.5 × 11.5 × 6 cm) contained within a cage (30 × 20 × 20 cm). The adults were then removed. The two cages were maintained exactly as in the first experiment and the adults studied in the same way.

Results

1. Viability. As expected from previous work (Butlin et al., 1983) overall viability declined steadily with density from an average of 34% in the replicates at 100 larvae per canister, to 13% in the 800 larvae replicates. The relative viabilities of the three genotypes could not be calculated because their starting frequencies were not known. Hardy-Weinberg expectations based on the parental inversion frequencies would have been misleading since there is strong sexual selection in favour of az and αf males (Butlin et al. 1982). However, in 8 of the 10 replicates more than 50% of the surviving adults were heterokaryotypes, suggesting that the viability of azf’s was, as expected, greater than that of the homokaryotypes. The proportion of heterokaryotypes increased with density in both males and females, although in neither case was the regression significant. (A logarithmic density scale was used and frequencies were transformed to angles. For males, b = 0.032 ± 0.056 and for females b = 0.0015 ± 0.039). This density effect is much smaller than that observed by Butlin et al. (1984), possibly because some density dependent selective mortality occurs in the first two days of larval life - that is, before the different density replicates were established in this experiment. There is some independent evidence that this is the case (Butlin 1983).

2. Development time. A linear relationship was seen between mean development time and larval density (both logarithmically transformed) (Fig. 1), and the regression was significant for both males and females (b = 0.144 ± 0.017, P < 0.001 for males; b = 0.186 ± 0.012, P < 0.001 for females). In other words, there was a marked increase in egg to adult development time with density. In the males there were differences between karyotypes in their intercepts (f2,26 = 29.15, P < 0.001) but not in their slopes (f2,24 = 0.49). This confirms that ββ males were smaller at all densities than az or αf males, which were themselves similar in size. In females there were no such differences (f2,26 = 0.25). This result is consistent with other studies of development time in C. frigida (Mayhew 1939; Day et al. 1980).

An increase in development time with increasing larval competition is a common observation in insects, (for example in Drosophila subobscura, McFarquhar and Robertson 1963, and in the pitcher-plant mosquito, Moeur and Istock 1980). However, Bakker (1961), using D. melanogaster, found the converse relationship. In his experiments, competition was purely exploitative – that is, it depended entirely on the absolute amount of food available. As density increased, only fast growing larvae were able to reach the “minimum survival weight” before the food was exhausted and, in consequence, mean development time was reduced. The observation in Coelopa of longer development times at higher densities probably indicates an interference element in the competition; the larvae interact physically or

![Fig. 1a, b. The relationship between mean development time (in days) from the estimated mean hatch time, and larval density for a males and b females. Karyotypes are indicated by the symbols: • az, • αf, • ββ.](image-url)