Studies on the Intraspecific Competition in Dung-Breeding Flies

IV. Effects of Larval Density on the Development of *Orthellia pacifica* ZIMIN (Diptera: Muscidae)

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Orthellia pacifica ZIMIN was tested for the effects of larval intraspecific competition. Newly hatched larvae were transferred to cattle dung and reared until adult emergence at thirty-one densities of between 1 to 301 larvae per 50 g of dung. As the density increased, reduction in the size of emerged adults, increasing mortality and shortening of the developmental period from larvae to adults were observed. These density effects, however, did not begin to occur at the same density levels. The adult size and developmental period began to decrease at the density of 21 larvae. On the other hand, increase in the mortality did not occur until the density of 121 larvae where the adult size had reached almost the lowest limit. These findings were discussed in relation to competitive advantage and larval habitat characteristics.

INTRODUCTION

Cattle dung pats in pastures constitute isolated and ephemeral habitats for larvae of dung-breeding flies. An excess of oviposition to dung pats, which is observed to occur frequently in pastures, would cause an intra- and/or interspecific competition among larvae. In some other insects an emigration behavior from original habitats is an ordinary response to escape from such population pressures, but in the case of the larvae of dung-breeding flies this behavior must be followed by a risk that the emigrants fail to obtain such requisites as food and shelter; this risk must often be mortal. Therefore, it can be expected that dung-breeding flies have developed some special traits to survive an overcrowding within respective dung pats. In this connection, many developmental characteristics of dung-breeding flies have been examined in certain species including *Musca autumnalis* DEGEER (VALIELA, 1969; BAY et al., 1970; WASTI et al., 1975; MOON, 1980), *M. hervei* VILL. (AMANO, 1987), *M. domestica* L. (KIRKWOOD, 1960; SULLIVAN and SOKAL, 1963; HAUPT and BUSVINE, 1968), *M. vetustissima* WALKER (SANDS and HUGHES, 1976), *Haematobia irritans* L. (PALMER and BAY, 1983), *H. thirouxipotans* BEZZI (DOUBE and MOOLA, 1987), *Orthellia caesarion* MEIG. (WASTI et al., 1975), *Scatophaga stercoraria* L. (AMANO, 1983; SIGURJONSDOTTIR, 1984) and *HYDROTEA* sp. (COTTON, 1978). Most of them reported that the outstanding symptoms of larval competition were the minimization of emerged adults and change in developmental period besides an increase in mortality. However, a few of them referred to the relationships between these developmental responses depending on larval density.

Orthellia pacifica ZIMIN is one of the dung-breeding species colonizing pastures most successfully in the Tohoku district of Japan. The present experiment was carried out to elucidate the three developmental responses of this species, i.e. adult size, developmental period and mortality, depending on various larval densities, with the aim of clarifying the mechanisms of the colonization of *O. pacifica* in pastures from the viewpoint of larval competition.

MATERIALS AND METHODS

Cow dung used in the present experiment was a homogenous mixture from cattle fed on only grass in pastures. Eggs of *O. pacifica* deposited on the dung pat were collected from the same pastures. Newly hatched larvae were reared on 50 g dung at different densities from 1 larva with increments of 10 larvae to a maximum of 301 larvae. The replicates were set up to secure at least 100 larvae per density, except for the lowest density (59 replicates).

Each cup (7.0 cm in diameter, 3.3 cm in height) containing 50 g dung along with larva(e) was placed into another cup (9.0 cm in diameter, 4.5 cm in height) where a 1 cm layer of soil was provided so as to allow the mature larvae to pupate in the soil, and the cup was covered with a fine meshed lid. They were left out undisturbed until adult emergence. The experiments were carried out at 24°C and 90–100% RH under a 16L–8D photoperiod. The date of emergence, head width and sex of adults were recorded.

RESULTS

Density effect on emerged adult size

Figure 1 (top) shows the relationship between the larval density and average head width of emerged adults. Adult head width was used as an index of body size. There was no significant difference in adult size between 1 and 11 larvae ($p > 0.05$ for both sexes, *t*-test), 3.43 mm average head width for females and 3.36 mm for males. However, the difference was significant between the densities of 11–21 larvae ($p < 0.05$ for both sexes, *t*-test). As the density exceeded 21 larvae, head width continued to decrease until it was 2.37 mm for females and 2.28 mm for males at 161 larvae. No further reduction was seen at densities greater than 161 larvae except for slight fluctuation. Average head width at densities greater than 161 larvae was 2.36 mm for females and 2.32 mm for males, which shows a total respective reduction of 31.3 and 30.8% compared with average one at 1–11 larvae.

The coefficient of variation was 2.6–8.0% throughout the observed range in both sexes.

Density effect on mortality

Figure 1 (middle) shows the relationship between larval density and mortality during immature stages. The mortality for densities up to 121 larvae was low, ranging about an average level of 22.9%. After that, an increase in mortality occurred appreciably with increase in density. The critical density level for the increase in mortality is markedly higher than that for the reduction in size shown before.

The sex ratio of emerged adults was about 0.5 through the density range of 1–221

Fig. 1. Relationships between the larval density and average head width of emerged adults (top), mortality in immature stages (middle) and developmental period from larvae to adults (bottom) in *Orthellia pacifica*.

larvae ($\chi^2=21.85$, $d.f.=22$, $p>0.05$), but it fluctuated above 221 larvae (Fig. 2). The sex ratio of the total adults which emerged at the densities over 231 larvae was not significantly different from 0.5 ($\chi^2=0.75$, $d.f.=1$, $p>0.05$), suggesting that the fluctuation in sex ratio may be simply attributed to a chance bias due to small sample size as a result of the high mortality in immature stages.

Density effect on developmental period

Figure 1 (bottom) shows the average developmental periods from larvae to adults at various larval densities. The average developmental periods at 1–11 larvae were 16.94 ± 0.70 ($\bar{x} \pm S.D.$) days for females and 16.66 ± 0.69 for males. As the larval density increased, however, the periods shortened in both sexes. Some individuals

Fig. 2. Relationship between average sex ratios (=female ratios) and larval densities of *Orthellia pacifica*. Vertical lines show 90% confidence limits.

emerged in as short a time as 13 days at higher densities. In a density range of between 1 to 151 larvae, a linear relationship between the average developmental period (Y) and average adult head width (X) was observed. The relationships were represented by the equations: $Y=1.52X+11.48$, ($r^2=0.81$, $p<0.001$) for females and $Y=1.42X+11.72$, ($r^2=0.87$, $p<0.001$) for males. With the density progressing over that level, the values of developmental period began to fluctuate more markedly than those of head width without any significant relationships between the both values ($r=0.12$, $p>0.05$ for females; $r=0.24$, $p>0.05$ for males).

DISCUSSION

In many insects, the most evident effects of overcrowding in larval stage have been reported to be the extension of developmental period and increase in mortality during immature stages (PETERS and BARBOSA, 1977). The increasing mortality is a ubiquitous feature under extremely high larval density conditions unless emigration is possible. This type of density response has also been observed in the house fly, *Musca domestica* (BOGGILD and KEIDING, 1958; SULLIVAN and SOKAL, 1963). However, the house fly does not normally colonize an open pasture despite its good capability of breeding in cattle dung there (FERRAR, 1979; AMANO, 1985). It breeds mainly in stable refuse of mixed straw, dung and urine, and also in other rotting matter such as composting heaps of manure around domestic livestock facilities (LARSEN et al., 1966; THIMIYAN et al., 1970; LYSYK and AXTELL, 1986). Manure in which it usually breeds is not strictly limited in quantity as is an individual dung pat, and it has the potential to increase in quantity and quality owing to decomposition, while a dung pat has no such possibility. As long as there is no quantity limitation in manure, larvae breeding there can escape the severe competition, if any, by a dispersal behavior or slowing their developmental velocity.

On the contrary, the larvae of many dung-breeding flies which actually colonize pastures show a reduction in developmental period under overcrowded conditions, e.g. *O. caesarion* (WASTI et al., 1975) *M. autumnalis* (MOON, 1980) *Scatophaga stercoraria* (AMANO, 1983), *M. vetustissima* (MATTHIESSON and HAYLES, 1984) and *M. hervei* (AMANO, 1987). In the present experiment with *O. pacifica* as well, the developmental period markedly decreased with increasing larval density levels.

Another characteristic sign in the development of the present species was a notable minimization of emerged adults. The change in adult size was clearly a sensitive indicator depending on larval density. Similar cases have also been reported in most of the dung-breeding flies mentioned earlier (BAY et al., 1970; MOON, 1980; AMANO, 1983, 1987).

O. pacifica larvae showed a trend to reduce the adult size at lower densities, but they were able to survive well at a high density up to 121 larvae/50 g dung without an increase in mortality. Then the mortality began to increase markedly where the adult size had almost reached the minimum possible for an individual. Few pieces in the literature have treated this relationship between an adult size and mortality against larval density in dung-breeding flies, but *S. stercoraria* and *M. hervei* showed similar responses to larval densities (AMANO, 1983, 1987). A consideration of these results of the three dung-breeding flies including the present species may indicate that high larva-to-adult survival at high larval densities can be realized by the ability to minimize individual size and shorten the developmental period. The nature of these findings should have general applicability to other dung-breeding Diptera yet to be studied, with allowance for differences in their biology. The species which has abilities to tolerate body size loss and to develop in a shorter time has a strong competitive advantage over species of other types (LEVOT et al., 1979). The ability of short cut development is considered to be adaptive for escape from the pressure of competitors, but is inevitably followed by a decrease in adult size and fecundity. However, the disadvantages would surely be outweighed by the adaptive advantage of avoiding mortality. This could explain their successful colonization in pastures throughout the season.

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