Influence of Group Size on Daily Per Capita Birth Rates of the Cabbage Aphid (Homoptera: Aphididae) on Collards

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ABSTRACT Daily per capita birth rates of the cabbage aphid, Brevicoryne brassicae (L.), increased 40-50% as numbers of adult female aphids in artificially created groups on kale plants increased from three or fewer to six or more adults. Reproduction was enhanced at a declining rate such that the maximal effect was observed at 10 females per group, with no further increase up to 27 females per group. Increasing the number of females per group enhanced per capita birth rates on potted kale plants under greenhouse conditions and on field-grown kale plants. Enhancement under field conditions was observed in warm (22°C) but not cool (15°C) periods.

KEY WORDS Insecta, Brevicoryne brassicae, birth rates, population size

The effect of density on total and daily fertility in insects varies greatly among species. Most frequently, high densities of mixed-sex populations are correlated with lower total and daily fertility; e.g., the blowfly Lucilia cuprina (Wiedemann) (Nicholson 1950), the alfalfa weevil, Hypera postica Gyll. (LeCato & Pienkowski 1972), grasshoppers (Smith 1970), and Drosophila melanogaster L. (Lints & Lints 1969). In some species, density has no apparent effect on fertility (e.g., the house fly, Musca domestica L. (Osborn et al. 1970)). Indirectly, fertility of populations of insects such as aphids may be enhanced for some species by increased group size, inasmuch as large groups of some species lead to improved nutritional quality of the plant at the feeding size, giving rise to larger individuals reared at such sites (e.g., the cabbage aphid, Brevicoryne brassicae (L.) (Way & Camell 1970)). In some cases, the same effect also occurs with groups formed by members of two distinct species feeding together; e.g., enhancement of growth of Drepanosiphum plantanoides (Schrank) when feeding at sites coinfested with Periphetus acercola (Walker) (Shearer 1976) and enhancement of Eulachnus agilis (Kaltenbach) when feeding at sites coinfested with Schizolachnus pinetti (F.) (Kidd et al. 1985). Because increase in body size is positively correlated to increased fecundity in many species (e.g., Aphis fabae Scopoli [Dixon and Wratten 1971]), aggregation of parents can result in increased fecundity of offspring. This effect, however, is distinct from the question of whether or not the fertility of females in the original ("parent") groups is raised by aggregation. Reports of such direct enhancement of per capita fertility by increased density are relatively rare, but they exist for the greenhouse whitefly (Xu 1983) and the aphid Uroleucon nigrotuberculatus (Olive) (Kareiva 1984), although a subsequent report by Cappuccino (1987) indicated a negative rather than a positive relationship between colony size and fertility in U. nigrotuberculatus.

The cabbage aphid forms dense colonies on kale. The advantages of this life history trait that have been experimentally demonstrated include more rapid developmental rates of immature stages, attainment of larger adult body size (Way & Camell 1970), and reduced levels of attack by the parasitoid Diaeretiella rapae (McIntosh) (Lopez & Van Driesche 1989). We confirm here earlier suggestions (Way & Camell 1970) of yet another advantage of colony formation in this species; i.e., enhanced per capita birth rates of individuals in larger groups.

Materials and Methods

Measurement of Per Capita Recruitment of Caged Females. The effect of numbers of adult apterous females per group on the per capita birth rate of cabbage aphids, Brevicoryne brassicae (L.), under greenhouse and field conditions was determined using leaf cages (3.4 cm diameter) constructed from clear plastic Petri dishes ventilated top and bottom with fine screen and held in place on leaves of kale plants (Brassica oleracea L., group acephala de Candolle cv. Georgia collards, a flat-leaved form, cv. Vates) by wooden clips. Unparasitized adult cabbage aphid females were taken from a greenhouse colony maintained on potted kale plants of the same variety in a greenhouse. Colonies of various numbers of adult females were created for experiments by transferring aphids into leaf cages with a fine-tipped brush. Aphids then moved by themselves onto leaves after cages were...
secured to leaves. Three trials were conducted, one in a greenhouse and two in a kale field.

Trial 1 was conducted 16 June–7 July 1986 on potted plants in a greenhouse during a warm period (average 35 ± 4.5°C in the greenhouse). Densities of one, three, five, and seven adults per group were created, and aphids were allowed to reproduce on the undersides of leaves for 3 d. The resulting numbers of offspring and surviving females were then counted. The trial was repeated five times, with 30 replicates per density each time; two leaf cages per leaf were placed on each of four leaves per plant, using two replicates of each treatment for each plant.

Trial 2 was conducted 5–26 September 1986 in a kale field at South Deerfield, Mass., during a cool period (average 15 ± 2.3°C) using 1, 3, 5, 7, 9, 11, 13, and 15 females per group. Aphids from the same greenhouse colony used in Trial 1 were placed in cages which were then placed on the undersides of recently fully expanded leaves on field plants. Aphids were allowed to reproduce for 3 d, then were examined to determine total progeny produced and numbers of females surviving. Ten replicates were used for each density, and the trial was repeated four times. During each repetition, treatments were randomly assigned to plants, using five leaves on each of 16 plants, with one cage per leaf.

Trial 3 was conducted 15–18 July 1987 on plants in a similar kale field in the same location as was used for Trial 2. The trial was run only once, during a warm period (average 22 ± 3.8°C). Using aphids from the same greenhouse colony as in previous trials, groups of 1, 3, 5, 7, 9, 11, 13, 15, 20, 25, and 30 adult aphids were placed in cages which were attached to leaves as in previous trials. Thirty replicates of each density were established at the same time; one cage was placed on each of five leaves on 66 plants. Because some aphids in Trials 2 and 3 died during the trial, treatment values were redefined from single densities to narrow ranges of density; for instance, colonies with 14 and 15 surviving adult females per colony were grouped in lieu of the original targeted density of 15 adults per cage and so on.

**Distribution of Adult Females per Colony in the Field.** To determine the group size typical of cabbage aphid colonies in a natural population, a plot of 'Vates' kale was established the first week of May 1987 at the University Research Farm at South Deerfield, Mass., with 60 cm interplant and 120 cm interrow spacings. Weeds were partially suppressed during the season by hand-pulling and

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**Fig. 1.** Per capita reproduction per 3-d interval for cabbage aphids in groups of varying numbers of initial females in a greenhouse (A), and in a kale field in South Deerfield, Mass. (B), in 1986–1987. Error bars represent SEM.
cutting. On 24 July, five leaves of similar age were chosen from each of 1,000 similar-sized plants; the first four rows at each end of the plot were excluded. The leaves were numbered 1–5 on tags stapled directly on the leaves. Leaves were young but fully expanded at the time of selection. Tagged leaves turned senescent after 4 wk and were replaced with a second set of 5,000 leaves selected in the same manner as the first group. Three times each week, 30–50 tagged leaves were picked using random number coordinates for row, plant, and leaf, and all cabbage aphid colonies were noted. For each colony, the numbers of adults and nymphs were noted. Data were pooled for the entire 8-wk sampling period, and the proportion of adults living in colonies with various numbers of adults per colony was determined.

Results

Per capita reproduction of female cabbage aphids was significantly influenced by colony size on potted plants held in a greenhouse at 35°C (significant at \( \alpha = 0.001 \), one-way analysis of variance [ANOVA], \( F = 24.4 \), df = 346) (Fig. 1A). The reproduction rate of females in colonies with either one or three adult females per cage was smaller than that of females in colonies of five or seven per cage (Tukey's test, significant at \( \alpha = 0.05 \)). On field plants under warm conditions (average 22°C), per capita reproduction of female cabbage aphids also was significantly influenced by colony size (Fig. 1B) (significant at \( \alpha = 0.05 \), one-way ANOVA, \( F = 2.79 \), df = 128), but under cool conditions (average 15°C) in the field on leaves of the same age, aphid density had no effect on reproduction (Fig. 1B) (one-way ANOVA, \( F = 0.16 \), df = 195). Thirty-eight percent of adult females observed in samples from the field population under study occurred in colonies containing four or more adult females (Fig. 2).

Discussion

Way & Cammell (1970) and others have suggested that aggregates of phloem-feeding aphids are treated by plants as the equivalents of rapid growth areas. Such “sinks” cause nutrients to be diverted from distant parts of the plant to the advantage of the aphid colony. Some aphids also are believed to actively secrete auxins such as indole acetic acid which are thought to actively direct nutrients to the auxin-enriched tissues (Dixon 1975). The documented effects of such sinks on aphids have included more rapid growth rates and greater adult weights (Way & Cammell 1970). Previous evidence for enhanced fertility, however, has been limited. Data of Way & Banks (1967) and Kareiva (1984) come from experiments in which predation on aphid colonies was uncontrolled. The report of Way & Cammell (1970), although widely perceived as demonstrating enhanced per capita fertility in the cabbage aphid because of aggregation, is inconclusive on this point because its experi-
mental design did not control for earlier maturation to adulthood of aphids in high-density groups. We present clear evidence, which is not confounded by either of these issues of experimental design, for enhancement of fertility by aggregation in the cabbage aphid. Our observations support the general concept of the “sink” hypothesis, assuming that under warm conditions, the most limiting factor governing the rate of progeny production is nutrient supply. Lack of enhancement of daily birth rates in Trial 2 implies that under cool conditions, reproduction rates were too low for the nutrient supply to be limiting. Thirty-eight percent of all adults sampled from the natural population occurred in groups large enough to raise per capita reproduction rates. This suggests that the effect of group size on fertility is likely to be of significance for the population dynamics of the species through the middle portion of the season (i.e., July, August) when temperatures are 20–30°C. For the cabbage aphid and any other species with such density-related per capita reproduction rates, knowledge of such rates and the spatial distribution of adult insects in the field population would be essential to estimate correctly net reproductive rates ($R_n$) that could be meaningfully applied to the actual field population. Similarly, knowledge of such density effects would be significant in the construction of time-specific life tables (as originally developed by Hughes [1962, 1963]), especially those in which the intrinsic rate of increase ($r_i$) of a population is first estimated from manipulated cohorts of individuals whose $l,m$ schedules are observed, and then used in conjunction with other data to construct the actual tables (e.g., Hutchison & Hogg 1985). As currently applied, no consideration is given to group size in making such calculations.

Acknowledgement

We thank Christopher Geczy, Ronald Mack, Anthony Saucier, and Dave Stanley for technical assistance, and Keith Dorschner for help in locating critical references. Financial support was provided by USDA Competitive Grants #84-CRCR-1-1385 and 86-CRCR-1-2171. The study was completed while the senior author was a LASPAU (Latin American Scholarship Program of American Universities) scholar.

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Received for publication 27 December 1988; accepted 27 February 1989.