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MATERNAL AGE AS A SOURCE OF VARIATION IN THE ABILITY OF AN APHID TO PRODUCE DISPERSING FORMS

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Introduction

Natural populations in favorable environments so seldom increase to the point where they endanger their own future that many ecologists suspect self-regulating mechanisms may be more common in the real world than earlier theorists were prepared to believe. Genetic changes arising from varying selective pressures in different environments or at different population densities may regulate numbers of some species (Baltensweiler, 1970; Chitty, 1960). Other species may be regulated through physiological responses of individuals sensitive to changing environments or population densities (Gruys, 1970; Kennedy, 1961).

Hypotheses of self-regulation stipulate that qualitative and quantitative changes within a population must be closely linked; that the numbers and proportions of different types of individuals within that population should in fact change between certain generations or at particular levels of abundance. To satisfy such hypotheses, therefore, there must be sufficient variability within and between generations to maintain the links between quality and abundance.

Maternal age at the time of an individual's birth, or egg order in species which reproduce only once, have been shown to cause remarkable variability within single families, particularly among the insects (e. g., Howe, 1967). Only a few workers have considered the possible influence of such variability on population dynamics, or its potential as a population-regulating mechanism (e. g., Murai and Kiritani, 1970; Visscher, 1971; Wattiaux, 1968; Wellington, 1957, 1960). There are, however, theoretical considerations which suggest that maternally-induced individual differences could provide an advantageous source of variability for a species, and that such differences could even facilitate the evolution of self-regulatory mechanisms at the population level (MacKay, 1974).

The present study was designed to explore the effects of maternal age on some ecologically important characteristics of insects. Two considerations affected the choice of a phenomenon suitable for monitoring in relation to maternal age. The

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process first of all had to be associated with the persistence of the organism in its habitat, but not so consistently present throughout each generation that its frequency of expression could not vary. Secondly, the process had to be easy to monitor; e.g., with on-off limits instead of a continum that would require regular measurements. The production of dispersing individuals by aphids during particular periods or in particular environments meets those criteria (KENNEDY and STROYAN, 1959). This paper describes the effect of maternal age on the ability of the aphid, *Acyrthosiphon pisum* (HARRIS), to produce its winged form.

MATERIALS AND METHODS

The Insect

The pea aphid, *Acyrthosiphon pisum* (HARRIS), is widely distributed on many legumes. Its life cycle is comparatively simple. In the spring, eggs overwintered on woody tissue of the previous year hatch and the young aphids begin to feed. Members of this first generation produce only live females parthenogenetically. This mode of reproduction continues for several generations during the summer.

Periodically, apterous females may give birth to nymphs which are destined to become winged adults. Whether the future adult is winged or wingless is determined just prior to its birth, most often by the mother's response to crowding or to host-plant deterioration (SUTHERLAND, 1969a, b). The resulting alatae or the more usual apterae both must pass through four nymphal instars before becoming adult. In the autumn, sexuales, which include males as well as females, are produced in response to changing photoperiods and temperatures. The sexuales mate and the females deposit the overwintering eggs on the woody parts of perennial legumes, often on their summer host.

Rearing Conditions

Aphids for all the experiments were reared on broadbeans, *Vicia faba* (var. Exhibition Longpod). Plants were started in a greenhouse under varying temperatures, light intensities and photoperiod, and grown singly in a mixture of sandy soil and peat in 10 cm plastic pots. The plants reached the hook-stage and were ready for use after 9-11 days in such conditions.

A plant on which aphids were to be reared was first isolated in a 909 cc unwaxed cardboard freezer carton which had its bottom removed so that the lower edge could be pressed into the soil. The top of this small cage was covered by a clear plastic lid. Light intensity at soil level in such cages approximated 100 ft-candles, which ensured healthy plant growth.

Aphids were transferred from old to new plants with a small, moistened brush. Both the rearing and the experiments were carried out in environmental chambers kept at 20±1°C, with a photoperiod of 16L : 8D provided by fluorescent "Daylight" lamps. Those conditions kept the clone reproducing parthenogenetically. Apterous females began to reproduce on the ninth day after birth, continuing for some 14 days. Alate females began to reproduce on the eleventh day, continuing for a further 17 days (MACKAY and WELLINGTON, 1975).

Stock Culture

A single parthenogenetic female was collected in September, 1972, from an alfalfa field at the University of British Columbia. Because it was necessary to have a daily supply of newly-matured aphids as nearly identical as possible, nine separate lines, one day apart in development, were established from the descendants of a single offspring of the original female. Only the young born during the first four days of the reproductive period were used to obtain these lines, so more than one generation was required to establish them. Each new line was required to pass through at least one additional generation before being used in the experiments.

Once established, each line consisted of a group of 20 apterous aphids obtained from days 1 and 2 of a female's reproductive output. Each day, one of these lines approached adulthood and provided one female to continue the line on a new plant, and up to 19 females which could be used in experiments.

Because the stock culture, once established, consisted of nine separate clones, there was a danger that they might develop different responses over several generations. To avoid such difficulties, the lines were re-established from a single individual prior to each major set of experiments.

Experimental Design

As an experiment involved three generations, a standard nomenclature was adopted to avoid confusion. The generations in each experiment were the grandparents, parents, and offspring (Table 1). The terms, "mother", "progeny", etc., were reserved for general descriptions.

Table 1. The experimental generations.

Generation	Differences Monitored
grandparents	early *vs.* late reproduction
parents	early- *vs.* late-born
offspring	alate *vs.* apterous

The study explores the question: does the age of a grandparent at the time of a parent's birth affect that parent's ability to respond to crowding by producing alate offspring? The grandparent was always the aphid which was observed as it aged through its reproductive period. The parents thus were early-or late-born, though they were all subsequently crowded at the same age. After that exposure of the parents to crowding, their offspring were monitored to determine whether they were winged or wingless morphs.

The crowding stimulus used by SUTHERLAND (1969a) to investigate *A. pisum*'s production of winged individuals was also applicable in the present study. SUTHERLAND found that groups of aphids crowded into small vials soon began to produce alate individuals when returned to their hosts, whereas aphids placed singly in such vials afterwards continued to produce only apterae. He concluded from these and other studies that encounters among crowded aphids stimulated the mechanoreceptors, particularly those on the antennae, and thus initiated the production of alatae. In the present study, the crowding stimulus was applied by holding a batch of ten aphids in a 2.5×5 cm plastic vial for eight hours (1100-1900 h) at 20°C and at the light intensity to which they were normally exposed.

To test the effect of maternal age on alata-production, a grandparent was isolated as a late fourth-instar nymph or teneral adult. The aphid was then transferred every few days to new plants in order to obtain four batches of parents, born at different times within the grandparent's reproductive period. Batch I parents were produced during days 1 and 2 of the grandparent's reproductive period. Batch II parents were born on days 4-5, Batch III on days 7-8, and Batch IV on days 10-11.

Some 15 aphids born during each of these four periods were reared together on the plant on which they had been produced. As each group neared the adult stage, ten healthy specimens were selected as members of the batch, isolated on separate fresh plants, and left to begin to reproduce. Each batch was assigned a randomly chosen position in an environmental chamber.

After two days, when all the adults in a batch had begun to reproduce, the crowding stimulus was administered. By that time, each parent had already produced 1-25 nymphs. All the offspring which had been produced during that pre-crowding period were collected and reared until their morph could be determined.

After crowding, the parents were returned to plants and allowed to reproduce for four days. They each bore 40 or more young during that period. (The four-day period was chosen because preliminary trials and SUTHERLAND's (1969a) earlier work both indicated that all the parents should stop producing alatae by the fifth day after they had been removed from crowding. In most instances, in fact, all the alatae were produced in the first 24 h.) The offspring were monitored for another six days, by which time the youngest had reached its fourth instar, unequivocally displaying its winged or wingless condition.

When apterous grandparents were required, they were obtained directly from the stock culture. In contrast, when alate grandparents were needed, ten great-grandparents were isolated from the culture, crowded after they began to reproduce, and then returned to their plants. Their post-crowding progeny were reared until the required winged individuals could be distinguished.

Simultaneous controls could not be arranged because of the time-span of the phenomenon being investigated. Thus there was a danger that observed differences might sometimes be influenced by transient external factors as well as by physiological changes in the grandparents. Since it was difficult to ensure that all such external influences had been excluded from each set of experiments, an experimental design was adopted which would expose any that might accidentally intrude.

Replicates were established sequentially instead of simultaneously, When one grandparent was beginning to produce its first batch, another was simultaneously producing Batch II, another, Batch III, and a fourth, Batch IV. As expected, some transient variations occurred during some of the days, but the method demonstrated that none of those variations initiated or maintained a trend that could bias the results.

In determining the effect of maternal age with apterous grandparents, 14 replicates were carried through in two groups several months apart. The two sets of data gave virtually identical results, and therefore could be pooled. With one exception noted later, the six replicates obtained for alate grandparents also could be pooled.

RESULTS

Apterous Grandparents

Table 2 shows that there was only a slightly greater response to crowding among Batch I parents than among those in the remaining batches: ~39% of Batch I parents produced some alatae, as opposed to ~29% of Batches II, III, and IV. But the numbers of alate offspring those parents produded differed markedly: Batch I parents produced more than twice as many alatae as the parents in Batches II, III, and IV (Table 3). In addition to the data of Table 3, those of Fig. 1 also show the greater strength of the response of Batch I parents compared with the responses of later-born parents.

Table 2. Effect of grandparental age at the time of parental birth on the numbers of ***parents*** which produced winged offspring in response to crowding: 14 ***apterous*** grandparents.

	Birth-order of parents during the grandparent's reproductive period.			
	Batch I[a]	Batch II	Batch III	Batch IV
Parents producing[b] only apterae	86(97)	100(97)	100(97)	102(97)
Parents producing[b] some alatae	54(43)	40(43)	40(43)	38(43)

[a] Batch I parents were born during first two days of the grandparent's reproductive period; Batch II-days 4-5; Batch III-days 7-8; Batch IV-days 10-11.

[b] χ^2 test for independence of parental response *vs.* batch = 5.50; $0.1 < p < 0.15$ Expected values assuming no effect are given in parentheses.

Most of the parents which produced large numbers of alatae were themselves born during the first two days of their own mothers' reproductive period. Most parents born later in their apterous mothers' reproductive period could scarcely produce any alatae in response to the stimulus.

Table 3. Effect of grandparental age at the time of parental birth on the numbers of ***winged offspring*** produced in response to crowding: 14 ***apterous*** grandparents.

	Birth-order of parents during the grandparent's reproductive period			
	Batch I[a]	Batch II	Batch III	Batch IV
Number of apterae produced[b]	4687 (4955. 9)	5577 (5466. 6)	5262 (5177. 5)	5181 (5107. 0)
Number of alatae produced[b]	591 (322. 1)	245 (355. 4)	252 (336. 5)	258 (332. 0)

[a] See Table 2 footnotes for Batch periods.

[b] χ^2 test for independence of offspring morph *vs.* batch $= 316.0$; $p \leqslant 0.005$. Expected values assuming no effect are given in parentheses.

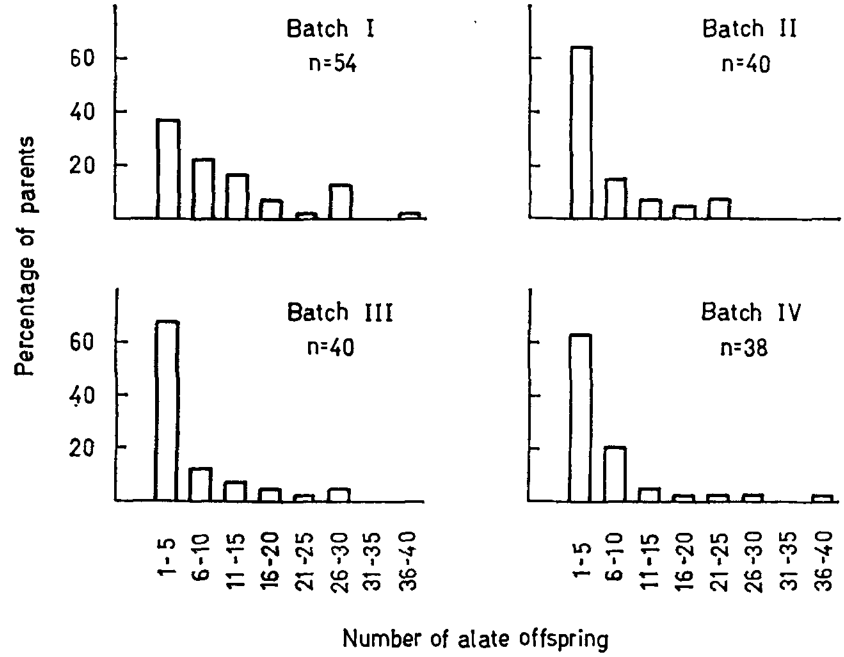

Fig. 1. The number of parents producing different numbers of alate offspring, expressed as a percent of the number of parents from each batch that responded (n). Parents were obtained from *apterous* grandparents. (Summarized from data for 14 apterous grandparents, 140 parents tested for each batch).

Alate Grandparents

Five of the six replicates of the alate morph had virtually identical parental responses to crowding. Table 4 shows the numbers of parents in the different batches of those five replicates which responded to the crowding stimulus, and Table 5 shows the numbers of alate offspring which those parents produced. In contrast to the results for apterous lines, Batch I parents borne by the five alate grandmothers did not produce any alate offspring in response to crowding. The later batches from the alate grandparents responded by producing some alatae, in much the same fashion as the comparable batches of parents borne by apterous grandparents (cf. Tables 2 and 4, Figs. 1 and 2).

Table 4. Effect of grandparental aged at the time of parental birth on the numbers of ***parents*** which produce winged offspring in response to crowding: 5 ***alate*** grandparents.

	Birth-order of parents during the grandparent's reproductive period			
	Batch I[a]	Batch II	Batch III	Batch IV
Parents producing only apterae[b]	50(37.25)	29(37.25)	35(37.25)	35(37.25)
Parents producing[b] some alatae	0(12.75)	21(12.75)	15(12.75)	15(12.75)

[a] See Table 2 footnotes for Batch periods.

[b] χ^2 test for independence of parental response *vs.* batch = 26.5; $p < 0.005$. Expected values assuming no effect are given in parentheses.

Table 5. Effect of grandparental age at time of parental birth on the numbers of ***winged offspring*** produced in response to crowding: 5 ***alate*** grandparents.

	Birth-order of parents during the grandparent's reproductive period			
	Batch I[a]	Batch II	Batch III	Batch IV
Number of apterae produced[b]	1846 (1772.5)	1881 (1926.3)	1966 (2006.0)	1819 (1807.2)
Number of alatae produced[b]	0 (73.5)	125 (79.7)	123 (83.0)	63 (74.8)

[a] See Table 2 footnotes for Batch periods.

[b] χ^2 test for independence of offspring morph *vs.* batch = 125.1; $p \ll 0.005$. Expected values assuming no effect are given in parentheses.

The sixth replicate of the alate morph displayed an interesting difference in its parental response to crowding. Unlike the Batch I parents produced by the other five grandparents, seven of the ten Batch I parents of the sixth replicate produced a total of 95 alatae after they were crowded. In this respect they behaved like the Batch I parents from the apterous grandparents described above. In contrast to the aberrant behavior of the sixth replicate's Batch I parents, its three subsequent batches of parents were not unusual in any way.

In Fig. 2 (Batches II, III, and IV), the progeny of all six grandparents could be grouped to show their similar responses to crowding. In contrast, the only positive response to crowding among Batch I parents arose among the progeny of the sixth, aberrant grandparent. The diagram for Batch I parents therefore shows how similar the reactions of that single lineage were to the responses of the morphologically

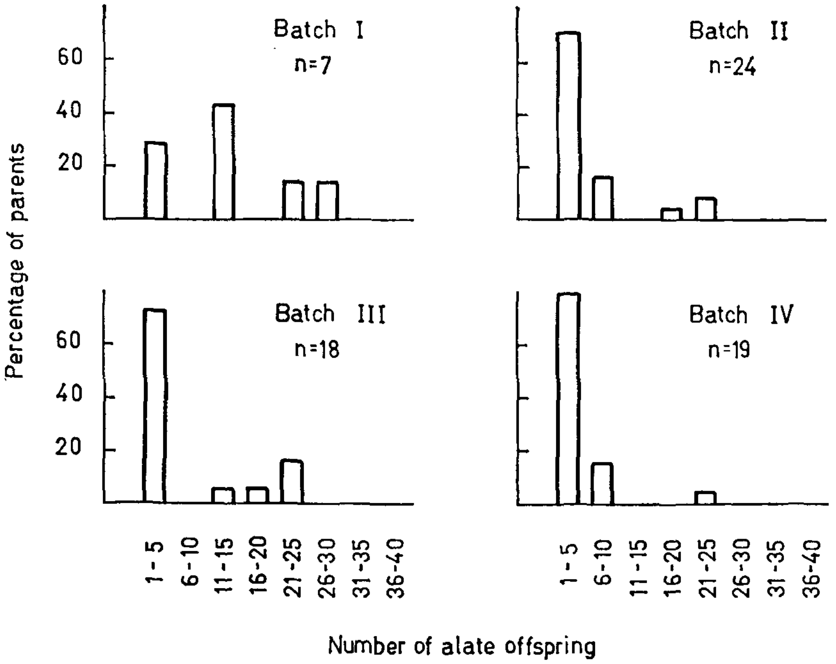

Fig. 2. The number of parents producing different numbers of alate offspring, expressed as a percentage of the number of parents from each batch that responded (n). Parents were obtained from alate grandparents. Summarized from data for 6 alate grandparents, 60 parents tested for each batch. (The histograms for Batches II-IV include parents descended from all six alate grandparents. The histogram for Batch I includes only the parents descended from winged grandparent Number 6, the sole alate individual which gave rise to Batch I parents capable of producing winged offspring. In that sense, grandparent Number 6 was "functionally apterous," as its Batch I progeny behaved like the early-born progeny of the morphologically apterous grandmothers of Fig. 1).

apterous lines illustrated in Fig. 1. In this one respect, at least, the sixth alate grandparent appears to have been functionally apterous.

DISCUSSION

Apterous individuals of *A. pisum* born during the first one-sixth of their apterous mother's reproductive period produce many more alatae than their later sibs after they are crowded. Part of that difference is due to the *proportion* of early-born progeny which respond. More important, however, is the far greater *intensity* of the reproductive response of early-born progeny, compared with that displayed by responsive progeny from the remaining five-sixths of the grandmother's reproductive period.

In contrast to apterous founders, alate grandparents normally do not produce early-born young which can in turn produce alatae. In the first one-sixth of their reproductive period, the alate grandparents instead bear only aptera-producers. In other words, while young apterae bear prolific alata-producers, young alatae bear only aptera-producers. On the other hand, both old and middle-aged grandmothers, whether winged or wingless, bear only relatively poor alata-producers.

Physiological Basis of Alata-production

Changes in the activity of the corpus allatum and in the concentration of juvenile hormone have been correlated with the production of alatae in some species of aphids (JOHNSON, 1959; LEES, 1961, 1966; WHITE, 1968; WHITE and GREGORY, 1972; WHITE and LAMB, 1968), but not in others (LECKSTEIN and LLEWELLYN, 1975). The presence of juvenile hormone or its analogues at the appropriate time certainly disrupts the normal development of wings. But other hormones may ultimately be shown to be involved, as the complicated endocrine changes are still not fully understood. In some species of aphids, the winged or wingless state is prenatally determined; in others, postnatal determination is the rule, and some may determine the morph either pre- or postnatally (LEES, 1966). Thus nymphal as well as adult endocrine systems may be involved.

Most aphids have small wing-buds at birth (JOHNSON and BIRKS, 1960). These buds continue to develop in proto-alate aphids, but degenerate in proto-apterae. WHITE (1971) found that the size of the progeny's wing-buds varied prior to birth, depending on whether the mother was newly-molted or older, and apterous or alate. She found these differences in size were correlated with changes in the size of the corpora allata in both the adult and the unborn nymph.

In addition to affecting the size of embryonic wing-buds, however, the mother's age may also influence the development and characteristics of the embryonic humeral system. The resulting effects could limit the progeny's later ability to produce alatae. As it is only the first one-sixth of the progeny of both winged and wingless mothers which differ so markedly from their later sibs, the sudden change may be associated with a discrete event (such as the larval-adult ecdysis), rather than a gradual change in the processes of maternal development. (Alternatively, the activity level of early-born aphids may differ sufficiently from that of their later sibs to make them more receptive to appropriate stimuli.)

Ecological Effects of Alata-production

Whether the differences resulting from birth order are artifacts of other physiological processes, or specifically evolved mechanisms, they can have ecological as well as physiological import. Birth-order differences can be considered in relation to the survival of an individual and its descendants, or viewed in relation to their effects on population processes. Both the evolutionary and the population consequences can be profitably considered in terms of DEN BOER's (1968) concept of "spreading of risk"; i.e., intra- as well as inter-generational variations may not be entirely due to the presence of some imperfectly adapted individuals, but may actually be adaptive, thereby diminishing the risk of extinction and lessening the amplitude of numerical fluctuations.

The Consequences for the Individual.

An apterous aphid appears to spread dispersive risks among its progeny in at least three ways. Firstly, its response to crowding or host deterioration varies over its lifetime. SUTHERLAND (1969a) found that production of alatae by *A. pisum* was lowered in older aphids. BONNEMAISON (1951) reported a comparable decrease in the ability of ***Brevicoryne brassicae*** to produce alatae as the mother's age increased, but also noted that the ability of ***Myzus persicae*** to produce alatae increased to a maximum midway through the reproductive period, decreasing again thereafter. Thus, the ratio of the two morphs among an aphid's progeny will be related not only to the intensity of the stimulus eliciting the production of alatae but also to parental age.

The second method of spreading dispersive risks has been illustrated here in *A. pisum*. An apterous pea aphid may produce only apterous progeny dring its lifetime, but they in their turn will differ in their ability to produce dispersers when they are appropriately stimulated. After that stimulation, two distinct maternal types, "alata-producers" and "aptera-producers", will be recognizable. But those maternal types will have originated at different times—early and late in their parent's reproductive period.

One result of that differentiation is that the original aphid's immediate descendants include some individuals capable of responding strongly to a stimulus to which the remaining sibs can only respond weakly, if at all. Each aphid therefore establishes several different lines of descendants that can cope with different eventualities; wingless residents destined to remain near their birthplace for another generation, and winged migrants capable of flying elsewhere. The founder thus increases the probability that at least one line of its descendants will survive, even in an uncertain environment.

Alate aphids appear to be more restricted than their apterous counterparts in their ability to produce dispersers. Most alatae of *A. pisum*, and those of many other species (LEES, 1966), seem unable to produce winged progeny, although some species display an increasing ability to do so later in life (JOHNSON and BIRKS, 1960). In addition, as shown here and elsewhere (LEES, 1966; SUTHERLAND, 1970), alatae may also be restricted in their ability to bear alata-producers; e. g., the progeny of winged *A. pisum*, unlike those produced by their wingless counterparts, in their turn are rarely more than weak producers of alatae.

The hormonal state required to develop functional wings may be incompatible with the state required for producing winged young or young that will become alata-producers. That incompatibility could be advantageous for an alate aphid and its progeny, as it would ensure that at least one generation remained on a new host before there was further dispersal.

Disadvantages resulting from a temporary inability to produce dispersers should be outweighed by the selectivity of the winged founder in choosing a plant on which to settle. Alate aphids often flit for long periods among apparently suitable plants before finally selecting and settling on one (WAY and CAMMELL, 1970). Initial selection of a highly suitable plant thus should reduce the need for more dispersers during the first few generations after establishment.

Finally settled on a plant, an aphid may spend its lifetime producing a large colony (e.g., *Aphis fabae*, WAY and BANKS, 1967) or it may bear only a few young before flying to another plant (e.g., *Myzus persicae*, JOHNSON, 1957). In the latter instance, the small group of progeny left on one host would all be from the same part of the mother's life-cycle and therefore should respond similarly to alata-producing stimuli. The survival of those nuclear groups which could not themselves produce many alatae would only be ensured if their host remained suitable for at least two generations. The question arises: does the searching behavior of an alate mother and her criteria for selecting hosts change after she begins to produce some young that can in turn bear alatae?

A third way in which an aphid may spread dispersive risks among its progeny has been reported by SHAW, (1970a, b; 1973a, b). He demonstrated that, contrary to previous assumptions, not every winged aphid flew before settling on a plant and reproducing; i.e., there was not such a complete dimorphism between "winged" dispersers and "wingless" non-dispersers as had hitherto been supposed. Among *Aphis fabae*, for example, he found some alatae that neither towered upward nor dispersed for long distances. Instead, they either flitted from plant to plant, or did not fly at all. The proportions of progeny with differing flight capacities in a laboratory population of alata-producers were affected by the circumstances in which presumptive alatae developed. Thus, if aphid densities decreased or host condition improved while proto-alatae were developing, fewer of the subsequent alatae showed strong dispersive tendencies. Thus the subsequent amount of long-range dispersal was smaller, and the proportions of local fliers and non-fliers were higher.

A comparable situation seems to have developed during the present study with the appearance of the aberrant alate grandmother. That individual clearly lacked the mechanism to suppress alata production by its progeny, a mechanism exhibited by all other alatae tested. In bearing more alata-producing parents than the other winged grandparents, it displayed a functional winglessness, despite its well-developed wings. We do not know whether mothers of a particular age class or aphids born at a particular point in their mother's reproductive period might produce the most active dispersers, but the question is worth further study.

The Consequences for the Population.

If all the members of a population responded equally to stimuli to produce alatae, there would be sudden peaks in aphid flight. Such peaks would drastically reduce a local population, making it more vulnerable to extinction. Moreover, if a period of unsuitable weather coincided with a peak, the dispersing migrants also might be lost. When only a fraction of each generation can respond strongly to the signal to produce alatae, however, the period of their production is extended, thus avoiding any difficulties associated with peaks in flight.

The apterous progeny of a single alata may form dense aggregations (e.g., *Aphis fabae*, WAY and BANKS, 1967; *Brevicoryne brassicae*, HUGHES, 1963) or they may be dispersed over the plant (e.g., *Acyrthosiphon pisum* ; *Myzus persicae*, VAN EMDEN *et al.*, 1969). Although in both instances alatae are eventually produced as numbers increase or the host deteriorates (BONNEMAISON, 1951; JOHNSON, 1965, 1966; LEES, 1961, 1967; SUTHERLAND, 1969a, b) such alatae may be more than a safety-valve for evading the consequences of local crowding. They may have somewhat different functions in spaced-out, as opposed to aggregating, species.

Species of aphids which form dense aggregations inflict severe and often lethal damage on their hosts. Such aphids are usually very patchily distributed through their habitats, however, so that many hosts may remain untouched for every one that is inundated. Such species can avoid dangerously frequent local extinctions by maintaining a high rate of alata production, dispatching a steady stream of dispersers into other parts of their habitat before their host dies (e.g., *Aphis fabae*, WAY and CAMMELL, 1972). In contrast, the production of alatae in species of aphids which are spaced more uniformly through the habitat appears to keep the many local populations so small that the hosts survive much longer; e.g., *Myzus persicae* (WYATT, 1965). To exploit the winged state in this fashion, however, such "spreaders" require a mechanism which makes them especially sensitive to small changes in density.

Whether alata-production reduces the risk of local extinction when hosts are inundated, or helps to stabilize smaller local populations at tolerable levels for the hosts, further examination of the effects of maternal age on the underlying strategy could prove rewarding. Age-related differences could provide the sensitive mechanism a species such as *Acyrthosiphon pisum* requires to regulate its density, by operating through the adult age-structure of a local population to dictate its level of response.

If population density and host condition were the only variables affecting the rate at which aphids produced alatae, all populations subjected to the same density and host condition might produce dispersers at the same rate. The addition of age-related effects, however, increases the flexibility of the population's response by providing historical as well as current information for the monitoring apparatus to digest. As a result, species which incorporate maternal age in their monitoring systems can modify their responses to enviromental signals to suit the recent direction of change as well as the present level of population density and host condition.

SUMMARY

Apterous parthenogentic females of the pea aphid, *Acyrthosiphon pisum* (HARRIS), begin to produce alate offspring soon after they have been subjected to crowding.

Females which were born early in their own parent's reproductive period respond most strongly to crowding, producing much larger numbers of alatae than their late-born sisters.

In contrast, the early-born daughters of most alate females do not produce winged offspring after being crowded. Some of their later-born sisters may produce a few winged individuals, resembling in this respect the late-born daughters of the apterous females.

Control of the production of alatae thus begins in the grandparental generation. Risk-spreading by means of differential dispersal becomes a less uncertain venture when local populations can modify their responses to environmental changes by utilizing past as well as present signals from their surroundings.

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アブラムシにおける有翅虫産生能力の変異の1因としての母虫の日令

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エンドウヒゲナガアブラムシ（***Acyrthosiphon pisum***）の無翅胎生雌はこみあい状態におくと間もなく有翅虫を産生しはじめる。母虫の生殖期間の初期に産まれた雌はこみあいに対して最も強く反応し，後期に産まれた雌に比べてずっと多数の有翅虫を産む。一方，有翅雌の場合にはそれが初期に産んだ雌からはこみあい状態にしても有翅虫が産まれないのがふつうであるが，後期に産まれた雌は若干の有翅虫を産み，この点で無翅虫が後期に産んだ雌に似る。いずれにしても有翅型の産生の制御は祖母の世代にはじまることになり，現在のみならず過去の環境条件にも左右されるわけで，このため分散による“危険の分散”はそれだけ確実性を減ずることになる。