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Ecology of host alternation in aphids

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Ecology, aphids, fundatrix specialization hypothesis, host alternation

Abstract. This paper reviews the evidence for the fundatrix specialization hypothesis and attempts to quantify the relative advantage of host alternation and define the conditions favouring the evolution of this way of life. Contrary to the predictions of the fundatrix specialization hypothesis there does not appear to be a barrier to some host alternating Aphidinae transferring their whole life cycle over to a secondary host plant. The coexistence of plants with asynchronous phenologies supplied the potential and the ability of aphids to produce a number of highly prolific generations in quick succession, which amplify the differences in performance on the two hosts and more than offsets the costs of transfer between hosts, supplies the means of exploiting this potential. That is, host alternation is not maladaptive and maintained by constraint but adaptive, at least in the Aphidinae.

INTRODUCTION

Most aphids show cyclical parthenogenesis in which each bout of sexual reproduction is followed by a sequence of asexual generations. That is, each clone is made up of many individuals, which are separated in space and may be particularly adapted for reproduction or dispersal. Ten percent of aphid species show host alternation (Eastop, 1986), which involves regular seasonal movements mainly between woody (primary) and herbaceous (secondary) host plants with sexual reproduction occuring on the primary host. Recently a lot of attention has been devoted to discussing whether such a way of life is adaptive or maladaptive (Moran, 1988, 1992; Mackenzie & Dixon 1990, 1991). The maladaptive scenario, or fundatrix specialization hypothesis, has focused mainly on the spring females (Fundatrices) that hatch from the overwintering eggs, which some authors believe to be so closely adapted to living on their primary host that they are unable to transfer to the secondary host although the later is thought to be generally nutritionally superior to the primary host (Mordvilko, 1928; Moran, 1988). This debate has diverted attention away from the ecological problems associated with host alternation, a phenomenon which in the Insecta is confined to the superfamily Aphidoidea.

The fitness of a clone is dependent on its success in maximising the collective performance over the whole life cycle, the evolutionary unit of Janzen (1977). In the case of host alternation this involves the sequential exploitation of two very different host plants. This paper reviews the evidence for the fundatrix specialization hypothesis and attempts to quantify the relative advantage of host alternation and define the conditions favouring the evolution of this way of life. This will be done mainly by reference to the subfamily Aphidinae as it is only in this group of aphids that the physiological tolerances of the spring females versus other morphs in the life cycle have been tested.

The role of 'fundatrix specialization' in maintaining host alternation in the Aphidinae

The spring females of several species of host alternating Aphidinae have been successfully reared on their secondary host plants (Table 1). This has mainly been achieved by transferring the aphid to the secondary plant at egg hatch. In *Cavariella aegopodii*, however, the eggs were laid, hatched and the emerging spring females reared to maturity on the secondary host plant. Although the spring females don't survive as well on the secondary host as they do on the primary host at bud burst they do survive and grow as well or better than those reared on the mature foliage of the primary host (Kundu & Dixon, 1994a).

TABLE 1. The species of host alternating Aphidinae whose spring females have been successfully reared on a secondary host.

Species	Host alternates between	Reference
A WOODY PRIMARY AND HERBACEOUS SECONDARY HOST		
Aphis fabae Scopoli	Spindle and bean	Dixon & Dharma (1980)
Cavariella aegopodii (Scopoli) *Cavariella pastinacae* (L.) *Cavariella theobaldi* (Gillete & Bragg)	Willow and Umbelliferae	Kundu & Dixon (1994a)
Metopolophium dirhodum (Walker)	Rose and grasses	Thornback (1983)
Myzus persicae (Sulzer)	*Prunus* and species of over 40 different plant families	Blackman & Devonshire (1978)
A PERENNIAL HERBACEOUS PRIMARY AND ANNUAL HERBACEOUS SECONDARY HOST		
Acyrthosiphon pisum (Harris)	Perennial vetches and annual *Pisum* spp.	Mordvilko (1928)
Uroleucon gravicorne (Patch)	Perennial *Solidago* and annual *Erigeron*	Moran (1983)

In eight species of Aphidinae the spring females are not so constrained to living on the primary host that they are unable to survive, mature and reproduce on the secondary host. That is, contrary to the prediction of the fundatrix specialization hypothesis there does not appear to be a physiological barrier to some host alternating Aphidinae transferring their whole life cycle over to the secondary host plant i.e., becoming autoecious. As aphids are small insects host alternation is undoubtedly very costly as few individuals will survive each host transfer. Therefore, if these aphids are not constrained to this way of life what are its advantages and under what conditions is it likely to have evolved?

Advantages of host alternation

Only as few as 1 in 100 are thought to make each transfer between hosts (Taylor, 1977). Host alternation involves at least two host transfers each season in most species. Thus host alternating clones need to be able to compensate for the large losses incurred in host transfer otherwise there will be a strong selection pressure to simplify the life cycle and for the aphid to become secondarily autoecious on either the primary or secondary host.

The fecundities recorded in the field for each generation of two host alternating aphids (Fig. 1) reveals that the potential amplification in the number of individuals in each clone

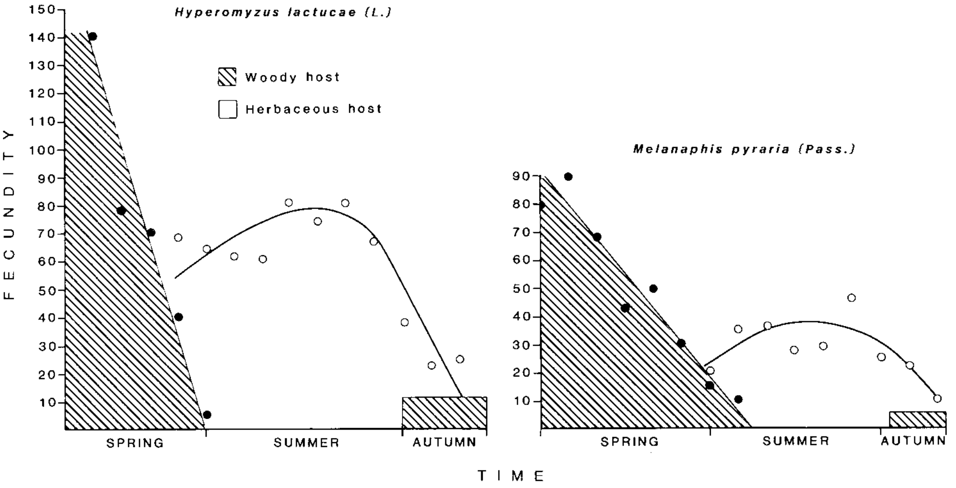

Fig. 1. The fecundity and number of generations that *Hyperomyzus lactucae* and *Melanaphis pyraria* achieve on their primary (●) and secondary (○) hosts in spring and summer, respectively, and the fecundity achieved by the autumnal migrants of these species on their primary hosts (after Karczewska, 1976, 1979).

on the primary host in spring more than compensates for losses incurred in the spring host transfer. Thus these clones are better represented at the beginning of the season on the secondary host than they would have been if they had overwintered there. In both these species the further amplification in numbers achieved on the primary host in autumn is probably not greater than it would have been if they had stayed on the secondary host. Thus the amplification in numbers of each clone achieved in spring on the primary host has not only to offset the cost of one host transfer, but of both host transfers. By virtue of the very high fecundities achieved on the primary host in the spring these aphids could more than compensate for as few as 1 in 10,000 making the two transfers.

The autumn migrants of most host alternating Aphidinae that have so far been studied either do not, or judging by the relatively few offspring they produce are unlikely to feed on the primary host (Table 2). This has been attributed to the short period remaining for ovulation and maturing additional embryos before leaf fall (Walters et al., 1984). Those of *C. aegopodii*, however, are a striking exception as they achieve a higher fecundity, feed and mature half their embryos on the primary host. This difference in the reproductive behaviour of autumn migrants is possibly associated with the pattern of leaf fall of their woody hosts. Willow, the primary host of *C. aegopodii* retains its leaves much later than do the primary hosts of many other host alternating aphids, e.g. *Malus*, *Prunus*, *Pyrus* and *Ribes*, and as a consequence the aphid can further amplify its numbers on the primary host.

As *Cavariella* can complete its life cycle on either its primary or secondary host it is possible to estimate the advantage of host alternation over non host alternation assuming that all individuals of clones with the later strategy make one host change in the third generation between willow trees. Figure 2 gives the relative success of the two strategies in terms of number of eggs produced and indicates that if at each host transfer 1% are successful then host alternation is advantageous over non host alternation even if there are three host transfers. If the success in locating a host is as little as 1 in 1,000 host alternation involving two host transfers is still advantageous. In the field we can expect 2 or 3 host transfers, which providing the success of moving from one host plant to another is in the order of at least 1% would result in host alternation being more advantagous than autoecy (Kundu & Dixon, 1994a).

TABLE 3. The relationship between the date on which the temperature first went below 10°C in autumn and time of leaf fall of apple, peak arrival of autumnal migrants of *Dysaphis plantaginea* and of the peak number of the sexual females they produce, and the ratio of the peak number of sexual females to peak number of autumn migrants (after Bonnemaison, 1959).

Year	1950	1952
Autumn	Late	Early
Temp < 10°C	25 October	19 September
50% leaf fall	20 November	24 October
Peak of autumn migrants	14 October	5 October
Peak sexual females	27 October	25 October
$\frac{\text{Peak sexual females}}{\text{Peak autumn migrants}}$	0.6	0.08

The above assumes that the aphid completes a certain number of generations and that its reproductive potential does not vary greatly from year to year. Annual variations in weather and activity of natural enemies, however, could have a dramatic effect on the number of generations and the fecundity achieved on each host plant, the proportion surviving each host transfer and the success of clones in producing eggs at the end of the season. Unfortunately there are very few field studies of host alternating aphids. However, there is statistical evidence that the weather during the spring migration significantly affects the proportion of aphids making the spring host transfer. Peak numbers of *Aphis fabae* in summer are dependent not only on the number present in the previous two years but are also strongly dependent on hot conditions in May when it colonizes secondary host

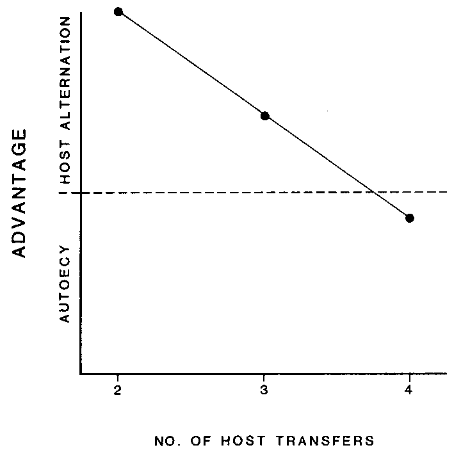

Fig. 2. Relative advantage of host alternation over non host alternation in *Cavariella aegopodii* in terms of eggs produced at the end of a season assuming different degrees of success in locating a new host and different numbers of host transfers for the host alternating form (After Kundu & Dixon, 1994a).

plants. The strong delayed density dependent effect associated with previous aphid abundance indicates that the abundance of the aphid may also be affected by natural enemy activity (Thacker et al., 1994). Low temperatures in autumn induces early leaf fall, which can have a dramatic affect on the number of aphids on the primary host that survive to produce egg laying females and the number of these females that survive to mate and produce overwintering eggs. For example, low temperature in inducing early leaf fall in apple has a dramatic affect on the ability of *Dysaphis plantaginea* to successfully produce sexual females and overwintering eggs (Table 3).

TABLE 2. The total number of embryos, well developed embryos and offspring produced by autumn migrants of host alternating Aphidinae, and whether they have been recorded as feeding as adults on the primary host.

	Number of			Feed as adults	Reference
	Embryos	Well developed embryos	Offspring		
Dysaphis plantaginea			9		Bonnemaison, 1959
Hyperomyzus lactucae			11		Karczewska, 1979
Melanaphis pyraria			6		Karczewska, 1976
Rhopalosiphum padi	7	7	5	No	Leather, 1982
Rhopalosiphum insertum	10	10	10	No	Dewar, 1977
Cavariella aegopodii	18	8	19	Yes	Kundu & Dixon, 1994b

If the onset of growth of the secondary host plant were to occur earlier then selection might begin to favour clones that stayed and completed their life cycle on the secondary host plant. This is especially so if the difference in fecundity on the primary and secondary host is not very great. That is, host alternation is only likely to prove advantageous if each season the primary host is available to host aphids well before the secondary host. If the two hosts are available over the same period then it only becomes advantageous if the fecundity on the primary host in the spring is much greater than that achieved on the herbaceous host. By completing a greater number of generations and only incurring the cost of some dispersal between hosts, which may not involve all the individuals of a clone in a particular generation, would put a secondarily autoecious form on an herbaceous host at an advantage over host alternating clones. Thus the existence of complementary patterns of growth in the primary and secondary host plants provides the conditions that make host alternation advantageous.

Opportunity for host alternation

Given that the quality of woody plants in summer is generally conceded to be in some way inferior to herbaceous plants as hosts for aphids (Davidson, 1927; Mordvilko, 1928; Kennedy & Booth, 1951; Dixon, 1971, 1985, 1990; Moran 1988, 1992) and that host alternation is adaptive then it is surprising that host alternation is so rare. A possible answer may be found in the association of host alternation with the dominant status of aphids' host plants. Significantly fewer (6%) of the aphids associated with the dominant species of trees in British woodland host alternate compared with the aphids (58%) associated with sub-dominant species of tree. Thus there appears to have been less opportunity for the evolution of host alternation in climax woodland situations dominated in summer by a few species of trees. The closed canopy characteristic of such woodland prevents the development of herbaceous plants during summer when the 'quality' of the trees for aphids is low. In contrast sub-dominant trees, like *Populus*, *Prunus*, *Pyrus*, *Salix* and *Ulmus*, live in more open habitats such as river banks where there is often a rich herbaceous flora in summer. Thus opportunity in terms of an abundant woody and an abundant herbaceous plant with complementary patterns of growth growing close together, i.e, a suitable plant community structure, could have played an important part in the evolution of host alternation. The more so because aphids are severely constrained by the very short period they can spend searching and their low efficiency in locating host plants (Dixon, 1990).

CONCLUSIONS

There appears to be no evidence to sustain the hypothesis that host alternation in the Aphidinae is maintained by the specialization of spring females to living on primary hosts. Assuming the primary and secondary host plants show complementary growth patterns then to host alternate is better than remaining on one host providing an aphid clone can amplify its numbers on the two hosts sufficiently to offset the high cost of transferring between hosts. If the spring flush of growth of the primary and secondary hosts coincided then host alternation would still be advantageous providing the fecundity on the primary host in spring was sufficiently higher than on the secondary host at that time to offset the costs of transfer between hosts. The fact that primary hosts generally start growing early

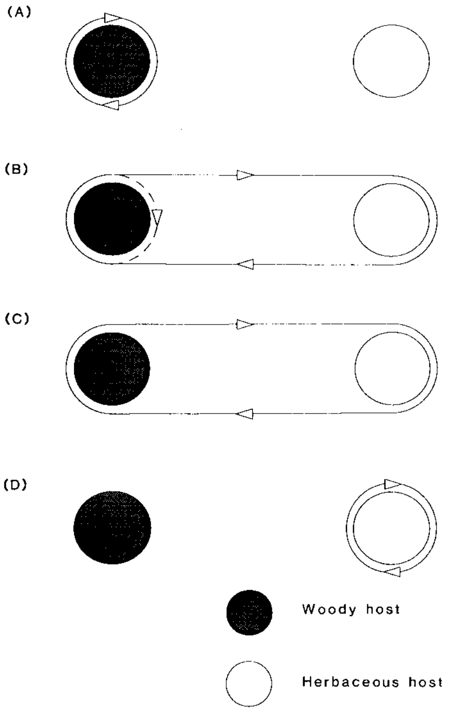

Fig. 3. Schematic diagrams of an autoecious life cycle on a woody host (A), host alternation between a woody primary host and an herbaceous secondary host with some clones (– – –▷) remaining on the primary host throughout the year (B), host alternation with all clones transferring seasonally between the primary and secondary host plants (C), and secondarily autoecious life cycle on an herbaceous host (D).

and at that time are a highly nutritious host for aphids whereas in summer they are a poor host for aphids when secondary hosts are actively growing and a good host makes host alternation so advantageous.

The system, however, is very sensitive to environmental changes that can shift the balance in favour of non host alternation. If the abundance of the secondary host plant were to decline then costs of host transfer would increase and selection would favour autoecy on the primary host (Fig. 3A) or if the secondary host varied in abundance from year to year then a polymorphism with some clones host alternating and others non host alternating is likely to evolve (Fig. 3B). Where both host plants are abundant then host alternation is the better strategy (Fig. 3C), but should the primary host become rare then host transfer again becomes costly and selection would favour a secondarily autoecious way of life on the secondary host (Fig. 3D).

Thus the coexistence of plants with asynchronous phenologies supplied the potential and the ability of aphids to produce a number of highly prolific generations in quick succession, which amplify small differences in performance on the different plants, supplied the means of exploiting that potential.

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