Eur. J. Entomol. **91**: 91–96, 1994
ISSN 1210–5759

Evolution of host range in aphids

PAVEL KINDLMANN[1] and ANTHONY F.G. DIXON[2]

[1]Faculty of Biological Sciences, University of South Bohemia, Branišovská 31,
370 05 České Budějovice, Czech Republic

[2]School of Biological Sciences, University of East Anglia, Norwich, NR4 7TJ, UK

Aphids, host specificity

Abstract. A simple model reveals one possible explanation of why aphids and organisms with a similar bionomy, i.e., have a high rate of population increase, a short adult life, and are time – limited dispersers, are so highly host specific. It indicates that small differences in host suitability amplified by the high rate of population increase over a number of generations could compensate for the losses incurred in searching for the best host plant.

INTRODUCTION

As for other herbivorous insects a problem faced by aphids is how to apportion their total fecundity among different species of plants so as to maximize their fitness. Aphids are both limited and poor dispersers (Dixon et al., 1987; Ward, 1987) with few surviving when migrating between plants (Taylor, 1977). One way of reducing the huge dispersal losses would be to have a wide host range, i.e., to be polyphagous. However, aphids are highly host specific (Dixon, 1985) even to the extent of selecting a particular subspecies of a plant (Hille Ris Lambers, 1979).

In considering the evolution of host range in herbivorous insects it is generally assumed that environmental constancy or uncertainty are the all important determinants of host specificity (Levins & MacArthur, 1969; Jaenike, 1978; Rausher, 1984; Ward, 1987; Michaud, 1990; Ward, 1992a) and that factors evoked to explain host-specificity must accomodate the huge losses incurred in moving between plants (Ward, 1992b). This paper highlights the role that the very high rates of population increase and short generation times shown by aphids might have played in determining their host specificity.

THE MODEL

Aphids have little control over the direction of their flight and are not able to recognise host plant species at a distance. Therefore, aphid migratory behaviour can be seen as a series of "trials", in which they land on plants at random and after probing decide whether to continue to search or to stay on the plant. Due to their short life and limited fuel reserves the number of "trials" is finite and small.

Assume for simplicity that an aphid can live on two host plant species, A and B, but not on other species of plants and the aphid's growth rates on these plant species are r_{mA} and r_{mB} where $r_{mA} > r_{mB}$. The proportion of the ground covered by the foliage of these plants is denoted by c_A and c_B and the length of the season the aphid can expect to live on each of these plants by t (common for both plant species). Assuming exponential growth, the increase in aphid numbers on these plants at the end of the season will therefore be $e^{t.r_{mA}}$ and $e^{t.r_{mB}}$, respectively. Assume further that an aphid has only fuel and/or time for one more trial and it is on B. If it decides not to fly but to stay and reproduce the relative increase in population size, its benefit R_n will be

$$R_n = e^{t.r_{mB}} \qquad (1)$$

If it decides to fly and try to find A, then there is a 'cost' as it may not find either A or B, and dies, the probability of this is $(1-c_A-c_B)$. The probability of finding B is c_B and the benefit, $e^{t.r_{mB}}$, the same as if it did not fly. The probability of finding A is c_A and the benefit $e^{t.r_{mA}}$. Therefore, the benefit associated with flying is

$$R_f = c_B.e^{t.r_{mB}} + c_A.e^{t.r_{mA}} \qquad (2)$$

Fig. 1. shows the minimum difference in population growth rates on A and B, $r_{mA} - r_{mB}$, required if $R_f > R_n$, and defines the conditions when the best strategy is to fly rather than stay on B and become polyphagous on both A and B. The dependent variables here are the length of the season, which varies from 50 to 100 days, and the risk of migration, expressed as the inverse of the relative cover of A, which is for convenience assumed to be the same as that of B. The risk of migration is expressed in terms of that number of aphids necessary if one on average is to survive and find a host plant. It ranges from 50 to 500 in Fig. 1. Empirical data suggest that this number will be in order of 100 (Taylor, 1977).

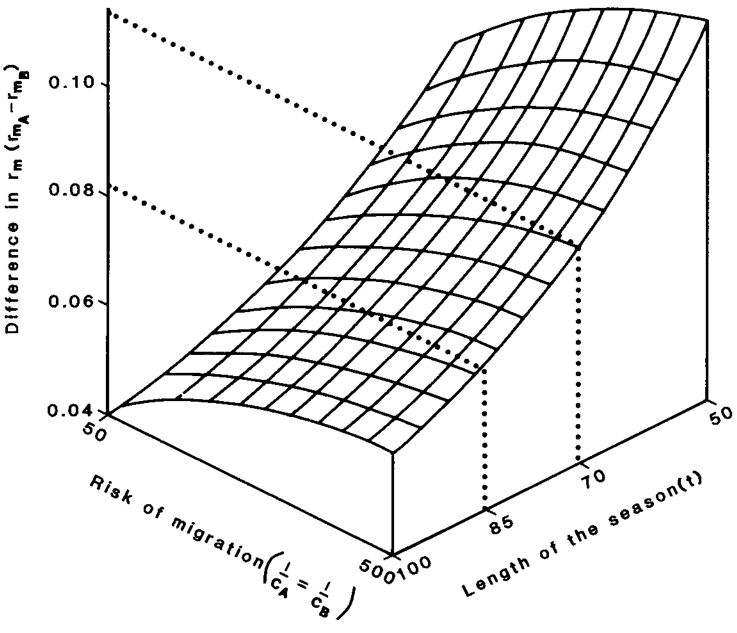

Fig. 1. The difference in population growth rates on the two plants, A and B, needed for it to be advantageous to change host if not on A, relative to the risk of migration and the length of the season.

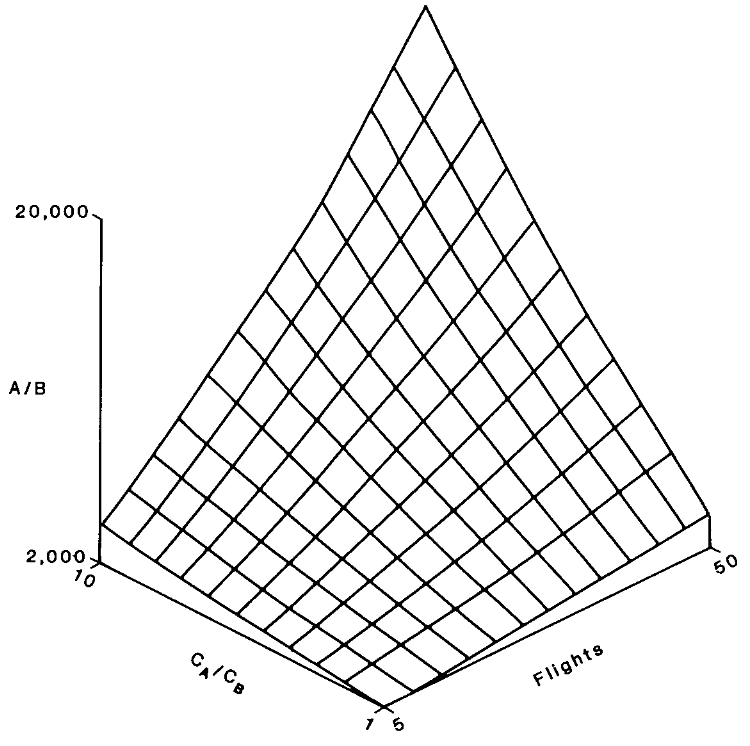

Fig. 2. The number of aphids on A relative to B at the end of a season, relative to the proportional cover of A and B, and the number of flights available to locate A. (Difference in r_ms = 0.1, length of season 60 days, proportional cover of B = 0.001 and A = 0.001 to 0.01).

Moreover, the relative covers of host plants that aphids live on seem to fall within this range (Dixon et al. 1987).

Aphid population growth rates, r_m,, may be as large as .5, if time is measured in days (Kindlmann et al, 1992). Therefore the difference needed (< .1 in most cases, Fig. 1) is small and such differences are frequently observed on plants of different species. Therefore, the strategy aphids should adopt in this case, is "fly" and become a specialist.

When aphids have fuel and/or time for several flights and are on B, then the preference for "fly" as opposed to "not to fly" should be even more pronounced. This is best illustrated by reference to the penultimate flight. Using the same argument as in the case of the last flight then assuming $R_f > R_n$, (2) becomes

$$R_{2f} = c_B.(c_B.e^{t.r_{mB}} + c_A.e^{t.r_{mA}}) + c_A.e^{t.r_{mA}} > R_f \qquad (3)$$

which defines the benefit associated with host specialization, if the aphid has two more flights while (1) remains the same. Therefore, if it is better to fly when only one further flight is possible, then it is necessarily better when an aphid can make several flights. By

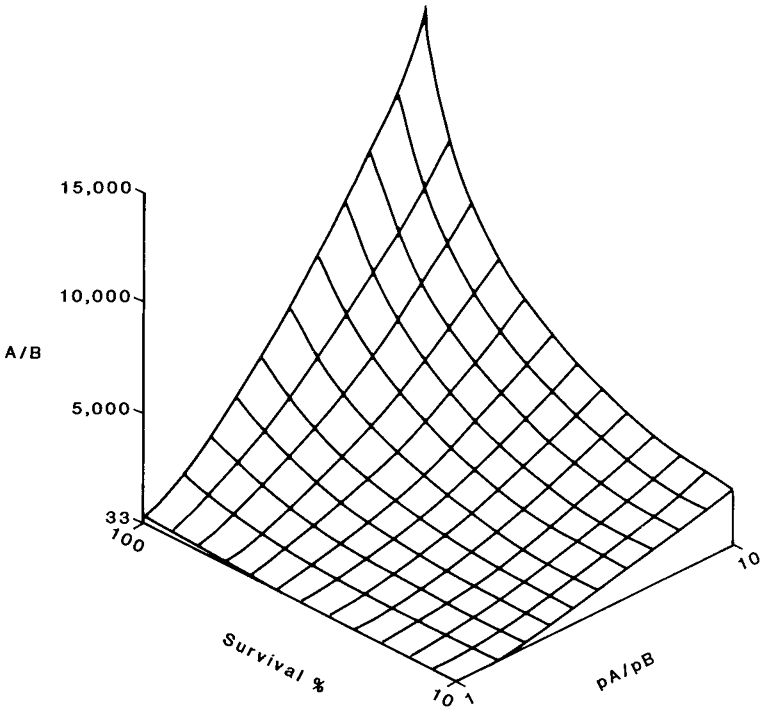

Fig. 3. The number of aphids on A relative to B at the end of the season, relative to the proportional cover of A and B and the percentage of aphids surviving each attempt to locate host A. (Difference in r_ms = 0.1, length of season 60 days, number of attempts 10, proportional cover of B = 0.001 and A = 0.001 to 0.01).

mathematical induction it is possible to generalise this conclusion for any particular flight in a sequence.

In Fig. 1. it is assumed that the relative covers of both host plants are the same, otherwise it would not be possible to depict this dependence. What happens, if they differ? Assume that the population growth rates on both hosts is the same, i.e., $r_{mA} = r_{mB}$. The dependence of the ratio of the population sizes at the end of the season on A and B, on the ratio of the relative covers of A and B, c_A/c_B, and the number of flights, D, an aphid can make to find a host is shown in Figure 2. The benefits were calculated assuming that host specificity on A gave

$$R_A = \left[1 - (1 - c_A)^D\right].e^{t.r_{mA}} \qquad (4)$$

and B

$$R_B = \left[1 - (1 - c_B)^D\right].e^{t.r_{mB}} \qquad (5)$$

The extremely large values of the ratio of benefits indicates that there is likely to be a strong selection pressure for preference for the slightly more common host plant. The same result is obtained, if instead of varying the number of flights, the percentage surviving is varied and again (4) and (5) are used (Fig. 3).

DISCUSSION

Parthenogenesis and the telescoping of generations have enabled aphids to achieve the very high rates of population increase and very short generation times usually associated with much smaller organisms (Dixon, 1992). The model presented here indicates that very small differences in the rates of population increase achieved on two species of plants amplified by clonal parthenogenesis over several generations makes it advantageous for aphids to seek out the species of plant on which they perform best in spite of the huge losses incurred in finding this plant. This would lead to most aphids being on the favoured host and most genetic changes occuring there on which selection could act resulting in more host specific adaptations, such as changes in morphology, physiology and phenology that render the aphid less able to exploit other hosts. Reinforced by such feedbacks monophagy represents an evolutionary stable state.

However, this assumes that aphid populations always grow exponentially, which would appear to be at variance with what happens in nature where within a season populations tend to increase and then crash in numbers. The increase phase is clearly exponential, but what of the population collapse. There is evidence that aphids scramble for resources (Mackenzie et al., 1994) and that the collapse in abundance is mainly driven by competition for resources resulting in most of the aphids migrating to seek resources elsewhere. Those that remain continue to grow exponentially within the constraints imposed by host quality and natural enemy activity. It is possible that the huge losses associated with migration stabilize both the within and between year fluctuation in abundance.

If the model is correct, then why aren't all aphids host specific? In addition to those species of plant that are consistently abundant enough to sustain a specific aphid (Dixon et al., 1987) there are many species of plants that vary too much in abundance from year to year or are just not abundant enough to sustain a specific aphid. However, polyphagous species of aphids by exploiting a range of host species could overcome the variation in abundance or low abundance of a particular species. That is, a group of plant species could sustain a species of aphid whereas an individual plant species of the group cannot.

CONCLUSIONS

This simple model reveals that there is a strong reason for organisms with a bionomy similar to that of aphids to become host specialists. Enormous growth rates, random location of host plants and short life, all result in strong selection to specialise on those hosts that have a slightly better quality and/or are slightly more abundant. Therefore in terms of the model there are no advantages in being polyphagous for the simple statistical reasons stated. Adaptations reinforce host specificity, but initially it is just a question of probability.

REFERENCES

Dixon A.F.G. 1985: *Aphid Ecology*. Blackie, Glasgow, 157 pp.

Dixon A.F.G., Kindlmann P., Lepš J. & Holman J. 1987: Why are there so few species of aphids, especially in the tropics. *Am. Nat.* **125**: 580–592.

Dixon A.F.G. 1992: Constraints on the rate of parthenogenetic reproduction and pest status of aphids. *Invert. Reprod. Dev.* **22**: 159–163.

Hille Ris Lambers D. 1979: Aphids as botanists? *Symb. Bot. Upsal.* **22**: 114–119.

Jaenike R. 1978: On optimal oviposition behaviour in phytophagous insects. *Theor. Popul. Biol.* **14**: 350–356.

Kindlmann P., Dixon A.F.G. & Gross L.J. 1992: The relationship between individual and population growth rates in multicellular organisms. *J. Theor. Biol.* **157**: 535–542.

Levins R. & MacArthur R.H. 1969: A hypothesis to explain the incidence of monophagy. *Ecology* **50**: 910–911.

Mackenzie A., Dixon A.F.G. & Kindlmann P. 1994: The relationship between the regional number of aphid species and plant species diversity. *Eur. J. Entomol.* **91**: 135–138.

Michaud J.P. 1990: Conditions for the evolution of polyphagy in herbivorous insects. *Oikos* **57**: 278–279.

Rausher M.D. 1984: The evolution of habitat preferences in subdivided populations. *Evolution* **38**: 596–608.

Taylor L.R. 1977: Migration and the spatial dynamics of an aphid, Myzus persicae. *J. Anim. Ecol.* **46**: 411–423.

Ward S.A. 1987: Optimal habitat selection in time – limited dispersers. *Am. Nat.* **129**: 568–579.

Ward S.A. 1992a: Environmental uncertainty and polyphagy in herbivorous insects. *Oikos* **63**: 506–512.

Ward S.A. 1992b: Assessing functional explanations of host-specificity. *Am. Nat.* **139**: 883–891.