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Phenotypic plasticity and fitness in aphids

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Aphid life-history, phenotypic plasticity, fitness, intrinsic rate of increase, wing dimorphism

Abstract. In holocylic aphid species many different morphs are produced during the phase of parthenogenetic reproduction. Because these morphs differ in their life-histories, research has been focused on how individual life-histories can be explained in the framework of maximizing the Malthusian parameter r_m. All these different morphs are produced by the same genotype. Since it is the genotype that selection acts on it is questionable whether the intrinsic rates of increase of individual morphs can be used to make inferences about the fitness of the genotype. A simple model is developed to investigate the relationship between individual r_m and clonal fitness in the case of wing dimorphism of aphids in summer. In the model, survival and fecundity of winged and unwinged morphs depend on the quality of their host plants, and unwinged aphids have to decide which morph to produce in the next generation to maximize the number of eggs produced at the end of the season. The model shows that clonal fitness depends on the sequence of morphs produced and that the relationship between individual and clonal rate of increase is not straightforward. The decision as to which morph to produce is influenced by the quality and distribution of the host plants and depends also on the time of the year. It is suggested that r_m-values of individual morphs should be treated with care when aphid life-history is to be explained.

INTRODUCTION

Aphids exhibit a remarkable complexity in their life-cycles involving the alternation of the host plants in spring and summer, sexual reproduction and the production of hibernating eggs prior to periods with adverse weather conditions, and parthenogenetic reproduction during favourable periods (Dixon, 1977, 1987; Moran, 1992a). In periods of parthenogenetic reproduction host-alternating species can produce morphs as different as fundatriginae, emigrants, unwinged (apterous) and winged (alate) virginoparae, as well as alate males, alate gynoparae and sexual females (Hille Ris Lambers, 1966). Because all these different phenotypes are produced by the same genotype, the diversity of forms in aphids is due to phenotypic plasticity. A commonly used measure of fitness in life-history theory is the intrinsic rate of increase, r_m, which can be calculated from the Euler-Lotka equation. In aphid biology, one normally analyses the life-history of particular morphs and uses the intrinsic rate of increase to compare the performance of different morphs. The solution to the Euler-Lotka equation, however, measures the fitness of a clone or a gene substitution (Stearns, 1992). The critical question for aphid fitness therefore is, how does the intrinsic rate of increase measured in particular morphs relate to the fitness of the underlying genotype? Because most aphids produce many generations in a single season the fitness of individuals produced early in the season is linked to the behaviour of phenotypes living late in the season. In holocyclic aphid species, sexual reproduction leads to a

recombination of genetic information in autumn. The life of a particular genotype starts in autumn when eggs are fertilized, and ends in the next autumn with the production of diapausing eggs. The fitness of the genotype depends on the fitness contribution of all the phenotypes that are produced in response to a particular environmental situation. Successful genotypes are those that produce a high number of copies of their genetic information. To understand the evolution of aphid life-histories it is therefore important to know the relationship between the performance of an individual that lives at some time in the season, and the fitness of the underlying genotype.

An example of this problem is the production of winged virginoparae in summer. Unwinged females feeding on a host plant can either produce apterous offspring that will feed on the same host plant, or they produce alatiform nymphs that can colonize other plants. Alate morphs that settle on new plants mostly produce apterous offspring which in turn can produce winged or unwinged offspring. The production of alate morphs is triggered by factors like crowding or bad plant quality (e.g. Kawada, 1987; Kidd, 1990). While alate females often have similar r_m-values to apterous females, their offspring are smaller at birth (e.g. Dixon & Wratten, 1971). Small birth weight in aphids has two consequences. First, a small weight at birth may result in a lower weight at adult moult (Dixon, 1977), which in turn is correlated with low fecundity (e.g. Dixon & Wratten, 1971). Second, survival in small offspring may be lower than in large offspring, especially when plant quality is poor or weather conditions are adverse.

If the number of eggs produced at the end of the season is taken as a measure for the reproductive success of the genotype, it is therefore likely that aphid fitness is influenced by the sequence in which winged and unwinged morphs are produced.

In this paper a simple model is developed to analyse the fitness consequences of the decision to produce winged or unwinged females for aphids feeding on different plant qualities at different times of the season. In particular, the model focuses on the relationship between the intrinsic rate of increase of winged and unwinged morphs, and the intrinsic rate of increase of the genotype.

THE MODEL

In the model the mean number of eggs produced at the end of the season, R, is chosen as the fitness measure of the genotype. For the sake of simplicity, a number of assumptions are made about the biology of our model system. The model concentrates on the period of parthenogenetic reproduction in a non-host-alternating species and assumes that the aphid produce 10 discrete generations a year. Each aphid is assumed to reproduce only once in its life and survival and fecundity depend on the quality of the host plant. The host plants of the aphids pass through a fixed sequence of developmental stages each of which represents a certain type of quality q ($q = 1 \ldots 5$). Developmental stage $q = 1$ corresponds to young plants, and plant quality $q = 5$ corresponds to senescent plants. Plant quality is highest in developmental stage $q = 3$. Survival and fecundity patterns differ between winged and unwinged morphs whereby $l_u(q)$ is the probability that an unwinged aphid that feeds on a plant of developmental stage q will survive upon reproduction, and $m_u(q)$ is the number of offspring an unwinged aphid produces on a plant of quality q. Similarly, $l_w(q)$ and $m_w(q)$ denote survival and fecundity of winged aphids feeding on developmental stage q of their host plant. Winged aphids are assumed to have a lower fecundity than unwinged

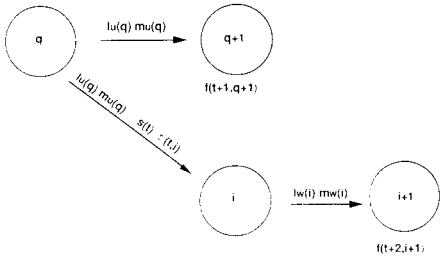

Fig. 1. Graphical illustration of the model. In each generation t and for each plant developmental stage q unwinged aphids have to decide whether to produce winged or unwinged offspring. See text for explanation.

morphs. From the survival and fecundity pattern the intrinsic rate of increase of an unwinged aphid that feeds on a plant of quality q can be calculated as $r_m(q) = \ln [l_u(q)m_u(q)]$.

Each apteriform nymph that is born on a plant of quality q has to decide whether it will produce winged or unwinged offspring (Fig. 1). Winged morphs are assumed to only produce unwinged offspring. The expected number of offspring an unwinged aphid can produce is given by $l_u(q)m_u(q)$. Because plant development progresses these offspring are born on a plant of quality q + 1 where they stay and reproduce. On plants of quality q = 5 mothers can only produce winged offspring to ensure the persistence of the clone. Winged offspring leave their original host plant and colonize new plants after larval development is completed. It is assumed that travelling takes no time. The probability that an aphid survives the journey from one plant to another, however, is given by the function s(t), where t refers to the t-th generation in the season (t = 1,...,10). The function s(t) reflects the changes in plant abundance over the time course of the season. Since at any time of the year, not all plants within the habitat are in the same developmental stage, another function function $\tau(t,q)$ is defined as the proportion of plants in generation t that are in developmental stage q. The term $s(t)\ \tau(t,q)$ therefore denotes the probability for a winged aphid to survive the travel and settle on a plant of quality q.

The intrinsic rate of increase of winged offspring is therefore calculated by averaging over the $r_m(q)$-values for winged offspring on the different plant qualities, each weighted by the relative frequency of the plant, i.e.

$$r_m(\text{winged}) = \sum_{q=1}^{q=5} \tau(t,q) \ln [l_w(q)\ m_w(q)] \qquad (1)$$

When an alate aphid settles on a plant of quality q in generation t, its unwinged offspring develop on a plant of quality q + 1 and have again to decide whether to produce unwinged or winged offspring in generation t + 2 (Fig. 1).

In the 10th generation, at the end of the season, each unwinged female produces 3 diapausing eggs.

Let f(t,q) be defined as the expected future reproductive success, i.e. the number of eggs produced by the end of the season, by a unwinged aphid that feeds in generation t on a plant of developmental stage q. Thus, f(1,q) is the fitness of a fundatrix that hatches on a plant of quality q. With the function f(t,q) the consequences of the decision of unwinged

aphids to produce winged or unwinged offspring for the fitness of the genotype can be analysed (Fig. 1). If an aphid decides to produce unwinged offspring, its expected future reproductive success is given by

$$f(t,q) = l_u(q)m_u(q)\, f(t+1,q+1) \qquad (2)$$

If the aphid decides to produce winged offspring, the offspring travel to a plant of quality i with probability $\tau(t,i)$, i=1,..5. On this plant, they produce unwinged offspring which find themselves on a plant of quality i + 1 in generation t + 2. Thus,

$$f(t,q) = l_u(q)m_u(q)\sum_{i=1}^{i=4} s(t)\,\tau(t,i)\,l_w(i)m_w(i)\,f(t+2,i+1) \qquad (3)$$

Equations (2) and (3) determine which decision is optimal from the clone's point of view. Working backwards from t = 10 where only eggs are produced the optimal decision, i.e. the decision which results in the highest number of eggs produced, can be calculated for every generation and for each plant quality (Fig. 1).

To find an expression for the intrinsic rate of increase of a clone, r_m(clone), over the whole period of parthenogenetic reproduction, it is assumed that there is a fixed probability p for each egg to survive the winter. A fundatrix that hatches from an egg in the next spring is assumed to find itself on a plant of quality q with probability 0.2, i.e. at the beginning of the season fundatriginae are evenly distributed among the plants of different qualities. The expected number of eggs, R, produced at the end of the season under the optimal policy is then found by averaging over the different plant qualities, i.e. $R = \Sigma\, 0.2\, f(1,q)$.

The rate of increase of a clone is then given by

$$r_m(\text{clone}) = \ln (0.5*p*R) / 10 \qquad (4)$$

where the factor 0.5 accounts for the fact that eggs only contain 50% of the mother's genes.

RESULTS

Table 1 shows the parameter-values that are used in the following calculations. Table 2 shows how the decision as to which morph to produce depends on plant quality and the time of the year. When only one generation is left until the end of the season (t = 9), all aphids should produce unwinged offspring. In generation 8, the optimal decision is to produce unwinged offspring on plant qualities 1 to 3, and to produce winged offspring on plant qualities 4 and 5. From generation 6 backwards, the optimal decisions become time-independent. From the clone's point of view, the optimal decision is to produce winged offspring on bad-quality plants (stages 4, 5) and to produce unwinged offspring on good-quality plants (stage 3) and on plants that will develop into good-quality plants in the near future (stages 1, 2). The fitness differences between aphids feeding on different plant qualities are enormous. When plant quality is bad and aphids have to produce winged offspring (stages 4, 5), the high mortality risks for travelling and the relative low frequency

of high-quality plant [$\tau(t,3) = 0.2$ for all t] result in a low expected number of eggs produced at the end of the season. In generation 1, the fitness of a fundatrix on a plant of quality 2 is more than 20 times higher than the fitness of a fundatrix feeding on a plant of developmental stage 5. Table 2 also shows that a decision based on f(t,q) may differ from a decision based on the relative magnitudes of the r_m-values of winged and unwinged offspring. The decision that maximizes the number of winter eggs produced is not necessarily the decision that maximizes the rate of increase of the next generation of aphids. The reason is that descendants of winged morphs have a lower fecundity than those born to unwinged morphs.

TABLE 1. Parameter-values used in the simulations. Fecundity and survival pattern of aphids depend on the plant developmental stage q and determine the intrinsic rates of increase r_m of unwinged morphs.

q	$l_u(q)$	$m_u(q)$	r_m	$l_w(q)$	$m_w(q)$
1	0.7	2.0	0.3365	0.7	1.0
2	0.8	3.0	0.8755	0.8	2.0
3	0.9	5.0	1.5041	0.9	3.0
4	0.7	3.0	0.7419	0.7	2.0
5	0.5	1.0	–0.6931	0.5	1.0

Intrinsic rate of increase of winged morphs is $r_m = 0.15$.
Other parameter-values are as follows: $s(t) = 0.5$ for all generations t (t = 1,..10).
$\tau(t,q) = 0.2$ for all t and all plant qualities q.

TABLE 2. Expected total number of eggs produced f(t,q) for aphids feeding in generation t on a plant of quality q when the aphid choses to produce the offspring type that maximizes its fitness. The characters indicate the optimal decision. w = the optimal decision is to produce winged offspring, u = the optimal decision is to produce unwinged offspring. The asterisk indicates situations in which the optimal decision differs from a decision which would be based solely on a comparison of the intrinsic rates of increase of the offspring types.

t	q = 1	q = 2	q = 3	q = 4	q = 5
10	3	3	3	3	3
9	4.2^u	7.2^u	13.5^u	6.3^u	0.0
8	10.1^u	32.4^u	28.4^u	4.0^{*w}	1.0^w
7	45.4^u	68.0^u	19.6^{*w}	9.2^{*w}	2.2^w
6	95.3^u	47.1^u	41.2^u	16.9^{*w}	4.0^w
5	66.0^u	99.0^u	75.9^u	22.4^{*w}	5.3^w
4	138.6^u	182.1^u	101.0^u	31.5^{*w}	7.5^w
3	254.9^u	242.4^u	141.9^u	54.3^{*w}	13.0^w
2	339.3^u	340.5^u	244.5^u	80.8^{*w}	19.2^w
1	476.7^u	586.8^u	363.5^u	117.9^{*w}	28.1^w

In Figs 2 and 3 the relationship between the rate of increase of winged and unwinged morphs, and the rate of increase of the clone is investigated. In Fig. 2, the r_m-value of winged morphs in all generations is increased by increasing the fecundity $m_w(q)$. Increasing the rate of increase of winged morphs increases r_m(clone) in a non-linear way.

In Fig. 3 the fecundities $m_u(q)$ (and therefore the rates of increase) of unwinged morphs are increased in only one generation. Independent of the generation in which the fecundity of alate morphs increases, the r_m-value of the clone increases. Although the effect of an increased aphid fecundity in one generation seems to be highest at the beginning of the

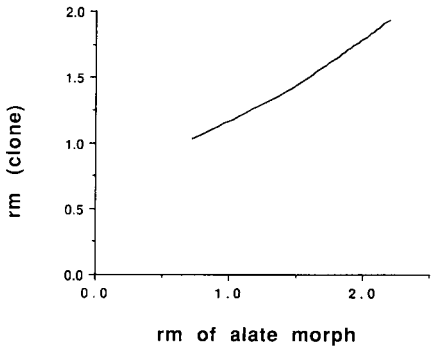

Fig. 2. Dependence of the rate of increase of the clone on the rate of increase of alate morphs. The r_m-value of alate morph is increased by increasing the fecundity $m_w(q)$. For each point in the graph the model is run once with the new parameter values to calculate the optimal policy [eqn (2),(3)] and the clonal rate of increase under this policy [eq. (4)]. For parameter-values see Table 1.

season, there is, however, no clear relationship between the time of the year at which this happens, and the r_m-value of the genotype. Thus, selection for increased fecundity may be different at different times of the year even within the same morph.

Table 3 analyses the trade-off between offspring number and offspring quality in winged aphids. Table 3 shows that when offspring born to winged mothers have lower fecundity than those born to unwinged mothers, the growth rate of the clone may decrease,

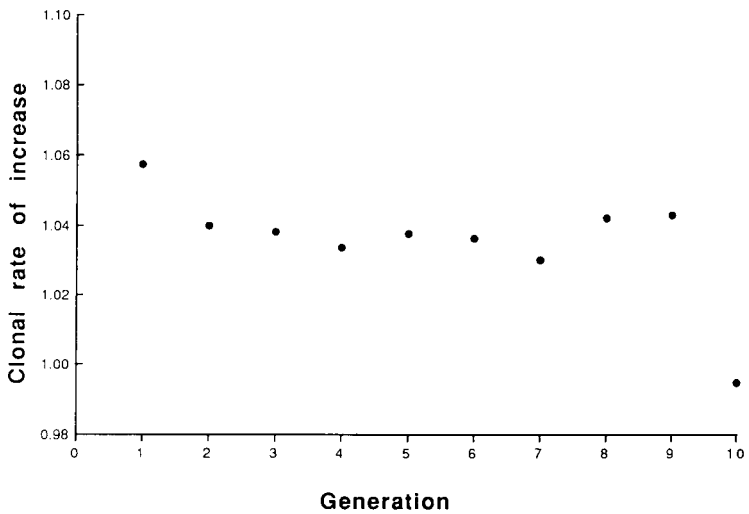

Fig. 3. Dependence of the clonal rate of increase on the time in which an increase in the r_m-value of a morph occurs. Parameter-values as in Table 1. Each point in the graph represents the result of one run of the model in which the fecundities $m_u(q)$ of apterous morphs in the respective generation are increased by 1 (as compared to the values in Table 1). Generation t = 10 shows the clonal rate of increase when the fecundity of apterous morphs is not increased.

although the r_m-values of winged and unwinged females born to unwinged mothers are the same.

TABLE 3. The trade-off between offspring number and offspring quality. It is assumed that an increase in the fecundity of alate aphids is only achieved by a decrease in the fecundity of their offspring. Winged aphids now have the same fecundity as unwinged aphids (cf. Table 1), but unwinged aphids born to winged mothers have a decreased fecundity (the fecundity is equal to that of winged aphids in Table 1).

Clonal r_m when offspring of alate females do not suffer from decrease in fecundity	Clonal r_m when offspring of alate females suffer from decrease in fecundity
0.995	0.758

DISCUSSION

In this paper a simple model has been developed to investigate how aphid fitness, as measured by the number of winter eggs produced, is influenced by the selective production of winged or unwinged morphs at different times of the year. Fecundity and survival patterns of apterous and alate aphids were assumed to depend on the quality of the host plant which in turn depended on the plant developmental stage.

The results of the model show that a decision based on the number of winter eggs produced may differ from a decision based on the intrinsic rates of increase of the two morphs. The reason for the difference is that r_m-values of particular morphs only account for offspring number, but not for offspring quality. When the number of eggs produced at the end of the season is maximized, the fitness of an aphid is not merely a function of survival and fecundity of the daughters alone, but depends on the performance of all descendants up to the time when eggs are fertilized. This is particularly important in winged aphids where the contribution to the overall reproductive success strongly depends on the probability of an aphid surviving the journey from one host plant to another (cf. Dixon et al., 1993). Furthermore, in winged offspring the trade-off between offspring number and offspring quality is particularly apparent since the former produce many small larvae early in life such that the intrinsic rate of increase of this morph is similar to that of unwinged aphids (e.g. Dixon & Wratten, 1971). The model shows that in many situations it may be advantageous for the clone to produce unwinged rather than winged offspring despite the similarity of the r_m-values.

Since plant quality was assumed to be correlated with developmental stage of the plant, the optimal decision as to which morph to produce depends not only on the current quality of the plant where the aphid feeds, but also on the future quality of the same plant, and on the relative frequency of host plants of other developmental stages in the habitat.

Finally, the optimal decision is also influenced by the time of the year. In our model, only unwinged aphids could initiate the production of eggs. At the end of the season, there may not be enough time left to ensure the successful development of two more generations, i.e. a winged and an unwinged. Thus, even on low-quality plants, aphids have to produce unwinged offspring.

The life-cycle of aphids is usually described as a linear sequence of different morphs each of which is produced as a response to particular environmental stimuli (e.g. Kawada, 1987). During most of the year, however, the same genotype is represented by more than one morph, e.g. in summer, where both winged and unwinged virginoparae are produced.

In life-history theory, the term 'phenotypic plasticity' is used for phenotypic variability due to environmental variation (Stearns, 1992). The term phenotypic plasticity emphasizes that it is an aphid's genotype that is adapted to environmental variation. The different morphs that occur during the life-cycle of an aphid are not isolated entities which are adapted to a particular environmental situation, but their sequential or parallel production is an adaptive response of the aphid clone. Recent work on dispersal polymorphism in insects has mainly been concerned with how this plasticity evolved (Roff, 1986) and how it has been maintained in evolution (Harrison, 1980; Moran, 1992b). In contrast, the work presented here concentrates on how the sequence of different morphs that are produced during the phase of parthenogenetic reproduction influences the fitness of the genotype. The model shows that even under the simplifying assumption made (semelparity, discrete generations etc.) there is no straightforward relationship between the fitness of the clone, and the intrinsic rates of increase of the different morphs. Thus, one should be careful in using r_m-values of particular morphs to explain complex life-history traits of aphids.

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REFERENCES

DIXON A.F.G. 1977: Aphid Ecology: Life cycles, polymorphism, and population regulation. *Ann. Rev. Ecol. Syst.* **8**: 329–353.

DIXON A.F.G. 1987: Seasonal development in aphids. In: Minks A.K. & Harrewijn P. (eds): *Aphids, their Biology, Natural Enemies and Control. Vol. A.* Elsevier, Amsterdam, pp. 315–320.

DIXON A.F.G., HORTH S. & KINDLMANN P. 1993: Migration in insects: cost and strategies. *J. Anim. Ecol.* **62**: 182–190.

DIXON A.F.G. & WRATTEN S.D. 1971: Laboratory studies on aggregation, size and fecundity in the black bean aphid, Aphis fabae Scop. *Bull. Entomol. Res.* **61**: 97–111.

HARRISON R.G. 1980: Dispersal polymorphism in insects. *Ann. Rev. Ecol. Syst.* **11**: 95–118.

HILLE RIS LAMBERS D. 1966: Polymorphism in Aphididae. *Ann. Rev. Entomol.* **11**: 47–78.

KAWADA K. 1987: Polymorphism and morph determination. In Minks A.K. & Harrewijn P. (eds): *Aphids, their Biology, Natural Enemies and Control. Vol. A.* Elsevier, Amsterdam, pp. 315–320.

KIDD N.A.C. 1990: Why is aphid flight density-dependent? *Acta Phytopathol. Entomol. Hungar.* **25**: 105–112.

MORAN N.A. 1992a: The evolution of aphid life-cycles. *Ann. Rev. Entomol.* **37**: 321–348.

MORAN N.A. 1992b: The evolutionary maintenance of alternative phenotypes. *Am. Nat.* **139**: 971–989.

ROFF D.A. 1986: The evolution of wing dimorphism in insects. *Evolution* **40**: 1009–1020.

STEARNS S.C. 1992: *The Evolution of Life Histories.* Oxford University Press, Oxford, 249 pp.