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*Journal of Animal Ecology*, Volume 62, Issue 1 (Jan., 1993), 182-190.

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# Migration in insects: cost and strategies

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## Summary

1. An optimal energy partitioning model is used to predict the optimum adult sizes of the soma, gonads and flight apparatus in insects. A comparison of the investment in gonads and lipoidal reserves in winged and unwinged individuals in species from three families of aphids is used to test the predictions and define the cost of developing a flight apparatus.
2. In accordance with theoretical predictions winged aphids had smaller gonads than wingless aphids and there appeared to be a trade-off between the investment in gonads and lipoidal reserves in both morphs.
3. Developing a flight apparatus prolongs development and resulted in a 20% reduction in gonad size.
4. The length of time for which aphids survived starvation was positively correlated with the relative size of their lipoidal reserves.
5. The relative size of the lipoidal reserves appeared to be negatively correlated with habitat quality and positively correlated with habitat fragmentation.
6. In accordance with theoretical predictions autolysis of wing muscles was correlated with a great increase in the size of the gonads and occurred in aphids that live in fragmented habitats.
7. The ecological significance of these findings are discussed in the context of the way in which phytophagous insects, and aphids in particular, might perceive their environment.

*Key-words:* aphids, habitat fragmentation, habitat quality, migration, trade-offs.

*Journal of Animal Ecology* (1993) **62**, 182–190

## Introduction

The oogenesis-flight syndrome (Johnson 1963, 1969) describes the trade-off between flight apparatus and gonads in insects. In migratory individuals, the development of ovaries is suppressed whilst in non-migratory individuals ovaries mature at the expense of the flight apparatus.

There are several specific estimates of the cost, in terms of developmental time and fecundity, of being fully winged in insects in which alary polyphenism is genetically (Roff 1984, 1990; Roff & Fairbairn 1991) or environmentally controlled (Dixon 1972; Dixon & Howard 1986; Dixon & Wratten 1971; Newton & Dixon 1990; Wratten 1977), but there are no general estimates of such costs for a particular group of insects. Aphids are an ideal group for such a study. The clonal structure of aphid populations with many species responding to environmental cues and switching from an unwinged (reproductive) to a winged (migratory) mode (Dixon 1977) presents the possibility of comparing winged and unwinged

individuals of the same genotype. In addition, most aphids are host-specific and their host-plants differ in abundance (Dixon & Kindlmann 1990) and show great temporal variability in quality (Dixon 1970) and spatial distribution, which are likely to be reflected in an aphid's ecology.

In this paper the optimal energy partitioning model of Kindlmann & Dixon (1989) is used to predict the optimum adult sizes of soma, gonads and flight apparatus in aphids. A comparison of the investment in gonads and lipoidal reserves in winged and unwinged individuals in species from three families of aphids is used to test the predictions and define the cost of developing and maintaining a flight apparatus. The variation observed between species is related to the abundance, dispersion and temporal changes in the quality of their food resources.

## Materials and methods

Adult winged and unwinged individuals that had just moulted, of different colour forms and gener-

ations, of 28 species of aphids, were either collected from the field or reared in the laboratory, at approximately 15°C and a 16-h photoperiod to produce winged virginoparae, or a 12-h photoperiod to produce winged gynoparae. Aphids that have recently moulted to the adult stage (day 0) are easily recognized by their callow appearance.

All weights were obtained using a Cahn electro-microbalance. Lipids were extracted using petroleum spirit AR 40–60. Intact aphids were killed with carbon dioxide and extracted, after drying at 38°C to a constant weight. An estimate of the lipid reserves available to an aphid for survival was obtained by starving them individually at 15°C in small specimen tubes, which were lined with damp filter paper. The aphids were examined two or three times per day, to determine whether they were still alive and, if required, a little water was added to the filter paper to keep it moist. The time of death of each aphid was noted.

To determine the proportion of the body made up of gonads, the aphids were first weighed and then dissected by gently pulling on the cauda until the abdomen ruptured and gonads were pulled free of the rest of the body. The gonads were cleaned by repeated flooding with distilled water before transfer to an aluminium foil strip that had been cleaned in methanol and weighed. The aluminium foil plus gonads was then dried at 38°C to a constant weight. The dry weight of the gonads was obtained by subtracting the weight of the aluminium foil (Brough, Dixon & Kindlmann 1990). Some aphids were kept for the first 7 days of their adult life on suitable host-plants before the size of their gonads were determined (day 7). The dry weight of the aphids was estimated from the relationship between fresh weight and dry weight obtained from another set of aphids that were dried to constant weight at 38°C.

Aphids for histological examination of their wing muscles were fixed in modified Duboscq-Brasil's fixative (Ponsen 1987), dehydrated, embedded in wax, and sectioned at 8 µm before staining with Ehrlich's haematoxylin and eosin. Alternatively, aphids were cleared in clove oil and then cut vertically in the median longitudinal plane with a small scalpel. The condition of the indirect wing muscle could then easily be observed under a stereomicroscope (Johnson 1957).

## Results

### THEORY

The observed trade-off between gonads and migratory organs could be seen in terms of competition for space or resources. For this to hold, however, the proportion of the remaining part – the soma – should remain relatively constant across species and morphs, i.e. Why do the gonads and migratory

organs always compete for the same proportion of the body? A further question is: Why do certain species autolyse their wing muscles and others do not? In this theoretical section an optimal energy allocation model is used to address the first question and whether a species goes in for wing muscle autolysis, or not, is explained in terms of the fragmentation of its habitat.

A theoretical prediction of the optimum adult sizes of soma ( $s_A$ ), gonad ( $g_A$ ) and migratory organs (wing muscles, wings and fuel for flight,  $m_A$ ) as a proportion of the adult weight ( $w_A$ ) can be obtained from a modification of Kindlmann and Dixon's optimum energy partitioning model for aphids (Kindlmann & Dixon 1989; Kindlmann, Dixon & Brough 1992; Kindlmann, Dixon & Gross 1992; Kindlmann & Dixon 1992). There are two cases:

*Aphids that autolyse their wing muscles.* In this case the original model can be used, but the constraint on the gonadal growth rate is greater and it takes the gonads longer to develop if wing muscles and lipoidal reserves are formed first. However, the model predicts that after wing muscle autolysis in early adult life about half the body should be made up of soma and the other half of gonads.

*Aphids that retain their wing muscles.* In this case  $g_A + m_A$  has to be used instead of  $g_A$  in the equation for nymphal growth, while the optimization criteria remain the same. The model predicts (unpublished results) that both at the adult moult and throughout early adult life about one-half of the body should be made up of soma and the rest partitioned between gonads and migratory organs.

In alates, however, the partitioning of energy within the body is part of another optimization problem; that of the timing and frequency of migration. This is concerned with the risk associated with migration, the proportion of  $m_A$  necessary to fuel flight, the optimum time for migration, and whether an aphid should autolyse its wing muscles. This is a very complicated problem and will be discussed in more detail in a later paper. The following is a simple illustration of the possible mechanisms.

The number of individuals in a population at a particular site at time  $t$  is  $N = N(t)$ , and the risk connected with migration is expressed as the probability  $p$  that an average individual will survive the migration. This risk can be seen as inversely proportional to the degree of habitat fragmentation. The reproductive success of an individual at a particular site is defined by  $rx f(N)$ , where  $x$  is the number of its offspring and  $r$  the potential rate of increase of the offspring under optimal conditions, i.e. in high-quality sites and in the absence of density dependence. The function  $f$  describes all the negative influences that either the environment or the number of individuals present (density depen-

dence) can have on the potential rate of growth of the population. The function  $f$  may also be dependent on site and time, as there may be differences between sites both in space and in time,  $t$ , as the quality of a site undergoes, e.g. seasonal changes. However, this is neglected here.

The migratory strategy is expressed in terms of the proportion  $q$ , of a clone that stays and reproduces at the original site, and the proportion  $(1 - q)$  that attempts to locate and reproduce at a new site. The fitness of the clone under such assumptions can be expressed as

$$F = qrf(N) + (1 - q)prf(M), \quad \text{eqn 1}$$

where  $M$  denotes the number of individuals of this species already present at the new site. The necessary condition for fitness to be maximized is  $dF/dq = 0$ , which gives

$$f(N) = pf(M). \quad \text{eqn 2}$$

Before plant quality deteriorates we assume  $N$  increases with time. If only a small proportion of sites are occupied then a migratory individual is likely to arrive at an empty site ( $M = 0$ ) and if  $f$  is a decreasing function of  $N$ , which is the usual case, then equation 2 defines the critical density,  $N_{\text{crit}}$ , for migration:

$$f(N_{\text{crit}}) = pf(O). \quad \text{eqn 3}$$

For illustration one can assume a logistic growth in equation 3 and look for the dependence of the interval between flights on habitat fragmentation, represented by  $1/p$ , in Fig. 1. From this figure it is evident that when  $1/p$  is low, there is a tendency to fly very early and often, while for a large  $1/p$  the time to migration increases dramatically. Thus, species living in non-fragmented habitats, where  $p$  is high, should always be winged but invest relatively little in fuel and retain the ability to fly throughout adult life (i.e. retain their wing muscles), even though it results in a reduced fecundity and lower population

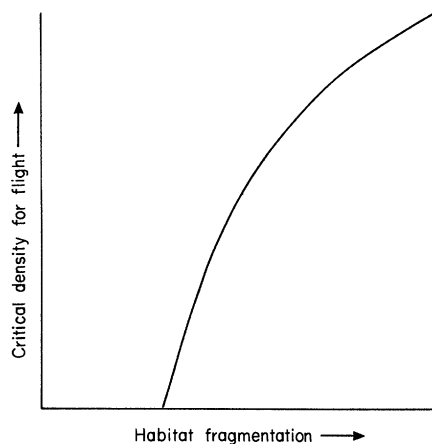


Fig. 1. Relationship between the critical density for flight and habitat fragmentation.

growth rate. However, in those species that occupy very fragmented habitats the optimum interval between flights may exceed the length of an individual's life. In such species there are advantages in a high investment in fuel but, on colonizing an empty habitat, to go for wing muscle autolysis, use all the energy for reproduction, and produce apterous offspring, i.e. switch from a migratory to a reproductive mode.

#### INVESTMENT IN GONADS

Not unexpectedly, winged aphids had smaller gonads than wingless aphids (Mann-Whitney,  $Z = -3.3$ ,  $P < 0.001$ ), i.e. the data set presented in Fig. 2 lends general support to the oogenesis-flight syndrome hypothesis and our model's prediction. Within a species, and even a clone, alatae had smaller gonads than apterae (e.g. *Megoura viciae*,  $t = 25.6$ ,  $df = 34$ ,  $P < 0.001$ ; Table 1). Surprisingly, however, there is considerable overlap between the apterae and alatae of the different species in the proportion of total dry weight made up of gonads. In addition there is considerable variation in gonad size in the various alate (e.g. *Aphis fabae*: 0.18–0.32) and apterous morphs (*Cryptomyzus ribis*: 0.51–0.61) of each species (Table 1). As the aphids included in this study exploit host-plants that vary greatly in abundance in space, and in quality in time, it is likely that the differences in gonad development are associated with host quality and the cost of locating high-quality feeding sites.

#### Trade-off between investment in gonads and lipid reserves

In both alatae and apterae there appears to be an inverse association between the proportion of the dry weight made up of lipid and gonads. Covariance analysis revealed that the slopes of the relationships for the two morphs are not significantly different ( $F_{\text{res}} = 2.2$ ,  $df = 33/8$ , NS;  $F_{\text{slopes}} = 3.1$ ,  $df = 1/41$ , NS) but that the elevations are different ( $F_{\text{elev}} = 15.1$ ,  $df = 1/42$ ,  $P < 0.001$ ) (Fig. 3). The gonads and most of the lipid reserves are located in the abdomen (unpublished results) and interspecifically the abdomen tends to make up a fixed proportion of the dry weight (Dixon 1985). If there were a trade-off between investment in gonads and lipid reserves one would expect the slope of the relationships in Fig. 3 to equal 1 but it is significantly less than 1, possibly because the gonads also contain lipid. An increase in the lipid content of the gonads would result in a decrease in the slope, e.g. the slope of 0.68 implies a gonadal lipid content of 32%. Some of the variation that is unaccounted for can be attributed to interspecific differences in the lipid content of the gonads (unpublished results). Another

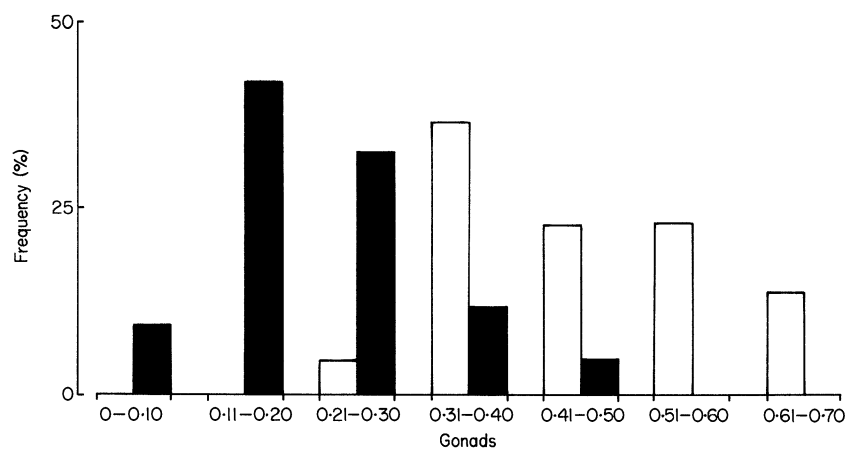


Fig. 2. Frequency distributions of the proportion of the dry weight made up of gonads for apterae (□) of 22 species and alatae (■) of 43 species of aphids.

Table 1. The proportion of the dry weight of apterae and alatae of aphids that is made up of gonads and lipid

Family	Species	Colour form/ generation/morph	Gonad	(n)	Lipid	(n)		
Apterae	Aphididae	<i>Acyrtosiphon ononis</i> (Koch)	Green	0.40	(18)	0.35	(34)	
		<i>Acyrtosiphon ononis</i> (Koch)	Red	0.46	(20)	0.22	(26)	
		<i>Acyrtosiphon pisum</i> (Harris)		0.60	(19)	0.13	(20)	
		<i>Aphis fabae</i> Scop.	1st	0.62	(20)	0.13	(20)	
		<i>Cryptomyzus ribis</i> (L.)	1st	0.61	(19)	0.15	(18)	
		<i>Cryptomyzus ribis</i> (L.)	2nd	0.51	(19)	0.24	(19)	
		<i>Megoura viciae</i> Buckt.		0.58	(20)	0.10	(20)	
		<i>Sitobion avenae</i> (Fab.)	1st	0.43	(38)	0.25	(18)	
		<i>Uroleucon cirsii</i> (L.)		0.42	(19)	0.33	(20)	
Lachnidae	<i>Tuberolachnus salignus</i> (Gmel.)		0.36	(25)	0.36	(20)		
Alatae	Drepanosiphidae	<i>Drepanosiphum platanoidis</i> (Schr.)	1st	0.26	(20)	0.22	(36)	
		<i>Drepanosiphum platanoidis</i> (Schr.)	2nd	0.11	(36)	0.28	(20)	
		<i>Eucallipterus tiliae</i> (L.)	1st	0.32	(20)	0.17	(40)	
		<i>Euceraphis punctipennis</i> (Zett.)		0.10	(20)	0.28	(20)	
		<i>Myzocallis boernerii</i> Stroyan	1st	0.49	(20)	0.19	(39)	
		<i>Myzocallis coryli</i> (Goeze)	1st	0.45	(20)	0.17	(40)	
		<i>Myzocallis coryli</i> (Goeze)	2nd	0.31	(19)	0.18	(19)	
		<i>Periphyllus testudinaceus</i> (Ferne)		0.33	(18)	0.29	(39)	
		<i>Therioaphis ononidis</i> (Kalt.)		0.27	(20)	0.24	(28)	
		Aphididae	<i>Acyrtosiphon pisum</i> (Harris)		0.18	(11)	0.31	(18)
			<i>Aphis fabae fabae</i> Scop.	Emigrant	0.18	(20)	0.28	(39)
			<i>Aphis fabae fabae</i> Scop.	Alate exule	0.32	(20)	0.24	(38)
			<i>Aphis fabae fabae</i> Scop.	Gynoparae	0.24	(20)	0.26	(39)
			<i>Aphis fabae solanella</i> Theobald	Gynoparae	0.21	(10)	0.35	(17)
			<i>Aphis sambuci</i> L.	Emigrant	0.12	(20)	0.38	(20)
			<i>Brachycaudus lychnidis</i> (L.)		0.27	(26)	0.25	(20)
			<i>Brevicoryne brassicae</i> (L.)		0.25	(20)	0.32	(20)
			<i>Cavariella aegopodii</i> (Scop.)	Emigrant	0.24		0.32	
			<i>Cavariella aegopodii</i> (Scop.)	Alate exule	0.20		0.32	
			<i>Cavariella aegopodii</i> (Scop.)	Gynoparae	0.18		0.34	
			<i>Cryptomyzus alboapicalis</i> (Theobald)		0.26	(20)	0.28	(20)
			<i>Cryptomyzus galeopsidis</i> (Kalt.)	Gynoparae	0.15	(20)	0.38	(20)
			<i>Cryptomyzus maudamantii</i> Guldemond	Gynoparae	0.17	(20)	0.36	(20)
			<i>Cryptomyzus ribis</i> (L.)	Emigrant	0.18	(20)	0.37	(18)
			<i>Macrosiphum albifrons</i> Essig		0.07	(20)	0.47	(21)
			<i>Macrosiphum artemisiae</i> (Boy de Fonsc.)		0.13	(20)	0.31	(20)
			<i>Megoura viciae</i> Buckt.		0.19	(16)	0.29	(20)
			<i>Metoplophium dirhodum</i> (Walk.)		0.29	(20)	0.22	(20)
			<i>Myzus cerasi</i> (Fab.)	Emigrant	0.26	(20)	0.21	(40)
			<i>Ovatus crataegarius</i> (Walk.)	Emigrant	0.21	(20)	0.39	(20)
<i>Rhopalosiphum padi</i> (L.)	Emigrant		0.28	(20)	0.31	(Dixon 1976)		
<i>Rhopalosiphum padi</i> (L.)	Gynoparae		0.27	(20)	0.35	(18)		
<i>Sitobion avenae</i> (Fab.)			0.20	(20)	0.37	(20)		
<i>Uroleucon cirsii</i> (L.)			0.10	(23)	0.45	(20)		
Lachnidae	<i>Tuberolachnus salignus</i> (Gmel.)			0.12	(14)	0.39	(20)	

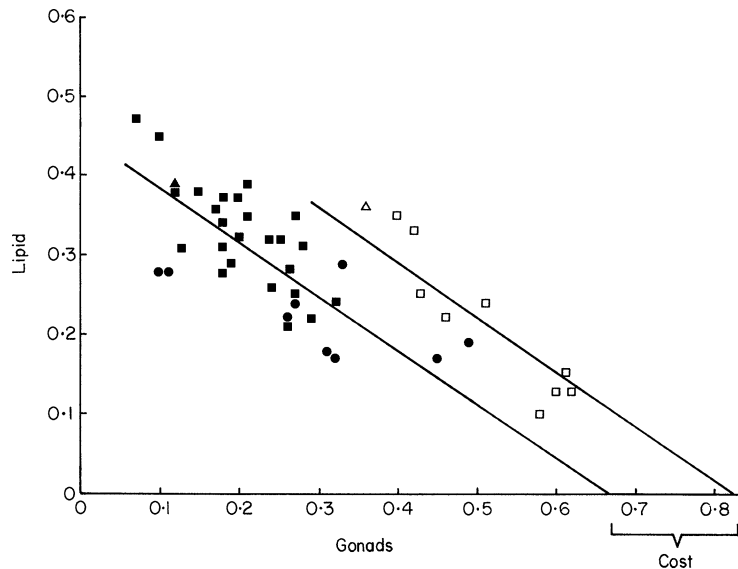


Fig. 3. Relationship between the proportion of the dry weight made up of lipid and gonads for apterae (open symbols) and alatae (closed symbols) (● Drepanosiphidae; □ ■ Aphididae; △ ▲ Lachnidae). The difference in the intercepts of the two trade-off curves on the  $x$ -axis indicates the cost in terms of gonad size of developing a flight apparatus.

factor that may account for some of the variation is the difficulty of rearing the various species under equally favourable conditions. This is important because in some morphs the proportion of the body made up of gonads and especially lipoidal reserves is related to adult weight (unpublished) and adult size reflects host quality (Dixon 1987). However, overall this interspecific comparison offers evidence in support of a trade-off between investment in lipid and gonads in both apterae and alatae.

As alatae invest in gonads and lipid reserves as well as a flight apparatus, an estimate of the cost of the latter based on a comparison of the relative size of the gonads in alate and apterous forms of the same species or even the same clone, could be misleading. Extrapolation of the relationships for alatae and apterae shown in Fig. 3, to where they intercept the abscissa, indicates that when corrected for lipid content the cost of developing a flight apparatus, assuming a linear relationship, is a 20% reduction in gonad size.

#### LIPID RESERVES AND SURVIVAL

Alatae utilize their lipid reserves when flying for long periods and, intraspecifically, individuals with large reserves are capable of flying for longer than those with small reserves (Cockbain 1961; Mercer 1979). Interspecifically, this relationship between flight duration and lipid reserves is also likely to hold. A relative estimate of the potential flight duration of different aphids can be obtained by starving them and recording the time for which they survive, assuming that survival is determined by the size of the lipid reserves.

The winged forms of three species tested in this way showed a clear trend. The species and gener-

ations that had the greater lipid reserve survived longest and metabolized more fat. This was also observed for individuals of *M. albifrons* (equation 3, Table 2). Both intra- and interspecifically, the trend in survival is also positively associated with weight, with the heavier surviving longer than the lighter. However, the results for the two generations of *D. platanoidis*, which did not differ in weight (Table 2), lend support to an alternative hypothesis; i.e. it was the relative sizes of the lipoidal reserves and gonads that were associated with the length of time they survived starvation. The relative sizes of the gonads and lipoidal reserves in the first generation sycamore aphids were 0.26 and 0.22, respectively, and were associated with a survival of 109 h, whereas in the second generation the corresponding values were 0.11 and 0.28, and 140 h (Tables 1 & 2).

In the case of apterae of *A. fabae*, the large individuals of the first generation survived starvation for a significantly shorter period than the smaller individuals of a later generation (Table 2). The length of time for which they survived was positively associated with the relative size of their lipid reserves (0.1 and 0.15, respectively; Dixon & Dharma 1980) and negatively associated with the relative size of their gonads (0.62 and 0.57, unpublished). Thus the evidence from apterae, although only based on one species, also favours the hypothesis that it is the relative investment in gonads and lipid reserves, rather than size, that determines the survival of aphids when starved.

#### LIPID RESERVES AND HABITAT QUALITY

A previous study of *Aphis fabae* revealed that apterous individuals that hatch from overwintering eggs (first generation) have proportionally smaller

**Table 2.** The average wet weight, time for which they survived starvation and the proportion of their dry weight made up of lipid before and after starvation for three species of aphid, where (*n*) is the number of observations. In addition, the relationships between wet weight and dry weight (equation 1), dry weight and lipid content (equation 2) and wet weight and time to death (equation 3) are given for *M. albifrons*

Aphid		Wet weight ( $\mu\text{g}$ )	Lipid as proportion of dry wt	Survival (h)	Lipid as proportion of dry wt at death
Alatae	<i>Myzocallis boernerii</i>	605 $\pm$ 9.9 (39)	0.19 $\pm$ 0.006 (39)	84.4 $\pm$ 4.45 (39)	0.028 $\pm$ 0.004 (34)
	<i>Drepanosiphum</i> 1st gen	1405.2 $\pm$ 51.2 (37)	0.21 $\pm$ 0.018 (36)	108.7 $\pm$ 5.6 (30)	0.061 $\pm$ 0.005 (29)
	<i>platanoidis</i> 2nd gen	1429.5 $\pm$ 45.5 (41)	0.28 $\pm$ 0.011 (38)	139.3 $\pm$ 6.7 (41)	0.067 $\pm$ 0.006 (41)
	<i>Macrosiphum albifrons</i>	1879 $\pm$ 83.09 (51)	0.47 $\pm$ 0.018 (21)	210.8 $\pm$ 11.04 (51)	10 $\pm$ 0.012 (51)
	Relationships for <i>M. albifrons</i>				
	Dry wt ( <i>y</i> )/wet wt ( <i>x</i> )	$y = -0.2 + 0.26x$	$r = 0.98$	$n = 18$	eqn 1
Lipid ( <i>y</i> )/dry wt ( <i>x</i> )	$y = -63.5 + 0.69x$	$r = 0.90$	$n = 21$	eqn 2	
Survival ( <i>y</i> )/wet wt ( <i>x</i> )	$y = 24.23 + 0.099x$	$r = 0.75$	$n = 51$	eqn 3	
Apterae	<i>Aphis fabae</i> 1st gen	1582 $\pm$ 46.9 (16)		64.8 $t = 4.02$	
	<i>Aphis fabae</i> 2nd gen	722.9 $\pm$ 33.7 (52)		106.6 $df = 66$ ***	

lipid reserves than the apterae of later generations (Dixon & Dharma 1980). A similar trend is present in the results for *Cryptomyzus ribis* presented in Table 1. The first generation individuals had proportionally smaller lipoidal reserves ( $t = 6.8$ ,  $df = 35$ ,  $P < 0.01$ ) and larger gonads ( $t = 3.8$ ,  $df = 35$ ,  $P < 0.01$ ) than individuals of the second generation. These trends are associated with the dramatic decline in host-plant quality that occurs after bud burst. That is, these trends appear to indicate that as host-plants cease growing and become less suitable for aphids they invest proportionally more in lipoidal reserves and less in gonads.

#### LIPID RESERVES AND HABITAT FRAGMENTATION

Winged aphids similarly show a seasonal trend, with first generation individuals having larger gonads and smaller lipid reserves than second generation individuals (*D. platanoidis* and *M. coryli* in Table 1; Dixon 1975). In addition, the Drepanosiphidae have on average proportionally larger gonads (0.29) and smaller lipid reserves (0.22) than the Aphididae and Lachnidae (0.20 + 0.33, respectively;  $t = 2.8$ ,  $df = 33$ ,  $P < 0.01$  and  $t = 4.3$ ,  $df = 33$ ,  $P < 0.01$ ; Table 1). The Drepanosiphidae are mainly deciduous tree dwellers whereas the Aphididae mainly live on herbaceous plants. That is, winged aphids that depend on locating plants characteristic of permanent climax communities have proportionally larger gonads and smaller lipid reserves than those that depend on locating short-lived plants that often have a very fragmented distribution. For example, the alatae of the species in the data set presented in Table 1, with the largest gonads and smallest lipid reserves, *M. boernerii*, lives on Turkey oak, *Quercus cerris*, and the species with the smallest gonads and largest lipid reserves, *M. albifrons*, lives on a herbaceous plant, *Lupinus* spp. An apparent exception, *T. salig-*

*nus*, which lives on *Salix* spp. but nevertheless has only relatively small gonads and large lipid reserves, is dependent not only on locating a willow tree but one that is close to a suitable ant colony. Unfortunately, the poor state of knowledge on the dispersion of plant species rules out a more rigorous analysis of the association between reproductive strategies and habitat fragmentation.

#### GONAD DEVELOPMENT IN ALATAE

Winged individuals of the Aphididae and Drepanosiphidae differ in that some show wing muscle autolysis and others retain the ability to fly throughout adult life (Dixon 1969; Haine 1955; Johnson 1957). Whether they retain their wing muscles or not appears to be associated with whether their gonads increase in size in early adult life. Generally, over the first 7 days of adult life the gonads of Drepanosiphidae, which retain their wing muscles, decrease in size, and those of Aphididae, which autolyse their wing muscles, increase in size (Table 3). The species that showed the most striking increase in gonadal size was *M. albifrons*. The two species of Aphididae (*B. brassicae* and *C. alboapicalis*) that showed a decrease in gonadal size also retained functional wing muscles for 7 days.

#### Discussion

The optimal energy allocation model for aphids predicts that the proportion of the body made up of soma should be the same for the virginoparae of all species of aphids and that there should be a trade-off between the investment in gonads and lipoidal reserves. In accordance with the theoretical predictions there appears to be a trade-off between the investment in gonads and lipoidal reserves in both the winged and unwinged morphs; as also previously reported in apterous individuals of the same clone

**Table 3.** The proportion ( $\pm$ SE) of the dry weight made up of gonads on day 0 and day 7 of adult life, the relative increase in the size of the gonads from day 0 to day 7 and the occurrence of wing muscle autolysis (+) in alatae of 11 species of aphids

Species	Day 0	Day 7	<i>t</i>	df	<i>P</i>	Relative increase	Muscle autolysis
<i>M. albifrons</i> *	0.07 $\pm$ 0.01	0.29 $\pm$ 0.02	13	38	***	4.14	+
<i>T. salignus</i> †	0.12 $\pm$ 0.02	0.31 $\pm$ 0.01	8.9	31	***	2.60	+
<i>A. pisum</i> *	0.18 $\pm$ 0.01	0.27 $\pm$ 0.02	4.6	37	***	1.50	+
<i>M. viciae</i> *	0.19 $\pm$ 0.01	0.53 $\pm$ 0.02	14.6	29	***	2.80	+
<i>B. brassicae</i> *	0.25 $\pm$ 0.01	0.20 $\pm$ 0.02	2.2	37	*	0.80	–
<i>C. alboapicalis</i> *	0.26 $\pm$ 0.01	0.16 $\pm$ 0.008	6.9	49	***	0.62	–
<i>D. platanoidis</i> ‡	0.26 $\pm$ 0.01	0.21 $\pm$ 0.01	3.9	37	***	0.81	–
<i>T. ononidis</i> ‡	0.27 $\pm$ 0.01	0.41 $\pm$ 0.01	14.7	36	***	1.52	–
<i>E. tiliae</i> ‡	0.32 $\pm$ 0.01	0.28 $\pm$ 0.03	1.3	38	NS	0.88	–
<i>M. coryli</i> ‡	0.45 $\pm$ 0.01	0.26 $\pm$ 0.01	12.9	51	***	0.58	–
<i>M. boernerii</i> ‡	0.49 $\pm$ 0.01	0.31 $\pm$ 0.01	8.8	39	***	0.63	–

\* Aphididae.

† Lachnidae.

‡ Drepanosiphidae.

and generation (Brough & Dixon 1989). Individuals of the unwinged morphs, the reproductive mode, which are present at bud burst in spring, when host-plant quality is generally very good, invest less in lipoidal reserves and more in gonads, than individuals of later generations, which are exposed to a much poorer host-plant quality. It is possibly more advantageous for individuals of later generations to move frequently within the habitat in search of better feeding sites and this is made possible by their greater investment in lipoidal reserves. This is the fine-scale population redistribution referred to by Harrington & Taylor (1990) and described for the apterae of three species of aphids by Hodgson (1991).

Although no hibernating apterous morphs are included in this survey they are known to have very large lipoidal reserves and very poorly developed gonads and can survive very long periods without feeding (Dunn 1959; Judge 1967). It is likely that such morphs are located at the top left of the trade-off curve for apterae in Fig. 3; the reproductive trade-off curve. That is, the relative investment in gonads and lipoidal reserves could be related to habitat quality, with those living in poor-quality habitats investing less in gonads and more in lipoidal reserves, than those living in favourable habitats.

Individuals of winged morphs, the migratory mode, show a similar trend to that observed in apterae. This is partly associated with seasonal trends in habitat quality, e.g. the differences between the first and second generation sycamore aphid (Table 1). However, the migration trade-off curve appears to be shaped more by the degree of habitat fragmentation to which each species is exposed. For example, aphids that move between dominant plants characteristic of climax communities (mainly Drepanosiphidae; Fig. 3) tend to have relatively large gonads and smaller fat reserves than aphids that seek out herbaceous plants (mainly Aphididae; Fig. 3) that are short-lived and markedly

clumped in their distribution. That is, winged aphids associated with a spatially predictable resource invest less in fuel and more in reproduction than aphids associated with spatially unpredictable resources.

As predicted, most of the Aphididae, which mainly live on herbaceous plants that are often spatially unpredictable resources, tend to go in for wing muscle autolysis after locating a suitable host-plant, whereas the Drepanosiphidae, which mainly live on trees that are spatially predictable and abundant resources, retain their wing muscles. Associated with wing muscle autolysis is a dramatic and often very rapid increase in the size of the gonads. Assuming that wing muscles compete with the gonads for resources, there are advantages in wing muscle autolysis and investing all the resources in reproduction. Wing muscle autolysis has the additional advantage of preventing an aphid accidentally being displaced from its host-plant, the diffusive losses of Roff (1986). Aphids that live on predictable and abundant plants also tend to be abundant per unit of resource (Dixon & Kindlmann 1990). Thus, they are likely to be more frequently exposed to intense intraspecific competition for resources and, therefore, retaining their ability to fly and so escape competition could be advantageous. Diffusive losses are unlikely to be serious for such aphids because their host-plants tend to be both abundant and more continuously distributed.

In addition to incurring an increased developmental time, aphids that develop a flight apparatus incur another cost: a 20% reduction in the potential size of their gonads. Both apterae and alatae show a trade-off between the size of their gonads and fuel reserves. In the aphid model this is a consequence of the optimal partitioning of energy. Although the rate of growth of aphids is limited by the amount of amino nitrogen in their food, aphids ingest large quantities of sucrose, virtually all of which is excreted (Dixon 1985). This sugar could be converted into



fat. During development winged forms appear to incorporate into their bodies a greater proportion (29%) of the sucrose they ingest than do unwinged forms (6%) and this has been associated with the higher fat content of the former (Kunkel & Hertel 1975). Thus, in addition to the constraint associated with the optimal partitioning of amino nitrogen there could be a further constraint, that of structural design, i.e. the principle of symmorphosis (Taylor & Weibel 1981; Dudley & Gans 1991; Sibly 1991). That the abdomen appears to make up 60% of the total weight in a number of species of aphids of a wide range of weights (0.6–3.0 mg) (Dixon 1985) also lends support to the idea that there could also be a design constraint.

The trade-off between gonadal size and fuel reserves has possibly enabled aphids to exploit plants that vary from being abundant and continuously distributed to those that are relatively uncommon and have a highly fragmented distribution. In the latter case the fact that aphids rarely fly to exhaustion and that their readiness to settle on a plant increases with flight duration (Kennedy & Booth 1963) enables them to test a large number of plants before their fuel is exhausted. The ability of Aphididae to switch from an apterous to an alate mode of development and waste their wing muscles has possibly been important in the successful exploitation of Angiosperms, and is in accordance with the theoretical predictions. Wing muscle autolysis not only enabled them to greatly increase their reproductive rate in later adult life (Newton & Dixon 1990), it also greatly reduced diffusive losses, which would have partly compensated for the high cost of locating host-plants with highly fragmented distributions.

This survey raises questions about the way in which phytophagous insects, and aphids in particular, perceive their environment. Is it in terms of permanent and temporary habitats (Southwood 1962, 1977; Groeters 1989; Groeters & Dingle 1989) or of the probability of locating and successfully competing for a suitable food source (Dixon 1969; Dixon *et al.* 1987)? The former hypothesis predicts that the incidence of migration is dependent on the permanency of an organisms habitat whereas the latter predicts it is dependent on its abundance.

Generally, plants survive for longer than it takes most phytophagous insects to complete their life cycle. In addition, when suitable vegetation forms a continuous cover over large areas, losses during migration are relatively low and the aphid abundant (Dixon & Kindlmann 1990). In such circumstances the ability to avoid competition by flying, possibly outweighs the cost of being able to fly. The aphids living in such habitats are frequently fully winged, although living in permanent habitats. A good example is that of the tree-dwelling Drepanosiphidae, which can produce a rare apterous morph, but nevertheless mainly produce only winged vir-

ginoparae. When the host-plant is uncommon and its distribution very fragmented then the losses incurred in migrating are likely to be very high and the aphid only infrequently abundant. Although the host-plants here are most likely to be herbaceous, and temporary habitats, nevertheless it is in such habitats that apterousness is likely to be favoured. On colonizing such vacant habitats, there are advantages for the colonist in wing muscle autolysis and producing apterae in order to exploit the resource, and later generations switching to alate production when the plant eventually becomes overcrowded. Thus, habitat abundance/fragmentation, rather than permanency, is likely to have been the major factor shaping the migratory strategies of insects. The existence of a range of habitat-related migratory strategies in aphids supports Johnson's (1969) contention that the migratory strategy of an organism, like its other life history traits, is subject to natural selection.

### Acknowledgements

This work was supported by NERC Grant GR3/8026 and Czechoslovak Academy of Sciences Grant 68001. The authors are indebted to Aulay Mackenzie for reading and commenting on the manuscript.

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Received 28 February 1992; revision received 30 April 1992