Evolutionary Ecology Research, 2002, **4**: 133–145

An experimental manipulation of the growth and dispersal strategy of a parasitic infection using monoclonal aphid colonies

David J. Hodgson*

Imperial College of Science, Technology and Medicine, Silwood Park, Ascot, Berks SL5 7PY, UK

ABSTRACT

Parasite life-history theory predicts the potential for prudent host resource use by monoclonal infections. Deterministic models show that prudence will be favoured if an infection suffers density-dependent limits to population growth on or in a host individual. This implies that the release of transmission stages throughout the infection cycle should maximize the reproductive output (and hence fitness) of a monoclonal parasite infection. This hypothesis was tested by experimentally imposing a maximum sustainable yield harvesting strategy on monoclonal aphid colonies grown in the laboratory. Harvesting increased colony longevity, but its effect on total dispersal and colony fitness (a measure that accounted for the timing of dispersal) was subtle. Harvesting increased dispersal and fitness due to adult unwinged dispersers, at the expense of nymphal dispersers. This effect is predicted to increase clonal fitness, since adult unwinged dispersers will have more chance of surviving dispersal costs and represent a unit of colony investment similar to the more specialized winged disperser morph. Despite this, unmanipulated aphid colonies showed a bang–bang dispersal strategy, suggesting that factors promoting late dispersal outweigh the influence of density-dependent colony growth on dispersal strategies in natural aphid populations. Candidate selection pressures include genotypic diversity within aphid colonies and interactions with natural enemies.

Keywords: aphid, *Aphis fabae*, clonal parasite, density dependence, dispersal, life history.

INTRODUCTION

Life-history theory describes the allocation of resources to growth and reproduction by an individual, based on the assumption that natural selection acts to maximize individual fitness (Stearns, 1992). Although developed for individual organisms, life-history theory can easily be applied to genotypically homogeneous aggregations of clonal organisms that represent both a local population and a genotypic individual. For such organisms, selection acts to maximize the fitness of the entire clone (Janzen, 1977; Hodgson, 2001). Parasitic organisms are often clonal; therefore, an understanding of the life histories of distinct

* Address all correspondence to David J. Hodgson, CEH Oxford, Mansfield Road, Oxford OX1 3SR, UK. e-mail: djhod@ceh.ac.uk
Consult the copyright statement on the inside front cover for non-commercial copying policies.

© 2002 David J. Hodgson

clonal aggregates will be of great importance to applied medicine and, in the case of the aphid system presented here, agricultural entomology.

Many aphid (Homoptera: Aphididae) species are serious pests of agricultural crops, due either to direct feeding damage or to transmission of viral diseases between plants. All species reproduce parthenogenetically for at least part of their life cycle (Dixon, 1998), thus colonies founded by a single female will be genotypically homogeneous. Monoclonal parasitic infections are predicted to evolve prudent strategies of resource use (Frank, 1996), in contrast to the virulent strategies predicted when parasite genotypes compete for host resources (Levin and Bull, 1994). *Aphis fabae* (Scop.), the species used in the experiments reported here, is a useful model organism for the testing of parasite life-history theory, since it forms large aggregations on individual host plants. The aggregative tendencies of the species (Kay, 1976) allows manipulations of investment in colony growth and reproduction without suffering the confounding variables to which traditional life-history experiments are prone (Partridge and Harvey, 1988).

The fitness of an aphid clone is determined by the number and fecundity of individuals representing that clone when sexual generations are induced by environmental cues (Janzen, 1977). This, in turn, is determined by the growth and reproduction of clone members during the parthenogenetic generations that precede the sexual generations (Hodgson, 2001). Populations on individual host plants rarely persist for the entire season of parthenogenesis (Dixon *et al.*, 1997); clonal fitness, therefore, also depends critically on the spread of the genotype between host plants via dispersal. Dispersal is a risky venture for individual aphids (Ward *et al.*, 1998), but is still favoured because individual interests subserve the fitness of the entire clone. Each individual member of a monoclonal aphid colony can represent a unit of colony investment in growth on the focal host plant, or transmission of the clonal genotype between plants via dispersal.

Simple deterministic models of aphid colony growth (see 'Methods') predict the optimal schedule of allocation of host resources to colony growth and dispersal, based on two patterns of colony growth. Both models assume that colonies are monoclonal and selected to maximize the number of dispersers produced over their lifespan, that all dispersers suffer the same probability of dispersal success and that colonies survive until a threshold is reached, when all colony members must disperse from the host plant. The intuitive results of these models are that exponentially growing colonies should not produce dispersers during colony growth, since their future reproductive contribution to the focal colony is lost. Instead, a bang–bang strategy is favoured: colonies should grow, then disperse. In contrast, colonies with density-dependent growth rates should self-harvest (release dispersers) during colony growth to reduce population pressure on the focal host plant. Neither model allows dispersing individuals to found their own colonies. This will alter the optimal dispersal schedule. Early dispersal, like early age at maturity in more traditional life-history models, will always increase fitness in the absence of trade-offs with other life-history parameters.

Density-dependent colony growth patterns gain support from published evidence in the aphid literature on density-dependent per capita growth rates (Ives and Settle, 1996; Heinz, 1998; Hodgson and Godfray, 1999), density-dependent dispersal responses (Shaw, 1970a,b; Dixon and Wratten, 1971) and genotypic variation in a clone's propensity to disperse (Lamb and Mackay, 1979). Despite this, laboratory-grown colonies appear to produce few dispersers early in colony growth (D.J. Hodgson, unpublished data). I performed an experiment to determine whether a simple maximum sustainable yield harvesting strategy

can affect colony fecundity (the number of dispersers produced during a colony's lifespan), colony fitness (a measure that includes the timing of disperser-production) and colony longevity. The experiment doubles as a test of density-dependent growth in aphid colonies, and an examination of the optimality of aphid colony growth and dispersal strategies under laboratory conditions. This is the first published attempt to alter directly, by harvesting individuals, the growth and transmission strategy of a parasitic infection. It also includes the first published study of the growth and dispersal strategy of an aphid colony from colonization of the host plant to death of the colony due to total dispersal or exhaustion of the host resources.

METHODS

Models of colony growth and dispersal

Consider a monoclonal colony founded by a single aphid. At time t, colony size N will be determined by the colony growth pattern (see below) and the loss of dispersers during growth. Dispersers will found a new colony with probability p, and all remaining aphids must disperse from the host plant at time threshold T.

1. Exponential growth

Colonies, initiated by a single foundress and releasing no dispersers until time T, will produce the following number of successful dispersers (D):

$$D = pN_T = pe^{rT}$$

where N_T is colony size and r is colony growth rate. A colony that produces a single disperser at time $t < T$ will have dispersal success:

$$D = p(1 + (e^{rt} - 1)e^{r(T-t)})$$

$$= p(e^{rT} - e^{r(T-t)} + 1)$$

Thus any early dispersers produced will reduce colony dispersal success by $p(e^{r(T-t)} - 1)$. As long as $r > 0$, the optimal strategy is to grow until time T, then release all colony members as dispersers.

2. Density-dependent growth

Dispersal serves to increase the spread of a genotype between hosts, but also to relieve any self-regulation occurring on the focal host plant. If we describe a colony in discrete time, then the growth of a colony with simple density-dependent growth, in the penultimate time period $T - 1$, can be written as:

$$N_T = N_{T-1} + rN_{T-1}\left(1 - \frac{N_{T-1}}{k}\right)$$

where k is the carrying capacity (asymptotic maximum size) of the colony.

The dispersal success of a colony producing m dispersers at time $T-1$ is, therefore:

$$D = p\left(N_{T-1} - m + r(N_{T-1} - m)\left(1 - \frac{N_{T-1} - m}{k}\right)\right) + pm$$

Expanding, differentiating with respect to m and setting to zero gives

$$m_{\text{opt}} = N_{T-1} - \frac{k}{2}$$

where m_{opt} is the number of dispersers that maximizes successful colony dispersal. Since negative dispersal cannot occur, m_{opt} will be zero when $N < k/2$. This is confirmed as a maximum, since:

$$\frac{\mathrm{d}^2 D}{\mathrm{d}m^2} = -\frac{2pr}{k}$$

which is negative for all reasonable values of p and k and for $r > 0$.

This result holds for all iterations back through a colony's lifespan. Thus a colony with simple density-dependent growth should grow until it exceeds half the carrying capacity, then release all individuals in excess of this threshold as dispersers. This result exactly mimics the simple maximum sustainable yield model of fisheries management presented by Schaefer (1954).

Colony growth and experimental design

Colonies of *A. fabae* were grown on individual *Vicia faba* var. Sutton Dwarf plants, grown in compost in 12 cm diameter pots. Fifty plants were isolated by surrounding them in a cylinder of clear plastic. A gauze-covered window and gauze lid allowed air to circulate around each plant. Plants were grown for 5 weeks, at 18°C and 16:8 L:D photoperiod, before aphids were introduced. A single winged adult was weighed, then placed on each plant to initiate the colonies; the height of the plant was measured as an indicator of inter-plant differences. Aphids were obtained from stock cultures of a single clone, maintained at Silwood Park.

Colonies were allocated randomly to one of three treatments. On day 10, before the experimental manipulation, colonies in treatments 2 and 3 were paired according to similarity in colony size.

1. *Control*. Colonies were left to grow and disperse without manipulation.
2. *Harvested*. Colonies were harvested according to the harvesting regime described below.
3. *Disturbance control*. Aphids were disturbed by lifting their abdomens with a fine paintbrush. The number of aphids disturbed on each plant was the same number as harvested from the paired treatment 2 plant. Disturbance controls were considered important due to the possible confounding effect of pheromone alarm release (Pickett *et al.*, 1992) during harvesting of colonies in treatment 2.

Manipulation of colony size

The carrying capacity of host plants could not be predicted before colony growth. Instead, a harvesting strategy was designed based on colony absolute growth rates. The daily growth rate of a colony is

$$\Delta N_t = (N_t + D_t) - N_{t-1}$$

where N is population size, t is time (in days) and D_t is the number of dispersers leaving the colony between days $t-1$ and t. With density-dependent growth, ΔN increases as the colony ages and then begins to decline. ΔN was monitored and the population size, N^*, at which it reached a maximum was noted. Harvested colonies were maintained at this size by removing aphids to simulate dispersal. Were plant quality to remain constant, this manipulation would be analogous to a maximum sustainable yield harvesting policy (Schaefer, 1954; Beddington, 1979). In contrast to constant effort or fixed yield harvesting strategies, this resulted in a dynamic harvesting regime, since N^* was maintained by a mixture of natural and experimentally imposed dispersal. Adult wingless aphids were chosen as the 'unit' of harvest, as they represent a distinct modular unit of the size of an aphid clone, they are a similar unit of resource allocation as the more specialized winged adults and they were less likely to disperse naturally than winged individuals (thus avoiding as much as possible the removal of an aphid that would have dispersed anyway). The number of aphids harvested was added to the number of dispersers released naturally by the colonies.

Monitoring the colonies

Colony size was monitored by counting daily all the aphids (adults and nymphs) on each plant, until the whole colony had either died or dispersed. Colony death always coincided with the death of the plant. The numbers of dispersing aphids were counted daily and consisted of all individuals that had left the plant and gathered on the gauze lid of the plastic cylinder surrounding the plant. The sum of the number of aphids removed experimentally and the number dispersing naturally was used when assessing total colony dispersal. Disperser age was accounted for by distinguishing between unwinged dispersers that were adults (identified by the presence of the anal cauda; Heie, 1986) or nymphs.

Colony growth rates and age distribution

Two problems were encountered with the harvesting regime. First, colony growth rates peaked early in the experiment and a low population density, N^*, was then maintained by the removal of aphids. Surprisingly, colony growth rates recovered in the control colonies and a second, higher peak growth rate was achieved. The earlier peak is probably an artefact caused by the initially non-overlapping generation structure in the young colony. On day 24, harvesting was relaxed to allow the colonies in treatment 2 to reach a higher N^*. The second problem was that, on some occasions, there were insufficient adult aphids in the colony that could be removed to reduce colony density to N^*. In these circumstances, all wingless adults were removed, and hence the densities temporarily remained above the threshold.

Colony fitness

Colony fitnesses were calculated to account for the timing, as well as the magnitude, of disperser production. The schedule of age-dependent dispersal for each colony was converted into an individual Leslie matrix format (Fig. 1; McGraw and Caswell, 1996); the eigenvalue of the matrix was used as an estimate of colony fitness. This method weights the

$$\begin{bmatrix} 0 & 0 & 2 & 3 & 1 \\ 1 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 \end{bmatrix}$$

Fig. 1. Hypothetical individual fitness matrix. The top row represents age-specific fecundities, the sub-diagonal survival of the individual (always equal to 1 for an individual matrix). Longevity is defined by the dimensions of the matrix (5*5). This individual lived for five time units, producing two, three and one offspring in the third, fourth and fifth time unit respectively. The dominant eigenvalue of this matrix is an estimate of the fitness of this individual and equals 1.618. Matrices for aphid colonies were much larger, ranging in dimension from 25*25 to 60*60 (in units of days).

contribution of each disperser according to its time of release: early dispersers contribute more, since they may colonize a new host plant and reproduce sooner than late dispersers. Colony fitness was first calculated using all dispersers, then using each dispersing morph (winged, adult unwinged, nymph) separately.

Statistical analysis

The number of dispersers, colony fitness and colony longevity were analysed using analysis of covariance within a generalized linear modelling framework (Crawley, 1993). Disperser numbers were log-transformed to cure skew and equalize variances. Colony fitness did not require transformation. Longevity analysis used the Weibull error distribution. The validity of these transformations and error structures were confirmed using standard diagnostics. In all the analyses, a full model was fitted, including treatments, covariates (foundress weight and plant height) and their interactions. Models were then simplified by removing non-significant interaction terms. Absence of mention indicates an interaction was not statistically significant. Covariates were retained in each model, whether significant or not, but only significant effects are reported here.

RESULTS

Harvested colonies had very different growth and dispersal patterns and longevities compared with control and disturbed colonies (Fig. 2). Harvesting removed, on average (± 1 standard error), 303.65 ± 45.78 adult unwinged aphids, compared to the 115.65 ± 19.25 released naturally by the harvested colonies. Harvesting maintained colonies at a lower size, as expected. Dispersal from unmanipulated and disturbed colonies occurred in the last days preceding colony death; nearly all dispersers were released after colonies had peaked in size. Harvesting altered this dispersal strategy by removing adult unwinged individuals throughout the colonies' lifespans (Fig. 2). Harvested colonies and their host plants survived longer than the controls (Weibull survival analysis: $G_2 = 42.15$, $P < 0.001$). Colony longevity increased with increasing plant height ($G_1 = 7.33$, $P = 0.007$) and with decreasing colonist weight ($G_1 = 6.75$, $P = 0.009$).

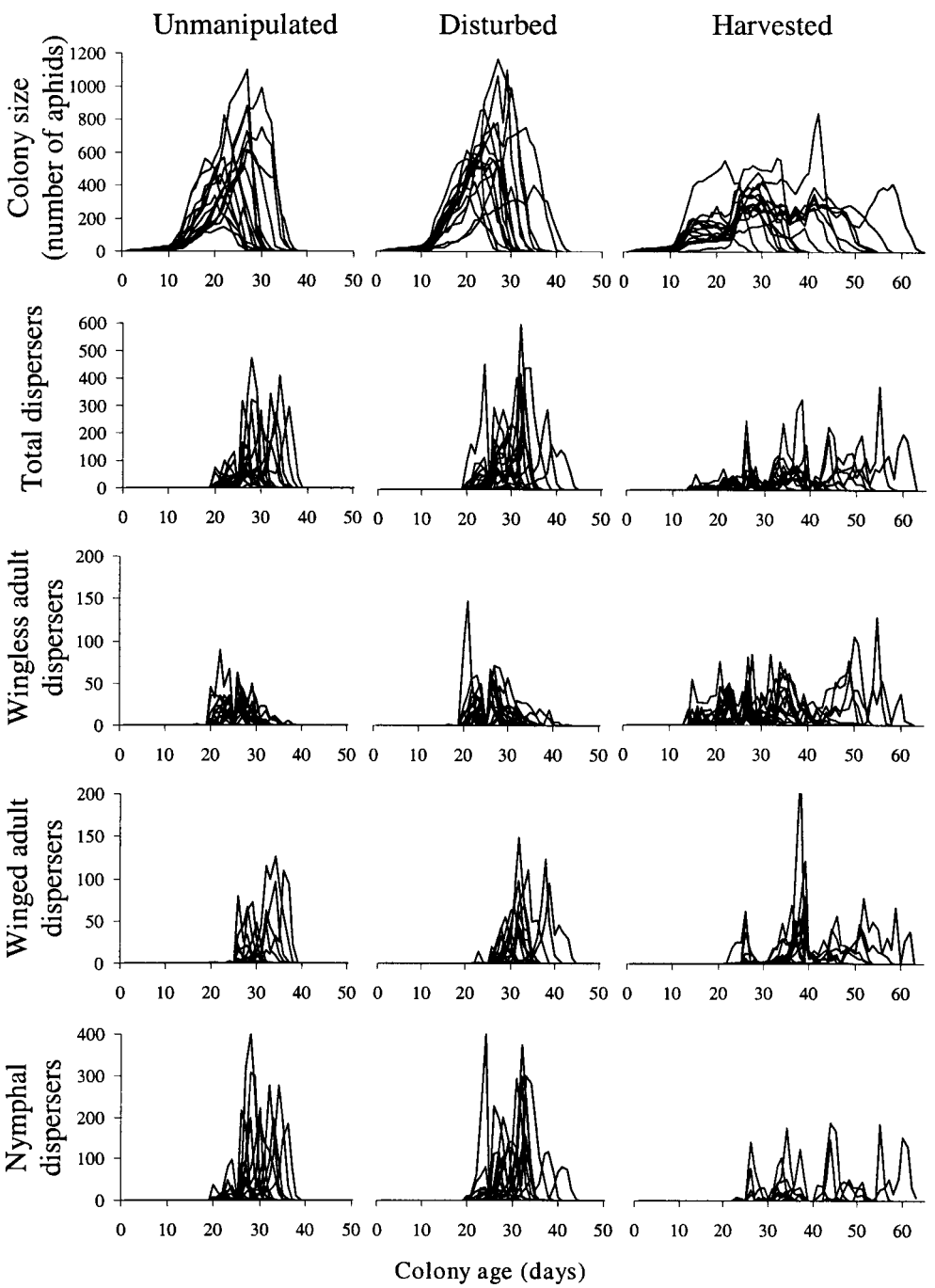

Fig. 2. Growth and dispersal patterns of monoclonal *A. fabae* colonies. Each column refers to one of the treatments. Each line represents a single colony. Dispersers are graphed together (second row) and according to aphid morph (rows 3–5).

The total number of dispersers produced was not influenced by treatment ($F_{2,45} = 1.69$, $P = 0.20$) (Fig. 3a), suggesting no impact of harvesting on the disperser production of the aphid colonies. The separation of the dispersers into age and morph categories demonstrated more subtle treatment effects. Adult unwinged disperser production was significantly influenced by harvesting treatment ($F_{2,45} = 15.70$, $P < 0.001$): combining the control and disturbance control treatments did not significantly decrease the fit of the statistical model ($F_{1,45} = 1.92$, $P = 0.17$), hence the difference was due to the increased number of adult unwinged dispersers in the harvesting treatment (which includes aphids removed as part of the manipulation) (Fig. 3c). This was mirrored by an influence of harvesting on nymphal dispersal ($F_{2,45} = 17.18$, $P < 0.001$). Combining the control and disturbance treatments had no impact on the fit of the model ($F_{1,45} = 1.81$, $P = 0.19$): the difference was due to a decrease in nymphal dispersal from harvested colonies (Fig. 3d). Winged disperser production was unaffected by treatment ($F_{2,45} = 1.29$, $P = 0.29$) (Fig. 3b), but increased with increasing plant height ($F_{1,45} = 4.05$, $P = 0.05$). The lack of effect of treatment on total dispersal was caused by the additive effects of increased adult unwinged dispersal and decreased nymphal dispersal.

Similar effects of harvesting on colony fitness were obtained. Fitness due to all dispersers was not affected by harvesting or disturbance ($F_{2,45} = 1.16$, $P = 0.32$; Fig. 4a), but increased with increasing colonist weight ($F_{1,45} = 6.34$, $P = 0.015$) and decreasing plant height ($F_{1,45} = 4.31$, $P = 0.044$). Fitness due to adult unwinged dispersers was significantly higher in the harvested treatment ($F_{2,45} = 10.86$, $P = 0.0001$) than the control or disturbance

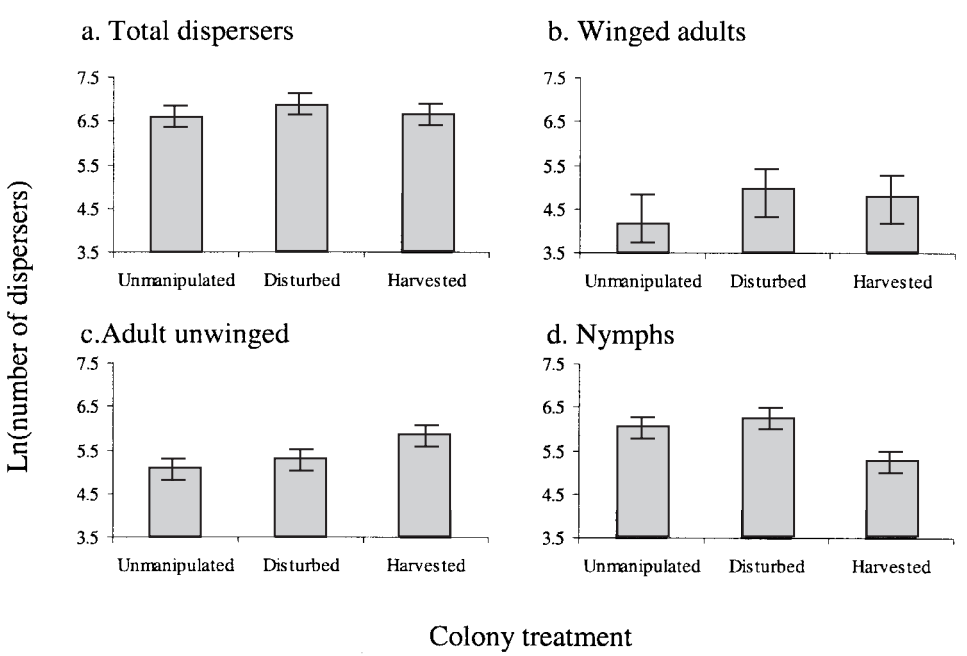

Fig. 3. Number of dispersers produced by monoclonal *A. fabae* colonies, according to harvesting treatment. Harvested colonies produced significantly more adult unwinged dispersers, and significantly less nymphal dispersers, than unmanipulated or disturbed colonies.

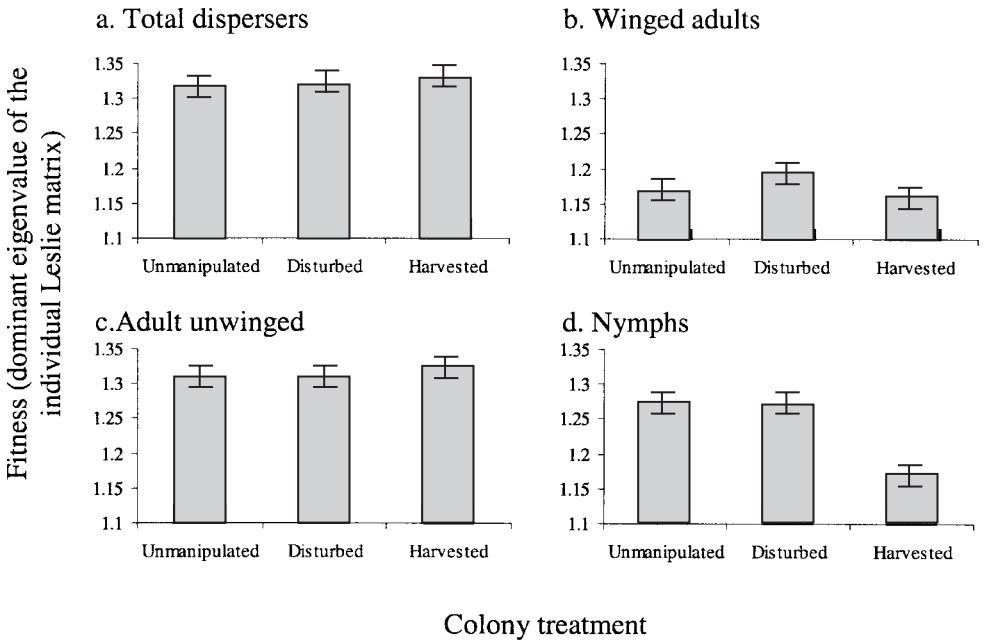

Fig. 4. Individual fitness of monoclonal *A. fabae* colonies, calculated using all dispersers or each dispersing morph. Harvested colonies had significantly higher fitness due to adult unwinged dispersers, and lower fitness due to nymphal dispersal, than unmanipulated or disturbed colonies.

treatments, which shared similar fitness ($F_{1,45} = 0.30$, $P = 0.59$; Fig. 4c). Adult unwinged fitness increased with increasing colonist weight ($F_{1,45} = 6.77$, $P = 0.013$) and decreasing plant height ($F_{1,45} = 6.06$, $P = 0.018$). These differences were mirrored, as in the disperser counts, by a decrease in nymphal disperser fitness in harvested colonies ($F_{2,45} = 36.14$, $P < 0.001$; Fig. 4d). Nymphal disperser fitness increased with decreasing plant height ($F_{1,45} = 5.23$, $P = 0.027$). Fitness due to winged adults was similar across treatments ($F_{2,45} = 1.61$, $P = 0.21$; Fig. 4b) and increased with increasing colonist weight ($F_{1,45} = 4.09$, $P = 0.05$).

DISCUSSION

Unmanipulated and disturbed colonies showed a growth-then-dispersal strategy, with the vast majority of dispersers being released after colonies had peaked in size. This mimicked the bang–bang optimal dispersal strategy predicted for exponentially growing colonies. Despite this, the imposition of early dispersal, according to a simple maximum sustainable yield (MSY) harvesting regime, increased colony longevity and favoured the release of adult dispersers over the lifespan of monoclonal colonies of *A. fabae*. The increased longevity of harvested colonies was expected due to a delay in exhaustion of host resources and did not itself indicate density-dependent colony growth. It was, however, expected to influence the fitness of harvested aphid colonies due to a shift in the timing of disperser production. In fact, colony fitnesses showed similar patterns to simple counts of dispersers. This may either

be because the fitness calculations were not sufficiently sensitive to disperser timing, or because the early dispersal imposed on harvested colonies was compensated for by the late dispersal due to increased colony longevity.

Had disperser morphs not been measured, the simple interpretation of these results would have been that harvesting does not alter aphid colony fecundity or fitness. More sensitive analyses revealed that harvested colonies produced more adult unwinged dispersers than unmanipulated and disturbed colonies. Why should the altered age distribution of dispersers in the harvested colonies affect clonal fitness? Adult unwinged dispersers will donate more to clonal fitness than nymphs, for three reasons. First, they can reproduce as soon as they find a new host. Second, they are larger and may have larger fat reserves to help survive dispersal costs. Third, they represent a unit of resource that a colony employing a natural MSY strategy could have used to produce equivalent numbers of the more specialized winged disperser morph.

These results demonstrate that aphid colony growth had a density-dependent component, since the imposition of self-harvesting via early dispersal increased the fecundity and fitness of colonies due to adult dispersers. Despite this, unmanipulated colonies did not show the predicted prudent dispersal strategy that would maximize clonal fitness. This result suggests that density-dependent colony growth is a relatively weak selective force shaping the dispersal strategy of aphid colonies.

There are five features of aphid colonies that may weaken selection for prudent dispersal strategies:

1. *Spatial distribution of genotypes*. Prudent strategies are only predicted for monoclonal populations (Levin and Bull, 1994; Nowak and May, 1994; Frank, 1996). If host plants are commonly shared by more than one genotype, then the naturally virulent colony growth patterns demonstrated here may be optimal. There is only limited information on the distribution of aphid clones in the field. Loxdale and Brookes (1990) showed that colonies of *Sitobion fragariae* were genotypically homogeneous. Raymond (1998) showed similar homogeneity in *A. fabae cirsiiacanthoides* colonies. In contrast, other studies have demonstrated genotypic heterogeneity at the scale of individual leaves or host plants (Wöhrmann and Tomiuk, 1990; Shufran *et al.*, 1991), or seasonal variation in the extent of within-site variation (DeBarro *et al.*, 1995). More studies of within-colony genotypic variation are required to determine the extent of genotypic population structuring in aphids.
2. *Knowledge of available resources and colony size*. Models of parasite population growth assume that they can respond to depletions in host resource and changes in population size, and predict the costs and benefits of dispersing. If aphids cannot respond to the remaining resources in an individual host plant, then their dispersal responses will be shaped by the quantity of resources offered by the average host plant. This may lead to an apparent growth-then-dispersal strategy on small host plants, such as were offered in these experiments.
3. *Environmental stochasticity*. Recent harvesting models suggest that extinction risk and stochastic variation in growth rates and carrying capacities of density-dependent populations may radically alter the optimal harvesting regime (Lande *et al.*, 1995, 1997). Such changes could be predicted by modelling the evolution of aphid colony virulence with stochastically varying growth parameters, or be determined by performing harvesting experiments in the field.

4. *Interclonal variation*. Only one clone of *A. fabae* was tested in these experiments. More clones should be tested to determine whether dispersal strategy is a heritable component of aphid colony phenotypes and whether other aphid clones have strategies that respond to density. Lamb and Mackay (1979) used crowding tests to demonstrate differences in the propensity to disperse in clones of *Acyrthosiphon pisum*; such experiments should be repeated using whole aphid colonies.
5. *Interactions with other species*. *A. fabae* is facultatively attended by ants. This interaction, although traditionally viewed as mutualistic (Way, 1963), may have some parasitic components (Stadler and Dixon, 1998). In particular, aphid dispersal is not in the ants' best interests and chemical interactions are known to reduce the number of winged adults produced by ant-attended aphids (Kleinjan and Mittler, 1975). Aphids are also attacked by a suite of specialist and generalist natural enemies. There is some evidence that high levels of clustering by aphids may provide them with selfish-herding benefits against predator attack (Kidd, 1982; Turchin and Kareiva, 1989). If this is an important effect, then clustering may be promoted via selection against clones with a propensity to disperse.

The observed bang–bang dispersal strategy of aphid colonies, despite the potential for increased clonal fitness via prudent dispersal, raises more questions than it answers. Aphid colonies, as model parasites, present a challenge to theoretical predictions of the evolution of parasite life histories. Several explanations of the observed lack of prudence are presented here, each of which deserves further study. Laboratory studies of aphid colony growth and dispersal should be performed with more aphid genotypes and with host-sharing between clones. Field studies are also required to determine whether results from the laboratory can be extrapolated to more natural systems.

ACKNOWLEDGEMENTS

I thank Professor Charles Godfray for supervision, Drs Angus Buckling and Rosie Hails for helpful criticisms of the manuscript and Dr Sophia Ratcliffe, Irma Adriaanse and Dr Karel Alders for practical assistance. The research was funded by a Commonwealth Scholarship.

REFERENCES

Beddington, J.R. 1979. Harvesting and population dynamics. In *Population Dynamics* (R.M. Anderson, B.D. Turner and L.R. Taylor, eds), pp. 307–315. Oxford: Blackwell.

Crawley, M.J. 1993. *GLIM for Ecologists*. Oxford: Blackwell.

DeBarro, P.J., Sherratt, T.N., Brookes, C.P., David, O. and MacLean, N. 1995. Spatial and temporal genetic variation in British field populations of the grain aphid *Sitobion avenae* (F) (Hemiptera: Aphididae) studied using RAPD-PCR. *Proc. R. Soc. Lond. B*, **262**: 321–327.

Dixon, A.F.G. 1998. *Aphid Ecology*. London: Chapman & Hall.

Dixon, A.F.G. and 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.

Dixon, A.F.G., Hemptinne, J.L. and Kindlmann, P. 1997. Effectiveness of ladybirds as biological control agents: patterns and processes. *Entomophaga*, **42**: 71–83.

Frank, S.A. 1996. Models of parasite virulence. *Q. Rev. Biol.*, **71**: 37–78.

Heie, O.E. 1986. *The Aphidoidea* (*Hemiptera*) *of Fennoscandia and Denmark*, *III*. Copenhagen: E.J. Brill/Scandinavian Press.

Heinz, K.M. 1998. Dispersal and dispersion of aphids (Homoptera: Aphididae) and selected natural enemies in spatially subdivided greenhouse environments. *Environ. Entomol.*, **27**: 1029–1038.

Hodgson, D.J. 2001. Monoclonal aphid colonies and the measurement of clonal fitness. *Ecol. Entomol.*, **26**: 444–448.

Hodgson, D.J. and Godfray, H.C.J. 1999. The consequences of clustering by *Aphis fabae* foundresses on spring migrant production. *Oecologia*, **118**: 446–452.

Ives, A.R. and Settle, W.H. 1996. The failure of a parasitoid to persist with a superabundant host: the importance of the numerical response. *Oikos*, **75**: 269–278.

Janzen, D.H. 1977. What are dandelions and aphids? *Am. Nat.*, **111**: 586–589.

Kay, R.H. 1976. Behavioural components of pheromonal aggregation in *Aphis fabae* Scopoli. *Physiol. Entomol.*, **1**: 249–254.

Kidd, N.A.C. 1982. Predator avoidance as a result of aggregation in the grey pine aphid, *Schizolachnus-pineti*. *J. Anim. Ecol.*, **51**: 397–412.

Kleinjan, J.E. and Mittler, T.E. 1975. A chemical influence of ants on wing development in aphids. *Entomologia Experimentalis et Applicata*, **18**: 384–388.

Lamb, R.J. and Mackay, P.A. 1979. Variation in migratory tendency within and among natural populations of the pea aphid, *Acyrthosiphon pisum*. *Oecologia*, **39**: 289–299.

Lande, R., Engen, S. and Saether, B.E. 1995. Optimal harvesting of fluctuating populations with a risk of extinction. *Am. Nat.*, **145**: 728–745.

Lande, R., Saether, B.E. and Engen, S. 1997. Threshold harvesting for sustainability of fluctuating resources. *Ecology*, **78**: 1341–1350.

Levin, B.R. and Bull, J.J. 1994. Short-sighted evolution and the virulence of pathogenic microbes. *Trends Microbiol.*, **2**: 76–81.

Loxdale, H.D. and Brookes, C.P. 1990. Temporal genetic stability within and restricted migration (gene flow) between local populations of the blackberry-grain aphid *Sitobion fragariae* in south-east England. *J. Anim. Ecol.*, **59**: 497–514.

McGraw, J.B. and Caswell, H. 1996. Estimation of individual fitness from life-history data. *Am. Nat.*, **147**: 47–64.

Nowak, M.A. and May, R.M. 1994. Superinfection and the evolution of parasite virulence. *Proc. R. Soc. Lond. B*, **255**: 81–89.

Partridge, L. and Harvey, P.H. 1988. The ecological context of life history evolution. *Science*, **241**: 1449–1454.

Pickett, J.A., Wadhams, L.J., Woodcock, C.M. and Hardie, J. 1992. The chemical ecology of aphids. *Annu. Rev. Entomol.*, **37**: 67–90.

Raymond, B.De H. 1998. Evolutionary and ecological aspects of host plant range in the *Aphis fabae* complex. Unpublished doctoral dissertation, University of York.

Schaefer, M.B. 1954. Some aspects of the dynamics of populations important to the management of commercial fisheries. *Inter-American Tropical Tuna Commission Bulletin*, **1**: 27–56.

Shaw, M.J.P. 1970a. Effects of population density on alienicolae of *Aphis fabae* Scop. I. The effect of crowding on the production of alatae in the laboratory. *Ann. Appl. Biol.*, **65**: 191–196.

Shaw, M.J.P. 1970b. Effects of population density on alienicolae of *Aphis fabae* Scop. II. The effects of crowding on the expression of migratory urge in the laboratory. *Ann. Appl. Biol.*, **69**: 197–203.

Shufran, K.A., Black, W.C. and Margolies, D.C. 1991. DNA fingerprinting to study spatial and temporal distributions of an aphid, *Schizaphis graminum* (Homoptera, Aphididae). *Bull. Entomol. Res.*, **81**: 303–313.

Stadler, B. and Dixon, A.F.G. 1998. Costs of ant attendance for aphids. *J. Anim. Ecol.*, **67**: 454–459.

Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.

Turchin, P. and Kareiva, P. 1989. Aggregation in *Aphis varians* – an effective strategy for reducing predation risk. *Ecology*, **70**: 1008–1016.

Ward, S.A., Leather, S.R., Pickup, J. and Harrington, R. 1998. Mortality during dispersal and the cost of host-specificity in parasites: how many aphids find hosts? *J. Anim. Ecol.*, **67**: 763–773.

Way, M.J. 1963. Mutualism between ants and honeydew-producing Homoptera. *Annu. Rev. Entomol.*, **8**: 307–344.

Wöhrmann, K. and Tomiuk, J. 1990. The population biological consequences of a mosaiclike structure in *Macrosiphon rosae*. In *Aphid–Plant Genotype Interactions* (R.K. Campbell and R.D. Eikenbary, eds), pp. 51–67. Amsterdam: Elsevier.