PREDATOR REPRODUCTION AND THE OVERALL PREDATOR-PREY RELATIONSHIP

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Abstract

Previous work described the effects of predation of pea aphids by adult coccinellids. That work has been extended to cover the entire reproductive cycle of the coccinellids. The relationship between amount of aphids eaten, and numbers of coccinellid eggs produced, was determined in the laboratory and used to predict numbers of eggs produced in the field. The survival rate of the eggs to adults, as a function of aphid density, was estimated in large field cages and in small enclosures. These relationships were incorporated into a population model for both predators and prey. The model has been validated against field data. It suggests that predator reproduction is optimized when conditions are very good. The significance for optimal foraging theory and biological control is discussed.

Introduction

Frazer and Gilbert (1976) described the predation by adult ladybird beetles, *Coccinella trifasciata* Mulsant, of pea aphids, *Acyrthosiphon pisum* (Harris), on alfalfa (lucerne). The present paper serves two purposes. Its first four sections extend the work to cover the full reproductive cycle of the coccinellids. The last two sections summarize the entire predator-prey relationship, and examine the implications for biological control and optimal foraging theory.

1. Field Cage Experiment

Six field cages, each 4×6×2 m high and covered with a clear plastic roof and screen walls, were erected in a 13×50 m plot of alfalfa. Each cage contained three 6 m rows of alfalfa. Into each of four cages 75 adult *C. trifasciata* were introduced (32 ♂, 43 ♀), a high but realistic density (section 5). The other two cages served as controls. The females were allowed to lay eggs for 18 days, when all surviving adults were removed. After a further 22 days, the new generation of beetles began to appear and the cages were searched daily for them. The soft, pale condition of the elytra indicated that the new beetles were caught within a day or two of emergence. The weather throughout the experiment was sunny and warm, with average daily temperatures of 24°C max. and 12°C min. inside the cages. Irregularities in the pattern of daily emergence (Fig. 2) are due to the fact that on sunny days, newly-emerged ladybirds sun themselves in full view, whereas on cloudy days, they remain in the undergrowth.

Aphid densities in each cage were estimated every 3-5 days, from samples each containing 18-45 plant terminals, as adopted in previous work. Figure 1 shows the changes in aphid density during the first 32 days of the experiment. The initial samples are inaccurate because of the low numbers of aphids per sample, while the final samples are biased because there were so many aphids that some were inevitably lost during sampling. Because of these sampling problems, densities were grossly underestimated after the 32nd day, but they remained well above 100 aphids/terminal in all cages.

Cage 1, which had the highest aphid density, gave the earliest emergence and the greatest total number of second-generation beetles (Fig. 2). Cage 5, with the lowest aphid density, gave the latest bulk emergence and the smallest total. Cages

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2 and 6 were intermediate. Figure 1 shows that, according to our samples, aphid density in cage 2 was consistently higher than in cage 6. If this difference was real, we would expect cage 2 to produce rather more beetles than it did. Otherwise, the timing and number of the new beetle generation accord exactly with the differences in aphid density. In each cage, the coccinellid larvae that hatched early found a lower prey density than those that hatched late: and those that hatched earliest in cage 1 found about the same prey density as the latest hatchling in cage 5. It is precisely the first-instar larvae which have the greatest difficulty in catching prey (cf. Dixon 1959 for *Adalia decempunctata* (L.)).

The larval survival rate was deduced as a function of aphid density from the data in Figs. 1 and 2. First, the model describing adult coccinellid and aphid population dynamics (Frazer and Gilbert 1976) was set to simulate the conditions in each cage. Only 60% of the beetles introduced into the cages were recovered at the end of 18 days. Most of the others were killed by spiders, and this mortality (3%/day) is included in the model. Figure 1 shows that aphid density increased faster in the control cages than in the four experimental cages, during the first 18 days when the adult beetles were present. This gives a numerical check on the predation rate. As Frazer and Gilbert point out, the precise effects of temperature, sunshine, and daylength on ladybird activity are still uncertain. The effect of adult predation on the rate of aphid increase, observed in Fig. 1, is predicted by the predation model only if the beetles remained fully active until they had satisfied their hunger. This does not mean that they were continuously in motion, but that conditions never inhibited beetle activity. And indeed, conditions were ideal in the long (17 h), warm and sunny days. Thus the estimated predation rate, inflicted by adult coccinellids, has been checked by comparing the changes in aphid density between the experimental and control cages.

Predation rate is then used to estimate the rate of egglaying in each cage. Ives (this series) investigated rates of egglaying in the laboratory. At normal field temperatures female *C. trifasciata* require 1.3 mg live weight of aphids per 'quip' for maintenance: here one 'quip' or quarter instar period is 6.5 day-°C above 4.0°C (Frazer and Gilbert 1976). Any additional prey are converted into eggs at the rate

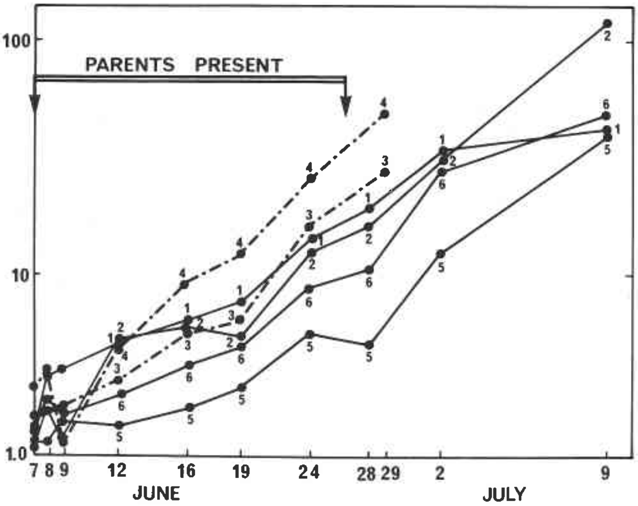

FIG. 1. Aphid densities in six field cages. Logarithmic scale of aphid numbers: physiological time scale (section 1). ——— cages with beetles, - - - control cages.

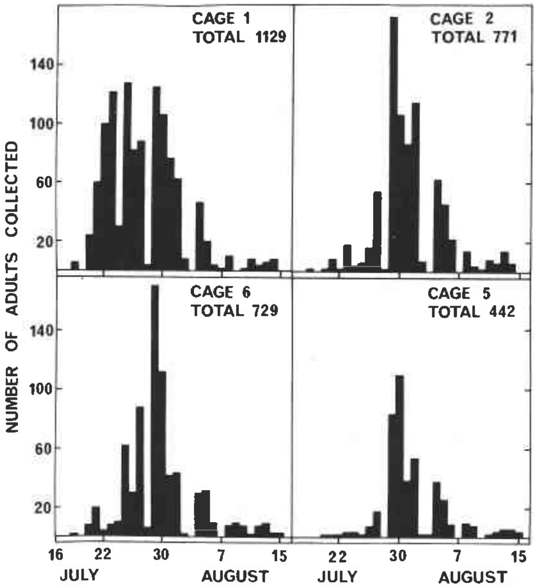

FIG. 2. Numbers of second-generation beetles recovered in the field cage experiment.

of 0.7 egg/mg of aphid. Temperature and prey density certainly affect the predation rate, but over the usual range of field temperatures, the conversion rates can be treated as constant (Ives, this series). Thus the adult predation rate automatically specifies the predator's reproductive rate. It is impossible to make a direct count of eggs laid in the field, since they are hidden in the undergrowth.

The overall survival rate, from egg to adult, was estimated by comparing the expected numbers of eggs laid with the numbers of adult beetles subsequently recovered at the appropriate emergence time, i.e. the time at which the eggs were laid plus the developmental period. We had previously estimated the developmental period (D-°C) of *C. trifasciata* from egg to adult, in the laboratory. Figure 3 shows the survival rate, plotted against the density of aphids present during the critical first larval instar. The curve in Fig. 3 is not estimated directly from the plotted points. Those points are inevitably biased because, although we know when the newly-emerged adult ladybirds were taken from the cages (Fig. 2), we do not know exactly when they hatched. Instead, the curve in Fig. 3 is the curve which, when used in the aphid population model, gives the correct total numbers (Fig. 2) and relative timing of beetles emerging in all four cages. It is the only survival curve that does so. The observed survival rate approaches 20% when aphid densities exceed 20/terminal, but it is very low at prey densities less than 8/terminal.

2. Field Observations

When aphid density in the cages was less than 4/terminal, very few larvae survived. The estimated survival rate at low density is therefore inaccurate, and further evidence is needed for the lower part of the curve in Fig. 3. In the field outside the cages, where aphid density never exceeded 2/terminal, many adult beetles were laying eggs. So we examined larval survival at low prey density in the open field. Ives (this series) estimated the numbers of parent beetles as they entered and left the alfalfa plot, using capture-recapture methods. Those numbers, and the observed aphid density and age-distribution, were used in the predation model to estimate the number of eggs laid. The number of larvae subsequently surviving to

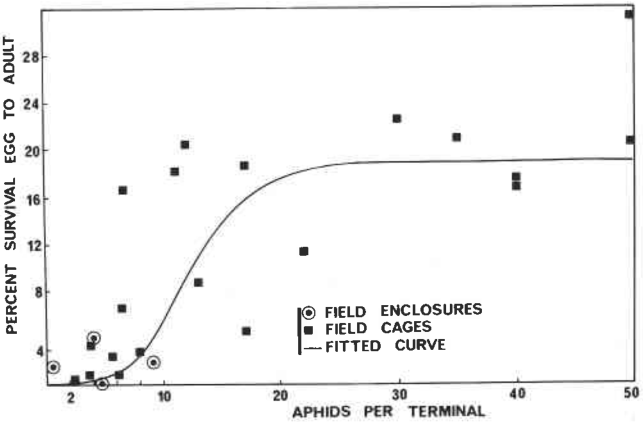

FIG. 3. Survival rate of *Coccinella trifasciata* from egg to adult, as a function of total aphid density present during the first larval instar.

adult was estimated in two ways: by calibrated walk-counts (Ives, this series) of the second-generation beetles, and by placing a cage over a 50 m^2 area of the plot, just before emergence, to trap the emerging beetles.

Neither method was very accurate, because few beetles emerged. Thirty-two beetles were recovered in the cage, which when adjusted *pro rata* by area, gives a total of 400 in the whole plot. The walking counts give an average of 120 beetles present in the plot every day. With daily loss of 20% (section 5), this requires a total emergence of between 250 and 500 beetles depending on the length of the emergence period, which is not accurately known. The value predicted by the population model, using the survival curve of Fig. 3, is 464.

The survival curve in Fig. 3 therefore combines the cage data (between 2 and 20 aphids/terminal) with the field data (0–2 aphids/terminal). This survival must be nearly optimal, since field conditions were continuously good. Possibly the cages excluded some predators or parasites of coccinellid larvae, but spiders were certainly active in the cages (section 1), and they killed many adult beetles.

3. Field Enclosure Experiments

The survival curve of Fig. 3 depends on predicted rates of egglaying. It was checked by four experiments with open enclosures, which estimated survival rates directly, from known numbers of eggs.

There were 24 enclosures, each consisting of a 2 m row of alfalfa (about 600 plants) enclosed by a 30 cm high sheet metal wall. To the inside of the wall was glued a plastic sheet sprayed with ‘Fluon’ so that no insect could walk out of the enclosure. Winged insects, including predators and parasites, could fly in and out. The first three experiments tested the survival rates of various numbers of coccinellid eggs or newly-hatched larvae (fed to repletion immediately after hatching), at initial aphid densities of 1–4/terminal. When the larvae were in their fourth instar, the plants were cut and the entire area searched. Few larvae survived: we did not realize at the time that such high aphid densities are needed for appreciable larval survival. The overall survival rates agreed with those predicted (Fig. 3), and there was no great influx of predators into the enclosures.

The fourth experiment began with aphid densities much higher than those in the surrounding field. Different numbers of coccinellid eggs or of newly-hatched larvae, separated from their egg masses and fed to repletion in the laboratory, were placed in the enclosures. The numbers per enclosure were realistic, ranging from

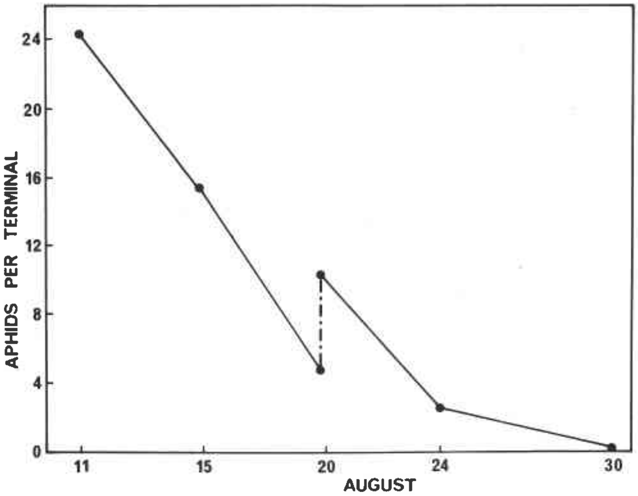

FIG. 4. Decline in pea aphid density during fourth field enclosure experiment. Physiological time scale. On 20 August, extra aphids were added.

100 to 500 eggs, or 40 to 275 larvae. The larvae were not placed in their enclosures until the eggs in other enclosures had hatched: thus all the larvae were of similar age, and they encountered similar aphid densities. Heavy rain followed by an influx of predators—mostly adult coccinellids, earwigs (Dermaptera), and chrysopids (Neuroptera)—rapidly reduced aphid numbers in the enclosures to the level in the field (Fig. 4). The larval survival rate agreed with previous estimates (Fig. 3). Survival of newly-hatched and fed larvae was higher than that of eggs. There was no effect of larval density on survival rate. An influx of predators made it impossible to assess the survival rate over the full range of aphid densities.

4. Larval Predation and Survival Rates

The formula for adult predation rate (Frazer and Gilbert 1976) may be converted to predict a predation rate for first-instar larvae. This does not involve the construction of a new predation model, but merely the substitution of larval values for the parameters of the predation formula. The conversion is bound to be crude, because the predation process cannot be observed directly in the field; the tiny larvae are quickly lost in the undergrowth. The parameters in the formula were estimated as follows. The voracity of first-instar *C. trifasciata* (i.e. the maximum live weight of aphids consumed per quip) was estimated by multiplying the observed voracity of first-instar *Adalia bipunctata* (L.) (Blackman 1967) by the ratio of the adult body weights of the two species. We chose *A. bipunctata* because it is similar in size to *C. trifasciata*. The probability of capturing an aphid (PE), and the average time spent searching one terminal (TS), were estimated by observing fourth-instar larvae searching in the field. The value of PE was then multiplied by the ratio of the values of PE for first- and fourth-instar larvae in the laboratory (Frazer *et al.*, unpub.). The value of TS was calculated in the same way. The predation formula, with these values substituted, predicts that the first-instar larvae can catch all the aphids they need, whenever the density of first-instar aphids exceeds 1/terminal. First-instar larvae depend on first-instar prey, since they have difficulty in catching second-instar aphids, and are unable to subdue older aphids. (Figure 3 is nevertheless plotted against total aphid density to facilitate the ensuing comparisons between adults and larvae.) In all our field samples, a density of 1 first-instar aphid/terminal occurs whenever total aphid density is between 4 and 6/terminal. There is therefore a discrepancy between the predation formula and the survival rate in Fig. 3, which demands a density of 20 aphids/terminal for maximal larval survival. This discrepancy might be explained in three ways: (1) inaccurate conversion of the predation formula for first-instar larvae, (2) increasing cannibalism of eggs or larvae at low aphid densities, (3) uneven aphid distribution. First-instar larvae are far less mobile than older larvae or adults. Therefore, a non-uniform distribution of first instar aphids in the field would reduce the average predation rate of first instar larvae, just as a non-uniform aphid distribution reduces the success of adult beetles in artificial laboratory conditions (Frazer and Gilbert 1976). Whatever the cause of the discrepancy, there are two basic reasons why larval survival during the first instar is so low: first-instar larvae have poor powers of search, and they can catch only the smallest aphids (Hodek 1973).

5. Exploitation of Aphids by Coccinellids

We shall now summarize the entire predator–prey relationship (Frazer and Gilbert 1976; Ives, this series) and consider the efficiency with which the ladybirds exploit the aphid population.

At Vancouver, *C. trifasciata* produces one generation a year. Overwintered adults fly into the alfalfa field on warm days from May to July. The number of beetles arriving does not depend on the density of aphids in the field. But if prey density falls below 0.3/terminal, the beetles cannot maintain their own body weight, and they leave the field. Even at higher prey densities, individual parent beetles do not stay long. At high temperatures, about 20% depart each day; the proportion declines as prey density increases. Trap catches of flying beetles (Ives, this series) prove that most of the 'departures' are genuine emigrations, not deaths. But the deathrate of 3% per day in the field cages (section 1) implies that at least 90% of the parent generation are dead by the end of July: and the capture–recapture work shows that most of the beetles alive in the field in August are indeed second-generation.

The adult beetles are fully active only in sunny, warm (above 15°) conditions. The predation rate therefore depends not only on predator and prey densities (and on prey age-distribution), but very importantly, on temperature. Since warm weather favours the beetles and cool weather favours the aphids, no steady state is possible, even in theory. We have twice seen the adult coccinellids reduce aphid numbers from 0.8 to 0.3/terminal in 2–4 days of warm weather. Thus the lower limit of 0.3 prey/terminal is actually achieved in practice. But there have never been enough coccinellids in the field to halt a steady increase in aphid density, once it exceeds 1/plant. The predation process is therefore intrinsically unstable: it sets no upper limit to prey density, and no upper or lower limit to predator density. The predator–prey relationship is 'stabilized' solely by the ladybirds' numerical response to prey density. (It may be objected that if we switch our attention from the field of alfalfa to the entire area over which the ladybirds operate, this 'numerical' response becomes a 'functional' response involving a switch to alternative prey. That objection, although correct, does not alter our view of the predator–prey relationship between *C. trifasciata* and *A. pisum*. It merely shows that the distinction between numerical and functional responses is, to that extent, arbitrary.)

Female coccinellids lay eggs at a rate determined by food intake (section 1). The survival of larval coccinellids is very poor, reaching a maximum of 20% at aphid densities greater than 20/terminal (Fig. 3). Since the parent beetles attack the same prey as their progeny, consumption of aphids by the parents must affect the survival of the larvae. The converse is not generally true, because very few larvae survive unless aphids are so numerous that the adults can take all the prey they need. The population model of section 1 has nevertheless been extended to include the effects of larval predation on aphid numbers. The necessary parameters of the voracious fourth-instar larvae were estimated by direct observation in the field: those for the young larvae are discussed in section 4. These larval predation rates have not been checked against prey population dynamics, as Frazer and Gilbert (1976) checked the adult predation rate. This extended population model may be used to assess the aphids' ability to support coccinellid reproduction in optimal conditions, and assuming no other aphid losses. A copy of the model may be obtained from the authors.

Figure 5 shows the predicted numbers of second-generation coccinellids produced by varying numbers of parent beetles, in an alfalfa plot containing 100,000 terminals. In the model, the parents lay eggs (at the rate determined by their food intake) for 34 quips—a realistic period (Frazer and Gilbert 1976, figs. 1a and 8) — and then leave the field. Curve A is calculated for an initial aphid density of 0.6/terminal, the number observed in the field in 1975 at the start of the coccinellid influx. The maximum total number of progeny is produced by 400 parents. Curve B predicts the rate of reproduction for an initial aphid density of 0.3/terminal, when the maximum number of progeny is produced by 200 parents. Curve C shows that, with an initial aphid density of 1.2/terminal, 750 parents produce the maximum number of progeny. Curve D recomputes curve A assuming that, after the 34-quip period of egglaying, the parents remain in the field, preying on aphids but laying no more eggs. The difference between curves A and D therefore illustrates the effect, on larval survival, of competition for food between parents and offspring.

We have records, for 1973 and 1975, of beetle densities in alfalfa plots at two different sites, described by Frazer and Gilbert (1976). At site 1, the initial aphid density in 1973 was 0.5. Daily counts of parent beetles fluctuated between 200 and 1300. At site 2 (fig. 8, Frazer and Gilbert 1976), initial aphid density was 0.7 and beetle counts reached a maximum of 1600, but declined to 500, when the alfalfa was cut. There is good reason to believe that these beetle counts underestimated the true numbers by a factor of 4 (Frazer and Gilbert 1976). So there is little doubt that beetle densities in both plots were too high for successful reproduction; and in both plots, aphid densities were driven down to 0.3.

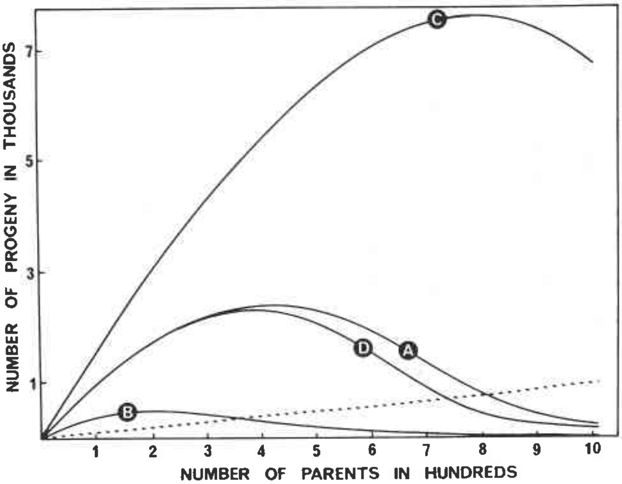

FIG. 5. Reproductive rates of *Coccinella trifasciata*, predicted by the computer model. For explanation of curves, see text. The broken line is the replacement rate of 1 progeny/parent, not allowing for overwinter mortality.

In 1975, coccinellid densities were estimated by capture–recapture (Ives, this series). Site 1 gave estimates in the range 200–900, with an average of 500: aphid density increased from 0.6 to 1.6. At site 2, the estimates varied in the range 800-1200, while aphid density increased from 0.3 to 1.0. So the densities of parent beetles, actually observed in the field, are frequently close to the values which, according to the expanded population model, permit the beetles to exploit the aphid population to the greatest advantage. The coincidence cannot be perfect, if only because the model is unavoidably imprecise, and because the parent beetles cannot predict the subsequent weather conditions which will affect the survival of their offspring. Moreover, the numbers of overwintered beetles arriving in a plot do not depend on aphid density within the plot. Therefore, although the proportion of beetles leaving the field at any given time does vary with the current aphid density, the absolute numbers remaining cannot adjust instantaneously to suit the current density.

But how reliable is the population model? Each part of it is firmly based on experimental evidence, but the synthesis has not been tested rigorously. Observations on reproduction in the field tend to support Fig. 5. In 1973 the alfalfa was cut before coccinellid larvae could mature, so that no test is possible of the predicted effect of excessive parental density. In 1975 the second-generation emergence at site 1 was about 400–500 beetles. This agrees (section 2) with the larval survival rates at the observed aphid densities. It does not agree with the numbers of second-generation beetles predicted by Fig. 5, because the observed aphid densities fell lower than those predicted by the model, which ignores effects of rainfall and of other predators. At site 2 in 1975, aphid densities remained below those in plot 1, and coccinellid reproduction failed. Thus the observations, if anything, support the model, but not conclusively.

If the model is correct, it tells us that the density of adult beetles in the field is fairly close to that which would best exploit the aphid population, assuming optimal conditions for larval survival. This result concerns the beetle *population*. It is not a necessary consequence of Fisher's (1930) theorem that natural selection acts to maximize average individual 'fitness', but may well be compatible with it. To consider the point further, we should need to study the reproductive success of beetles which leave the alfalfa plot to seek alternative prey elsewhere.

The agreement between the observed beetle densities, and those in Fig. 5, offers considerable comfort to the practical ecologist. We have studied all the parts of the complete reproductive cycle of a natural predator. No glaring numerical inconsistency has appeared, and so the coccinellid–aphid case supports our assumption that reasonably accurate, realistic, and quantitative pictures of complete predator–prey relationships can be obtained in the field.

6. Discussion

Events in Britain in 1975–76 are admirably consistent with our view of the predator–prey relationship. Both summers were unusually sunny and warm, and the intervening winter was mild. In both years, a rapid spring build-up of aphid numbers was followed by a large summer production of coccinellids, especially *Coccinella septempunctata* L. In 1976, enormous swarms of ladybirds (but not of other aphid predators such as chrysopids or syrphids) occurred throughout the country. For example a large field of cabbage (*Brassica oleracea* var. *capitata* L.) in Lancashire had no less than 0.8 adult *C. septempunctata*/plant, and no aphids were found on a sample of 200 plants (N. Gilbert, pers. obs., Rothamsted Exp. Sta. Rept. 1976).

This supports our belief that high temperatures and high prey densities are necessary for intensive coccinellid predation and reproduction.

There are several practical conclusions. Frazer and Gilbert (1976) argued that no study of predation can be trusted until the predicted predation rates are reconciled with the observed prey population dynamics in the field. This paper now shows that, to understand the complete predator-prey relationship, we must study not only the predation process, but also its effect on the population dynamics of both predator and prey. Where juvenile and adult predators attack the same prey species, a study of the predators' entire reproductive cycle is required. A similar conclusion holds for optimal foraging theory (Pyke *et al.* 1977). Optimal rates of adult food intake would entail disastrous survival for the progeny. Unless the optimum of section 5 is a fortuitous artifact, optimal foraging theory must in such cases include the population dynamics, not just the search process.

The aphid density in the field is limited by a combination of several species of predator and parasite, and sometimes by fungal epidemic. On five occasions, aphid density in field cages that excluded syrphids, chrysopids and some other predators, rose to more than 50/plant, although the normal complement of coccinellids, spiders, and parasites was present. Aphid density in the open field rarely exceeds 10/plant. The cages did not obstruct any mass emigration of aphids, because very few winged individuals were produced. When aphid density in the open enclosures was artificially increased to 24/plant (Fig. 4), there was a rapid influx of predators, and aphid density declined. Yet the predator complex never completely exterminates the aphids over more than a few square metres; instead, the various forms of mortality compensate each other (Charnov *et al.* 1976). The introduction of an exotic species of predator is therefore unlikely to reduce aphid numbers, because its depredations would be compensated by reduced effectiveness of the predators already present. If, instead, the aphids were restricted by their food supply (which is certainly not the case here), an introduced predator might reduce their numbers effectively. In other words, a predator or parasite introduction is more likely to succeed against a pest held down by its food supply, than against prey already held down by other predators. This conclusion may, of course, be vitiated by considerations of the relative timing of predator and prey generations.

The intrinsic instability of the predator-prey relationship makes it very difficult to use coccinellids alone for biological control of aphids throughout the season. Reasonable reproduction of the ladybirds requires an aphid density of about 8/terminal, at least occasionally; but very large numbers of coccinellids would be needed to prevent aphid numbers from rising above that level, once attained. And if the adult beetles are not to leave the field when their prey density sinks too low, they must be rendered incapable of flight either by surgery (Ignoffo *et al.* 1977) or genetically. Theoretically this is not impossible, for many flightless mutants are known in other insect species (e.g. Lindsley and Grell 1967), and wing-reduced morphs are known for about 100 species of coccinellid (Pope 1977).

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