COCCINELLIDS AND APHIDS:

A Quantitative Study of the Impact of Adult Ladybirds (Coleoptera: Coccinellidae) preying on Field Populations of Pea Aphids (Homoptera: Aphididae)

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ABSTRACT

This paper examines the quantitative effect of predation by a ladybird beetle, **Coccinella trifasciata,** on field populations of pea aphid, **Acyrthosiphon pisum.** Field studies showed that no mathematical function, involving only the current densities of predator and prey, can predict the true predation rate. We studied the components of the predation process in detail, first in the laboratory, and then in the field. We derived a new, empirical (not theoretical) formula for predation rate, which includes predator and prey densities, predator voracity, prey age-distribution, and temperature. Temperature has a single effect on the rate of aphid development, but a double effect on the predation rate, so that coccinellids are much more effective predators at high temperatures, than at low. Field cage experiments, with known numbers of beetles, revealed that all current methods of counting adult coccinellids in the field greatly underestimate their true numbers. When this fault is rectified, the new formula correctly predicts the predation rate.

The study shows that it is possible to investigate a predator-prey relationship, in the field, in considerable detail, in order to predict the predation rate over a wide range of circumstances. The study reveals several sharp, qualitative, differences between the predation relationship observed in the laboratory, and the same relationship observed in the field. All laboratory studies must therefore be suspect, until verified in the field. In particular, arthropod predation studies must allow for effects of temperature on both predation rate and prey population dynamics. The coccinellid-aphid relationship permits no equilibrium, or steady state, so that conventional definitions of stability do not apply. The coccinellid's functional response is inherently unstable: the relationship is stabilized solely by a numerical response. Implications for biological control are discussed.

Contents

Introduction

Morris *et al.* (1963) pioneered the use of life tables for insects which have more or less discrete generations. Hughes (1963) and Hughes and Gilbert (1968) produced a "variable life-table" model of the cabbage aphid, which has overlapping generations. That model assessed the impact of a parasite on the aphid (Gilbert and Hughes 1971). The parasite had no serious effect on aphid abundance, which is restricted by competition and crowding. In similar analyses of other insects (Hassell 1969, Gutierrez *et al.* 1971, 1974a, b; Wratten 1973, Gilbert and Gutierrez 1973), natural enemies also had scant effect on prey numbers. Yet many parasites and predators effectively reduce the numbers of their prey (e.g. Frazer and van den Bosch 1973, DeBach 1974).

In 1972 we began to study field populations of pea aphid, *Acyrthosiphon pisum* (Harris) on alfalfa, *Medicago sativa* L. After the first year it was obvious (§ 1) that coccinellid predators significantly affect aphid density in the field. This paper analyses the predation process (§§ 4 & 5). This is the first time that Holling's (1964) "component analysis" has been applied to predation in the field, and tied into the life table approach of Morris *et al* (1963).

1. BACKGROUND

This section describes the field biology, and proves that the predation rate cannot be a function of current predator and prey densities alone.

Sampling and Field Biology

Alfalfa, *Medicago sativa* L., cv. Alfa was sown in 1971 at the University of British Columbia. The plot consisted of 18 rows each 25 m long and 1 m apart. The crop was cut three times during the summer of 1972, whenever about 10% of the plants were in flower. This approximated the commercial practice in the region.

A population of pea aphids, *Acyrthosiphon pisum* (Harris), became established on plants in 1971, overwintered as eggs, and reappeared in 1972. Pea aphids normally infest the actively growing terminals of alfalfa. We began sampling aphids in April and took samples about once weekly throughout the summer. A sample comprised 20 plastic bags, each containing ten terminals collected directly in the field. Pea aphids readily drop off a plant when it is cut, but care was taken to ensure that no aphids were lost. The bags were taken to the laboratory, where the aphids were beaten off the plants onto a sheet of paper, sorted under the microscope into four juvenile instars and adults, and counted. The fourth instar and adult aphids were separated into winged and wingless morphs.

Hymenopterous parasites, *Aphidius ervi ervi* Haliday, *A. smithi* Sharma & Subba Rao, and *Praon pequodorum* Viereck, attack the aphids. The parasites are themselves attacked by the hyperparasites *Asaphes vulgaris* Walker, *A. californicus* Girault, and *Dendrocernus* near *niger* Howard. To estimate the parasitization rate we dissected all aphids of the third and later instars in every sample, and recorded the numbers and sizes of parasite larvae they contained.

Large numbers of adult coccinellids invaded the alfalfa plot between May 9 and July 18. The commonest species were *Coccinella trifasciata perplexa* Mulsant, *C. t. subversa* Leconte, *C. undecimpunctata undecimpunctata* L., *C. johnsoni* Casey, *C. californica* Mannerheim, and *Cycloneda munda* Say. To sample for coccinellids, observers walked on either side of each row of alfalfa counting all visible beetles. At the same time we counted the parasite mummies. Aphidiid parasites pupate inside or below the dead, eviscerated host aphid, which is transformed into a shell, or "mummy". This gives a second estimate of the parasitization rate.

At the start of the season, aphid numbers began to increase (Fig. 1, May 9-25). After the beetles had arrived (May 25-31), the aphid population declined to a low level, which it

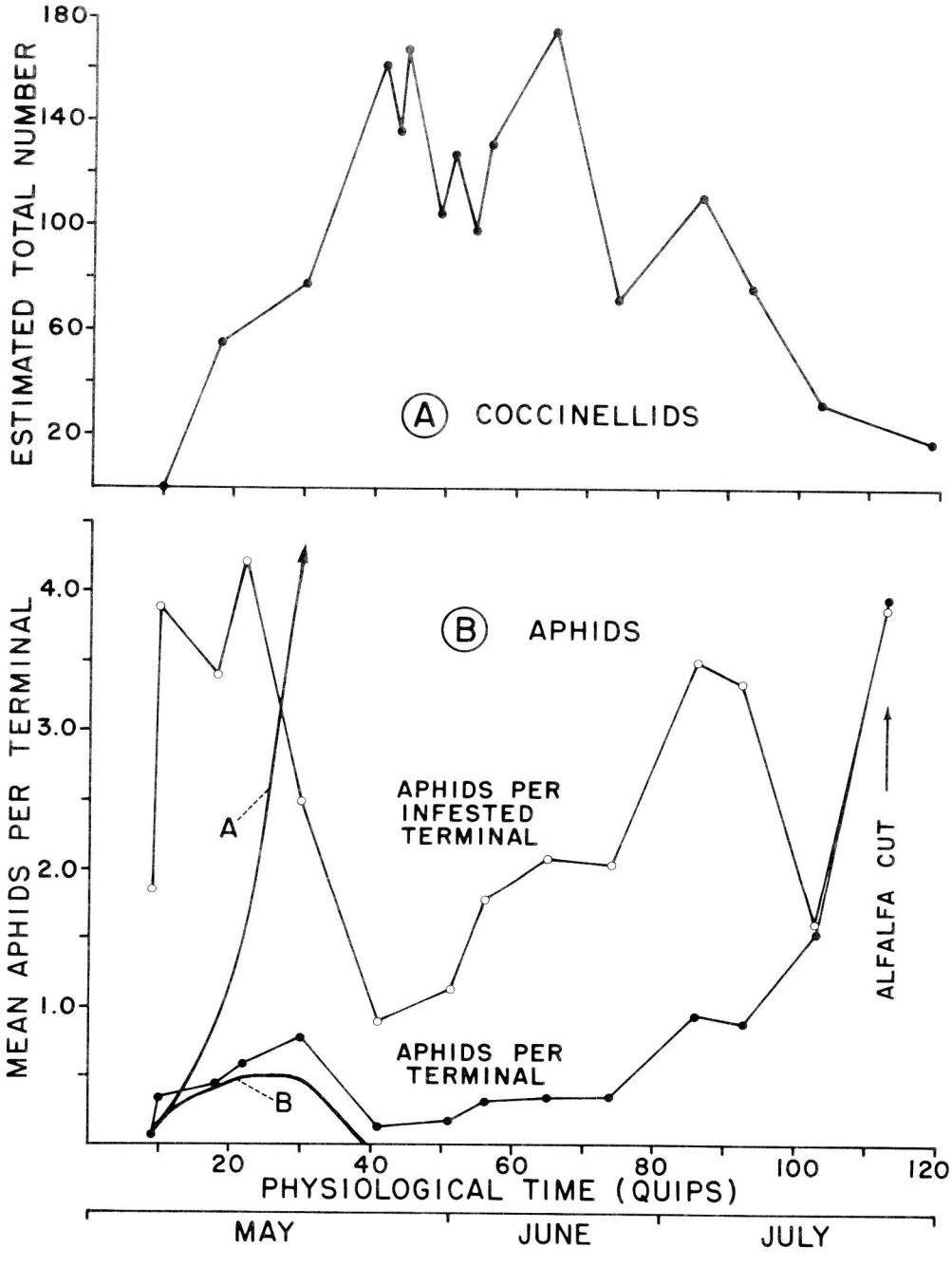

FIGURE 1A. Coccinellids of all species in the whole plot; 1B, aphids per terminal, both in 1972. Each aphid sample contained at least 160 plants. The fall in 'aphids per infested terminal' beginning at q 84 is probably due to an inaccurate estimate of p (see text). Curves A and B (1B) are computed by Appendix 1 in the absence and presence of coccinellids.

maintained throughout the period of maximal coccinellid numbers (May 31-June 21). Thereafter, coccinellid numbers fell sharply, and the aphids again increased (June 21-July 18) until the alfalfa was cut. We shall concentrate on the early period shown in Fig. 1. Later in the season, the aphids were attacked by many other natural enemies of aphids, eg. Chrysopids, Nabids, Mirids, Spiders, Syrphids, and Coccinellid larvae. At the same time, the alfalfa plants grew so big that the aphid samples became unreliable.Nevertheless, the aphid population dynamics during the first half of the season are sufficiently simple to permit some understanding of the underlying processes. Our task is to explain the course of aphid numbers shown in Fig. 1.

Biological parameters

An aphid goes through four instars before becoming adult. We estimated the duration of each instar, and the pattern of adult fecundity, by rearing aphids in the laboratory at each of four constant temperatures (10°, 15°, 20°, 25°). The development rate increased linearly with temperature in this range, so that a given instar required a constant amount of 'physiological time', measured in day-degrees above a threshold temperature of 4°C (Campbell *et al.* 1974). Since this physiological time-scale is the aphid's own time-scale, we adopted it for this study. The first three instars each took about the same amount of physiological time, which we adopted as the aphid's basic time-unit, one 'instar-period'. The fourth instar took longer; 1½ instar-periods for wingless aphids, and 1¾ for winged. To accommodate these varying periods, we adopted one quarter-instar-period, or 'quip' (q), as the unit of physiological time. For the pea aphid at Vancouver, one quip equals 6.56 day-degrees C above the threshold temperature of 4°C.

Parthenogenetic wingless aphids mature after 18 q, begin to reproduce at 19 q and can survive to 90 q. The physiological time-scale compensates for the effects of temperature, not only on development, but also on reproduction. For reproduction, the compensation is not quite perfect, but on the physiological time-scale, the time pattern of reproduction was nearly the same for the four temperatures. In other words, on this scale, both the total fecundity and the reproductive pattern are effectively independent of temperature.

Population Model

These development times and fecundities allowed us to predict the rate of aphid increase, assuming that all individuals survive to age 90 q. This we did by a simple simulation model (Appendix 1). We first converted calendar time in the field to physiological time, using a computer program (Appendix 2) which fitted sine curves to daily maximum and minimum air temperatures, and integrated them above the developmental temperature threshold (Morris & Bennett 1967). Each day in the field calendar was converted to its equivalent in physiological time, beginning arbitrarily on May 1, 1972.

There was a large discrepancy between the aphid model (curve A, Fig. 1) and observed aphid densities. The data indicated heavy mortality while the coccinellids were present. The age distributions (not shown) agreed. From 0-22 q, the aphids increased in numbers (fig. 1) at the rate predicted by the simulation model. No beetles were seen until 20 q. During 20-40 q, there was an influx of beetles, and the aphid population began to decline. The beetles remained in large numbers during 40-70 q, and the aphid population remained low. Most of the beetles left the plot between 70-120 q, whereupon the aphid population resumed its exponential increase.

The beetles had some direct effect on the aphids, as indicated by changes in the average number of aphids per *infested* terminal. The probability p that a sample unit of n terminals contains no aphids is f^n, where f is the frequency of uninfested terminals. From the values of p observed in the samples we estimate the corresponding f and $p^{1/n}$. The average number of aphids per terminal is then divided by (1-f), to estimate the average number of aphids per *infested* terminal. During the period May 9-19 (9-22 q, Fig. 1), that number increased from 1.9 to 4.2, since the population consisted of adults and their progeny, living on the same plants. The frequency f of unoccupied terminals was considerably greater than would be predicted by a random, i.e. Poisson, distribution with the observed mean number of aphids per terminal. When the beetles arrived during 20-40 q, the average number of aphids per infested terminal fell to its minimum level of one, a probable result of the activity of the beetles. When beetles search plants, they catch only a small proportion of the aphids and scatter the rest on the plants. When the beetles left, the aphids became aggregated again as the mean density increased.

At first the simulation model used the simplest possible predation function. The beetle's voracity was measured by feeding average-sized aphids to adult *C. trifasciata* in the laboratory. It was recorded as a number of aphids; later, we used biomass. If there are b beetles per terminal, and each eats k aphids per q, the demand for aphids will be kb per q. If there are a aphids per terminal, each aphid must expect to be eaten kb/a times per q. If the beetles search at random, the aphids will escape predation with a frequency equal to the zero term of the Poisson distribution, which in this case equals $\exp(-kb/a)$, a crude expression that worked well in previous cases (Hughes &

Gilbert 1968, Gilbert & Gutierrez 1973). When this survival rate, calculated in the model for every q, was applied in the population model, the aphid numbers rapidly decreased to zero (curve B, Fig. 1). But the field counts of beetles probably underestimated the true numbers, since some beetles escape notice. We therefore concluded that:

(1) The beetles were sufficient in timing and numbers, to explain the early season reduction in the aphid population.
(2) The success of the beetles in finding aphids at low density was considerably less than that predicted by random search.
(3) No conceivable mathematical function which includes only the current average numbers of predators and prey, can predict the survival rate of the prey: aphid and beetle numbers were much the same at 30 q and 90 q, yet at 30 q aphid numbers declined, and at 90 q they increased (Fig. 1). The true predation rate must therefore be affected by some other factor, which might be some characteristic of the predator or prey populations, e.g. age distribution or aggregation (cf Hassell & May 1973), or some environmental factor. We decided to study the predation process in detail.

2. PREDATION IN THE LABORATORY

Holling (1966) has shown how to study the actual process of predation with great realism. Rather than invoke theoretical functions and assumptions, Holling studied the detailed behaviour of the predators and prey, to determine the important biological parameters which predict the 'functional response'. But his approach is too complex for application in the field. We needed a simpler model of predation, at once realistic but simple enough for field use. We decided to study predation in an artificial arena to identify those essential components which must unavoidably be measured in the field. To avoid duplication of symbols, we shall freely mix algebraic and FORTRAN notations.

Methods

The tests were made in standard greenhouse flats each containing 12 small alfalfa plants arranged in a 3 x 4 grid. Each plant had a single stem with many of its leaves removed, so that the aphids could easily be seen. To make the aphids visible when on the ground, the soil was covered with white sand. The sand was kept wet because the beetles made poor traction on dry sand. The aphids and beetles were confined by a transparent plastic cage 29 cm x 45 cm and 21 cm high. To prevent the insects from walking up the walls of the cage, its lower rim, which rested on the sand at the edge of the flat, was coated with Fluon (a brand of polytetrafluoroethylene dispersion supplied by Imperial Chemical Industries Ltd.). All the coccinellid species found in the field, except one, readily flew off the plants and landed on the cage, so nullifying the test. The exception was *C.u. undecimpunctata,* which we adopted for the laboratory work.

We re-defined 'hunger' as that weight of aphids which a beetle will voluntarily eat until satiated. We established the hunger curve by feeding forty beetles until they refused to eat aphids presented directly to them, then starving them for various time periods at 24 ± 1°C, and weighing them. Each was again fed to repletion, and its increase in weight recorded. After 24 hours' starvation, males of *C. u. undecimpunctata* will eat a maximum of 2.0 mg. of aphid on average, and females about 3.0 mg. We therefore write HGR = 2.0xH for males, and 3.0xH for females. The curve for H (Fig. 2A) is of the type $H = 1 - \exp(-kt)$ (Holling 1966). Thus we shall use H for the *relative* hunger, the same for both sexes, and HGR for the *absolute* hunger.

The laboratory tests were done in a controlled room at 24.0 ± 1°. We placed aphids in known numbers and instars on the 12 plants, and left them to settle. Then we chose a beetle of known sex, which had been starved for a predetermined time at constant temperature, so that its initial hunger HGR could be estimated (Fig. 2A). Dixon (1959) has shown that a coccinellid changes its search pattern when it makes contact with an aphid, even if it does not capture the aphid. Therefore, each time the beetle climbed onto a plant, we recorded its hunger HGR and the time TLC since the beetle last contacted an aphid. At the start of each test we allowed the beetle to make contact with an aphid but not to capture it. Both HGR and TLC were thus established at the start of each test.

The beetle was placed on the sand inside the cage, where it began to search the plants for aphids. For every visit to a plant, we recorded the following: plant height; the number of trifoliate leaves; numbers and instars of the aphids on the plant at the start of the visit; numbers and instars of aphids which were eaten, which fell from the plant but returned to it, and which fell and left the plant for another; whether or not the beetle made contact with an aphid on the plant; and the lengths of time which the beetle spent in searching the plant, stationary on the plant, moving on the ground after it had left the plant, and stationary on the ground.

A beetle is stationary when it is eating, cleaning its appendages or resting, usually when it is not hungry. A beetle detects aphids only when it contacts them with its maxillary or labial palps. After contacting an aphid, the beetle scours the locality very thoroughly, making frequent turning movements. When a beetle searches a plant, many of the aphids on

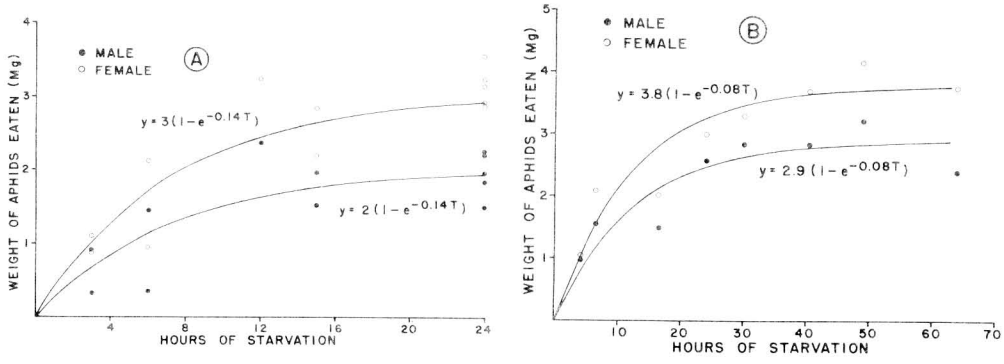

FIGURE 2A. Hunger, HGR, curves of Coccinella **undecimpunctata** at 24°C; B, C. **trifasciata** at 20°C. Each point is a mean value from about 40 beetles. The physiology underlying the variability in hunger has not been explored, but females tend to vary more in weight than males because captive females may lay eggs, and may or may not eat them.

that plant fall off, and so avoid predation. The aphids rarely left plants unless disturbed. We tallied the aphids as they moved from plant to plant, by means of counters which were moved correspondingly from square to square of a checkerboard. In this way, the current population of any plant was known whenever a beetle climbed onto it. A beetle can capture and eat aphids of all sizes, and the average time taken to consume an aphid is directly proportional to the aphid's weight (Fig. 3). But not all pea aphids are equally at risk. The older and larger aphids drop from plants much more readily than the young ones, so that first and second instar nymphs are those most vulnerable to predation. Large aphids which have fallen off a plant can find their way onto a new plant much more readily than can small aphids. In particular, a winged adult is largely immune from predation, partly because it readily falls off the plant, and partly because the beetle usually seizes the aphid by its wings and so cannot eat it without first letting go, whereupon the aphid usually escapes.

We made fifty such laboratory tests, each lasting an hour or more. Altogether, 2,020 plant visits were recorded, with varying numbers and distributions of aphids. When two beetles were placed in the cage together, they searched independently.

Analysis

The next step is to determine, from the data collected in the laboratory tests, the 'components' of the predation process (Holling 1966). The measurements taken were very variable, but regression analysis revealed the following relationships, which were similar for both sexes. The probability, PC (Table 1) that a beetle would make contact with an aphid on a given plant was proportional to the beetles' hunger, HGR, and to the number of aphids on the plant. That probability was never very

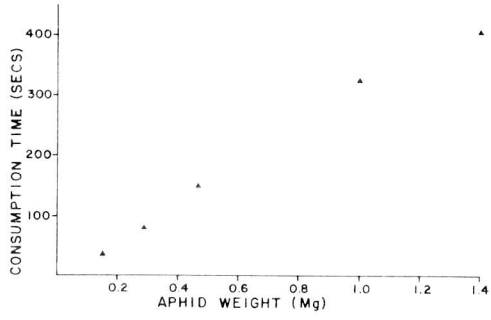

FIGURE 3. Times taken by adult C. **undecimpunctata** to eat various instars of aphid at 24°C. Each point is a mean of between 9 (adult) and 70 (1st instar) aphids.

TABLE 1. Variable Names and Their Meaning

AWT—weight (mg) of one aphid; which varies with instar (Table 2).
HGR—hunger (mg) of aphid (Fig. 2).
H—hunger, on a relative scale from 0 (replete) to 1 (fully hungry).
PC—probability that a beetle will make contact with an aphid.
PE—probability that a beetle will eat an aphid.
PL—probability that an aphid will leave a plant.
TLC—time (sec) since a beetle last contacted or ate an aphid.
TS—time (sec) spent searching a plant.

great. If no contact was made, the time, TS, which the beetle spent on the plant, increased with plant size and decreased with TLC, the time since last contact. According to the regression analyses, 'plant size' is best expressed as the simple product of plant height and the number of leaves. The probability, PL, that any given aphid shall leave a plant increases with TS. If contact was made, the probability, PE, that the beetle ate any given aphid was proportional to HGR. Since older aphids fell off and escaped predation more easily than younger ones, the probabilities PL and PE had to be corrected by factors appropriate to the different aphid instars (Table 2) present on the plant.

When no aphids were eaten, TS increased with plant size: when some were eaten, TS increased with the total number of aphids on the plant, and additional time elapsed while the beetle ate its prey and cleaned its mouth parts. Time spent in eating was proportinal to the biomass of the aphid eaten (Fig. 3). Whether or not any aphid was contacted, PL increased with TS: but PL (with contact) exceeded PL (no contact), because the beetle searched the plant more thoroughly after it had made contact. The beetle also spent time on the ground, while moving between plants. If the beetle was hungry (HGR was large) or if it had recently contacted an aphid (TLC was small), it spent a relatively short time on the ground.

These relationships were built into a simulation model of the predation process. Since the relationships are all linear, the model uses average values; for example, TS is actually very variable, even allowing for plant size, etc., but the model uses the average value appropriate to the particular circumstances. Since the model represents events in the laboratory only, we shall not describe it in detail: but later we shall present a similar, but simpler, model of predation in the field (Appendix 3). The laboratory model was checked, and the values of PE and TS were altered in order to reproduce the timing and frequencies of eating and leaving observed in all the various experimental conditions.

We then analysed the laboratory model to see which features could safely be omitted—especially those difficult to measure in the field. The most important conclusion was that although contact certainly influenced the behaviour of individual beetles, its effect could be absorbed into the values of PE and PL, and so the whole mechanism of contact could be omitted, provided the PE and PL were modified appropriately. This was fortunate, since it would be almost impossible to observe TLC in the field. However, the contact mechanism might cause PE to increase with the number of aphids on the plant. But an analysis of the numbers of aphids eaten on plants with varying initial numbers of aphids, showed no tendency

TABLE 2. Values of AWT, FACTE and FACTL

Average weights (mg) of aphids in the field (AWT) in 1973 and 1974. Aphids in the laboratory were generally lighter (cf. Appendix 3). When a beetle visits a plant, each aphid on that plant is eaten or leaves the plant, with *relative* frequencies FACTE and FACTL respectively. The frequencies were estimated during the laboratory tests. They must be multiplied by appropriate constants to give absolute frequencies PE or PL.

Aphid	AWT	FACTE	FACTL
Instar 1	0.17	1.68	0.64
Instar 2	0.33	1.28	0.68
Instar 3	0.91	0.75	1.05
Instar 4	1.88	0.52	1.13
Adult wingless	3.82	0.46	1.29
Adult winged	2.15	0.36	1.97
Mummy	1.88	0.57	—

for PE to vary; except that once one aphid had been eaten, other aphids on the same plant were slightly more likely to be eaten. The effect could be ignored, leaving hunger as the sole driving mechanism.

3. PREDATION IN THE FIELD

This section converts the laboratory predation model to represent the same process in the field, and uses it to predict the survival rate of aphids in the field. As far as possible, we measured all the model's parameters again, by watching and timing beetles in the field.

Timing

In the first series of field observations, we watched beetles searching at a low aphid density of about 0.2 per terminal. One observer followed the beetle's progress over the vegetation, while another timed and recorded each visit to a new plant. In this way, we estimated the average time, TS, which a beetle spends on a plant when no aphid is eaten. The estimate of TS, i.e. 51.3 sec (Appendix 3), is the average of 504 plant visits.

It was not necessary to measure the sizes of the alfalfa plants in the field. They were generally larger than those in the laboratory, with more leaves and branches. But the beetles did not search the entire plant; instead, they primarily searched the sunlit canopy of contiguous leaves and stems, where most of the aphids were. Most importantly, neighbouring plants touch, and so both aphids and beetles walked or flew freely from plant to plant. The beetles spent no time on the ground while searching for aphids, and the time spent on any plant did not depend on that plant's overall size.

Probability of Capture

In another series of field observations, we seeded lengths of row with high densities of aphids, and watched the beetles search for them. The average density of aphids on these plants was determined afterwards by sampling. That density, multiplied by the total number of plants visited (286), gave the total number of aphids at risk, 1746. Of those, 32 were actually eaten, giving a frequency PE of capture of 0.018. In the model, PE equals a constant times the relative hunger H. This constant is tentatively deduced as follows: since the beetles flew in from other parts of the field where aphids were scarce, we assumed that the beetles were very hungry, with H=0.88, corresponding to 15 h starvation as set initially in the model (Appendix 3). The constant must therefore be 0.018÷0.88, so that PE=0.0205 x H. This equation is re-examined in Appendix 4. The value of PE is much lower in the field than in the laboratory, because in the field a beetle makes only a cursory search of each plant, but searches many more plants in a given time. The same series of field observations gave the average time spent on one plant when aphids were eaten. In the laboratory model, PE was a function of time searching, which in turn was a function of plant size. In the field model, PE is no longer affected by plant size, and therefore the distinction between time searching and not searching is no longer required. Regression analysis of the field data shows that the time spent on a plant increases with the number of aphids eaten; so in the model, it appears as a linear function of the total weight of aphids eaten (Fig. 3).

Probability of prey movement

We could not directly measure PL, the probability of an aphid leaving a plant, because it was impossible to see how many aphids left during a visit by a beetle. However, PL must depend on the beetles' searching behaviour in much the same way as PE. Therefore, to estimate PL in the field, we took the frequency with which aphids fell off the plants in the laboratory, and changed it in the same proportion as the observed change in PE. The resulting value of PL must clearly be suspect; fortunately, analysis of the model showed that within reasonable limits, the value of PL had little effect on the predation rate. This does not, of course, imply that the aphids' behaviour in leaving the plant did not affect the predation rate, for that behaviour affected PE as well as PL. Having thus obtained overall values for PE and PL, we used the same factors (Table 2) as were observed in the laboratory, to compute the probabilities for each aphid instar. This was unavoidable, since it was impossible to count all the aphids of each instar on a plant in the field without disturbing them. However, these corrections were reasonable, because the relative frequencies depended more on the behaviour of the aphids than of the beetles. Most of the aphids captured by beetles in the field, were the youngest, as in the laboratory.

We now use these rules to develop the field model for predation (Appendix 3). It is impossible to determine the sex of each beetle encountered in the field without unduly disturbing it, and so the field model assumes a 1:1 sex ratio.

Effects of Temperature

The model describes events during one q at 18.5°C, the average temperature during the field observations. But the times spent on each plant are related to the speed at which beetles move and thus to temperature. We placed beetles of the three species on vertical poles in the laboratory, and timed their walking speeds at different temperatures. The result (Fig. 4) shows that the beetles' walking and searching speed has about the same temper-

ature threshold as the aphids' rate of development, and so we may use the same physiological time-scale for both predators and prey. The field predation model therefore describes the predation process during one q at any ambient temperature.

Temperature has an additional effect on coccinellids. At low temperatures, many of the field beetles are inactive (Fig. 7), even though they are capable of motion (Fig. 4). The physiological time-scale thus allows for the effect of temperature on the beetles' speed of search when active, but not for the variable amount of activity. Therefore, the number of beetles actually present at any given time must be multiplied by an activity coefficient, to give the effective number of active beetles. At first, we used the data in Fig. 7 to estimate the activity/temperature relation, with a temperature threshold of 8.7°C. But later we found (§ 5) that the counts in Fig. 7 are still biassed. The field cage experiments in § 5 demand that the temperature threshold be reduced to 4°C, the same value as for beetle movement. The algorithm used to calculate the approximate average temperature, for each q in the field, appears in appendix 5. Despite several attempts, we have not obtained a **direct** estimate of the activity/temperature relation, which is complicated by effects of sunshine and by some kind of circadian rhythm. But the fact that temperature has a double effect on the beetles, and a single effect on the aphids, has important consequences for the predator-prey relationship (§ 6).

Analysis

The aphid survival rates, predicted by the field predation model, will now be applied to the aphid population model. It would be possible to build the predation simulation model directly into the aphid population model, by calculating the survival rate *de novo* whenever it is needed. To do so would take impracticable amounts of computer time. The results of the predation model are best expressed as empirical functions which can be used directly in the population model.

The predation rate must depend on beetle density, and on aphid age-distribution, density and possibly aggregation. All these parameters must therefore appear in the empirical function. The problem is not really so complex. For the model shows that the overall survival of a mixture of aphids of different ages is about equal to the weighted average of the predicted survival rates of the individual age groups. For example, it shows that the survival of 0.2 adult + 0.6 instar I aphids/plant (total density = 0.8) is, very nearly, ¼ of the survival of 0.8 adults/plant + ¾ the survival of 0.8 first instar/plant. Moreover, the survival rate must be squared when the beetle density is doubled, since the beetles search independently of each other. The model shows just that effect, which incidentally proves that the model's time-step of one q is short enough, as far as the beetles are concerned: that is, within one q, no beetle can destroy so many aphids that it seriously reduces the number of prey available

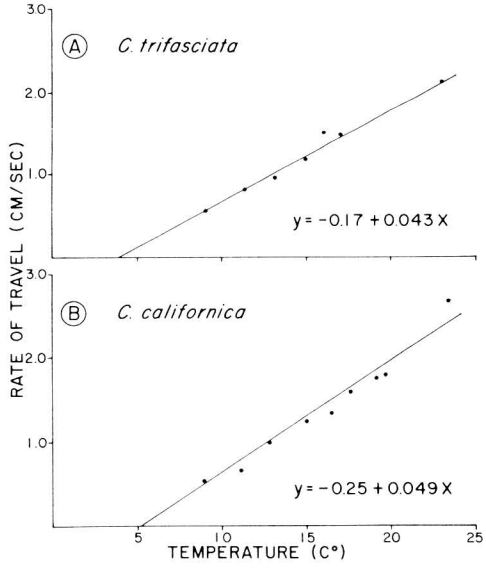

FIGURE 4. Effect of temperature on coccinellid walking speeds. Each point is a mean of about 40 observations.

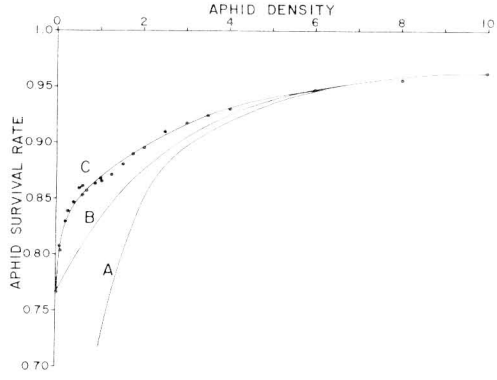

FIGURE 5. Survival rates per q, computed by Appendix 3, of second-instar aphids attacked by C. trifasciata. Coccinellid density=1/60 plants. Curves A, B, C are fitted in Appendix 4.

to other beetles. These circumstances permit us to analyse the predation model, using beetles at a fixed density, and aphids of one instar only. We used second instar aphids, and beetles at the highest density observed in the field, *viz.* 1 per 60 plants. We chose this case because it gives high aphid mortality, and therefore accurate estimates of survival rates. For each aphid density, the model (Appendix 3) was run many times, using different random numbers: the average survival rates predicted for varying aphid densities are shown in Fig. 5. They do not lie precisely on a smooth curve because they are estimated by this 'Monte Carlo' method, which estimates the survival rate from a finite number of trials.

The effects of aphid distribution or aggregation on predation rate are slight according to the field predation model. At average densities of less than one per plant, the survival rate is slightly lower when the aphids are highly aggregated on few plants, than when well spread out on isolated plants. That is because, having found one aphid, a beetle easily finds the others on the same plant. There is no such effect at high aphid densities, when a beetle can find enough aphids irrespective of their distribution.

By contrast, the laboratory predation model showed a great effect of aphid distribution (Fig. 6): the predation rate might be three times greater when the aphids were clumped, than when they were well spread out. This was an effect of timing, which persisted after the contact mechanism was eliminated from the model. It arose because, in the laboratory, the beetles could not climb directly from one plant onto another, and therefore spent a long time

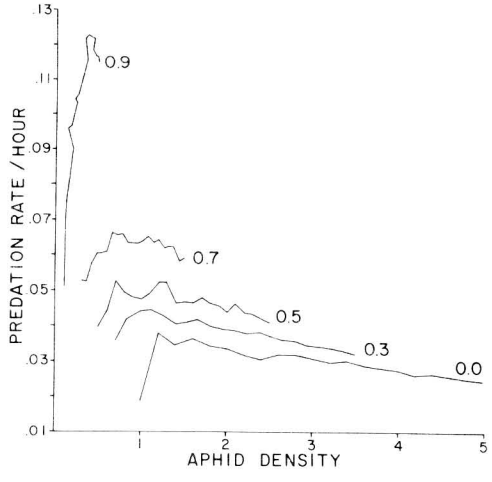

FIGURE 6. Predation rates per beetle-hour at 24°C, computed by the laboratory predation model, of second instar aphids when attacked by C. **undecimpunctata.** Coccinellid density = 1/100 plants. Different lines refer to different initial proportions of uninfested plants, as marked.

on each plant. In the field, however, the beetles moved directly from plant to plant, and thus visited many more plants for each aphid caught.

A predator-prey relationship might indeed be stabilized by predators scattering their prey (cf. Huffaker, Shea & Herman 1963), but not in our alfalfa plot, where the predators ranged freely and quickly over the area. We therefore ignored the slight effect of aphid distribution found in the field predation model, because it was equivalent at most to a 5% increase in beetle density, which is well within the accuracy of our field counts.

The next task was to fit an empirical function for survival from predation. We already knew how to deal with varying beetle densities and mixtures of aphid instars, so we needed only to fit a curve to the predicted points in Fig. 5. This was done (Appendix 4) and the resultant expression for the survival rate of aphids of instar I is

$$\underline{s} = \exp\left(\frac{-5.7}{AWT(\mathrm{I})} \times \frac{b}{a}\ (1 - \exp(-\underline{k}a))\right)$$

where $\underline{k} = 2.6 \times AWT\ (\mathrm{I}) \times \underline{FACTE}\ (\mathrm{I}) \times (0.654 + 0.026/\underline{a} + 0.075))$. This expression for s gives the fitted curve C in Fig. 5. By contrast, curve A is the random search curve, discarded in§1.

During the period 1 - 121 q of 1972 (Fig. 1), field densities of aphids were always less than one per plant. At these densities, the survival rate predicted by the model is very much higher than the random rate (Fig. 5), for the following reason: random search implies that the beetles can find aphids immediately, whereas the model imposes a time restriction. At low aphid densities, there is far too little time within a single q for a beetle to visit enough plants to find all the aphids it needs. Little wonder that random search in § 1 incorrectly predicted the demise of the aphid population.

4. BEETLES AND APHIDS COMBINED —FIRST ATTEMPT—

This section tries to reconcile the predicted predation rate with the observed survival rate of aphids in the field. By the time we had completed the field predation model, we had obtained population records from a new season which showed that the 1972 beetle counts were inaccurate. We therefore shall not use the 1972 data further, but instead describe the field methods used in 1973.

Sampling and field biology

Two plots of Alfa alfalfa were sampled 0.8 km apart on the grounds of the University of British Columbia. Plot 1 was that sampled in 1972. Plot 2, sown in 1972, consisted of 26 rows each 15 m long and 1 m apart. When the alfalfa was cut infrequently, the plants produced numerous lateral branches which made our sampling units of plant terminals ambiguous and ill-defined. We therefore departed from standard commercial practice in 1973 by cutting more often, whenever the plants reached about 1 m in height. All the rows were cut simultaneously on plot 1, but even- and odd-numbered rows of plot 2 were cut alternately, so that half the rows always contained tall plants bearing aphids. We sampled the even and odd rows of plot 2 separately, whereas plot 1 was sampled as a unit. Aphid samples were taken by cutting individual plant terminals and beating aphids off. The small-scale distribution of aphids over the plants does not seriously affect the predation rate in the field (§ 3). We looked for consistent large-scale patchiness, by taking samples from a regular grid pattern over the whole alfalfa plot. There was none. The number of terminals per sample varied between 40 and 400, according to the aphid density. Aphid samples were taken from each plot at least once a week, but 2-3 times a week during warm periods, when aphids were developing quickly.

The 1972 method of counting coccinellids and parasite mummies gave reproducible results; but we later found it to be inaccurate because mummies are easily overlooked and beetles are most easily seen when temperatures are high. Instead, we randomly chose between 40 and 70 short (30 cm) lengths of row, and searched them thoroughly for beetles. Beetle numbers changed rapidly (Fig. 8), and so we sampled almost daily during the main period of attack. Each beetle was classified by species, and according to whether it was moving or stationary when first sighted (Fig. 7). The ambient temperature inside a Stevenson screen placed on the ground in the plot was also recorded. The same species of coccinellids were found as in the previous year, but since *C. johnsoni* was observed freely mating in the field with *C. californica*, we counted them as one species. The dominant species was again *C. trifasciata*, which was three to five times as common as *C. californica*. The other species were comparatively rare.

We counted mummies at least twice weekly by the same method used for beetles. The mummies were classified as unemerged, emerged or preyed upon. The latter are easily recognized because the edges of the irregular holes made by coccinellids or the punctures made by chrysopids and nabids are darkly stained; the circular emergence holes of primary parasites and the irregular emergence holes of hyperparasites are not stained. We took samples of unemerged mummies from time to time and reared them at constant temperature, to estimate the sex-ratio of the parasites, their age-distribution, and rates of hyperparasitization.

The numbers of plants per foot of row were counted at various times through the season, to

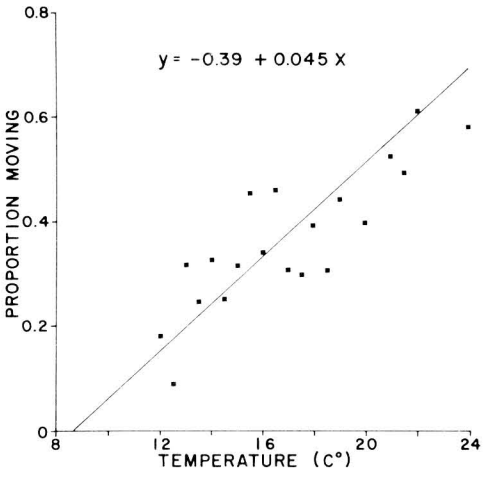

FIGURE 7. Effect of ambient temperature on proportion of C. trifasciata observed moving in field counts. For absolute numbers, see Fig. 10.

reconcile the two methods of sampling, *viz.* aphids/terminal, and beetles/length of row. We made checks by enclosing all the plants in one-foot lengths of row in plastic bags, cutting the plants at the base, and counting all the aphids and mummies found in the bags. Consistently, the average number of mummies/ft. was about twice that observed in the regular counts, mainly because mummies on the underside of the leaves or low on the plant, had been overlooked. The regular counts therefore are multiplied by the appropriate factor to correct for this under-estimate. Equally consistently, and irrespective of average plant height, total numbers of aphids/ft. were only half those predicted by multiplying the number of plants/ft. of row by the average number of aphids/plant derived from aphid samples. This is not unreasonable, since tall plants are much more heavily infested than the short ones. We therefore divided the counts of plants per foot by the appropriate correction factor to give the number of effective plants per foot.

Synthesis

Next we insert into the population model the aphids' rate of survival from predation, calculated by the field predation model, and using the new beetle density *b*. We make no distinction between the different species of coccinellids, but equate them all to *C. trifasciata*, which was always in the majority.

On plot 2 (1973), a generation of parasites matured during the period of coccinellid attack (Fig. 8). The mortality due to parasitism must therefore be inserted into the aphid population model. The best estimate comes from the field counts of mummies, and we therefore include in the model an amount of parasitization which reproduces the observed pattern of parasite mummies, both in time and numbers. We used the following method: the developmental threshold for the parasite *Aphidius ervi* is 4.2°; thus the two physiological time-scales are in proportion throughout the period of beetle attack. The length of time spent by a parasite in the mummy can therefore be equated to a fixed amount of the aphid's physiological time, namely 15 q.

It is the juvenile aphids between ages 4 q and 17 q which bear the brunt of the parasite attack (A. Campbell, pers. comm.). Laboratory tests showed that parasitized aphids, collected in the field in their fourth instar, can produce up to 26 progeny before the parasite pupates and kills the aphid. We therefore represent parasitism in the following way: parasitized aphids are not distinguished from unparasitized aphids in the model until the time comes for the parasite larvae to pupate. Then a proportion of aphids in the appropriate age-range is converted into parasite mummies. The correct proportion of parasitized aphids will thus produce their appropriate number of progeny before they die. The proportion of aphids converted into mummies, varies with time. The proportions were chosen by trial-and-error, to give the observed numbers and time-pattern of mummies in the field.

The parasite mummies are themselves subject to coccinellid attack, and therefore form a distinct class of prey in the predation model. The model gives the observed proportion of preyed-upon mummies, only when the predation rate on mummies is reduced to one-third the predation rate of first instar aphids (Table 2). Unlike healthy aphids, parasitized aphids often move to the upper surfaces of leaves, where beetles rarely search. The mum-

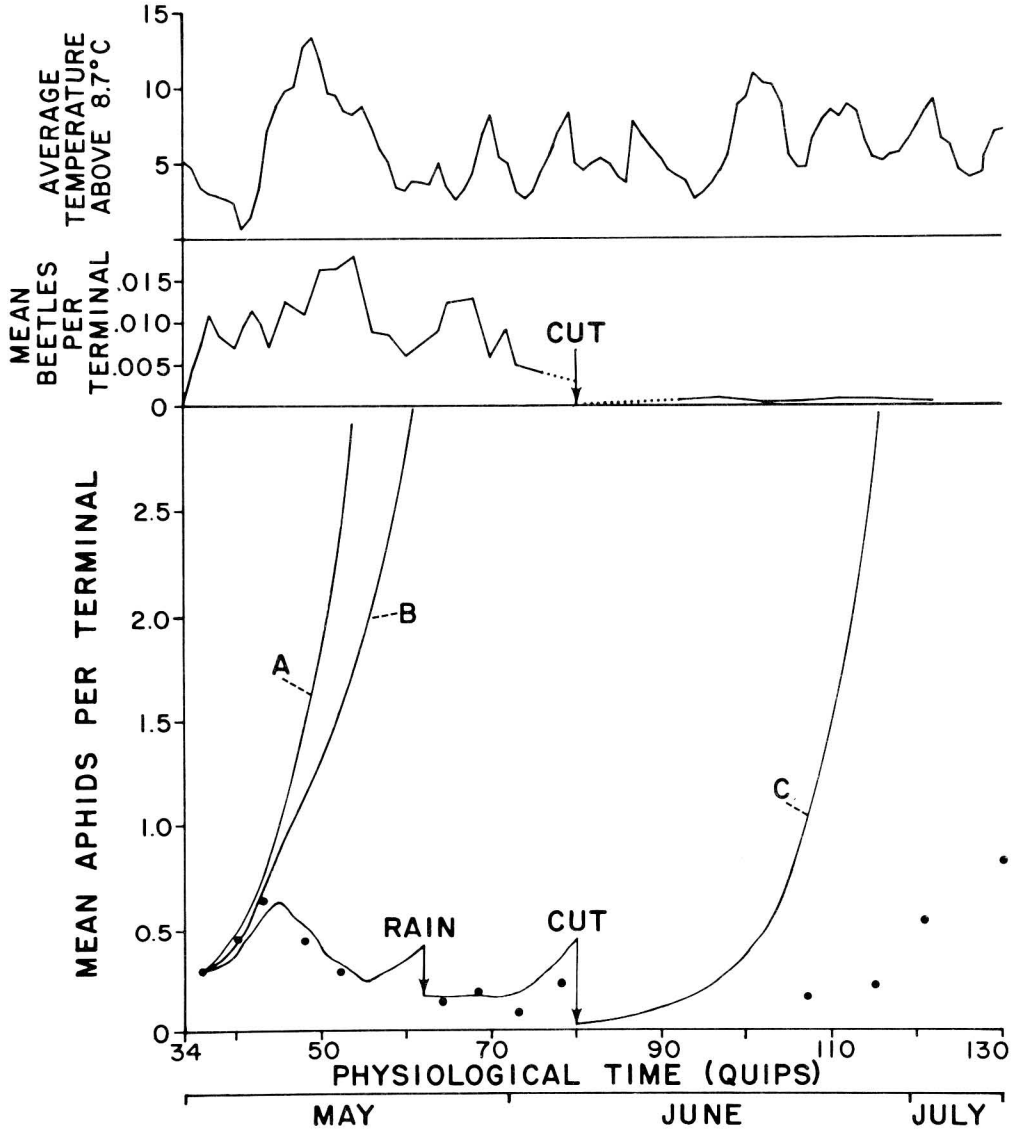

FIGURE 8. Numbers of beetles and aphids in 1973, plot 2, even-numbered rows. The upper section shows the weighted average temperature/q. TEMP, above the activity threshold 8.7°C. It is computed by Appendix 5 and used in Appendix 6. The middle section shows the field counts, COCC, of beetles/plant. The temporary increase in beetle numbers during q 60-q 65 occurred when the odd-numbered rows of alfalfa were cut, and the beetles moved to the uncut even-numbered rows. The lower section shows the observed numbers of aphid/plant, together with three curves computed by Appendix 6. The population model reproduces the effect of heavy rain at q 62 by imposing the appropriate survival rate on the aphids; similarly when the alfalfa was cut at q 80. These survival rates were found empirically by comparing aphid densities before and after the event. Precisely the same survival rates were observed on plot 1 and on the odd-numbered rows of plot 2.

mies therefore suffer an unexpectedly low rate of predation.

Fig. 8 shows the population dynamics of aphids and beetles on the even-numbered rows of plot 2, during and immediately after the period of beetle attack in May and June, 1973. The physiological time-scale starts on March 1, 1973. The pattern of events was very similar on the odd-numbered rows of plot 2, and on plot 1, i.e., the coccinellids arrived when the aphids were increasing in numbers, and the aphid population then declined, the beetles left, and the aphids again resumed their exponential increase. The same thing had happened in 1972 (Fig. 1).

Aphid numbers never exceeded an average of 0.7 per terminal during the period shown in Fig. 8, and so no density-dependent competition for food can be invoked. The population model simply combines fecundity rates for the aphids with the predicted survival rates from coccinellid and parasite attack. To explain the observed changes in aphid numbers the model must predict rates of survival from parasitization and predation, equal to those which the aphids actually experienced in the field. The predicted effects of parasitization and predation are too low to prevent a steady increase in simulated aphid numbers (curve B, Fig. 8). If the number of beetles is arbitrarily quadrupled, the model simulates the observed aphid numbers well enough for the period 15-79 q during the beetle attack (curve C, Fig. 8). We are out by a factor of four.

The curves in Fig. 8 were computed (Appendix 6) using the laboratory estimate of aphid fecundity. Much later we found (§ 5) that fecundity in the field is consistently only 30% of the laboratory estimate. This largely explains why curve C (Fig. 8) rises too fast during the period 80-130 q, when few coccinellids were seen. But it does not explain the discrepancy during the period of beetle attack. Using the true aphid fecundity, the observed number of beetles must be doubled, if the population model is to reproduce the field data. Fig. 9 shows the results of laboratory experiments to test the effect of high temperatures on aphid fecundity. There was no effect until the temperature exceeded 27°C, which was the highest temperature observed in the field. Thus the new population model gives a better approximation of the true mortality, than the 'random search' of § 1; but it now seems to underestimate the beetles' destructiveness.

5. BEETLES AND APHIDS COMBINED —SECOND ATTEMPT—

This section reconciles the predicted predation rate with the prey population dynamics.

In 1974, we erected four cages on plot 1. Each cage was 5 x 6 x 2 m high, and contained three rows of alfalfa each 6 m long. The cages were covered with translucent plastic and screening, which together admitted light, fresh air and rain. The temperatures recorded in the cages were sometimes a few degrees higher, during the day, than those in the field outside. We used the cages to compare aphid population dynamics in the presence and absence of known numbers of coccinellids. These were first-generation beetles bred in the laboratory, partly to eliminate parasitism, but mainly because we could not rely on collecting enough beetles from the field, early in the season. Figs. 11-13 show the results of three successive experiments, made for different purposes and in different conditions. The first was to determine the number of ladybirds needed to make an obvious reduction in aphid numbers, without driving them down too low. It also examined the possibility that the aphids might suffer mortality, over and above the direct predation, when beetles drive them off the plant; for example, when the youngest aphids fall off a plant in the laboratory, they have difficulty in finding a new plant. This explains why they fall off so much less readily than the older aphids (Table 2), even though they suffer a greater rate of predation in consequence. The weather during this first experiment was cool and wet.

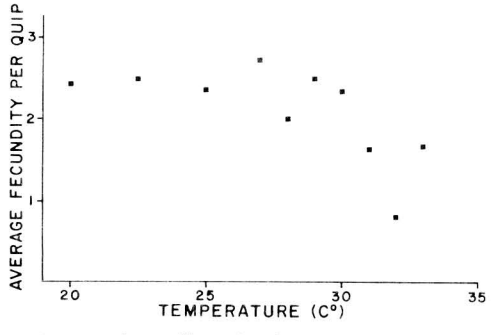

FIGURE 9. Effect of temperature on fecundity of aphids collected in the field and kept at constant temperature in the laboratory. Each point is a mean of about 20 adult aphids.

The second experiment, in warmer weather, was done in duplicate to see how much variation might occur between replicates. The third experiment, during a period of cloudy, warm weather, was started at variable aphid densities, partly to check for density-dependent restrictions on the rate of aphid increase, and partly to compare the predation rate at different prey densities. Each experiment ran until the alfalfa plants were too large for accurate sampling (§ 4), or until an incipient fungal epidemic threatened the aphids. After each experiment, the surviving coccinellids were removed and counted, the cages were sprayed with a short-lived insecticide, and the alfalfa was cut and allowed to grow for two weeks before the next experiment began.

Standard counts, as described in § 4, never revealed more than 25% of the true beetle numbers, even at high temperatures up to 28° and at low aphid densities. The ladybirds spent most of their time in the stubble at the base of the alfalfa. This observation itself can explain the remaining discrepancy: the beetle counts in the field (Fig 8) almost certainly underestimated the actual numbers present. The number of moving beetles (Fig. 10) increased steadily with temperature, but there was no corresponding decrease in the observed number of stationary beetles, which might be expected if all beetles had been visible.

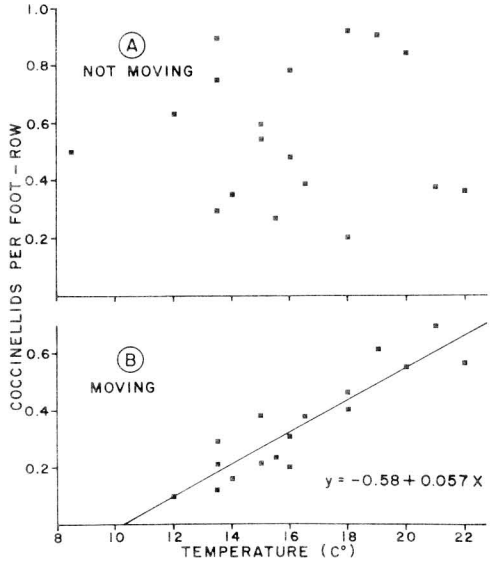

FIGURE 10. Effect of ambient temperature on numbers of C. **trifasciata** observed moving (10B), and not moving (10A), in field counts (cf. Fig. 7). Each point is the mean of counts from about 60 row-feet.

Analysis of cage experiments

Details of the individual experiments appear in the legends to Figs. 11-13. Each figure shows the means of successive aphid samples, together with the simulation curves generated by the computer. All broken curves refer to control cages without beetles. These curves all show the same rate of aphid increase, or, in other words different sections of the same curve of exponential population increase. They are not exponential at the start of the experiment, because of the initial, non-equilibrium, age-distributions. The relative rate of increase is the same at all aphid densities, but it is far less than would be expected from the aphids' fecundity, estimated in the laboratory. In fact, the broken curves are generated by imposing a 70% reduction in fecundity. We do not know the cause of this discrepancy, which has occurred consistently throughout the whole study, and in later work. Probably it means that fecundity in the field (which cannot be measured directly) is only 30% of that in ideal laboratory conditions. The discrepancy might alternatively be due to predation, at a constant rate of 70% throughout the season, acting on newly-born aphids only (to give the right age-distributions). In the control cages, we had to impose extra mortality of 1.3%/q on aphids of all ages. This 'background' mortality is ascribed to the numerous hunting spiders *Erigone metlakatla* Crosby & Bishop, observed in the cages. There was also a certain amount of parasitization, which we estimated

from counts of mummies (§ 4), and which increased from 0.3%/q in the first experiment to 1.0% in the third.

The 'disturbed' curve in Fig. 11 refers to a cage which contained no coccinellids, but in which the alfalfa was disturbed by hand four times/q, causing some aphids to fall off the plants, as they do when approached by a ladybird. If such aphids do not climb back onto a new plant, the rate of population increase will be reduced. There evidently is some reduction, but not much. The disturbance caused by a beetle is much less than that which we made by hand.

The unbroken curves in Figs. 11-13 were generated by imposing the additional mortality attributed to beetle attack. They assume that the predation occurs independently of the background mortality, i.e. that the overall survival rate is the product of the two separate survival rates. This is a very reasonable assumption, because each coccinellid searches independently of other predators and parasites.

The ladybirds also suffered mortality, mostly from predation by a web-spinning spider, *Enoplognatha ovata* (Clerck). We could not spray to control the spiders, for fear of provoking an outbreak of mites. Therefore, although we introduced known numbers of male and female beetles during each experiment, we do not know the exact numbers alive at any given time. After the end of each experiment, we collected ladybirds from the cages until few, if any, remained. We then computed the survival rate needed to reduce the initial numbers of beetles introduced to the final numbers recovered. The mortality proved to be rather more than 2%/q in all three experiments. The numbers of beetles shown in Figs. 11-13, although accurate at start and finish, thus depend on the assumption of constant survival rates. Our subsequent conclusions are not seriously affected by reasonable deviations from that assumption. At the end of each experiment we took bag samples (§ 4) to convert the numbers of beetles and mummies to a per-terminal basis.

Figs. 11-13 cover a range of field temperatures and aphid densities. We used more than twice as many beetles per cage in cool (Fig. 11), as in warm conditions (Fig. 13). If our understanding of coccinellid predation is reasonably complete, we should be able to apply a single formula (with appropriate temperatures, beetle numbers and initial aphid densities) to all three experiments. It is possible to do so. Every curve in Figs. 11-13 is computed by the same program; and all the parameters in that program, except three, have been estimated from other sources. Two parameters, *viz.* aphid fecundity and background mortality, were dictated by the aphid numbers observed in the control cages. The third parameter is the coefficient which specifies how beetle activity increases with temperature (§ 3). The curves require that beetle activity be, on average, 0.018 times the temperature above 4°C. This is merely an overall parameter chosen to reconcile the unbroken curves with the observations. The computer program, not listed here, is very similar to Appendix 6. We think that the agreement is good, bearing in mind the differences between replicates in Fig. 12. It could easily be improved by minor adjustments. The only serious discrepancy is in Fig. 11, where the computer predicts that increased temperatures, towards the end of the experiment, should have prevented the final increase in aphid density. In fact the weather remained continuously cloudy, which may have depressed beetle activity; we certainly need further information about the effect of weather on beetle activity. Otherwise, the agreement between observation and prediction is acceptable, and so we have a single formula, given in § 3 and used in Appendix 6, which satisfactorily predicts the predation rate over a wide range of temperatures and prey densities.

DISCUSSION

It does not follow that the components of the formula necessarily reproduce the biological details correctly. For example, we have ignored the fact that the hunger curve, used in the field predation model of § 3, refers to *C. undecimpunctata* (Fig. 2A), not to *C. trifasciata*. The hunger curve for *C. trifasciata* (Fig. 2B) was estimated at the end of the investigation, using beetles taken from the field cages. The observations in Fig. 2B were taken at 20°C. The curves in Fig. 2B predict a maximal consumption/q of 5.5 mg/beetle, as compared with the 5.7 mg for *C. undecimpunctata*, used in § 3. Thus the two species agree very closely in this respect, and there is no need to change the formula of § 3. But P.M. Ives informs us that female *C. trifasciata*, kept in the laboratory and fed *ad libitum*, ate only 4.4 mg per q on average. The reason is undoubtedly that given in § 3, that the initial hunger level of 0.88, used in our calculations, is too high for a well-fed beetle. There is therefore some residual ignorance about the voracity of coccinellids in the field, but it is unimportant here: for the computer program generates the same unbroken curves in Figs. 11-13, whatever the maximal consumption (within reasonable limits), provided that the temperature coefficient for beetle activity is altered accordingly. Thus the residual errors in beetle activity cancel the remaining errors in beetle voracity, to give identical predictions of the predation rate.

Whatever the true average level of coccinellid activity may be, it is certainly very low. Watching the predation process in the

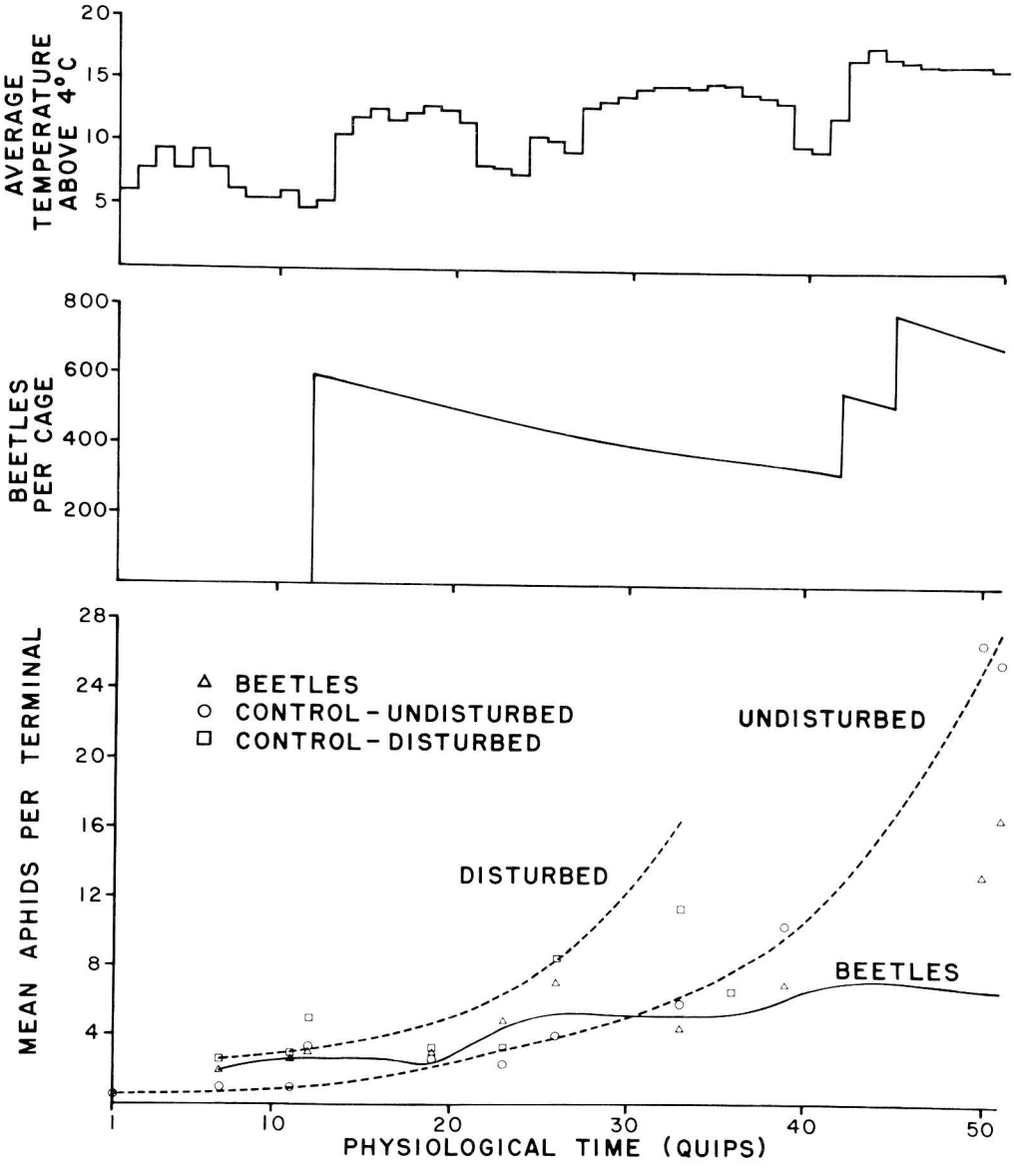

FIGURE 11. First cage experiment. In the lower section the points represent observed sample means but the curves were computed. Each sample in Figs. 11-13 contained about 27 plants, except at the start and end of each experiment, when each sample contained about 36 plants. The curves are largely independent of the observations—see text. The 'undisturbed' curve shows the exponential increase in the absence of ladybird predation. The 'disturbed' curve is computed on the assumption that mechanical disturbance of the plants, causing some aphids to fall off, causes no mortality. The solid line curve predicts the effect of predation by the numbers of beetles shown in the middle section, at the weighted average temperatures shown in the upper section. Compared with Figs. 12 and 13, temperatures were low and the number of beetles needed to show any obvious effect was consequently large. There was a fourth cage containing half the number of beetles shown here, which gave results intermediate between the 'undisturbed' and unbroken curves. To avoid confusion, those results are not shown.

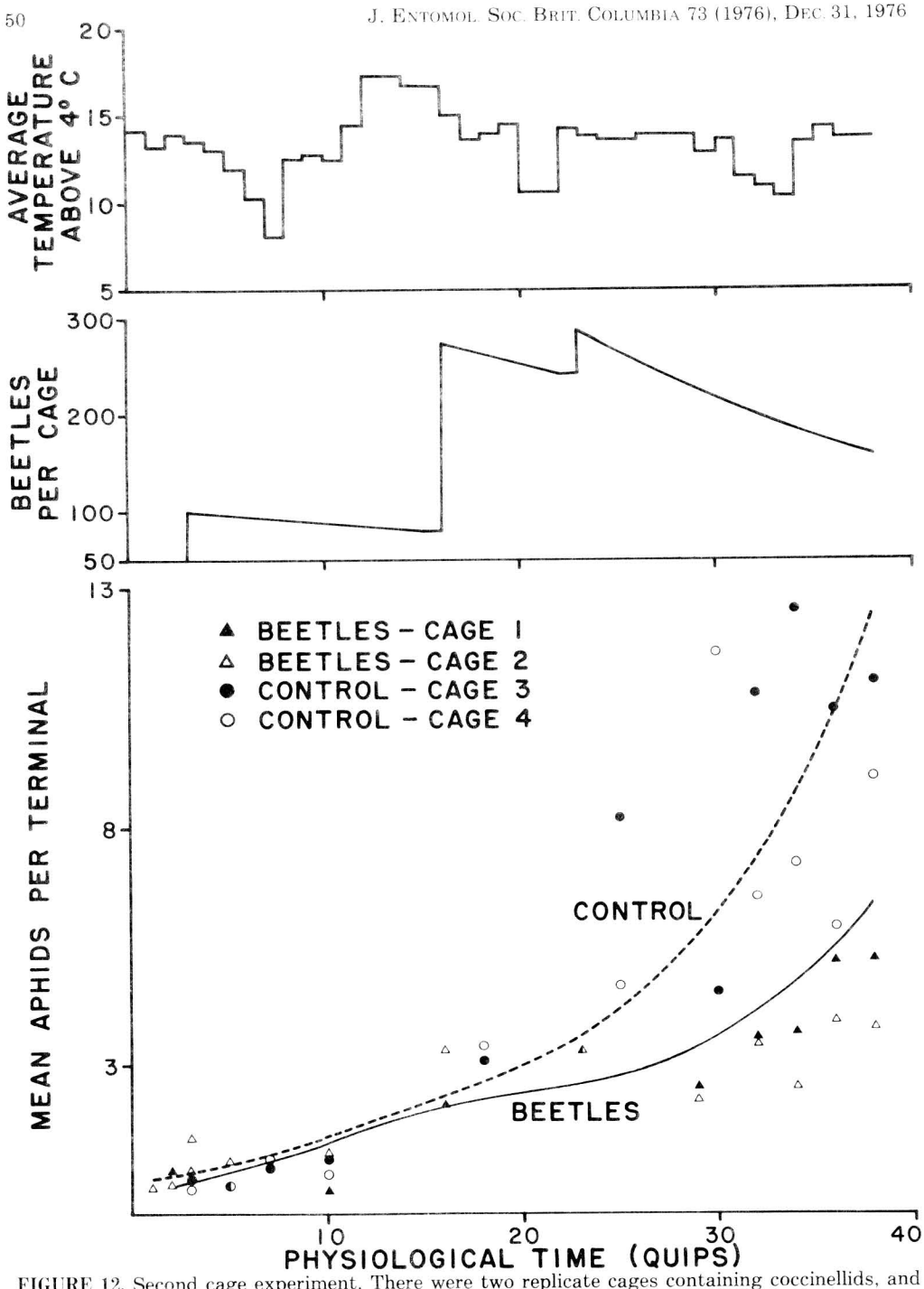

FIGURE 12. Second cage experiment. There were two replicate cages containing coccinellids, and two controls. Only one curve has been computed for each pair of cages. The differences between cages 1 and 2, and between 3 and 4, measure the variation experienced between replicates. These differences must be borne in mind during any examination of Figs. 11-13. Beetle numbers were the same at the start, but declined more in cage 1 than in cage 2, which partly explains the difference in aphid numbers. The number of beetles shown in the middle section is the average for the two cages.

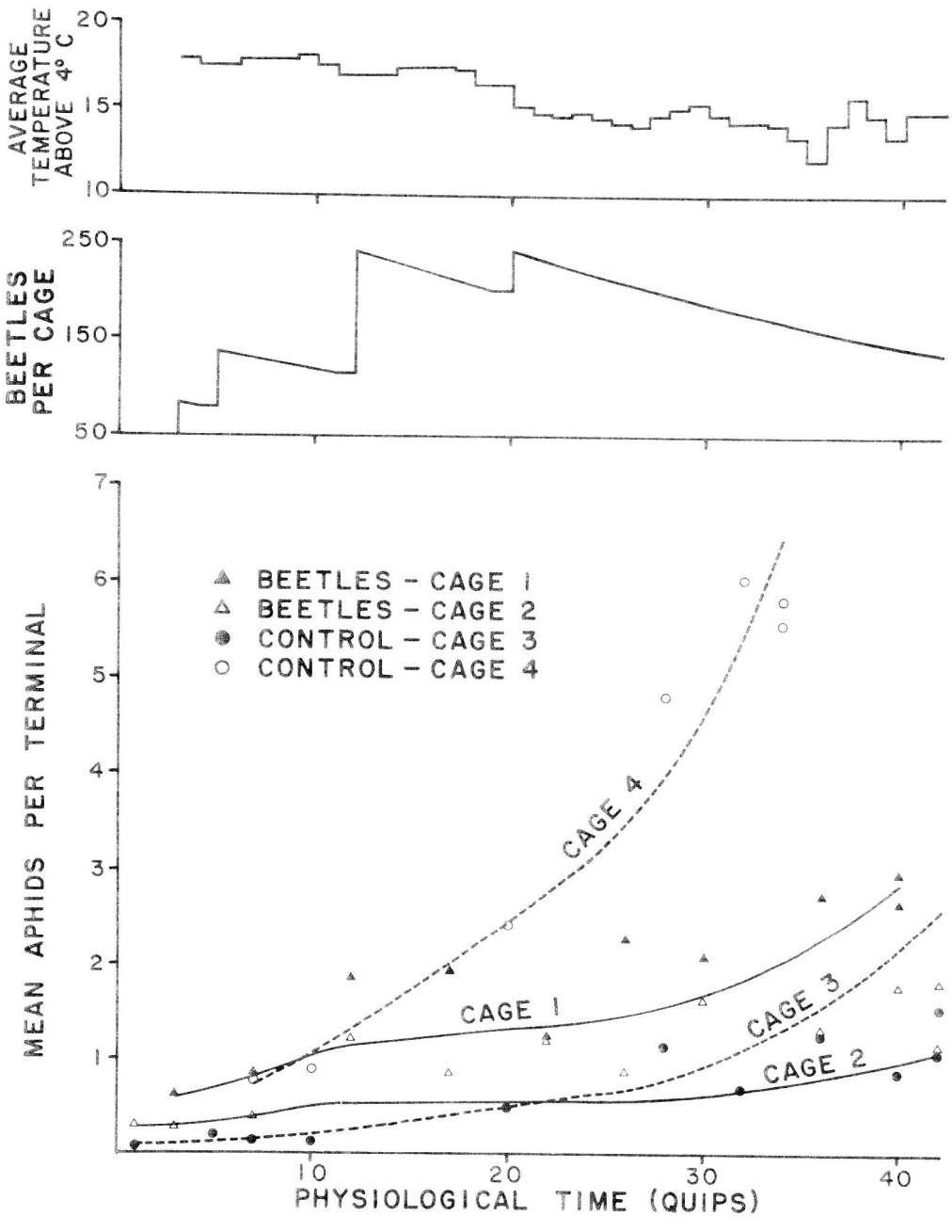

FIGURE 13. Third cage experiment. Different cages were deliberately started at different aphid densities, to examine the effects of aphid density on predation rate and rate of aphid increase. The curves predicted for cages 2 and 3 disagree with the data, but only within the limits of variation revealed in Fig. 12 (see text). The curve for cage 2 remains level from q 11 to q 25, but then begins to rise as temperatures and beetle numbers decline. This illustrates the principle that no equilibrium between aphid and coccinellid numbers can be permanent. Figs. 11-13 have different scales for aphid density. The number of beetles shown in the middle section is the average for the two cages: More survived in cage 1 than in cage 2, and the curves are computed accordingly.

laboratory, we saw a hungry predator anxiously scouring its universe for prey. Watching a population of beetles in a field cage in conditions almost identical with those of the open field, we saw the ladybirds spending a good three-quarters of their time motionless in the stubble. In the laboratory, there was nowhere to hide. The contrast between laboratory and field could not be greater.

The cage experiments give some information about possible interactions between predation and parasitization rates. If parasitized aphids suffer a higher predation rate than unparasitized, there will accordingly be a relative shortage of parasite mummies in the cages containing beetles. No large or consistent difference was seen: such heterogeneity as did occur was restricted to the first experiment, where the parasitization was begun by emerging overwintered adults.

The new formula for predation rate still does not resolve the discrepancy between observation and prediction in Fig. 8. In fact, it makes it worse, because beetle activity is less than we previously supposed (§ 4). We now need four times as many beetles as were actually observed, to produce the decline in aphid numbers shown in Fig. 8, 35-79 q. We can readily believe that, as in the field cages, there were four times as many beetles present as appeared in the samples. Although we have a good estimate of the predation rate, we still have no sure way of sampling beetle numbers in the field. Standard methods using sweep nets, walking counts, or suction machines, are hopelessly inaccurate. Our intensive counts find only a fraction of the numbers actually present, and that fraction must vary with aphid density, temperature, and probably the time of day. The adult coccinellid, at first sight so conspicuous an animal, is in fact very cryptic.

6. CONCLUSIONS

Laboratory v. field studies

The coccinellid-aphid relationship, observed in the field, differs from that in the laboratory in three major respects. The distribution of prey affects the predation rate in the laboratory but not in the field (§ 3). Predators observed in the laboratory were more active than those in the field (§ 5). Temperature has an overriding effect in both laboratory and field—a fact which would not be noticed at constant temperature in the laboratory. Moreover, it has a differential effect on predation rate, and on population dynamics of the prey. This means that predation and population studies on insects *must* include temperature as an essential component, and that studies of predation alone, unlinked to population dynamics can be meretricious. It also means that laboratory studies alone are unreliable, because some vital aspect of the true, i.e. the field relationship may be completely overlooked in the laboratory.

Holling (1966) pioneered the detailed behavioural and physiological approach to the study of predation and discussed the advantages of his approach, over more superficial methods (Holling 1964). Holling's work was so detailed that it could be done only in the laboratory: but the method can be simplified and applied in the field, to predict predation rates which can be reconciled with the population dynamics of the prey. Thus Holling's approach, offering precise predictions over a wide range of contingencies, may be combined with the broader realism of quantitative field studies, as first attempted by Morris (1963). Two major conclusions are therefore that (1) laboratory studies of ecological relationships must not be trusted until verified in the field, and (2) it is in fact possible to make detailed predator-prey studies in the field, to explain the observed impact of predation on the prey population.

Stability

The coccinellid-pea aphid relationship sharply contradicts existing theories on insect predators and prey, and of ecological stability. It permits no steady-state, or equilibrium, between predators and prey. It is true that, for any given aphid density and temperature, there is some number of coccinellids which could keep aphid numbers constant, once the aphid age-distribution had settled to a steady-state: but the ladybirds rarely approach the necessary predator prey ratio, even at high temperatures. Moreover, the relationship would be unstable. Curve C (Fig. 5) shows a monotonic increase of survival rate with aphid density, so that any chance increase in aphid numbers will allow the aphids to gain, and the beetles could not thereafter restore the balance. Conversely, the slightest decrease in aphid numbers would allow the beetles to drive the aphids towards extinction. Moreover, the required number of beetles depends critically on temperature, so that even a slight change in temperature would upset the equilibrium. There is nothing in the coccinellid-aphid functional relationship to prevent either a continual increase in aphid numbers, or a continual decline towards extinction. We have twice observed such a decline in the field (Figs. 1 and 8), which was arrested because the predator left the field when the prey density became very low. The conventional definition of stability (Hassell & May 1973), as a tendency to return towards some steady-state or equilibrium (which need never be actually reached), does not apply here, where the relationship is completely unstable, but extremely resilient (Holling 1973). The

functional response is unstable, and the relationship is stabilized only by the predator's numerical response.

Some technical considerations

To assess the impact of predators on their prey populations, we must compare the numbers of prey actually observed, with the numbers that *would* be observed, in identical field conditions, but in the absence of the predators. This is very difficult to do, especially if the comparison is to cover all conditions normally encountered in the field. The method used here, of dissecting the predation process and tying it into the population dynamics of the prey, is perhaps the only fully reliable method used so far. The chief technical difficulty in the field was not to observe the process of predation but to estimate the density of predators, for which we still have no satisfactory method.

Several theories of predation embody the concept of a predator's, or parasite's, area of search. Our predator is limited at low prey densities, not by its capacity for prey, but by the time available to search for them. This is equivalent to a limited area of search, since the predator cannot search the whole area within the time available. We believe it is better to think in terms of timing, rather than of area of search, partly because it emphasizes the dynamic nature of the predator-prey relationship, and partly because the aphids play hide-and-seek with the beetles. Even if a ladybird could search the whole area, it still would not find all the aphids.

This study offers cold comfort for biological control workers. Since the coccinellid-aphid relationship is unstable and incapable of a steady-state, we cannot expect the coccinellids to keep aphid numbers low for any length of time. Usually the beetles merely slow the increase in aphid numbers. At high temperatures, the beetles can certainly depress aphid numbers (Figs. 1 and 8); but we have seen this happen only during unusually warm periods early in the season; and even then, the beetles quickly left the field in search of other prey. The coccinellids' double temperature requirement, and their mobility, make them ineffective predators, in that they rarely restrict the density of their prey. To use ladybirds as effective and permanent agents for biological control, we must direct their natural behaviour to a quite unnatural end.

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References

Campbell, A., Frazer, B. D., Gilbert, N., Gutierrez, A. P. and M. Mackauer. 1974. Temperature requirements of some aphids and their parasites. **J. Appl. Ecol. 11**, 431-438.

DeBach, P. 1974. Biological control by natural enemies. Cambridge University Press, Cambridge.

Dixon, A. F. G. 1959. An experimental study of the searching behaviour of the predatory coccinellid beetle **Adalia bipunctata** (L.) **J. Anim. Ecol. 28**, 259-281.

Frazer, B. D. and R. van den Bosch. 1973. Biological control of the walnut aphid in California: The interrelationship of the aphid and its parasite. **Environ Ent. 2**,561-568.

Gilbert, N. and A. P. Gutierrez. 1973. A plant-aphid-parasite relationship. **J. Anim. Ecol. 42**, 323-340.

Gilbert, N. and R. D. Hughes. 1971. A model of an aphid population—three adventures. **J. Anim. Ecol. 40**, 525-534.

Gutierrez, A. P., Morgan, D. J. and D. E. Havenstein. 1971. The ecology of **Aphis craccivora** Koch and subterranean clover stunt virus. I. the phenology of aphid populations and the epidemiology of virus in pastures in south-east Australia. **J. Appl. Ecol. 8**, 699-721.

Gutierrez, A. P., Havenstein, D. E., Nix, H. A. and P. A. Moore. 1974a. The ecology of **Aphis craccivora** Koch and subterranean clover stunt virus II. A model of cowpea aphid populations in temperate pastures. **J. Appl. Ecol. 11**, 1-20.

Gutierrez, A. P., Havenstein, D. E., Nix, H. A. and P. A. Moore. 1974b. The ecology of **Aphis craccivora** Koch and subterranean clover stunt virus III. A regional perspective of the phenology and migration of the cowpea aphid. **J. Appl. Ecol. 11**, 21-35.

Hassell, M.P. 1969. A population model for the interaction between **Cyzenis albicans** (Fall.) (Tachinidae) and **Operophtera brumata** (l.) (Geometridae) at Wytham, Berkshire. **J. Anim. Ecol. 38**, 567-576.

Hassell, M. P. and R. M. May. 1973. Stability in insect host-parasite models. **J. Anim. Ecol. 42**, 693-726.

Holling, C. S. 1964. The analysis of complex population processes. **Can. Ent. 96.**, 335-347.

Holling, C. S. 1966. The functional response of invertebrate predators to prey density. **Mem. ent. Soc. Can. No. 48.**

Holling, C. S. 1973. Resilience and stability of ecological systems. **Ann. rev. Ecol. & systematics 4**, 1-23.

Huffaker, C. B., Shea, K. P. and S. G. Herman. 1963. Experimental studies on predation: complex dispersion and levels of food in a acarine predator-prey interaction. **Hilgardia 34**, 305-330.

Hughes, R. D. 1963. Population dynamics of the cabbage aphid **Brevicoryne brassicae** (L.) **J. Anim. Ecol. 32**, 393-424.

Hughes, R. D. and N. Gilbert. 1968. A model of an aphid population—a general statement. **J. Anim. Ecol. 37**, 553-563.

Morris, R. R. **et al.** 1963. The dynamics of epidemic spruce budworm populations. **Mem. ent. Soc. Can. No. 31.**

Morris, R. F. and C. W. Bennett. 1967. Seasonal population trends and extensive census methods for **Hyphantria cunea. Can. Ent. 99**, 9-17.

Wratten, S. D. 1973. The effectiveness of the coccinellid beetle, **Adalia bipunctata** (L.), as a predator of the lime aphid, **Eucallipterus tiliae** L. **J. Anim. Ecol. 42**, 785-802.

Appendices 1, 3, 5 and 6 will be sent upon request to either author.

Appendix 2

Algorithm to compute physiological time in the field

This method was devised by Morris & Bennett (1967), but the algorithm has not been published. Successive daily maximum and minimum field temperatures are stored in an array **X**. The algorithm fits a sine curve between two successive values of **X**, and integrates it above the threshold temperature *thresh*. It therefore calculates *two* increments (from min to max and from max to min) for each calendar day. Each increment, B, is calculated in day-degree units if the original temperatures are Fahrenheit, B will be in a day-°F., and similarly for Celsius. The algorithm is applied to successive pairs of values **X(I)**, **X(I+1)**, where I =1, 2, 3 . . .

```
   IF(X(I).LE.X(I+1))GO TO 2
   XMAX=X(I)
   XMIN=X(I+1)
   GO TO 4
 2 XMAX=X(I+1)
   XMIN=X(I)
 4 Y=XMAX+XMIN-2.*THRESH
   IF(XMIN.LT.THRESH)GO TO 6
   B=.25*Y
   GO TO 10
 6 IF(XMAX.GT.THRESH)GO TO 8
   B=0.
   GO TO 10
 8 T=ARCSIN(Y/(XMIN-XMAX))
   B=.125*Y*(1.-.63661977*T)+
     .079577472/(XMAX-XMIN)*COS(T)
10 CONTINUE
```

Appendix 4

Derivation of the expression for survival rate

The problem is to fit a curve to the data points in Fig. 5. At high aphid densities, when the beetles have no trouble in finding aphids, the survival rate s must approach the 'random search' survival rate $\exp(-kb/a)$, for the appropriate value of k, which is deduced as follows: In the model, each beetle starts with hunger **H**=0.88, corresponding to a starvation time of 15 hours. If such a beetle were suddenly presented with all the aphids it needed, it would eat an average of 5.7 mg. of aphids in the first q. This quantity is deduced from the hunger curve when an average beetle eats its fill, and thereafter eats a whole aphid whenever it becomes hungry enough to do so. Therefore, the beetle will eat 5.7/**AWT** aphids, each of weight **AWT** (Table 1), so that the appropriate value of k is 5.7/**AWT**. Curve A (Fig. 5) is the random search survival $s = \exp(-5.7b/(\mathbf{AWT}\text{-}xa))$, or for mathematical convenience

$$-\log s = 5.7\ b/(\mathbf{AWT} \times a)$$

This defines the required curve at the top end of the scale in Fig. 5. We shall now derive a theoretical value for $-\log s$ at the other end of the scale, when aphid density is very low. In the model, a beetle takes 51.3 seconds to visit one plant, provided that no aphid is found and eaten. At 18.5°C, 1 q lasts 40,000 seconds, in which time each beetle can visit 780 plants. Since there are b beetles per plant, each plant will receive an average of m=780 b visits/q. Any given plant will actually be visited r times, where r follows the Poisson distribution with mean, i.e. the probability of exactly r visits

is $e^{-m}m^r/r!$. We shall suppose that the aphid density is almost zero, so that most plants carry no aphids, but a few plants have a single aphid. In such circumstances, the beetles will be completely hungry (H=1). The probability of an aphid being eaten, when a beetle visits its plant, is **PE**, estimated from field observation to be 0.0205, which is the value of **PE** used in the field predation model of Appendix 3 to compute the data points of Fig. 5. The probability that one aphid survives one visit by the beetle is therefore (1-0.0205), and so the probability that it survives r successive visits is $(1-0.0205)^r$. The average survival rate s will therefore be the average value of this expression for all values of r, i.e. $\sum_r (1-0.0205)^r e^{-m} m^r/r!$, which reduces to $s = \exp(-0.0205\ m)$. Since $m = 780\ b$, it follows that, at near-zero aphid density,

$$-\log s = 0.0205 \times 780\ b. \qquad (2)$$

The required survival curve must therefore agree with expression (1) at high aphid densities, and with (2) when the aphid density a approaches zero. There are many such curves, but an obvious one (mathematically speaking) to try is:

$$-\log s = 5.7b\ [1 - \exp(-ka)]/(\mathbf{AWT} \times a) \qquad (3).$$

This expression approaches (1) for large values of a, and it also satisfies the requirement stated in §3, that if the beetle density b is doubled, the survival rate s is squared. Expression (3) agrees with (2) as a tends to zero if the appropriate value, namely

$$0.0205 \times 780 \times \mathbf{AWT} / 5.7 \qquad (4).$$

is chosen for the parameter k. When the value of **AWT** for second-instar aphids is substituted in (3), we get curve B of Fig. 5.

It is obvious from Fig. 5 that curve B still does not fit the data points very well. Although there are many other curves which satisfy the requirements of (1) and (2), it is unlikely that any equally simple formula will give a better fit than curve B. Rather than try one formula after another, it is better to tailor (3) to fit the data points. In expression (3), the term $(-5.7b/\mathbf{AWT} \times a)$ represents the random search of expression (1), while the term $[1-\exp(-ka)]$ reflects the fact that, at low aphid densities, the beetle has insufficient time to catch all the aphids it wants. Indeed, when expression (4) is substituted for k, the value of ka turns out to be the number of aphids which a beetle can expect to catch in a given time, divided by the number of aphids required to keep the beetle satiated during that time. Mathematically speaking, we could alter the terms for either random search or insufficient time; but since curve B gives a poor fit only at small aphid densities, it makes better biological sense to modify $[1 - \exp(ka)]$. The value of k is evidently not constant, but must vary with the aphid density a. Its value ko, when $a = 0$, must still be given by (4). From each survival rate computed by the predation model (Fig. 5), we deduce the appropriate value of k in (3). Fig. 14 shows the values of k/ko for varying aphid densities. When a 'greater than' 4, the value of k/ko is of no concern because the insufficient time factor $(1 - \exp(-ka))$ then has little effect on the survival rate.

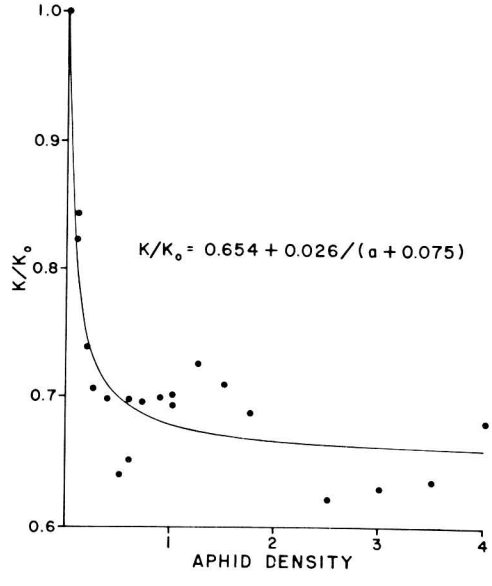

FIGURE 14. Values of k/ko deduced from Fig. 5 and the curvilinear regression, weighted according to the accuracy of each point.

In Fig. 14, a rectangular hyperbola has been fitted to the values of k/ko by non-linear regression, weighted according to the accuracy of each point, giving the formula $k/ko = 0.654 + 0.026/(a+0.75)$. This formula contains two independent empirical parameters, because k/ko must equal unity when $a=0$. We call k/ko the 'hunger correction', for the following reason: the curve for k/ko remains unchanged when we alter **PE**, **PL**, **TS**, or the instar of the aphids concerned. Such changes (with the exception of **PL**) will, of course, alter the survival rate s directly from the formula for ko. However, an acceleration of the beetle's digestion (i.e. of the rate at which its hunger **H** increases with time) does increase the value of k/ko somewhat, whenever the aphid density, a, exceeds one per plant, but has little effect at lower densities, when the beetle is continuously very hungry. For example, according to the predation model, the beetle's average relative hunger **H** is 0.64 at aphid density $a=1$, but 0.91 at $a=0.1$. It appears, then, that the shape of the k/ko curve in Fig. 14 is largely due to the fact that, the fewer aphids there are, the hungrier the beetle remains, and the more anxiously it searches. It must be remembered that changes in hunger level affect not only k/ko, but the random search term as well.

We thus end up with expression (3), but with

$$k = 0.0205 \times 780 \times \mathbf{AWT}[0.654 + 0.026/(a+0.075)]/5.7 \quad (5).$$

We then get curve C in Fig. 5, which fits the computed data points well. Finally we must reconsider the value of **PE**, since it varies according to the aphid instar. In face, **PE** equals some constant times **FACTE** (Table 2). We recorded the instar of every aphid which we saw captured in the field, and the average value of **FACTE** for those aphids is 1.07. To reproduce the estimated overall value of **PE** (0.0205), we write **PE**=0.019 x **FACTE**, since 0.019 x 1.07=0.0205. The figure 0.0205 in (5) must therefore be replaced by 0.019 x **FACTE**, and we then have the formula for survival rate used in Appendix 5. This means, incidentally, that the estimated overall value 0.0205 should not be used in Appendix 3, since **FACTE**=1.28 for second-instar aphids (Table 2), giving a corresponding **PE**=0.019 x 1.28=0.024. This error does not affect the analysis in this Appendix, since the k/ko curve is unaffected by changes in **PE**.