

**SIMULATING THE EFFECTS OF CLIMATE CHANGE ON *SITOBION*
AVENAE F. (HOMOPTERA: APHIDIDAE) AND *COCCINELLA*
SEPTEMPUNCTATA L. (COLEOPTERA: COCCINELLIDAE)**

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ABSTRACT

This study investigated how the predicted increase in global temperature would affect the interaction between the cereal aphid, *Sitobion avenae* F. (Hemiptera: Aphididae), and its coccinellid predator, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). A model describing the summer population dynamics of *S. avenae* (Carter *et al.*, 1982) was modified and updated. New equations describing the dependence of aphid development and reproduction on temperature were formulated. A new submodel, describing the population dynamics of *C. septempunctata*, was incorporated into the model. The predatory interaction between *C. septempunctata* and *S. avenae* was described using a modified form of the temperature-mediated functional response equation proposed by Mack *et al.* (1981). A sensitivity analysis showed that the output of the model, which compared well with field observations, was not greatly affected by small changes to the parameters of the equations used in the submodel. Stochastic elements were incorporated into the model; aphid and coccinellid immigration were simulated by sampling randomly from distributions fitted to observed patterns of immigration. Three temperature regimes: hot, moderate and cold, were defined by ranking and splitting the years from 1965 to 1992 according to the mean temperature between April and August. The temperature data from the years assigned to each regime were then used to formulate an equation to describe the daily temperatures within the five months.

The model was run for each regime, and the output showed that both coccinellid predation and increased temperatures caused a decrease in aphid abundance. The model also highlighted several more subtle effects of increased temperature on the interaction between *S. avenae* and *C. septempunctata*. The importance of the model predictions for future control of aphid populations in cereal crops is discussed.

Chapter 1: INTRODUCTION

1.1 GENERAL INTRODUCTION

1.1.1 Aim of the study

The aim of this study was to produce a simulation model that enabled qualitative estimates to be made of the effect of the predicted increase in mean global temperatures on the outcome of the interaction between the cereal aphid, *Sitobion avenae* F. (Homoptera: Aphididae) and its coccinellid predator, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae).

1.1.2 Cereal aphids as pests

Three species of cereal aphid are commonly found in the crops in the United Kingdom, *Sitobion avenae*, *Rhopalosiphum padi* (L.) and *Metopolophium dirhodum* (Wlk.). Of these, *S.avenae* is usually found in the greatest numbers (Carter *et al.*, 1980; Carter *et al.*,1982; Vereijken, 1979; Vickerman and Wratten, 1979). The losses due to damage caused by these species can be up to £100 million in an average year (Tatchell, 1991).

Damage is caused in several ways; one of the most important is the direct damage caused by feeding, which causes yield loss due to a reduction in the number of heads, 1000 grain weight and grain number (Vickerman and Wratten, 1979). *S.avenae* causes the greatest losses via direct damage because of its tendency to feed on the ears of cereals at the base of the spikelets (Kolbe, 1969; Rabbinge *et al.*, 1979; Vereijken, 1979; Vickerman and Wratten, 1979; Watson and Dixon, 1984). By feeding on the ears, *S.avenae* reduces the supply of assimilates to the grain, leading to a reduction in grain size and weight (Wratten, 1975). *S.avenae* also affects the grain quality, reducing the percentage of grain protein by imposing a direct reduction in nitrogen available to the plants. Kolbe (1969) estimated that *S.avenae* feeding on the ears of winter wheat at a density of 25 to 50 aphids per ear, which is not uncommon in Britain, caused a yield reduction of 25 percent.

Indirect damage can be caused by the production of honeydew, which encourages the growth of fungi and moulds (Tatchell, 1991; Vereijken 1979). Fungal growth can account for as much as 50 percent of the total yield losses in Britain. This led Vereijken (1979) to state that fungal growth is as important as direct damage.

Cereal aphids also act as vectors for many plant viruses, including Barley Yellow Dwarf Virus (BYDV), which is a major problem in winter sown cereal crops in Britain (Dean, 1974a; Kolbe, 1969; Tatchell, 1991; Vereijken, 1979). Plant viruses reduce the yield of crops directly, by up to 30 percent in the case of BYDV (Kolbe, 1969), and may even persist through to the next generation of crops.

Aphids can be controlled to prevent the direct yield losses, and the spread of viruses, either by spraying or by natural enemies. It is possible that enhanced control by natural enemies caused by increasing global temperatures could lead to a reduction in the use of pesticides. A reduction in pesticide use is beneficial because it decreases the chance of environmental damage to the field and also the chance of the pest developing resistance through overuse, and there is an economic benefit through reduced inputs.

1.1.3 Natural control of cereal aphids

Control of pest populations has been defined in many ways (Beddington *et al.*, 1978; Milne, 1957; Solomon, 1949; Solomon, 1964; Thompson, 1930; Watt, 1965). These definitions all contain one essential element, the regulation of population numbers. With aphids, the concern is to regulate the population numbers below the threshold at which economic injury occurs, which is usually defined as five aphids per tiller (Oakley and Walters, 1994).

The natural regulation of population numbers is controlled by many factors, which are either density-dependent or density-independent (Milne, 1957; Solomon, 1949; Solomon, 1964; Van Emden, 1972). Density-independent factors, such as climate (Solomon, 1949; Van Emden, 1972) act on the whole population with the same effect regardless of the density of the population. Density-dependent factors, however, show an effect that depends upon the density of the

population at the time when the factor is acting.

Density-dependent factors can act either directly, where the effect increases as the density of the population increases, or inversely, where the effect decreases as the population density increases (Solomon, 1964). This thesis is concerned with a direct density-dependent factor, predation by the natural enemies.

There are three categories of natural enemies of the cereal aphid *S.avenae*: pathogens, parasites and predators. The pathogens, which do not always act in a density dependent manner, comprise mainly fungal species belonging to the genus *Entomophthera*. Three species commonly attack *S.avenae*: *E.planchiana*, *E.aphidis* and *E.thaxteriana* (Hagen and Van den Bosch, 1965; Vickerman and Wratten, 1979; Wilding, 1970.). These fungal species have no strict specificity and the severity of their attack is determined by moisture factors, such as rainfall and relative humidity (Hagen and Van den Bosch, 1965; Vickerman and Wratten, 1979).

The main parasites belong to the families *Aphidiidae* and *Aphelinidae* (Carter *et al.*, 1982; Hagen and Van den Bosch, 1965; Powell, 1982; Powell and Wright, 1988). The *Aphidiidae* are host specific; whereas the *Aphelinidae* can parasitize several hosts, but both genera attack mainly first and second instar aphids, which prevents the aphids from reaching reproductive maturity (Hagen and Van den Bosch, 1965). Superparasitism, the depositing of more than one egg in a host, is rare in both genera.

Predators can be split into two categories, the polyphagous predators that feed on several types of prey and the aphid-specific species. The polyphagous species belong to many taxa including Carabidae (ground beetles), Staphylinidae (rove beetles), Dermaptera and (Linyphiidae) money spiders (Dennis and Fry, 1992). The aphid specific species are generally members of the families Chrysopidae, Syrphidae (hoverflies) and Coccinellidae (ladybirds) (Dennis and Fry, 1992; Hagen and Van den Bosch, 1965; Rautapaa, 1972; Vickerman and Wratten, 1979).

The effectiveness of these natural enemies in controlling aphid numbers is governed by many factors. The most important factor is synchronisation (Dean, 1974c; Van Emden, 1966;

Vickerman and Wratten, 1979), as is stressed in the following quote from Dean (1974c):

"Synchronisation of a natural enemy and aphid population is essential if natural enemies are to exert any kind of control. "

In the case of an aphidophagous insect, synchronisation is defined as the time relationship between the attack on the aphid population and the lifespan of an individual aphid (Van Emden, 1966). It is generally acknowledged that the earlier the natural enemy species attack the aphid population, the better is likely to be the control.

Pathogens are not well synchronised, due to their dependence on moisture factors. They generally only reach high levels of infestation when the aphids have already reached the threshold for damage (Hagen and Van den Bosch, 1965). Parasites, however, have a high degree of synchrony with the aphids and can be an effective controlling agent (Dean, 1974c; Hagen and Van den Bosch, 1965; Vickerman and Wratten, 1979).

Polyphagous predators are present early in the season and are therefore generally well synchronised with the aphid populations. The effect of predation by polyphagous predators is not fully understood, and their full importance in the field ecosystem is still emerging. Of the aphid-specific predators, chrysopids are known to enter the crop only when the density of aphids is high. This means that there is very little synchrony and chrysopids are unlikely to be effective controls (Hagen and Van den Bosch, 1965). Syrphids have been shown to be effective in controlling aphid numbers (Hagen and Van den Bosch, 1965), but parasitism of the syrphids themselves affects the degree of control that they can exert.

In the United Kingdom, the aphid-specific predators that receive the most attention from scientists because of their abundance and ease of study, are the ladybirds or coccinellids (Banks, 1954a, 1954b, 1955, 1956, 1957; Carter, 1982, 1985; Carter and Dixon, 1982, 1986; Carter *et al.*, 1984; Dixon, 1959; Mills, 1981, 1982; McLean, 1980; Perrin, 1974; Wratten, 1973). These species also appear in large numbers when aphid density is high (Hagen and Van den Bosch, 1965), but their synchronisation is dependent upon climatic variables (Hagen and Van den Bosch,

1965; Rautapaa, 1972), which makes their effectiveness variable.

The major coccinellid attacking *S.avenae* is *Coccinella septempunctata*. Rautapaa (1975) has shown, in cages, that control can be obtained with this species. In the United Kingdom, possible control of *S.avenae* by *C.septempunctata* was observed in the field in 1980 (Carter *et al.*, 1982; Chambers *et al.*, 1986).

Overall, instead of a single species being the major controlling factor, all the natural enemies interact to form a complex which acts to regulate the number of aphids (Chambers *et al.*, 1982, 1986; Thompson, 1930; Vickerman and Wratten, 1979), for which climatic factors determine the relative efficacy of the component natural enemies at different times.

1.1.4 The effect of climate change on pests and their natural enemies

The predicted increase in mean temperature for the United Kingdom, due to climate change, is between 1°C and 5°C by the year 2045 (Cammell and Knight, 1992; Parry *et al.*, 1989; Porter *et al.*, 1991; UK Climate Change Impacts Review Group (UKCCIRG), 1991; Warrick *et al.*, 1990). The warming is predicted to be greater in the winter compared to the summer (Cammell and Knight, 1992; Houghton *et al.*, 1990; Parry *et al.*, 1989; Porter *et al.*, 1991; UKCCIRG, 1991; Warrick *et al.*, 1990). The warmer temperatures will probably cause the development rates of pests, such as aphids, to increase (Cammell and Knight, 1992; Harrington and Woiwod 1995; Parry *et al.*, 1989; Parry *et al.*, 1990; Porter *et al.*, 1991), leading to more generations per season and greater numbers (Parry, 1992; Porter *et al.*, 1991). The natural enemies are likely also to show increased development rates, and could exert greater control if their response to temperature increase was proportionally greater than that of the aphids (Cammell and Knight 1992).

Higher temperatures might also effect natural enemy functional response (i.e. the response to the prey density), searching rate and handling time (Cammell and Knight, 1992). Hodek (1973) has shown that *C.septempunctata* can control *Aphis fabae* during hot seasons, but cannot in cooler seasons. This suggests that it might be possible for *C.septempunctata* to control *S.avenae* in the warmer climate predicted for the United Kingdom in the future.

By contrast the warmer winters may allow pests, such as aphids, to survive and develop over the winter (Parry *et al.*, 1989; Porter *et al.*, 1991), possibly resulting in larger numbers of aphids early in the season when crops are more vulnerable to attack (Parry, 1992). Indeed, in the UK, the winter of 1988/1989 was exceptionally mild and the large number of overwintering aphids led to heavy infestations (Porter *et al.*, 1991; UKCCIRG, 1991).

Natural enemies might also show enhanced survival and activity in milder winters (Cammell and Knight, 1992), leading to a greater synchrony with pests and resulting in an early collapse of the pest populations. However, greater synchrony may not occur if the natural enemy species has to enter an obligatory diapause, as do many parasites (Cammell and Knight, 1992). Then, the pest would benefit from enhanced reproduction and development due to the higher temperatures and could escape control, either through its increased numbers or because it was in an unfavourable stage for the parasite to attack (Cammell and Knight, 1992).

In general, the effect of an increase in mean temperatures upon the natural control of pests is uncertain. The determining factor is likely to be the differential response of the natural enemies in relation to the pests (Cammell and Knight, 1992; Farrow, 1991; Porter *et al.*, 1991).

1.1.5 Approaches to the problem

In this study, it was decided to concentrate on the two specific species, *S. avenae* and *C. septempunctata* rather than produce a model describing all the aphid and natural enemy species, as this would lead to an extremely complex model which would be tedious to use and hard to validate since insufficient data are available for validation. Concentration on specific species meant that a realistic model, which was relatively easy to validate, could be constructed from data available in the literature. The model was kept simple so that it could be adapted for other aphid and predator species and would require minimal computing time.

The aphid species chosen was *S. avenae* because it had been well studied previously, is a major pest species in the cereal ecosystem, and an existing model describing its biology was available in the literature (Carter *et al.*, 1982). A strategy of adaptation of the available model allowed

more time to be devoted to modelling the biology of the predator, and the interaction between the two species.

Coccinella septempunctata was chosen as the predator species because it has been well studied, due to its wide distribution throughout Europe, and it is also a major predator of *S. avenae* in Europe.

Once the two species had been chosen, a general approach to the problem was outlined, and details of this are given below. Several sequential stages were identified, leading to the production of a model that would enable qualitative predictions of the likelihood of aphid outbreaks under predicted increases in global mean temperatures.

The initial step was a review of *S. avenae* and *C. septempunctata* biology, focusing particularly on the interaction between the two species, which was felt to be an important prerequisite to the construction of a biologically realistic model. A review of the general modelling literature was also conducted to identify the advantages and disadvantages of different types of model and approaches to modelling. This allowed the possible pitfalls to be identified and avoided.

After completing these reviews, which form the rest of this chapter, the model simulating the summer population dynamics of *S. avenae* published by Carter *et al.* (1982) was examined with specific reference to the biology of *S. avenae*. Each section of the model was assessed separately for biological realism, and any necessary changes were made. A detailed description of the model, the changes made and their validation are given in Chapter two.

Attention was then focused on modelling the biology of *C. septempunctata*, and its predation of *S. avenae*. Three possible approaches were available for modelling the biology of *C. septempunctata*: constructing a model *ab initio*, constructing a separate model based on the approach used in the construction of the existing *S. avenae* model, and modification of the *S. avenae* model. A combination of the middle and latter options was chosen, and involved building a separate sub-model for the coccinellids which was incorporated into the existing model for *S. avenae*. This approach was followed for several reasons: modification of the existing model kept

the construction time to a minimum and provided the simplest solution to the problem, many of the components required for modelling the biology of *C. septempunctata* were included in the existing model, and since the layout of the model was known, it was a simple task to incorporate equations describing the biology of *C. septempunctata* into the appropriate section of the model and relatively easy to pinpoint problems.

The predatory interaction was thought to be crucial with respect to possible control. A review was undertaken to determine the advantages and disadvantages of the large number of coccinellid predation models available, which ranged from a simple empirical function (Tamaki *et al.*, 1974) to a complex spatially dynamic model (Frazer and Gilbert, 1976). Because the aim was to discover the effect of increased temperatures on populations, the approach chosen was a temperature mediated functional response model (Mack and Smilowitz, 1982). This incorporated the effect of temperature on the important parameters of the interaction directly, used equations that were simple but realistic, and required parameters that were available in the literature.

The review of predator and coccinellid models, and details of how the *C. septempunctata* model was constructed are given in Chapter 3.

Once a complete model describing the dynamics of *S. avenae*, *C. septempunctata* and the interaction between the two had been constructed and validated, the next step was to convert the deterministic retrospective model into a stochastic predictive model, in order to allow a range of possible outcomes to be simulated, mimicking natural variation, instead of producing a single answer.

The incorporation of stochastic elements was achieved by removing the reliance of the model on field observations, which made it retrospective, since it could only mimic events that had already occurred and not predict future events. The driving variable (the variable which affects the majority of processes within the model), temperature, was considered first. Under the predicted changes in climate, the average temperatures seen in the future might well be similar to those presently considered as hot years, and so previous summer temperatures for 28 years were classified into three regimes, cold, average or hot. The process of classification is described in

Chapter 5.

Secondly, to remove the dependence of the input to the model on counts made in the field and in suction traps, distributions were fitted to immigration data for both the aphids and coccinellids. This approach enabled the starting point of the distributions to be shifted between temperature regimes, since immigration is likely to occur earlier at the higher temperatures; data to fit most of these distributions was available. The fitting of the distributions and the differences between the temperature regimes are described in Chapter 5.

The final stage was to run the model using the different temperature regimes for a range of scenarios and to compare the results. The results and a discussion of their significance for future aphid control are given in Chapter 5.

1.2 BIOLOGY OF *SITOBION AVENAE*

1.2.1 Life Cycle

The aphid life cycle is complex, with a high degree of polymorphism found throughout the world. In Britain, *S. avenae* is a non-host alternating species spending the whole year on *Graminae* (Carter *et al.*, 1980; Carter *et al.*, 1982; Phillips, 1916; Watt, 1984; Williams and Wratten, 1987). In Britain., the population of *S. avenae* usually consists of holocyclic clones, which overwinter as eggs, and anholocyclic clones, which overwinter parthenogenetically and are usually the most numerous (Carter *et al.*, 1980; Carter *et al.*, 1982; Dixon, 1973, 1977; Hand, 1980, 1983; Höller, 1990; Parish and Bale, 1990; Phillips, 1916; Weber, 1985; Williams, 1987; Williams and Wratten, 1987).

This section provides a general description of the life cycle of *S. avenae* (Fig. 1.1) , with the main features being covered in more depth later. In Spring, the eggs laid by the oviparae on *Graminae* the previous winter hatch producing parthenogenetic fundatrices. The fundatrices then produce one or more parthenogenetic generations before winged alate emigrants appear, fly off and colonize cereal crops (Carter *et al.*, 1980; Phillips, 1916). Once the emigrants have colonized

the cereals in early summer, reproduction throughout the summer is parthenogenetic, with the production of apterous exules. These apterae (wingless aphids) have a high reproductive rate which allows the rapid increase in numbers characteristic of aphids (Ankersmit and Rabbinge, 1980; Carter *et al.*, 1980; Carter *et al.*, 1982; Kieckhefer *et al.*, 1989; Markkula and Myllymaki, 1963; Parish and Bale, 1990; Vereijken, 1979; Watt, 1984). In late summer, the increasing number of aphids on the plants combines with the decreasing quality of the host plant and the shortening daylength to act as a stimulus for the production of alatae (winged aphids) (Carter *et al.*, 1980, Carter *et al.*, 1982; Dixon, 1973, 1977; Rabbinge *et al.*, 1979; Vereijken, 1979; Watt and Dixon, 1981). When alatae reach the adult stage they migrate from the crop to other *Graminae*.

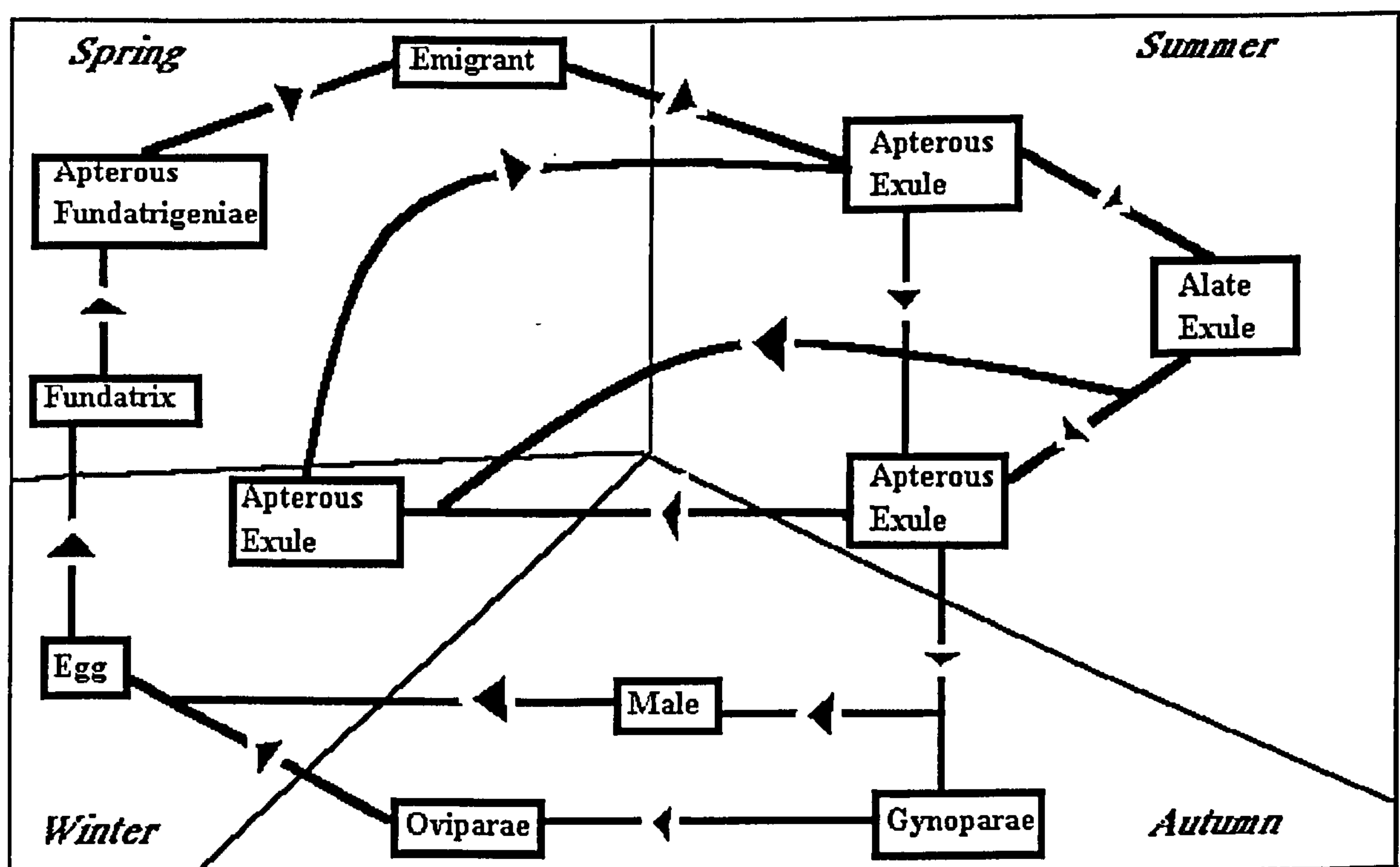


Figure 1.1: Life Cycle of *Sitobion avenae* .

In holocyclic or sexual clones, the apterae produce alatae in two phases between which reproduction ceases. The first phase is the production of gynoparae, which give birth parthenogenetically to the apterous, egg-laying oviparae. The second phase consists exclusively of alate males (Carter *et al.*, 1980; Carter *et al.*, 1982; Dixon, 1973; Watt, 1984). The pause

between the production of gynoparae and males leads to a synchronisation in the appearance of males and oviparae, making mating more likely (Carter *et al.*, 1980; Carter *et al.*, 1982; Dixon, 1973; Watt, 1984). After mating, oviparae lay cold-hardy eggs, which undergo an obligatory diapause and do not hatch until the next spring.

In asexual clones, the alatae produced migrate either within the crop or to other *Graminae*, where the aphids overwinter and reproduce parthenogenetically (Carter *et al.*, 1980; Carter *et al.*, 1982; Dixon, 1973; Höller, 1990; Parish and Bale, 1990; Williams, 1987; Williams and Wratten, 1987).

1.2.2 Phenology and population development

In this section the actual timings of each part of the life cycle are given. Since the majority of the work performed on *S. avenae* in Britain has taken place in Southern England, the timings presented here relate specifically to this area and may not be valid for more northerly areas.

The Spring egg hatch usually occurs in April (Carter *et al.*, 1980; Phillips, 1916), and the rapid increase in numbers due to reproduction of the fundatrices takes place throughout April, so that by the end of April the alate emigrants are beginning to appear. Migration into the crop commences in May, with the alates predominant before the onset of flowering, especially in wheat (Carter *et al.*, 1982; Dean, 1977; Rabbinge *et al.*, 1979). The alatae settle on the leaves of wheat and produce the more fecund apterae, which reproduce quickly and allow numbers to build up (Ankersmit and Rabbinge, 1980). Parthenogenetic reproduction by the apterae continues throughout June and July on the leaves and on the ears once they have emerged, due to the movement of the adults to the ears (Carter *et al.*, 1982; Dean, 1978). Dispersal through the crop in June and July is aided by the restlessness of newly emerged adult apterae. Temperatures in June and July can have a major effect on reproduction and development and hence on the aphid population, which led Dixon (1977) to suggest that above average temperatures in June combined with early infestation of the crop were the most likely circumstances that would cause populations to reach damaging levels.

Towards the end of June and in early July, the high densities of aphids, deteriorating crop state

in terms of food quality for the aphids, and shorter daylengths promote the production of large numbers of winged alatae (Carter *et al.*, 1982; Dean, 1978). The alatae then emigrate from the crop, and by early August few if any aphids remain in the crop (Dean, 1978). The emigrant alatae settle on *Graminae* in late July and early August and overwinter there as parthenogenetic apterae, although some eggs may be produced (Carter *et al.*, 1980; Dean, 1978). The whole process then begins again in April when the warmer temperatures promote egg hatch and cause the reproductive rate of the apterae to increase.

1.2.3 Polymorphism in *S. avenae*

In *S. avenae* there are two main morphs, the wingless apterous morphs and the winged alate morph. The apterae, which reproduce parthenogenetically, are generally heavier than the alatae and more fecund (Carter *et al.*, 1980; Carter *et al.*, 1982; Dixon, 1973; Parish and Bale, 1990; Simon *et al.*, 1991; Wratten, 1977), although fecundity varies with several factors including crop growth stage, aphid size and age (Carter *et al.*, 1982; Watt, 1979, 1984; Weber, 1985), and temperature (Dean, 1974b). The greater fecundity of the apterae is presumed to be due to the lack of wing muscles, since wing muscle development competes with developing embryos for limited nitrogen supplies (Dixon, 1976; Wratten, 1977).

Reproduction in apterae begins early in adult life after a short pre-reproductive period (Dean, 1974b; Simon *et al.*, 1991). The reproductive rate is greatest early in life (Watt, 1979) and Simon *et al.* (1991) observed that the reproductive rate was greatest on the first day, declining exponentially thereafter. The reproductive life of approximately four weeks is followed by a post-reproductive phase which may last up to ten days (Lopez *et al.*, 1989). The post-reproductive phase provides an advantage to the population via aggregative feeding (Simon *et al.*, 1991).

Due to their long reproductive life and high fecundity, apterae are primarily responsible for the rapid build up of aphid numbers and the dispersal of aphids through a crop (Dean, 1978).

The alate morphs can be either sexual, gynoparae or males, or parthenogenetic alate exules. The alate exules are produced by apterae in response to many stimuli, which include crowding, host

plant quality, temperature and the developmental stage of the crop (Carter *et al.*, 1978; Carter *et al.*, 1982; Dixon, 1973, 1977; Rabbinge *et al.*, 1979; Vereijken, 1979). In *S. avenae* crowding is thought to be the main stimulus involved in the induction of alatae. Crowding acts both pre-natally and post-natally (Carter *et al.*, 1980) via tactile stimulation (Dixon, 1976). Alatae are produced almost exclusively by apterae although Dean (1978) observed that alatae that have not flown produce alatae as easily as apterae.

Alatae have a longer development time than apterae (Lopez *et al.*, 1989; Markkula and Myllymaki, 1963; Simon *et al.*, 1991) and fly as soon as they have moulted to the adult stage (Carter *et al.*, 1980; Vereijken, 1979), but if prevented from flying, the newly-emerged adults show a pronounced restlessness (Williams and Wratten, 1987). Alate aphids show two distinct peaks in diurnal flight activity, which generally occurs before reproduction, especially if the alate nymph has been crowded (Dean, 1973). The peaks occur in the morning and the evening and are caused by the alate adults requiring a teneral period, after moulting, before flight can occur. Dixon (1973) suggested that the early morning peak consisted mainly of aphids that had moulted the previous evening and completed their teneral period overnight, whereas the evening peak consisted of aphids that had moulted and completed their teneral period during the day.

In flight, alates are at the mercy of the wind currents due to their small size, but most flights last no longer than two hours (Dixon, 1973). Initially, aphids fly away from long-wavelength light and towards short-wavelength light, but after flying for a while they become attracted by the long-wavelength light emitted by cereal crops, with a further attraction to yellow drawing the aphids towards plants of optimum physiological age (Dixon, 1973). After migrating, the alate adults lose their wing muscles and begin to reproduce, achieving a higher daily fecundity than apterae (Wratten, 1987).

The sexual morphs, gynoparae and males are produced in response to a shortening photoperiod in the autumn months, in two phases. The gynoparae appear first, followed by a brief reproductive pause before the males are produced (Carter *et al.*, 1980; Carter *et al.*, 1982; Dixon, 1973; Watt, 1984). This brief pause allows the males to develop at the same time as the apterous oviparae. On moulting to the adult stage, the males fly to the oviparae and mate with them. After

mating, the oviparae lay cold-hardy eggs.

The response to short daylength is controlled by a photoperiodic receptor located in the mid-dorsal region of the head, but low temperature is also able to promote the production of sexual morphs (Dixon, 1973). The fact that the sexual morphs are not produced under short daylength conditions in the spring has led to the postulation of an "interval timer" which prevents the induction of sexual morphs in the spring, although it is possible that the aphids react to the rate of change of daylength rather than to daylength itself (Williams, unpublished).

1.2.4 Overwintering of aphids

As outlined earlier, *S. avenae* is able to overwinter either as eggs or as parthenogenetic apterae. In Britain, *S. avenae* mainly overwinters parthenogenetically, although in particularly severe winters only eggs, which are better able to withstand extreme temperatures, are likely to survive (Höller, 1990). The eggs are elliptical and yellow when first laid, but change colour on exposure to the environment, eventually turning black (Phillips, 1916). The egg shell consists of three layers (Peterson, 1917), an outer semi-transparent layer, an inner black and elastic membrane and an innermost thin transparent membrane. The outer layer is initially soft, but hardens upon exposure to weather conditions, becoming tough and impervious to water, while the inner black and elastic layer remains permeable to water (Peterson, 1920).

The hatching of the eggs is determined by temperature and humidity (Hand, 1983; Peterson, 1920), with low temperatures breaking the diapause. However a prolonged exposure to low temperatures may act to prevent hatching in some cases (Hand, 1983). Before hatching occurs, the outer layer of the egg splits, the timing of which is influenced by evaporation. Once the outer layer of the egg has split, the air humidity is extremely important in determining the number of aphids that eventually emerge (Hand, 1983; Peterson, 1917, 1920). Humidity is important because the outer layer prevents the developing embryo from water loss; once this protection has been removed the embryo is very susceptible to desiccation. This led Peterson (1920) to suggest that an early rupture of the of the outer layer is likely to be detrimental, with hot weather causing the egg to dehydrate.

Although some eggs have been found in winter (Hand, 1980), *S. avenae* is more commonly found as parthenogenetic apterae. The apterae are able to withstand cold temperatures by using their ability to supercool (Knight and Bale, 1986), and it has been noted that if nymphs are exposed to subzero temperatures for short periods, high proportions develop as apterae (Parish and Bale, 1990). Aphids are able to acclimatize to low winter temperatures (Williams, 1987; Williams and Wratten, 1987); during a normal winter nymphal survival is approximately ninety-seven percent in clip-caged aphids.

Acclimatized apterae have a later reproductive peak than normal, but total nymphal production is similar to that found in the summer (Williams and Wratten, 1987). Although most overwintering aphids are apterae, some alatae are found, but in very low numbers, possibly due to their susceptibility to wind and rain (Parish and Bale 1990). Overwintering alatae show a slowed development, a shorter lifespan and poorer reproduction than apterae. The alate reproductive effort has two peaks, with more progeny produced late in their reproductive lives. The alates are therefore at a disadvantage compared to the apterae during the winter.

The overwintering survival of the parthenogenetic apterae and alatae is very important. It influences the timing and amount of alate immigration in the spring and therefore the summer population dynamics (Williams, 1987).

1.3 BIOLOGY OF *COCCINELLA SEPTEMPUNCTATA*

1.3.1 Life cycle of *C. septempunctata*

C. septempunctata is common throughout Europe (Butler, 1982; Hagen, 1962; Hodek, 1973), and shows geographical variation in life cycle characteristics throughout its range. In Britain, the life cycle consists usually of one generation per year (univoltine) with dormancy in the form of hibernation throughout the winter (Bodenheimer, 1943; Hagen, 1962; Hodek, 1973; McLean, 1980; Sundby, 1968). A generalised life cycle is shown in Fig. 1.2, followed by a full description.

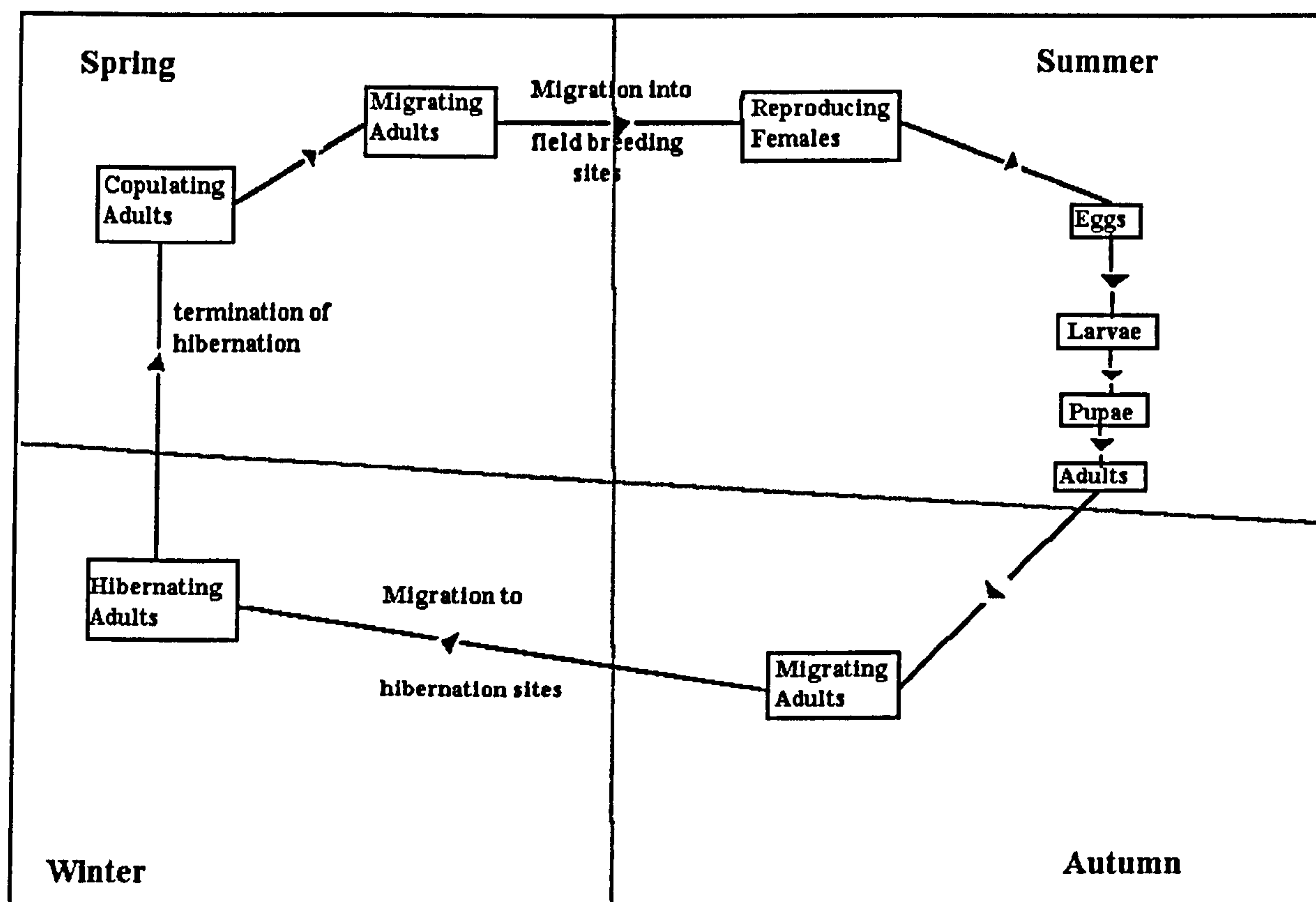


Figure 1.2: Life cycle of *Coccinella septempunctata*.

In spring, coccinellid dormancy is broken by lengthening days and rising temperature, and the adults become more active (Hodek, 1962; Honek, 1990; Shand *et al.*, 1972; Sundby, 1966). Copulation takes place while the coccinellids are still aggregated at the hibernation site (Hodek, 1973; Singh & Malhotra, 1979). Migration into field breeding sites occurs throughout April and May (Hagen, 1962; Hodek, 1965, 1973; Shand *et al.*, 1972; Sundby, 1966). The adults remain in the field only if aphid density exceeds a threshold (Adams, 1984). There is a slight delay before reproduction begins, during which ovariole maturation occurs in the females (Sundby, 1968). Reproduction begins as soon as the female coccinellids have eaten enough food to produce eggs, which usually occurs above a threshold aphid density (Ghanim *et al.*, 1984; Honek, 1978).

The female coccinellids lay their eggs in clusters close to aphid colonies (Dixon and Guo, 1994; Hodek, 1975; Singh and Malhotra, 1979); ovipositing behaviour lasts up to 3 months in some cases (Rhamalingham, 1987; Sundby, 1966, 1968), after which the females die. The males live longer than the females, but none survive to the autumn.

The coccinellid eggs hatch after approximately one week (Banks, 1956) and the newly hatched larvae remain with the egg shells for twelve to twenty-four hours before dispersal (Banks, 1956, 1957; Hodek, 1973). The larvae then develop through four instars before pupating to the adult form (Hodek, 1973; Singh and Malhotra, 1979). The development time of the immature coccinellids from egg through to adult varies with temperature (Hodek, 1958, 1973; Kawauchi, 1983, 1986; Michels and Behle, 1991; Sethi and Atwal, 1964; Singh and Malhotra, 1979), but the adults emerge usually in July/August (Hagen, 1962; Honek, 1990). The newly emerged adults feed in the field for approximately three to five days before they emigrate to the hibernation sites (Zaslovsky and Semyanov, 1986) in August and September (Hagen, 1962; Honek, 1990; Sundby, 1966) where they overwinter before emerging in the next spring.

In summary, the coccinellid life cycle consists of four main stages: emergence of old adults and their immigration into field breeding sites; oviposition by female coccinellid adults and the development of this new generation to adults; emigration of this new generation of adults to hibernation sites; hibernation of the new generation. This style of life cycle is extremely plastic (Honek, 1990) and enables the coccinellids to take full advantage of their major prey source, the ephemeral aphids.

1.3.2 Phenology and population development

During late April and early May coccinellid adults that overwintered emerge from their hibernation sites (Hagen, 1962; Shands *et al.*, 1972; Sundby, 1966) due to the rise in air temperature (Hodek, 1962). Ovariole maturation and copulation occur a few days after emergence, while the adults are still aggregated at the hibernation sites (Hodek, 1973).

The adult coccinellids migrate to the fields shortly after emergence; this migration lasts from April to June (Honek, 1990). The adult coccinellids will remain in the field only if there is enough food available (Adams, 1984; Honek, 1980). Adams (1984) estimated that the threshold abundance of aphids required for a coccinellid adult to remain in the field was 10 aphids per m². Once the coccinellids adults have settled in the field, ovariole maturation in the females continues, but only if the aphid density is above a threshold (Adams, 1984; Honek, 1978, 1980),

estimated to be 0.1 aphids per tiller or approximately 38 aphids per m² (Adams 1984). Honek (1980) noticed that these thresholds seemed to remain constant between years, showing only a very small variation.

The time taken to complete ovariole maturation constitutes the pre-reproductive delay which lasts up to a maximum of 10 days (Rhamalingham, 1987). As soon as ovariole maturation is complete, oviposition by the female coccinellid begins.

The eggs, which are laid in the vicinity of the prey (Hodek, 1973), are spindle-shaped or oval, and yellow in colour (Hodek, 1973; Singh and Malhotra, 1979). The eggs are usually deposited in clusters on the underside of the leaves of the plant, with cluster size varying from 29 up to 71 eggs (Hodek, 1973; Singh and Malhotra, 1979). A few hours before the eggs hatch, they darken and turn light grey (Banks, 1956; Singh and Malhotra, 1979); hatching usually occurs after approximately seven days (Banks 1956).

The newly hatched larvae emerge through an apical split in the chorion of the egg. The head, thorax and legs are gradually drawn free of the embryonic cuticle and chorion by slow forward and backward movements (Banks, 1956). Once the larva is free, it rests on top of the egg shell where it remains for one hour while its cuticle hardens. The larvae then eat the egg shells, and remain in the proximity of the egg-shells for twelve to twenty-four hours after eclosion (Banks, 1956, 1957; Hagen, 1962; Hodek, 1973). The newly hatched larvae often eat unfertilized eggs (Banks, 1956; Hagen, 1962; Hodek, 1973), and will also eat unhatched eggs, although Banks (1956) observed that in small egg batches the larvae often show a synchrony in hatching which acts to prevent cannibalism. The consumption of unfertilized and unhatched eggs allows the larvae to survive longer (Banks, 1954a), and allows them more time to find their first aphid.

The first instar larvae are black with four dark black patches on each abdominal segment. They have pronounced spines, and prominent white areas (Singh and Malhotra, 1979). The second instar larvae have some orange patches on the abdomen, and on moulting to the third instar, the orange patches appear on the thorax, while the fourth instar larvae have white/yellow patches on the head. Just prior to pupation, the fourth instar larvae become inactive and attached to the

leaf surface using the posterior of the abdomen; this stage is known as the prepupa (Singh and Malhotra, 1979; Hodek, 1973). The pupa varies in colour from a shining yellow through to a yellowish black (Singh and Malhotra, 1979) depending on the environment. However, the pupa is not totally immobile and may wave around, especially if disturbed (Hodek, 1973). The whole developmental process from egg through to adult takes approximately ten to fifteen days (Hagen, 1962).

Adult coccinellids are spherical in shape and have orange or red elytra with black spots of an irregular shape (Singh and Malhotra, 1979). On emergence from the pupa, the elytra of the adult are soft, matt and light coloured, without a pattern. The hind wings protrude from under the elytra and normal coloration is acquired with age (Hodek 1973).

Approximately three to five days after the imaginal moult, the newly emerged adults experience a migratory urge, which is not influenced by photoperiod, and occurs before reproduction or diapause (Zaslavsky and Semyanov, 1986). Adults migrating to overwintering sites are attracted to raised areas in the landscape where they aggregate at the base of plants or in small cracks under tree bark, stones, etc. (Hodek, 1973; Hagen, 1962; Honek, 1989). After feeding to increase fat levels the coccinellids enter dormancy, which is discussed in detail in the next section.

1.3.3 Dormancy in *C. septempunctata*

C. septempunctata shows a range of dormancies depending on geographical location. In Britain and Europe, the dormancy usually takes the form of hibernation (Hagen, 1962; Hemptinne, 1988; Hodek, 1962, 1973; Hodek and Cerkasov, 1961; Honek, 1989, 1990; Mariedra *et al.*, 1992; Okuda and Hodek, 1989; Sundby, 1966). The precise mechanisms which induce diapause in coccinellids are unknown, but it is thought that temperature and photoperiod are important factors in Britain (Hagen, 1962; Hodek, 1973; Hodek and Cerkasov, 1961; Hodek *et al.*, 1984; Honek, 1989, 1990; Zaslavsky and Semyanov, 1986). Kawauchi (1986) suggested that low temperature and short photoperiod induces diapause in *C. septempunctata*. This supports the main reason proposed to explain diapause, that is the avoidance of periods unfavourable for growth and development (Hodek, 1973; Hodek and Cerkasov, 1961; Hodek *et al.*, 1984).

Hodek and Cerkasov (1961) found that the hibernation of *C. septempunctata* had two distinct phases. The first phase was an obligatory diapause (Hagen, 1962) that occurred whilst environmental conditions still favoured growth and development. The second was a quiescent period during which resumption of activity and development can be evoked by favourable conditions (Hodek and Cerkasov, 1961). This observation led to the hypothesis that imaginal diapause synchronized life history with seasonal changes in environmental conditions, resulting in coccinellids being active only when the environment was most favourable. Hodek (1962) suggested that diapause was most likely caused by an inherited tendency to an obligatory univoltine life cycle.

Hibernation takes place at the same sites every year, although during years of high coccinellid abundance, new sites may be used. These sites all have several characteristics noted by Honek (1989). They are usually positioned so that they have access to sunshine, oriented to the south-west, south or southeast. If the sites are on a slope, the preference is for a small gradient between 0° and 20°. Most coccinellids tend to hibernate where there is bare ground or discontinuous plant cover, and the site must have a warm and dry microclimate. These characteristics lead to hibernation mainly in grass tussocks, under loose stones, or under dead leaves and other debris.

During their migration to hibernation sites, coccinellid show a hypsotactic response (Hagen, 1962; Hodek, 1973) which leads to large aggregations at the overwintering sites. Once the coccinellids arrive at the hibernation site, they use geotactic and thigmotactic responses to hide in small places, such as under stones or in cracks in rocks. Hagen (1962) suggested that odour may be important in the formation of aggregations, allowing the coccinellids to return to the same site each year.

Dormancy is broken by photoperiod in the Spring (Hodek, 1973), but temperature may also have an effect (Hodek, 1962), since dormant coccinellids may be active during sunny days in winter. Resumption of activity occurs whilst the temperature is rising and the days are lengthening, but full details are still unknown.

Before entering hibernation, the coccinellids undergo several physiological changes. Firstly, the adults empty their digestive tract, after extensive feeding to develop large fat bodies (Hagen, 1962; Hodek, 1973) and stores of glycogen (Hagen, 1962; Hodek, 1973). Ovarian development ceases and many dormant female coccinellids have undifferentiated germaria (Hodek and Cerkasov, 1961). Spermatogenesis in males continues throughout hibernation, although it is often arrested by low temperatures during the winter months (Hodek, 1973). During dormancy, their metabolic rate is very low and the fat stores are used as the main source of energy, although glycogen may be used, especially if the temperatures are less than 0°C (Hodek, 1973).

The search for food is quite intense, and a more detailed description of the strategies used by coccinellids is given in the next section.

1.3.4 Feeding and searching behaviour of *C. septempunctata*

The main food source of *C. septempunctata* is aphids, which by their nature have patchy distributions. The coccinellids have therefore adapted their searching behaviour so that they are more efficient predators when food is clumped (Murakami and Tsubaki, 1984).

Coccinellids show two main types of searching behaviour, a rapid random walk and intensive searching (Carter and Dixon, 1984; Ferran and Deconchat, 1992; Hagen, 1962; Hodek, 1973; Marks, 1977; Murakami and Tsubaki, 1984; Nakamuta, 1982, 1985, 1986). The rapid random walk occurs before the coccinellid encounters a prey and is characterized by a linear path and high walking speed (Ferran and Deconchat, 1992). They tend to move along leaf edges, or raised surfaces such as veins (Hodek, 1973; Marks, 1977) and it is believed that this increases the chance of them encountering aphids, which feed on the veins of leaves. The coccinellids show positive phototaxis and negative geotaxis (Hagen, 1962; Hodek, 1973; Marks, 1977), although the negative geotaxis declines as searching continues (Marks, 1977) and if the coccinellid reaches the ground, then it traverses across the ground for a set interval of time before it will begin to climb again, preventing the coccinellid from climbing the plant that it has just left (Hodek, 1973).

Nakamuta (1983) has observed that during both searching behaviours, coccinellids keep their

antennae parallel to the searching substrate and the maxillary palps perpendicular to the substrate, but there is occasionally some movement of the head which is associated with vibration of the maxillary palps, which are used to detect aphid body fluids (Nakamuta, 1985).

The rapid random search enables movement between prey patches to be as quick as possible, and is designed to increase the chance of the coccinellid encountering a prey patch. Early studies of the searching behaviour of coccinellids gave rise to the idea that coccinellids could detect prey only by direct contact (Hagen, 1962; Hodek, 1973; Marks, 1977), but it has now been shown that coccinellids can perceive prey visually, even if only from close range (Ferran and Deconchat, 1992; Nakamuta, 1985; Stubbs, 1980). Stubbs (1980) calculated the distance at which the visual perception of aphids occurred for adult coccinellids as 1.04cm, and 0.69cm for fourth instar larvae. There is some variation in perception distance and some coccinellids appear to detect prey only by direct contact. Stubbs (1980) also suggested that the level of hunger experienced by the coccinellid may affect prey perception.

Once a prey has been contacted, the coccinellid switches its searching behaviour to intensive searching. This type of searching is characterized by much slower movements, with fan-shaped movements of the body and much greater turning resulting in a tortuous or sinuous path (Ferran and Deconchat, 1992; Hagen, 1962; Hodek, 1973; Marks, 1977; Murakami and Tsubaki, 1984; Nakamuta, 1985). Marks (1977) identified two main components in this intensive searching by larvae. In the first stage, the abdomen is fixed to the substrate and head and legs are moved through 180°; this lasts for approximately five to ten seconds. In the second stage larvae make frequent turns through 360°, with head and legs moving to alternate sides of the mid-line of the abdomen. This pattern of searching increases the probability of encountering another prey within a patch (Carter and Dixon, 1984; Murakami and Tsubaki, 1984; Nakamuta, 1985). The switchover from random walk to intensive searching is elicited by prey contact (Carter and Dixon, 1984; Nakamuta, 1985, 1986); the prey does not necessarily have to be captured or consumed.

If a second prey is not found, then the coccinellid reverts back to the random walk behaviour described earlier in this section. The time taken for reversion is determined by the type of prey

contact (touching or eating), and also the size of the most recently consumed prey (Nakamuta, 1986).

If a prey is captured the coccinellid consumes its prey in one of two ways. The first method is external digestion, where the coccinellid sucks some of the body fluids out of the aphid and then regurgitates them back into the aphid along with digestive juices. The coccinellid then sucks back the pre-digested food (Hagen, 1962; Hodek, 1973); this method is usually used by the smaller coccinellid instars. The second method is to eat the entire prey using a chewing action; this method is usually used by the larger coccinellid instars and adults (Hagen, 1962; Hodek, 1973).

However, aphids are not totally helpless and they possess several defence mechanisms which can prevent capture, including kicking the coccinellid, shedding an appendage, dropping off the plant or moving out of the way (Hodek, 1973). The latter method is not always successful as during a search coccinellids often retrace their steps and may find aphids that had moved during a later traverse of a previously searched area (Marks, 1977). Cannibalism of smaller coccinellid instars may also occur if, while searching a hungry coccinellid encounters a smaller larva or egg.

In summary, coccinellids have adapted to the patchy distribution of their prey by developing two searching behaviours: a fast random walk which minimizes the time spent moving between patches, and a slow sinuous intensive search which is elicited by prey contact and maximises the probability of discovery of further prey within a patch.

1.4 MODELLING

1.4.1 What is a model?

Modelling is often used in biology and ecology, but what exactly is the definition of a model ? Frenkiel and Goodall (1978) defined a model as a representation of some part of the real world in another form. This is a very broad description covering physical, descriptive and mathematical models (Jeffers, 1982). Mathematical models are used in ecology because of their ability to cope with the large numbers of complex relationships often found in ecological systems. Mathematics

can be thought of as a language which minimizes the difficulties of incorrect interpretation, a common problem when using word-based languages, and which expresses ideas of great complexity in a simple fashion (Jeffers, 1982).

Most ecologists think of a mathematical model as consisting of a set of equations representing the concepts of the behaviour of a system found in nature (Barlow and Dixon, 1980; France and Thornley, 1984; Frenkiel and Goodall, 1978; Streifer, 1974), but it is more than this. A model encompasses the whole conceptual construct concerned (Association of Applied Biologists, 1991; Skellam, 1973). This conceptual structure is addressed later in this chapter.

1.4.2 Uses of ecological models

Ecological models are orderly and logical representations of complex and dynamic relationships (Jeffers, 1982). They have a wide range of uses, the three main ones being: as an aid to the understanding of a relationship; as an aid to the identification of areas that may require further research due to a lack of understanding or data, and hence act as a guide for future research (Frenkiel and Goodall, 1978; Gilbert and Gutierrez, 1973; Norton, 1979); and for prediction. This last point is an area fraught with many difficulties. A model is useful for prediction only if it is able to mimic existing data, and a measure of the error in the predictions is incorporated (Gardner *et al.*, 1980). The dangers of prediction are hinted at in the following quote by Skellam (1973).

" Roughly speaking a model is a peculiar blend of fact and fantasy, of truth, half-truth and falsehood. In some ways a model may be reliable, in other ways only helpful and at times and in some respects thoroughly misleading."

In addition to these three main uses, Worner (1991) suggests that models can be used to define problems, organise thoughts, generate interesting hypotheses and as standards for comparison. Carter (1985) suggests that models can be used as experimental tools for examining the effects of changes on ecological systems.

1.4.3 Types of model

There are several types of model, which can be used to describe population dynamics (Hodek and Kindlmann, 1988; May, 1973), ranging from simple analytical models, such as those described by Wyatt (1983), through to complex simulations, such as the model described later in this thesis. Analytical models contain only a few equations and enable a complete or partial mathematical analysis of the behaviour of the model. Simulation models, however, are designed to include the majority of the features of the modelled population, because they strive for reality (Hodek and Kindlmann, 1988), but with the penalty of producing often very complex models, the behaviour of which can be understood, if at all, only by actually running the model and examining its output.

Simulation models were used in this project because of their ability to take account of the complex ecological processes involved in population dynamics (Ankersmit and Rabbinge, 1980; Fransz, 1974; Frenkiel and Goodall, 1978). The reality of a simulation model is dependent upon the closeness of the analogies used to the real world (Frenkiel and Goodall, 1978). Here, the complexity of aphid and coccinellid behaviour warranted the use of a simulation model, and in fact Carter and Rabbinge (1980) stated:

"Simulation models are not an end in themselves but a means to an end, and the only means for a thorough aphid study."

The fact that simulation models are tools rather than answers to problems is reinforced by the following statement from Gilbert and Hughes (1971).

" Only if we choose the right criteria and ask the right questions will we get any enlightenment from a model."

1.4.3.1 *Types of simulation model*

Simulation models can be differentiated into several types according to their properties and the

level at which they work (France and Thornley, 1984; Frenkiel and Goodall, 1978; Jeffers, 1982). However, there are only two major types: deterministic and stochastic.

Deterministic models work on the basis of logical deduction, and once the state of the system has been entered into the model, along with initial inputs, the future state of the system is uniquely defined (France and Thornley, 1984; Fransz, 1974; Frenkiel and Goodall, 1978). This means that the model has a set trajectory which is able to be predicted exactly from the initial and boundary conditions (Association of Applied Biologists, 1991). The unique solution of deterministic models is their main disadvantage, since random events occur frequently in ecological systems.

Stochastic models, on the other hand, are able to account for random events because they include random variables in the form of statistical treatments or explicit variables (France and Thornley, 1984; Fransz, 1974; Frenkiel and Goodall, 1984; Jeffers, 1982; Smith, 1952). In this case there is no set trajectory, and only the probability distribution of the trajectory can be determined from the initial and boundary conditions (Association of Applied Biologists, 1991). The ability to account for random events makes stochastic models more realistic and hence more useful for prediction (Watt 1961), but only if the equations used in the model are biologically meaningful and realistic. There are three major drawbacks associated with stochastic models: the greater complexity of the model leads to longer running times; the variability of the models makes them difficult to validate; and the increased complexity may hamper interpretation of its behaviour.

1.4.4 Constructing a model

As was mentioned earlier, a model is not just a set of equations, but the whole process of building and testing. This process has been split into a number of stages (Association of Applied Biologists, 1991; Carter, 1980; DeWit and Rabbinge, 1979; France and Thornley, 1984; Gutierrez *et al.*, 1984; Murthy *et al.*, 1990), detailed below:

The first stage involves defining the objectives of the proposed model (Association of Applied Biologists, 1991; Carter, 1980; DeWit and Rabbinge, 1979; France and Thornley, 1984; Gutierrez

et al., 1984; Murthy *et al.*, 1990). This is an extremely important step as these chosen objectives will determine the structure of the model that is required (Carter, 1980).

Once the objectives of the model have been defined, the next step is to determine its structure (Carter, 1980; DeWit and Rabbinge, 1979; Murthy *et al.*, 1990). The initial model structure may be determined by listing all the components, interactions and mechanisms that are important in the model (Association of Applied biologists, 1991; Carter and Rabbinge, 1980). This list can be continually refined throughout the modelling process (Carter and Rabbinge, 1980). Having produced a complete list of all the model components, a diagrammatic representation of the conceptual structure of the model (Carter and Rabbinge, 1980) can be produced and decisions made about how to represent the included items (Association of Applied Biologists, 1991).

Any model component can be represented as one of the three main types of variable: driving, state or rate (Carter and Rabbinge, 1980; DeWit and Goudriaan, 1978; DeWit and Rabbinge, 1979; France and Thornley, 1984). Driving variables are continuously measured variables, which influence the system from outside and characterise interactions at the boundaries of the system, such as the effect of temperature, which can be considered as data inputs varying autonomously with time (Carter and Rabbinge, 1980; DeWit and Rabbinge, 1979; France and Thornley, 1984). State variables can be considered as variables which quantify the state of the system at any time (Carter and Rabbinge, 1980; DeWit and Rabbinge, 1979; France and Thornley, 1984), although DeWit and Rabbinge (1979) further defined state variables as variables which can be measured instantaneously, even when time stands still. State and driving variables affect the third major type, the rate variable. Rate variables give the values of flows of materials between state variables and their value is determined from the state and driving variables using rules based upon knowledge of the biological processes taking place (Carter and Rabbinge, 1980; DeWit and Rabbinge, 1979; France and Thornley, 1984). Rate variables also determine how state variables change with time (France and Thornley, 1984).

Carter and Rabbinge (1980) define two further variables, auxiliary variables, also described by France and Thornley (1984), which are intermediate variables used to enhance understanding, and output variables, which are the values that the model produces for the user.

The third stage in model construction is model formulation (Association of Applied Biologists, 1991; Carter and Rabbinge, 1980; DeWit and Rabbinge, 1979; France and Thornley, 1984; Murthy *et al.*, 1990). The aim in this stage is to quantify the relationships that make up the model and to define the output of the model (Carter and Rabbinge, 1980). This produces a model blueprint (Association of Applied Biologists, 1991) that may be constructed using well defined techniques (DeWit and Rabbinge, 1979).

Once the model has been constructed and output is able to be produced, the next step is to validate and verify the model (Carter and Rabbinge, 1980; DeWit and Rabbinge, 1979; Murthy *et al.*, 1990). Verification is the comparison of the structure and behaviour of the model with that of the real system (Carter and Rabbinge, 1980). This process is important as it is able to identify any areas of the model where the behaviour of the model differs from the real system, which may indicate a possible lack of understanding. DeWit and Goudriaan (1978) believe that verification can take place at several levels from the level of the individual, through the level of the population, to the field level.

Validation, on the other hand, is the quantitative comparison of output from a model with the observed results (Carter and Rabbinge, 1980; Gutierrez *et al.*, 1979; Jeffers, 1982; Rabbinge *et al.*, 1979; Zhou and Carter, 1989). Validation should be an ongoing process (Frenkiel and Goodall, 1978), and any data used for validation should be independent of the data used to build the model (Carter and Rabbinge, 1980; Jeffers, 1982; Rabbinge *et al.*, 1979). Feldman *et al.* (1984) noted that validation is often aimed only at the end values of a simulation, whereas the validation of a sequence of modelled variables representing the time-dependent behaviour of a process is also important. They developed a statistical process which quantified the closeness of model prediction to observed values.

Carter and Rabbinge (1980) warned that calibration of models to obtain a better fit, during validation, was undesirable as it lowered the explanatory value of the model and often degenerated into little more than a sophisticated curve fitting process.

If a model fails to be validated then it is inadequate for the goal in mind (Murthy *et al.*, 1990).

The model's assumptions have then to be examined and new assumptions made.

Once the model has been verified and validated, the final stage is its manipulation and implementation, which can be defined as the process of experimenting with the model (Carter and Rabbinge, 1980). Sensitivity analyses are often conducted at this stage because of their usefulness in detecting errors (DeWit and Goudriaan, 1978). There are two types of sensitivity analysis, fine and coarse (Carter and Rabbinge, 1980). For a coarse sensitivity analysis, whole processes are omitted from the model (Ankersmit and Rabbinge, 1979). In a fine sensitivity analysis, small positive and negative changes are made to the model parameters. Both coarse and fine sensitivity analyses can be used to show which parameters have the greatest influence on the model, and which parameters are responsible for deviations between predicted and observed values (DeWit and Goudriaan, 1978; Kocabas *et al.*, 1992; Jeffers, 1982; Rabbinge *et al.*, 1979).

Sensitivity analyses can also be used to obtain coefficients of variance for parameters (France and Thornley, 1984), which can then be ranked in an aid to model simplification, although this would of course lead to a loss in realism, and is not immediately useful in determine how parameters effect the fit of the model to observed data. By varying several parameters concurrently, the effects of interactions between parameters can be tested (Jeffers, 1982). The results of a sensitivity analysis can also help to improve insight into the system and to suggest further experiments (Rabbinge, Ankersmit and Pak, 1979), and may also provide an accurate measurement of the confidence merited by a model (Worner, 1991).

1.4.5 Problems with simulation models

Simulation models, although being able to handle complexity, are not without their problems. The main drawback with simulation models is estimation of the values for the large number of parameters that are required by the model (Carter and Rabbinge, 1980). This problem stems from the complexity of the ecological system being modelled, although Gilbert and Hughes (1971) felt that a simulation model did not have to be very sophisticated to throw some light on an ecological relationship. Another difficulty related to the complexity of the model is the logistical

problem associated with gathering all the data necessary for its construction and validation (Watt, 1961). Worner (1991) calculated that an adequate sample size for the validation of a simulation model was twelve populations monitored for twelve seasons, which would require a large long term sampling effort, and is outside the scope of most modelling projects, which tend to be short term. Gutierrez *et al.* (1984) also referred to this problem in relation to predator-prey models, which are rarely tested in the field due to the lack of data. They concluded that modelling efforts should be closely linked to detailed field and laboratory studies.

A model will be of limited use if it contains little understanding of individual functions in the model (DeAngelis *et al.*, 1975), or if a clear understanding of the behaviour of the major components of a model and their interactions is lacking. These are required in order to discern the behaviour of the total system. This means that before a model is constructed, suitable mathematical formulations for the mechanisms of each type of factor are required by the modeller (Watt, 1959); this is again related to the availability of adequate data.

Another major drawback with simulation models is the variance associated with model output. It has been estimated that a four percent error in model parameters can lead to up to forty percent variation in model output (Gardner *et al.*, 1980; Worner, 1991). Such large error terms imply that only gross changes in the system can be reliably predicted. However the use of stochastic models may relieve this problem, by producing a distribution of possible outputs.

As long as the limitations of simulation models are recognised, they will remain important in gaining qualitative insights into ecological systems, provided that they are based on a prior understanding of the process involved (Onstad, 1988).

Chapter 2. THE *SITOBION AVENAE* POPULATION DYNAMICS MODEL

Carter *et al.* (1982) proposed a simulation model (SAM7) to describe the summer population dynamics of *S. avenae* on winter wheat. It was felt that SAM7 was inadequate in its representation of aphid development and reproduction, due to the use of a linear representation of development, in spite of evidence of curvature (Dean 1974b), and also because reproduction was assumed to only occur between 10°C and 30°C. This chapter provides a brief description of SAM7, before detailing the changes made to the aphid development and reproduction processes.

2.1 DESCRIPTION OF THE MODEL

SAM7 uses an hourly time step, with temperature as the driving variable. The hourly temperatures are assumed to follow a sine curve, estimated from the daily maximum and minimum temperatures. The maximum temperature is assumed to occur at 1400 hours and the minimum temperature at sunrise. The times for sunrise are calculated according to the latitude of the site being modelled.

The model is divided into three main submodels; crop, aphid and natural enemy. A description of the processes involved in each submodel is given below.

2.1.1 The crop submodel

The crop submodel calculates the growth stage of the crop at the end of each day, based on an algorithm proposed by Frazer and Gilbert (1976) that uses a polynomial equation based on the accumulated number of day-degrees (D°) above 6°C. The number of day-degrees above 6°C is calculated following the equations shown below.

$$\begin{aligned} D_d &= 0.25 * Y & T_{mx} > 6.0, T_{mn} > 6.0 \\ D_d &= 0.125 * Y * (1.0 - 0.64T_r) + 0.0795 * (T_{mx} - T_{mn}) * \cos(T_r) & T_{mx} > 6.0, T_{mn} < 6.0 \\ D_d &= 0.0 & T_{mx} < 6.0, T_{mn} < 6.0 \end{aligned}$$

where: D_d = number of day degrees (D°) above 6°C ; $Y = T_{mx} + T_{mn} - 12.0$; T_{mx} = daily maximum temperature ($^\circ\text{C}$); T_{mn} = daily minimum temperature ($^\circ\text{C}$); and $T_r = \text{asin}(Y / (T_{mx} - T_{mn}))$.

Carter *et al.* (1982) used this simplified equation because the primary objective of SAM7 was to model the aphid population dynamics. The full model ends when the crop submodel predicts that crop growth stage is greater than 86.3 (Zadoks *et al.*, 1974); at this stage the crop is no longer suitable for aphids.

2.1.2 The aphid submodel

The aphid submodel can be split into several sub-processes which describe basic aphid biology in a crop during the summer. The first sub-process is immigration. The number of alatae entering the field is estimated from the number of alatae caught in a Rothamsted Insect Survey (Woiwod and Harrington, 1994) suction trap by multiplying the trap catch by a deposition factor (Taylor and Palmer, 1972).

The model then considers the development and survival of the aphids. Aphids develop by accumulating hour-degrees (H°), calculated from a threshold of -3.6°C , towards a total for each instar using the following equation.

$$H = T - (-3.6) = T + 3.6$$

where: H = hour-degrees (H°) accumulated during hourly timestep; and T = temperature during hourly time step ($^\circ\text{C}$).

On reaching this total for an instar, those aphids are moved into the next instar and the process reiterates. This is often referred to as a BOXCAR routine (DeWit and Goudriaan, 1978), and it means that all aphids of the same physiological age develop simultaneously through the various life stages. Fourth instar alate nymphs are assumed to emigrate immediately after moulting to the adult stage.

The longevity of adult aphids varies with crop growth stage, becoming shorter as the

crop ages. In order to cope with this, the model assigns different longevities according to the age of the crop. The model also assumes that fourth instar alate nymphs take longer to develop than fourth instar apterae due to their need to produce wings.

The proportion of aphids that survive an instar is set. Survival is calculated hourly from the assumed probability that an aphid survives the instar by adjusting for the proportion of the instar completed by the aphid concerned. This adjustment is required since the length of each aphid instar is dependant upon temperature. The equation used is shown below.

$$S = 10^{(\log_{10}(I) \frac{H_i}{H_h})} = I^{\frac{H_h}{H_i}}$$

where: S = proportion of aphids surviving for the hour; I = proportion of aphids surviving to complete instar (Dean, 1974b); H_i = Length of instar in hour degrees (H°); H_h = hour degrees (H°) accumulated in hour being considered.

The third sub-process deals with the reproduction of aphids. It is assumed in SAM7 that alate adults immigrating into the field are reproductively mature, but that apterous adults that develop within the modelled field are subject to a pre-reproductive delay.

Reproduction is assumed to occur only in the temperature range 10°C to 30°C. The reproductive rate is assumed dependent upon the morph of the adult aphid, temperature and crop growth stage. Apteræ have a higher reproductive rate than alatae (Wratten, 1977). The maximum reproductive rate is assumed to occur at 20°C, and was estimated from the data of Dean (1974b). When the crop growth stage is between 59 and 73 the reproductive rate is increased, in accordance with the observation of Watt (1979) that reproduction is greater on ears than on leaves.

The number of nymphs produced by the aphids in a given hour is calculated by multiplying the reproductive rate by the number of H° accumulated over that hour and by the number of aphids. The proportion of nymphs that will be alate is the calculated from the equation shown below.

$$Al = 2.60D_a + 0.847C - 27.189$$

where: Al = percentage of nymphs that will be alate; D_a = density of aphids (/tiller);
C = crop growth stage according to the decimal scale of Zadoks *et al* (1974).

2.1.3 Natural enemies submodel

The natural enemies included in the model are the seven-spot ladybird, *Coccinella septempunctata*, parasitoids and fungal pathogens.

The effects of parasitoids and fungal pathogens are calculated directly from data input from field counts of the number of mummified or infected aphids. The effect of *C. septempunctata* is covered in more detail below.

The number of aphids in each instar is first converted to aphid units (Lowe, 1974), where one aphid unit is equivalent to one adult, 1.5 fourth instar nymphs, 2 third instar nymphs, 3.5 second instar nymphs or 5 first instar nymphs. The aphid units are then summed to give an overall total, and a subtotal is formed of the number of aphid units in the first three nymphal instars.

Predation is assumed to occur only if the temperature is in the range 15°C to 30°C. The number of predators in each instar is obtained from field counts. The number of aphid units assumed to be killed by the predators in a given hour is calculated from the consumption rates of the predator for each instar, the number of predators in each instar, and the number of H^o accumulated for that hour.

If the number of aphid units is less than three, the number of aphids surviving is assumed to increase linearly as the aphid density decreases. This allows for the fact that at low aphid densities, coccinellids do not eat aphids at the maximum rate.

2.2 CHANGES MADE TO THE MODEL

2.2.1 Changes to aphid development

SAM7 was inadequate to describe aphid development, due to the use of a lower development threshold of -3.6°C, which is very low compared to the value of 3°C suggested by Williams and Wratten (1987). This value was obtained by Carter *et al.* (1982) by fitting a linear regression through the data of Dean (1974b) (Figure 2.1), for which the standard errors are unavailable. They assumed aphid development, D , was linearly related to temperature, t , in the range 10°C to 22.5°C, with H° accumulated calculated by adding 3.6 to the temperature. Between 5°C and 10°C, the number of H° accumulated increased linearly from 0.1 to 13.6, and below 5°C, the number of H° accumulated was set to 0.1. Between 22.5°C and 25°C the number of H° accumulated was set to 26.1, and between 25°C and 30°C, the number of H° accumulated was decreased linearly towards 0.1, being set at 0.1 for all temperatures above 30°C.

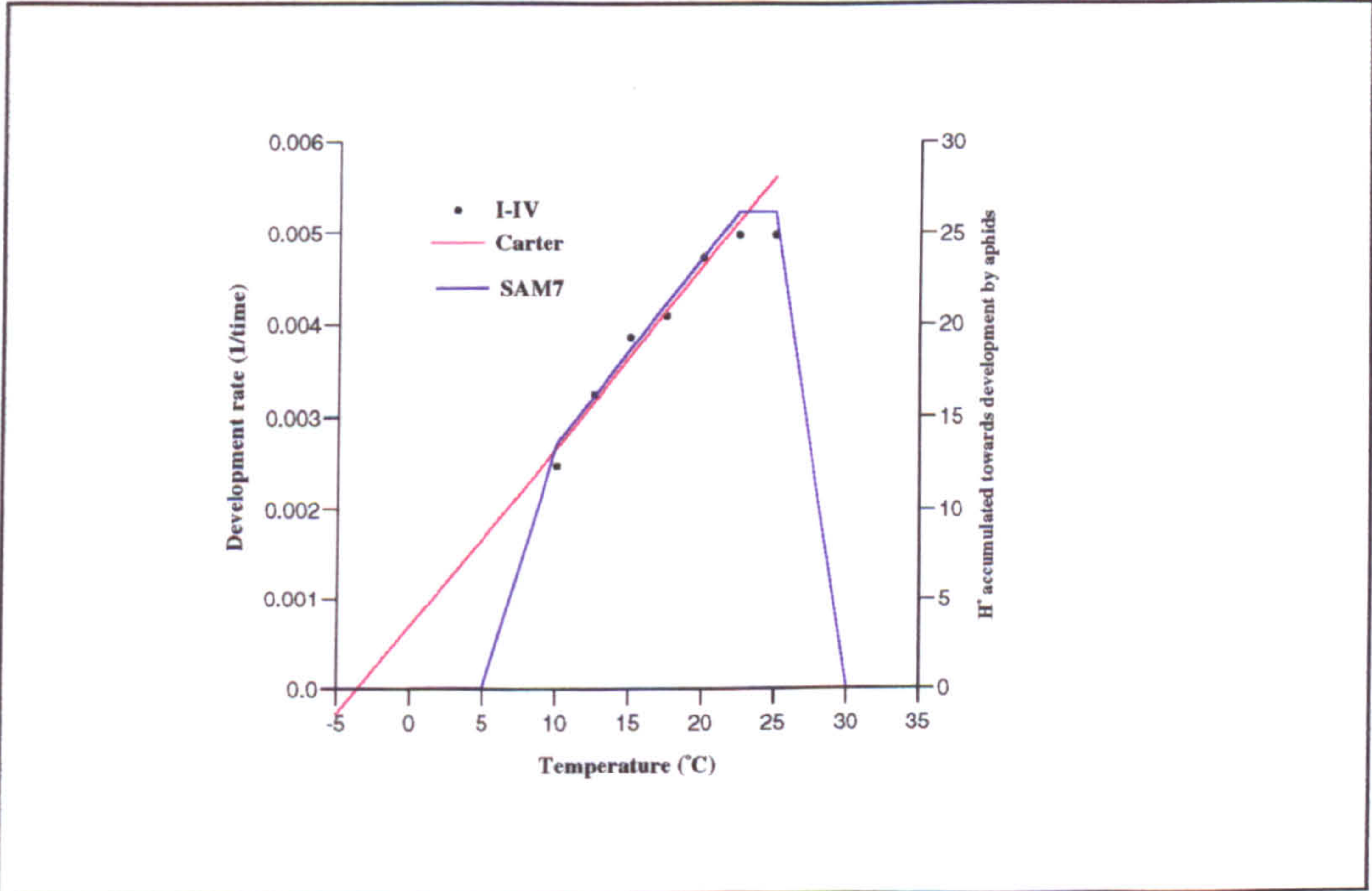


Figure 2.1: A graph showing the regression line fitted to the pooled developmental data of Dean (1974b) by Carter *et al.*(1982), and the representation of development used in SAM7.

More recent data were reviewed concerning the effect of temperature on the development of *S. avenae* (Lykouressis, 1985; Kieckhefer *et al.*, 1989) in addition to the data of Dean (1974b). All three datasets showed evidence of curvature at high temperatures, but the data of Dean (1974b) were a different shape to the data from the other two sets, which had been monitored less frequently and covered a narrower range of temperatures. These two sets also predicted higher development rates, with the data of Lykouressis (1985) showing little curvature, but that of Kieckhefer *et al.* (1989) showing curvature occurring as low as 22°C.

In order to choose the most appropriate dataset, the experimental methods used in obtaining the data were examined critically. The dataset of Dean (1974b) was chosen because it had the largest number of replicates; also sampling was done more often than in the other two experiments. Another advantage was that this was the dataset used to parameterize SAM7, and so the new model would be directly comparable.

To account for curvature in the data, it was decided to follow the example of Stinner *et al.* (1974), who suggested that a sigmoid relationship could be used to describe the effect of temperature on insect developmental rate. Dean (1974b) reported separate results for each instar, so separate generalized logistic relationships were derived for each instar, instead of using a general curve for all instars, which was the method adopted in SAM7. The data were fitted using non-linear regression in the package GENSTAT (Payne *et al.*, 1978).

A major problem of the logistic curve was that the abscissa (temperature) was an asymptote to the curve, so that a value for the lower developmental threshold, t_0 , where $D = 0$, could not be obtained. A solution to this problem was obtained by linearizing the curves below their point of inflexion. To do this, the gradient of the line was set equal to that of the curve at the inflexion point and this was calculated by differentiating the generalised form of the logistic curve, to give the equation shown below.

where: D = development rate (/hour); C = value of upper asymptote of curve; b = a slope parameter; m = value of dependent variable at the inflexion point; and x = the

$$\frac{dD}{dt} = \frac{-C(-b)(e^{-b(x-m)})}{[1+e^{-b(x-m)}]^2}$$

dependent variable (temperature (°C)).

At the inflexion point, $x=m$, which when substituted into the above equation gives a value of $Cb/4$ for the gradient. At the inflexion point $D = C/2$. Since the gradient was now known, the value of the threshold was calculated by rearranging the following equation:

$$\frac{\frac{C}{2}}{m-t_0} = \frac{Cb}{4}$$

$$\text{i.e } t_0 = m - 2/b.$$

The appropriate values were substituted in this equation, and the values for the lower development threshold of each aphid instar were calculated (Table 2.1) via linear interpolation.

Based on recent studies (Williams, 1987; Williams and Wratten, 1987), it was felt that a negative value for the lower development threshold was unrealistic for instars I and IV, and therefore a threshold of 0°C was adopted for all instars, as this was close to the mean value (-0.53°C); this also made the calculation of H° easier.

Instar	Lower Development Threshold
I	0.965°C
II	-1.05°C
III	0.967°C
IV	-3.013°C

Table 2.1: The lower developmental thresholds for the aphid instars.

Equations describing the linear effect of temperature on the developmental rate of the aphid instars below the point of inflexion were then calculated using the revised lower development thresholds.

The decision to linearize the curves below their inflexion point was supported by the work of Williams and Wratten (1987), who showed that there was no curvature in the relationship between developmental rate and temperature in the temperature range 3°C to 13°C. Since temperatures in the model do not often drop below 5°C, the assumption of a linear relationship below the point of inflexion was reasonable.

The next step was to determine how the developmental rate of the aphid instars was affected by temperatures above 25°C. The data of Dean (1974b) showed a decline in rate at 27.5°C. A line was fitted through the value predicted by the logistic curve at 25°C and the data-point at 27.5°C, which gave the upper developmental thresholds shown in Table 2.2, via linear interpolation.

Instar	Upper Development Threshold
I	41.0°C
II	41.3°C
III	39.0°C
IV	42.0°C

Table 2.2: Upper developmental thresholds of the aphid instars (Standard errors are unavailable since the values were derived via linear interpolation, since data were limited).

The equations describing the effect of temperature on the development of aphid instars (Figure 2.2.) are shown in general form below, with the parameter estimates shown in Table 2.3

$D = 0.0$
 $D = b_{li} \ t$

$t \leq 0.0$
 $0.0 < t \leq t_{li}$

$D = a_i / (1 + \exp(-x_j (m_i - t)))$	$t_{1i} < t \leq 25.0$
$D = c_i - b_{2i} t$	$25.0 < t \leq t_{2i}$
$D = 0.0$	$t_{2i} < t$

where: D = Development rate (1/time); the subscript, i , relates to the instar concerned; b = constant (slope of regression line); c = constant (intercept of regression line); a = constant (lower asymptote of the logistic equation); m = constant (upper asymptote of logistic equation); x = constant (slope parameter of logistic equation); and t = temperature ($^{\circ}\text{C}$). The standard errors of the regression coefficients are given in Table 2.3, where they were able to be estimated. The linear relationships were derived by linear interpolations and ,therefore, standard errors are not available for these parameters.

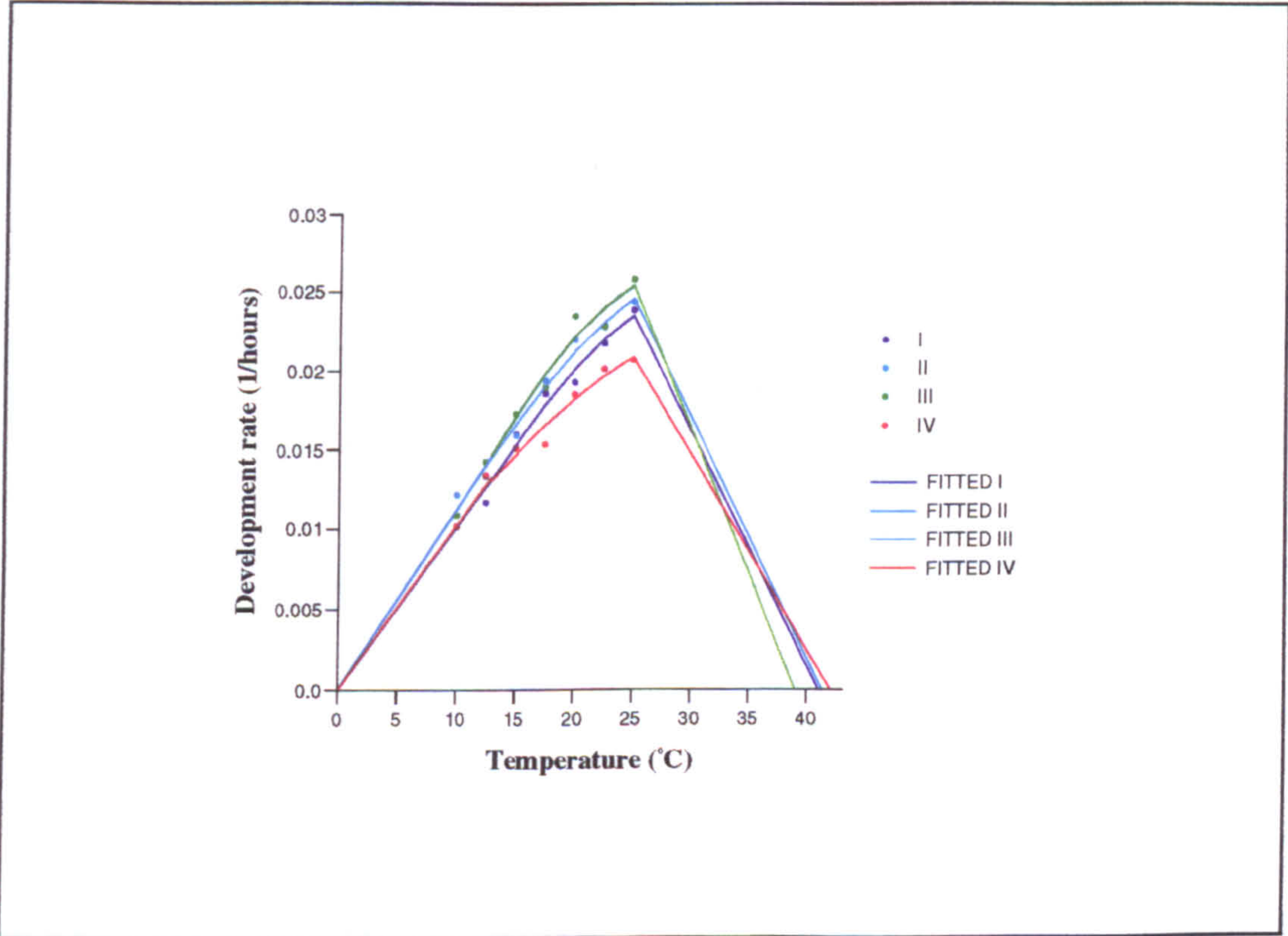


Figure 2.2: Graph showing the equations fitted to the data of Dean (1974b) to describe the effect of temperature on the developmental rate of the aphid instars.

The development of adult aphids was treated in a similar way to that in SAM7, via the accumulation of H° towards a total. This method was used due to the lack of data describing the effect of temperature on the developmental rate of adult aphids. Also

there was no way of estimating the age of the number of aphids which were estimated as immigrating into the field. Consequently, the longevity of these adults was assigned a constant value derived from the data of Dean (1974b).

Instar (i)	b_{1i}	t_{1i}	a_i	x_i	m_i	t_{2i}	c_i	b_{2i}
1	0.00101	13.45	0.02718 ±0.003	0.1602 ±0.038	13.45 ±1.54	41.0	0.0600	0.00146
2	0.00112	13.00	0.02903 ±0.003	0.1423 ±0.034	13.0 ±1.75	41.3	0.0620	0.00150
3	0.00112	12.67	0.02849 ±0.003	0.1709 ±0.044	12.67 ±1.33	39.0	0.0702	0.00180
4	0.00102	12.07	0.02461 ±0.004	0.1326 ±0.046	12.07 ±2.46	42.0	0.0517	0.00123

Table 2.3: The parameter estimates in the equations describing the relationship between temperature and development rate in the four aphid instars.

2.2.2 Changes to aphid reproduction.

In SAM7, reproduction was assumed to occur only in the range 10°C to 30°C. Data from Williams and Wratten (1987) and Dean (1974b) suggested that aphids were able to reproduce at temperatures below 5°C, and even at temperatures close to 0°C. Therefore, it was decided to use a lower threshold of 0°C, as with development, which ensured continuity throughout the model, and was computationally convenient.

In SAM7, the reproductive rate (nymphs/adult/H°) was treated as a constant, with a

value equivalent to the maximum value observed by Dean (1974b). Only the number of H^o changed with respect to temperature. However, a constant reproductive rate is unlikely, and in the amended model the reproductive rate was allowed to vary with respect to temperature. The relationship between temperature, t , and reproductive rate, R , was assumed linear as there was no evidence of curvature in the data. The line was fitted between the data at ($R = 0$, $t = 0$) and the maximum value observed by Dean (1974b) at $t = 20^{\circ}\text{C}$. Above 20°C , the reproductive rate was assumed to decrease linearly to zero at 30°C . The equations, which were derived separately for each morph to take account for the differing reproductive rates between apterous and alate morphs (Dean 1974), are shown below and the parameter estimates are presented in Table 2.4.

$$\begin{aligned}
 R &= b_1 t & 0.0 \leq t \leq 20.0 \\
 R &= a_2 - b_2 t & 20.0 < t \leq 30.0
 \end{aligned}$$

where: R = reproductive rate (Nymphs/adult/ H^o); a = constant (intercept of regression equation); and b = constant (slope of regression equation). The standard errors of the parameters in this equation were unable to be estimated since the relationships were derived by linear interpolation.

Morph	b_1	a_2	b_2
Apterous	0.00031	0.0186	0.00062
Alate	0.00024	0.0144	0.00048

Table 2.4: Parameter estimates for equations describing the effect of temperature on reproductive rate.

Watt (1979) observed that the reproductive rate of *S. avenae* was greater on the ear than on the leaf. Therefore, the reproductive rate obtained from the above equations is accurate only when the crop growth stage is outside the range 59 to 73. Within this range the assumed reproductive rate is increased by a factor of 1.6 to account for the observations of Watt (1979). If the crop growth stage is greater than 80, then the

reproductive rate is set to zero, since the crop is then no longer suitable for aphid reproduction.

The number of nymphs produced per female per hour is obtained by multiplying the reproductive rate by the number of hour degrees for each hour, and this value is shown at different temperatures in Figure 2.3. The total number of nymphs produced in any hour is then obtained by multiplying this value by the number of adults.

The predicted nymphal production of *S. avenae* was compared with data available from the literature (Dean 1973, Chaudhury *et al.* 1969, Ferreres *et al.* 1989 , Kieckhefer and Gellner 1988, Lykouressis 1984, Sotherton and Van Emden 1982) (Figure 2.3). The figure shows that there is a general agreement between the new equations and the published data. However, the published data consisted mainly of studies performed at single temperatures. Several wheat varieties were used in the studies, and the variety of wheat can have a large affect on aphid reproductive rate, according to the resistance of the wheat variety to aphid feeding. These two factors meant that accurate estimation of the fit of the new equations to actual data was hampered by interstudy variability.

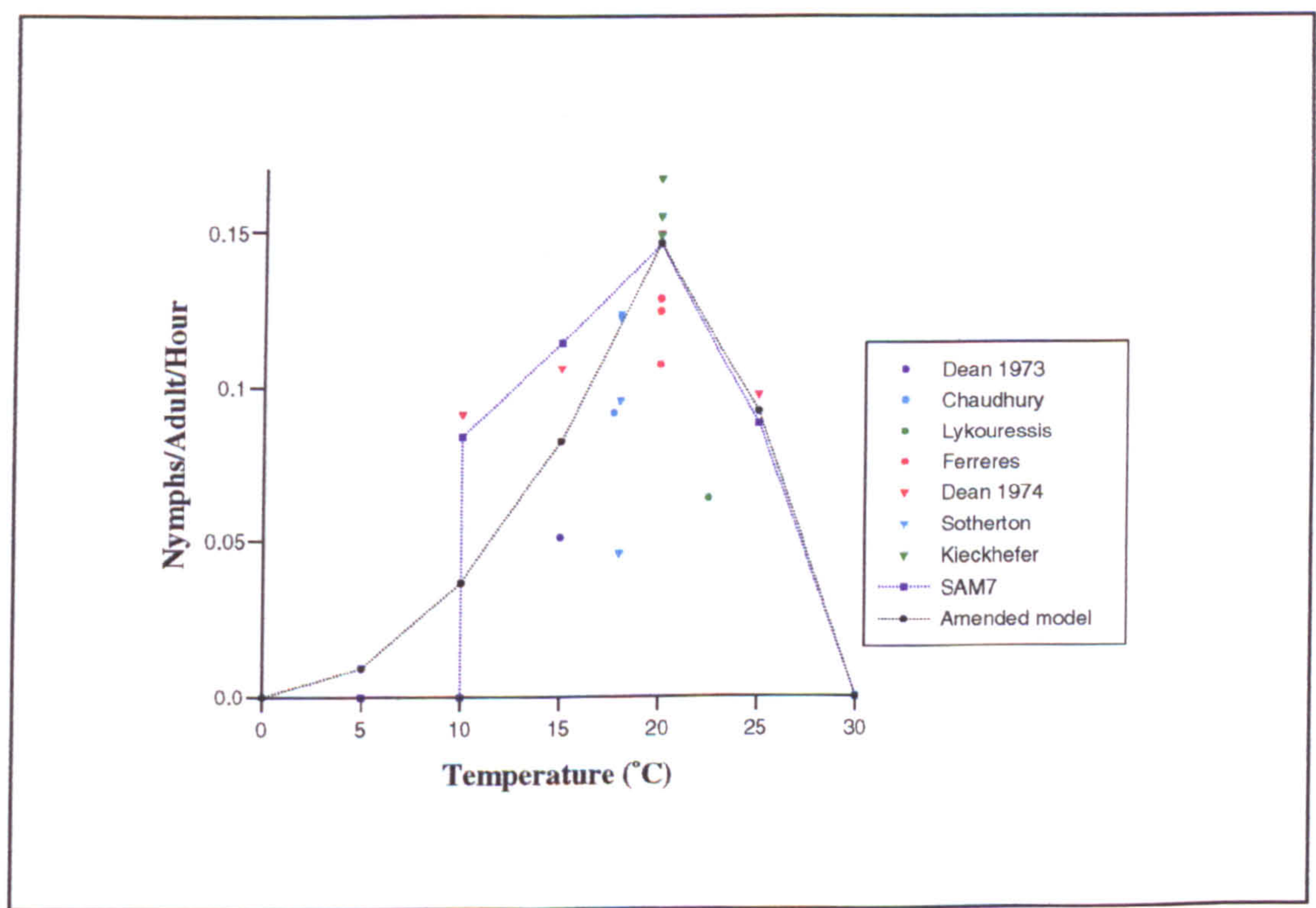


Figure 2.3: The effect of temperature on the production of nymphs by adult apterous *S. avenae*.

2.3 COMPARING THE PERFORMANCE OF THE AMENDED MODEL WITH SAM7

2.3.1 Comparison of SAM7 and the amended model with field data

To determine the effects of the changes to SAM7, it was necessary to compare the output of the new model (SACSIM) to that of SAM7. It was decided to compare the two models with data for the year 1976, as this was one of the years used to validate SAM7. The field data for this year was obtained from the University of East Anglia (A.F.G. Dixon *pers. comm.*), and only data from two fields in 1976, and one field in 1977 were available with counts in the form of numbers per tiller, which could be easily compared with the output of SAM7 and SACSIM, other fields having counts made by D-vac suction sampling.

During the lengthy process of comparing the output of SAM7 with that published by Carter *et al.* (1982), it was noticed that there was a discrepancy between the published results and the output of SAM7; some of the lines of code used in SAM7 were longer than the permitted length, and hence information and decimal places were being missed when running the model. Once this had been corrected, the published model and SAM7 produced similar output. After further investigation it was discovered that the fourth instar apterae in SAM7 were not accumulating H^o correctly; this was corrected also.

Having corrected these errors, the models were run and SAM7 and the published model were found to agree closely. The small discrepancy remaining was due to an amendment in SAM7, which produced a more efficient predation routine, that was absent from the published model.

Initial comparison revealed some errors in SACSIM, which were corrected before a full comparison was made. SAM7 and SACSIM were then run using the data from 1976 (Figures 2.4 and 2.5) and 1977 (Figure 2.6). Data were used from two fields in 1976 and one in 1977. The data came from the field counts used by Carter *et al.*

(1982) to validate SAM7.

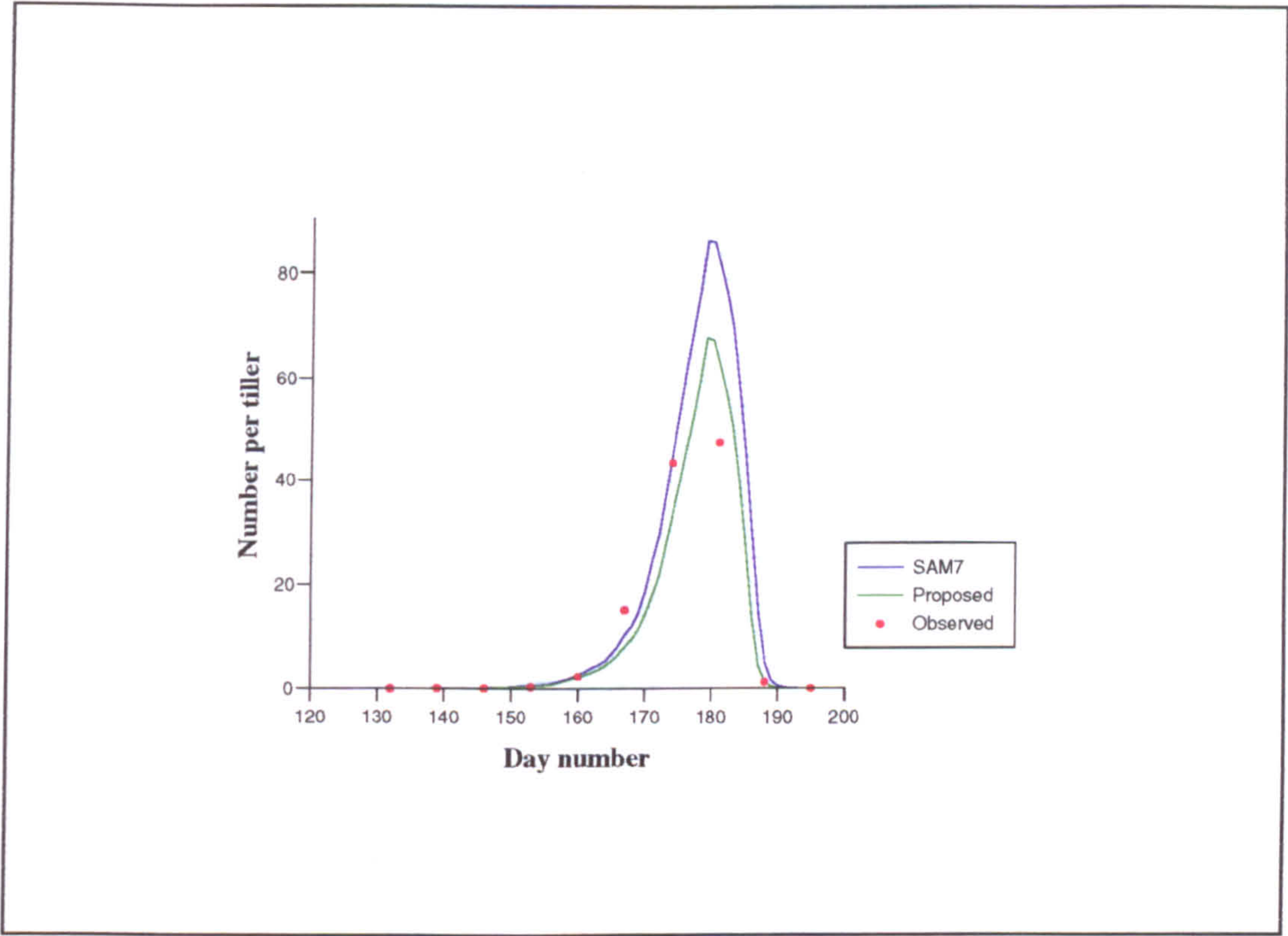


Figure 2.4: The predictions from SAM7 and SACSIM and field observations for field 1 in 1976.

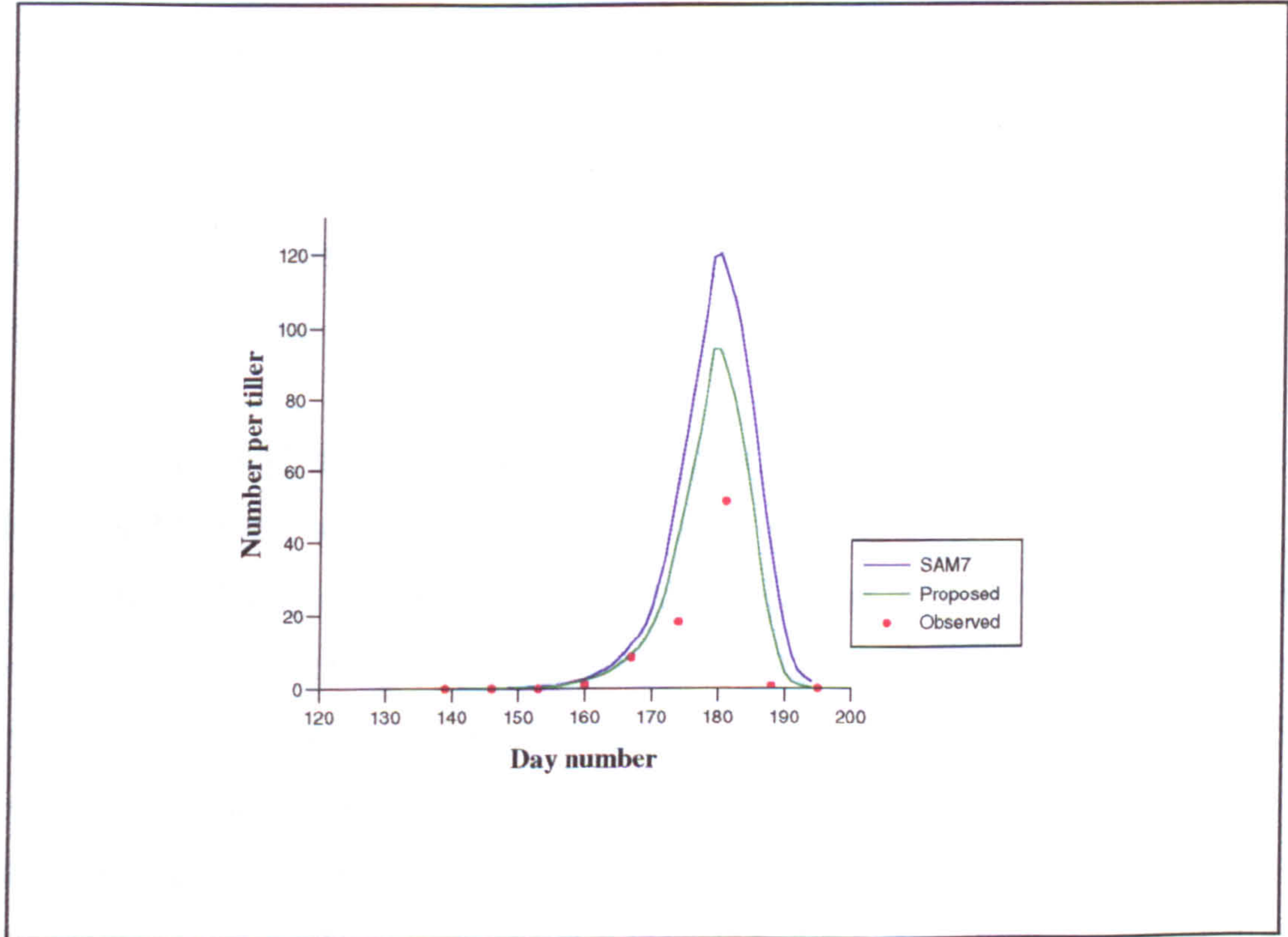


Figure 2.5: The predictions from SAM7 and SACSIM and field observations for field 2 in 1976.

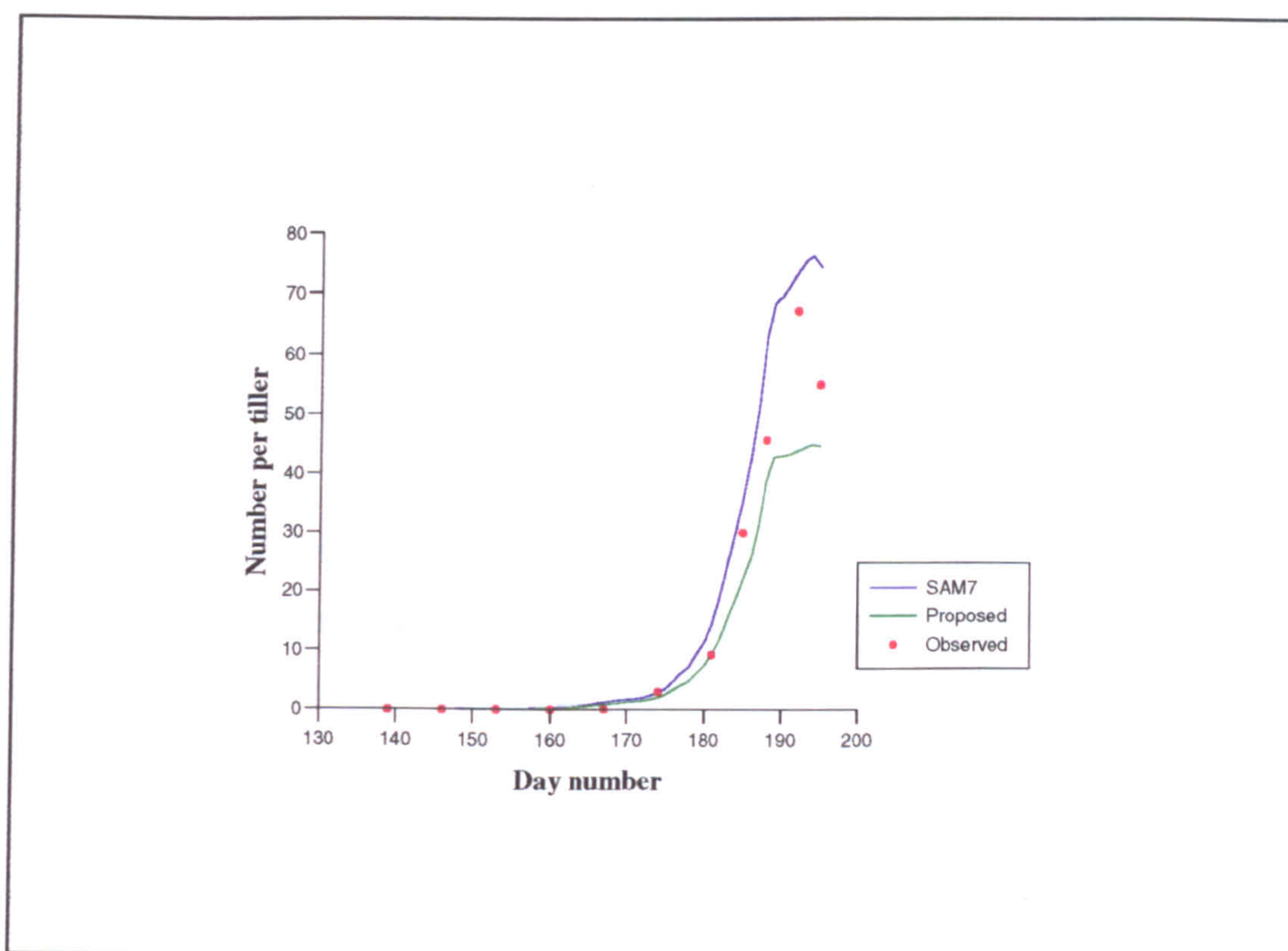


Figure 2.6: The predictions from SAM7 and SACSIM and field observations for field 1 in 1977.

The predictions of the model for both fields in 1976 were reasonable, with SACSIM closer to the observed values and predicting a smaller maximum number of aphids than SAM7. Even so, SACSIM predicted higher maximum numbers than were observed in the field, but this was because *C. septempunctata* is not the only predator of aphids, and the observations of smaller aphid numbers are the result of predation by a whole complex of natural enemies.

For 1977, although the predictions of SACSIM were closer to the observed values than SAM7, they were slightly smaller than the observed values. In 1977, the temperatures throughout most of the season were in the range 10°C to 20°C, and it is within this range that the equations of SAM7 predict larger values for the development and reproductive rates than SACSIM. This explains why the predictions of SACSIM are so much lower than those of SAM7, but not why they are slightly lower than the observed values. The presence of field to field variation could easily account for the differences between the predictions of SACSIM and the observed numbers, especially

since suction trap counts are used to provide a measure of aphid immigration. Suction traps are representative of a large area (Taylor, 1973), and therefore have a low spatial resolution. This means that the model is unable to account for the characteristics of individual fields, such as aspect, slope, soil characteristics and other variables known to affect crops and their insect fauna.

2.3.2 Comparison of SACSIM with SAM7

SAM7 and SACSIM were run using input data for 1984, 1985, 1988 and 1988 (Carter, N. personal communication), which consisted of suction trap counts for the aphids and field counts of coccinellids and aphid parasites. However, the field observations on the number of aphids were unavailable and therefore the output of the two models could not be compared with field observations.. The aim of this comparison, independent of field observations, was to see how the changes made to SAM7 had affected the output of the model. The output of SAM7 was also compared with runs of the SACSIM model where the changes to development , or reproduction were included separately. The output of SAM7 and SACSIM is shown separately for each morph in Figures 2.7 to 2.14; note the different scales on each graph. The version of SACSIM used for this comparison includes the amendments to both development and reproduction.

The results from this comparison show that SACSIM predicts greater numbers of apterous nymphs than SAM7, but lower numbers of apterous adults. SACSIM also predicts that the peak number of adults and nymphs will occur later than predicted by SAM7. For the alate nymphs, SACSIM again predicted lower maximum numbers than SAM7, but in this case the timing of the maximum numbers was earlier than predicted in SAM7. There was a particularly large discrepancy between the two models for alatae in 1989 because the temperatures favoured the greater reproduction of the aphids in SAM7 compared to SACSIM.

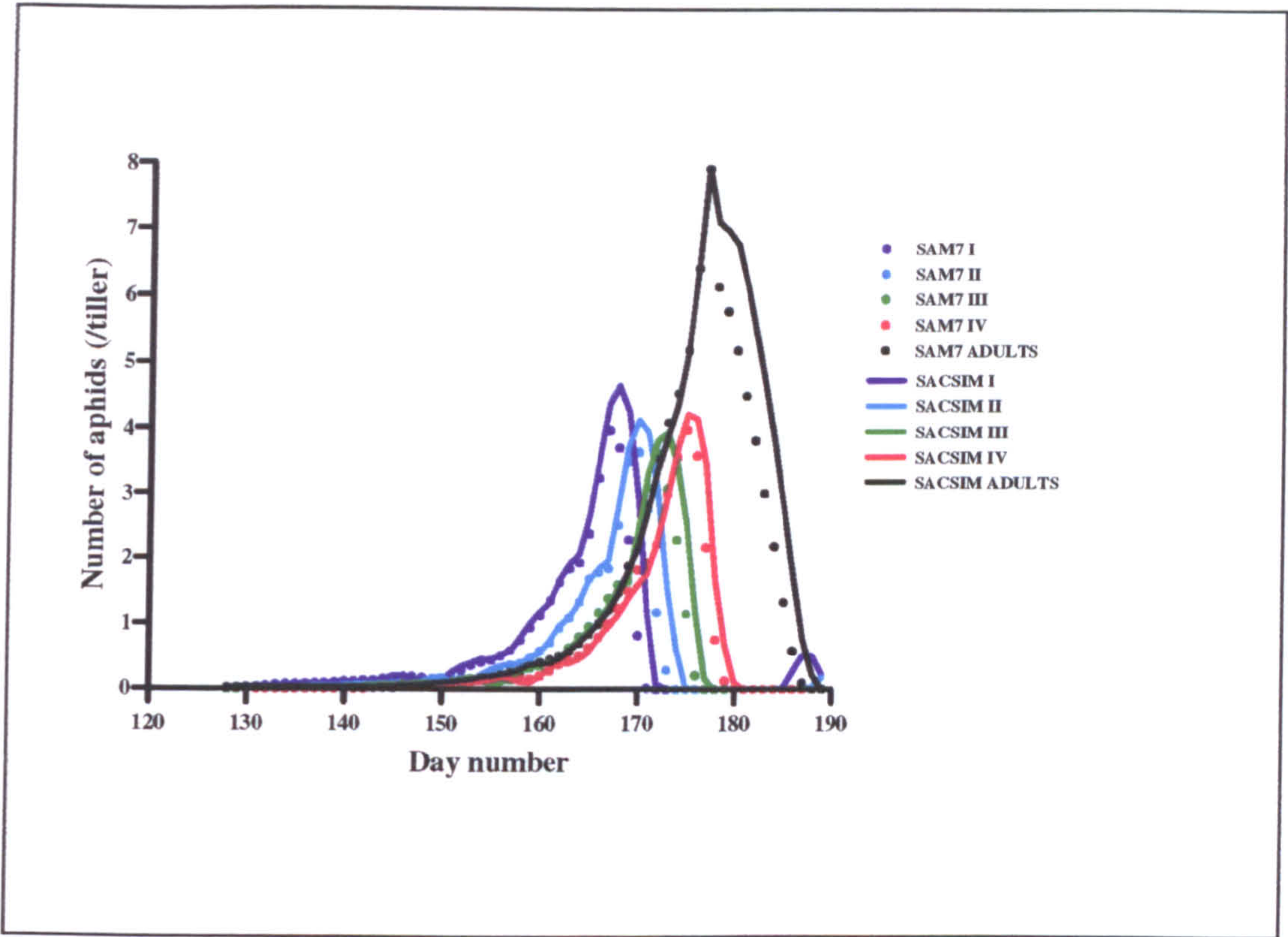


Figure 2.7: Comparison of output from SAM7 and SACSIM for apterae in 1984.

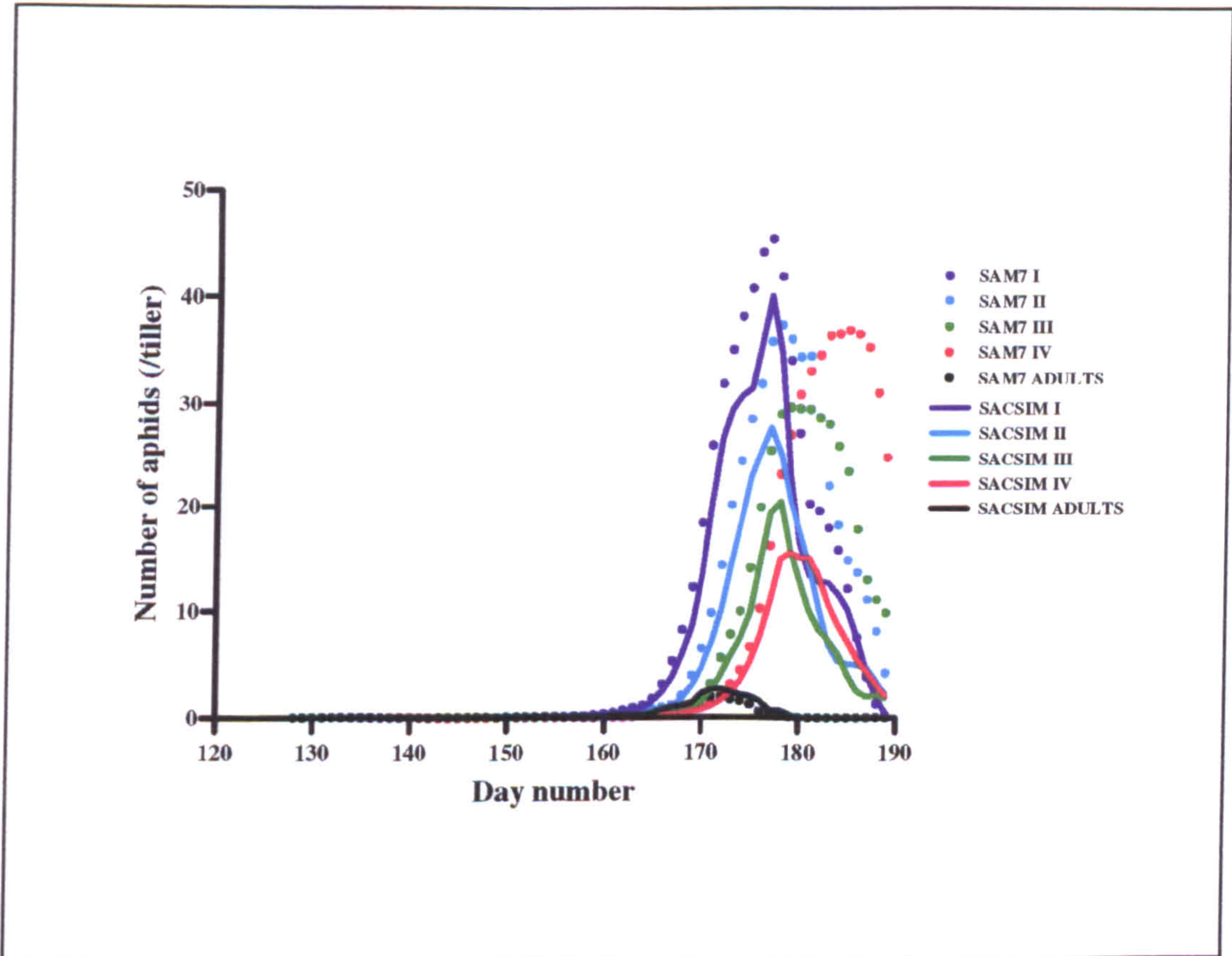


Figure 2.8: Comparison of output from SAM7 and SACSIM for alatae in 1984.

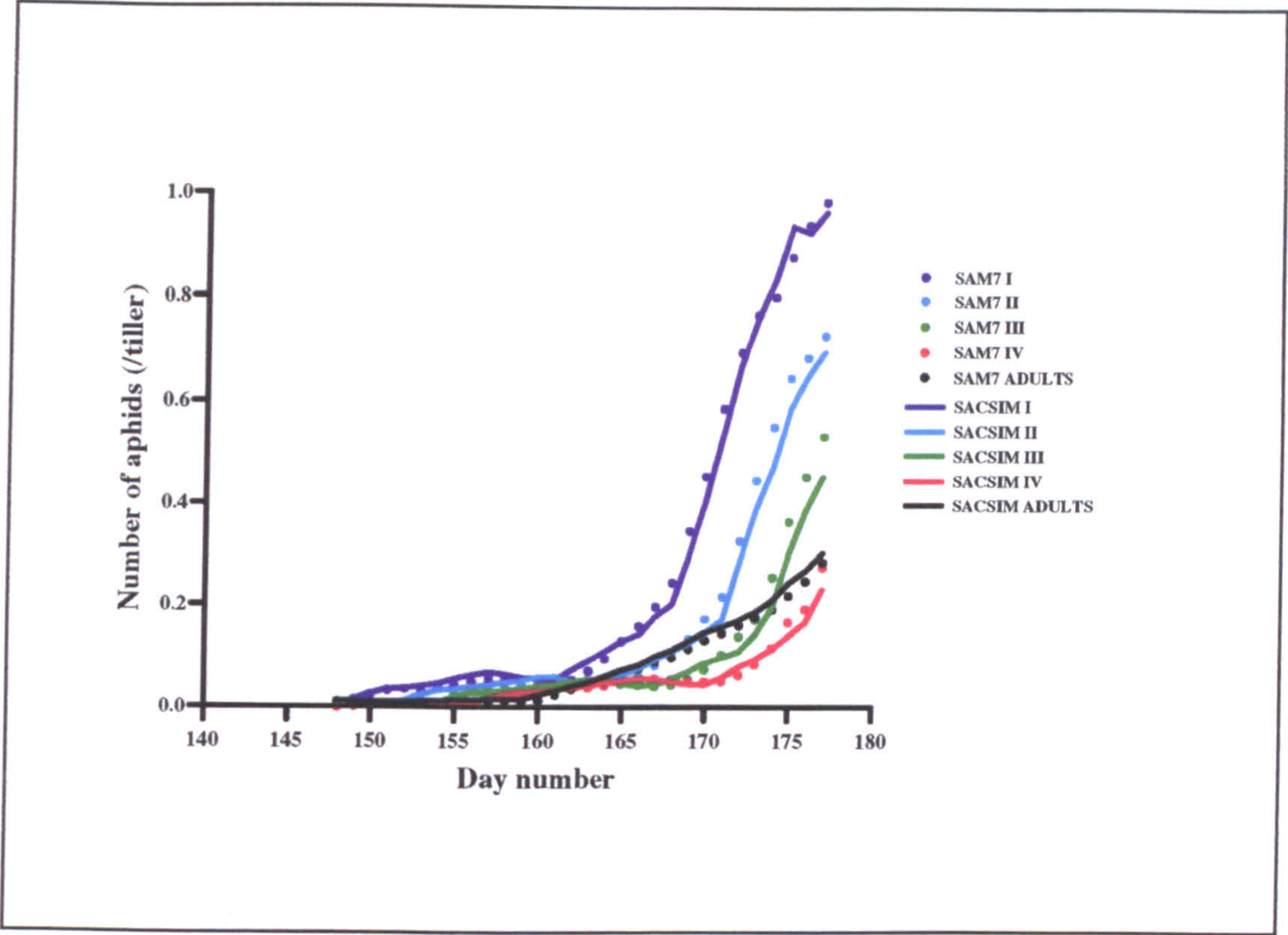


Figure 2.9: Comparison of output from SAM7 and SACSIM for apterae in 1985.

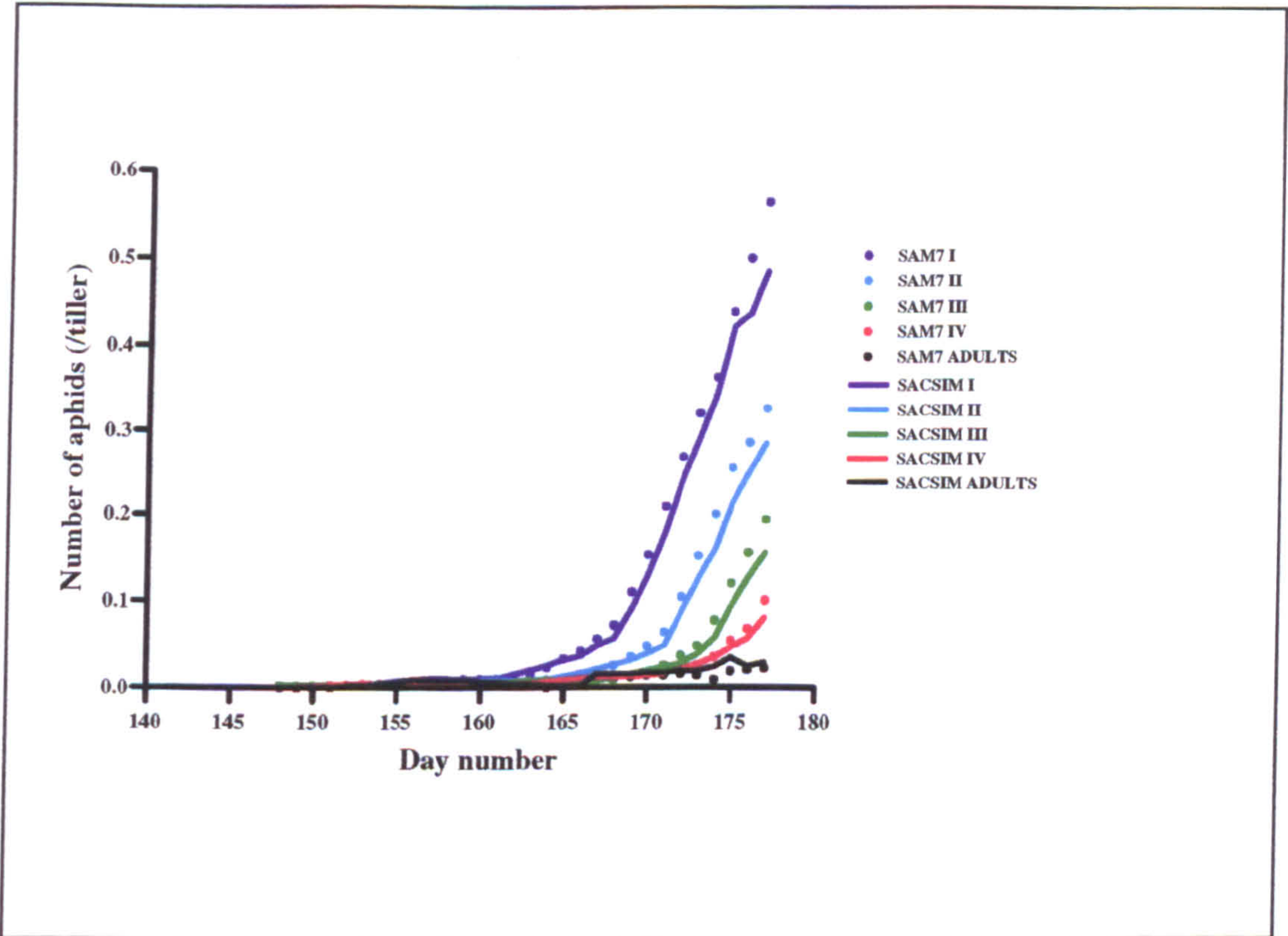


Figure 2.10: Comparison of output from SAM7 and SACSIM for alatae in 1985.

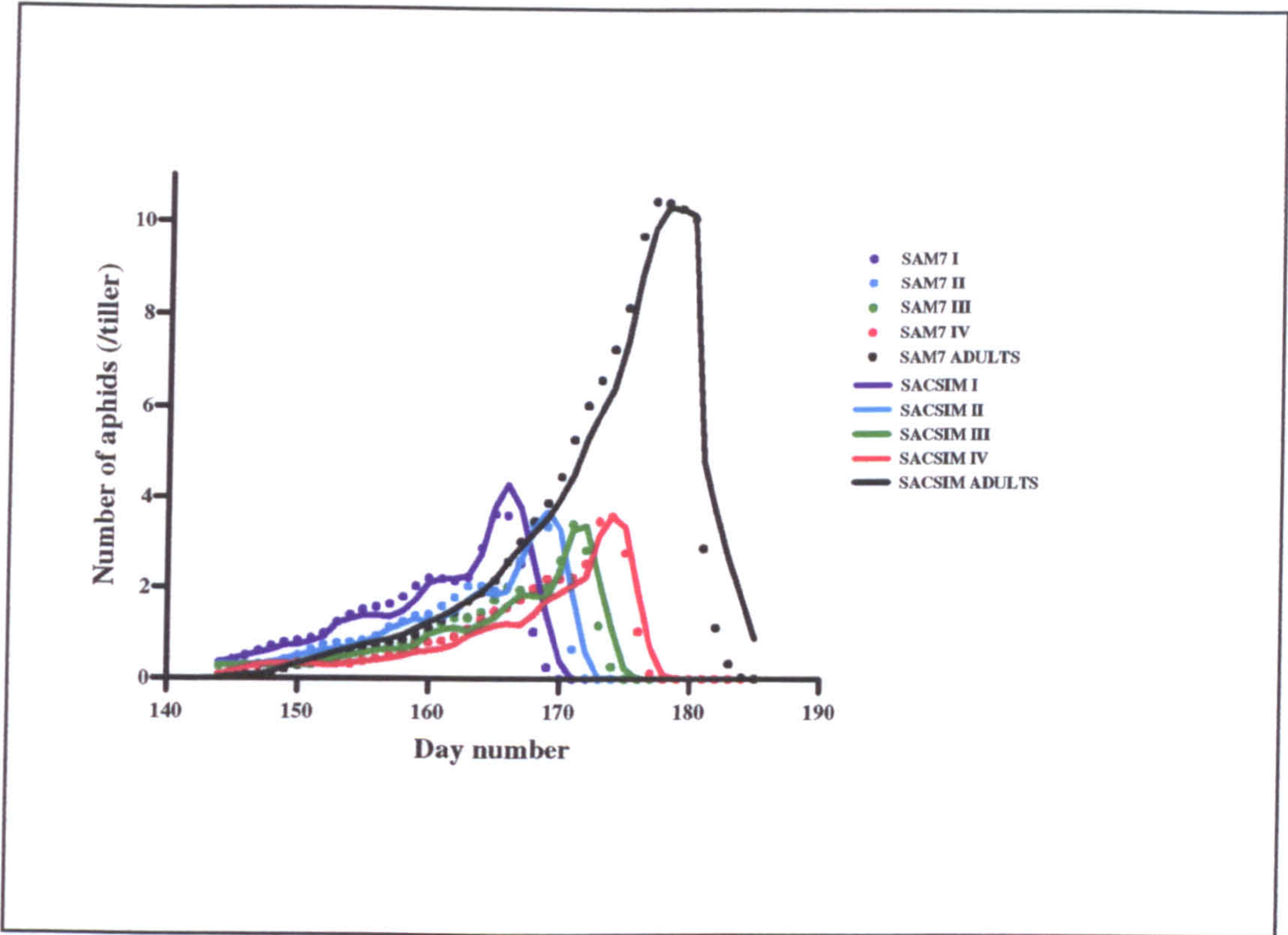


Figure 2.11: Comparison of output from SAM7 and SACSIM for apterae in 1988.

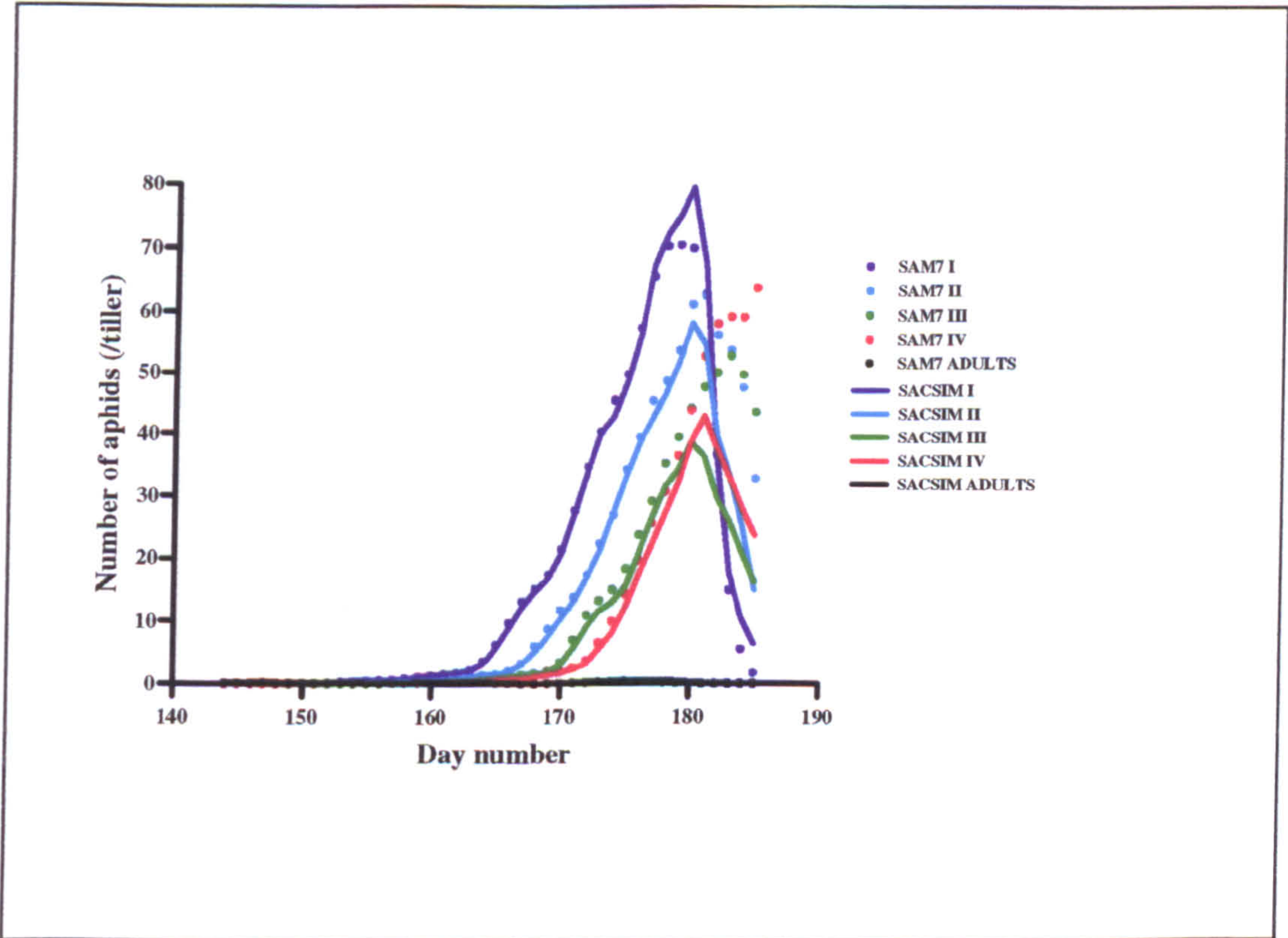


Figure 2.12: Comparison of output from SAM7 and SACSIM for alatae in 1988.

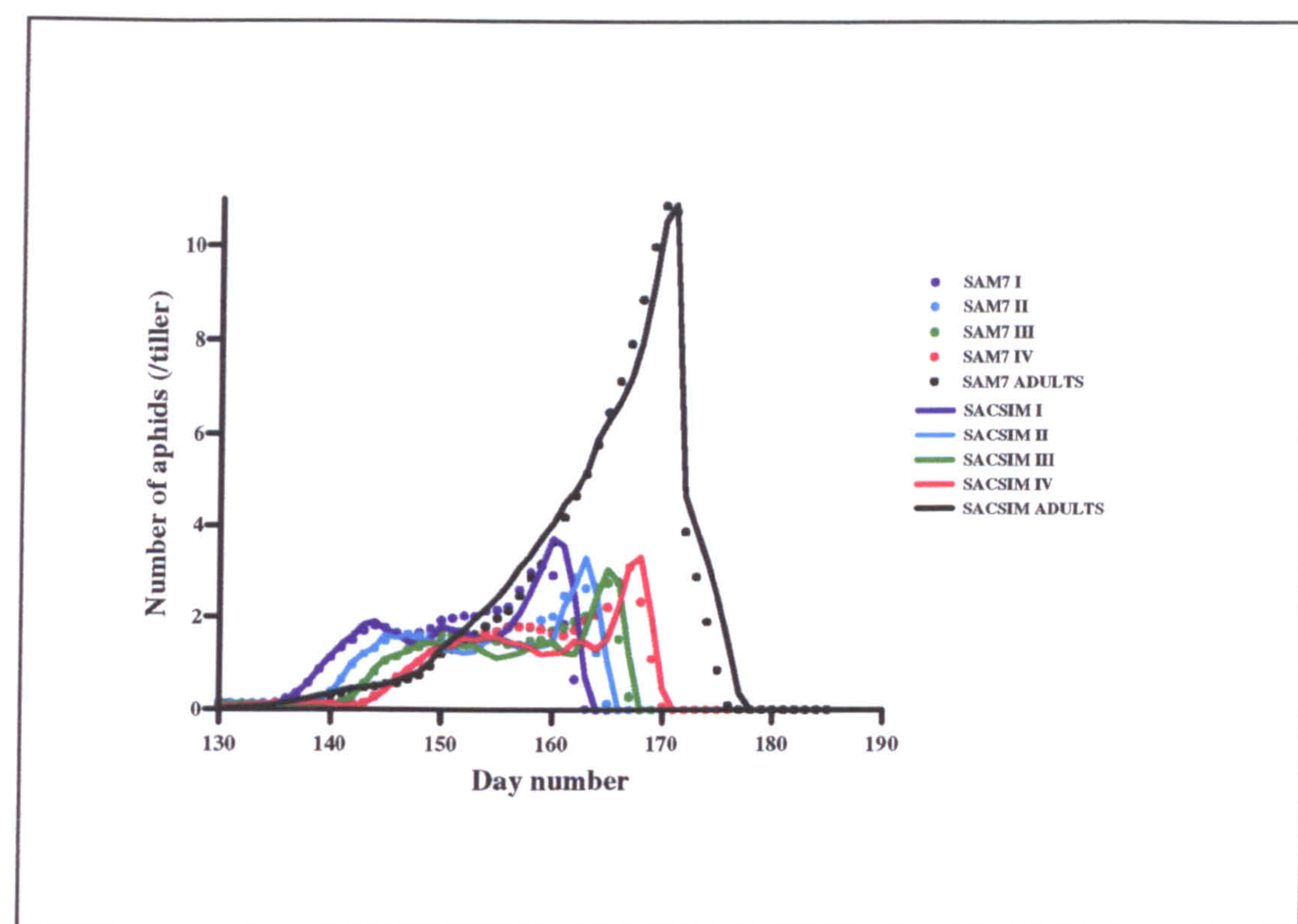


Figure 2.13: Comparison of output from SAM7 and SACSIM for apterae in 1989.

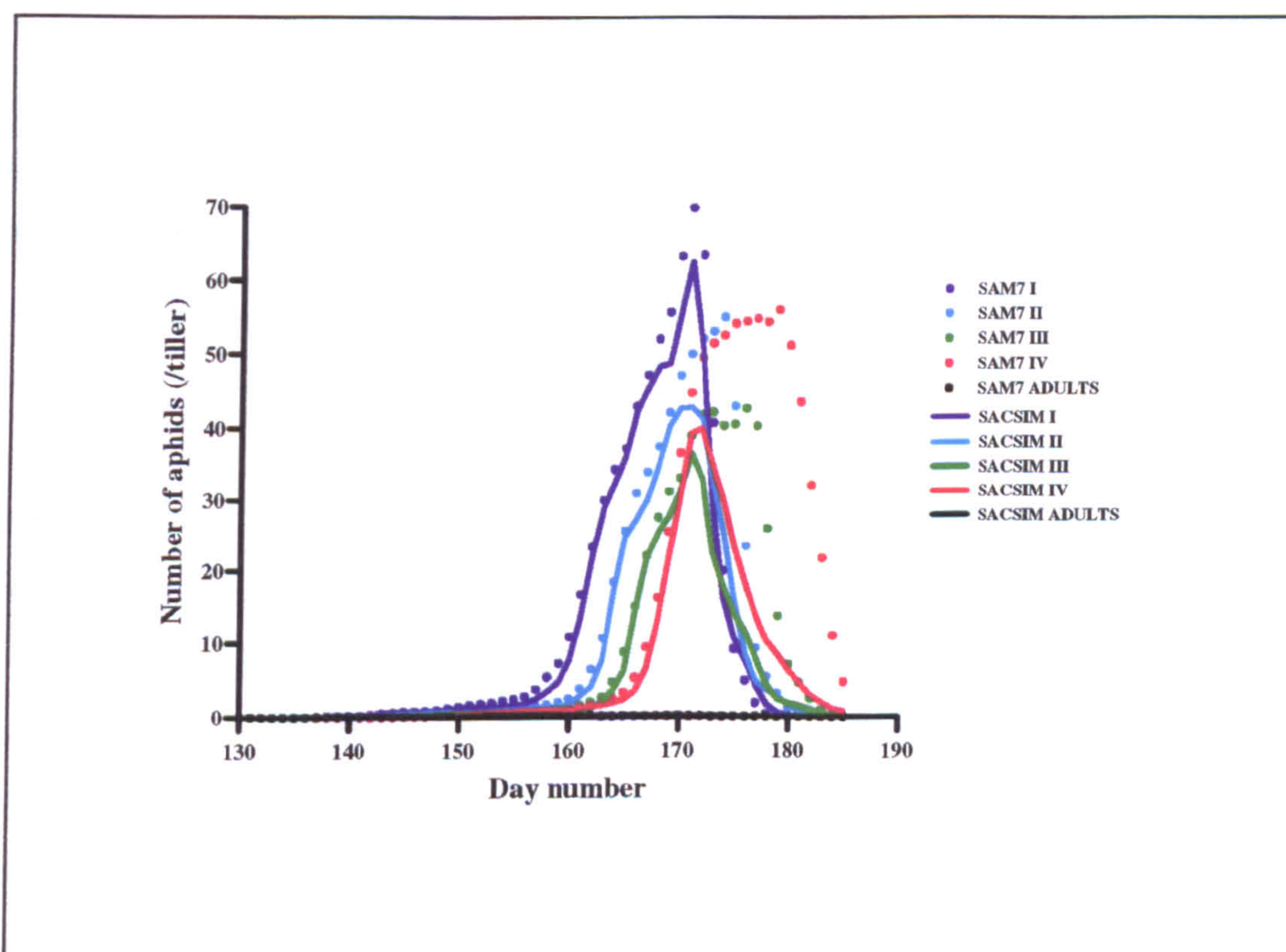


Figure 2.14: Comparison of output from SAM7 and SACSIM for alatae in 1989.

The comparison of the output of SACSIM with those models where either development or reproduction alone were altered suggested that the timing of the maximum numbers of apterae was affected by the changes to the equations for reproduction. The timing of the maximum numbers of alatae, however, was affected mainly by the changes to the development equations. The maximum numbers predicted by SACSIM seemed to be determined by a combination of the changes to both development and the reproduction, but with the latter having the greatest effect.

When the aphids were totalled over all the instars, the timing of the maximum value of this total predicted by SACSIM was the same as SAM7, but SACSIM predicted a lower value for this total number of aphids compared to SAM7.

2.4 SUMMARY AND DISCUSSION

A description of a model (SAM7) describing the summer population dynamics of *S. avenae* (Carter *et al.*, 1982) was presented in this chapter, followed by a description of the improvements made to the model (SACSIM).

These changes, made to the development and reproduction equations used in SAM7, affected the maximum number of aphids predicted by the model. The differences between the predictions produced by SACSIM and SAM7 were affected by temperature in the simulations.

At low temperatures, the development rate predicted by SACSIM is lower than that predicted by SAM7, but at high temperatures it is likely that the development rate predicted by SACSIM will be greater than that of SAM7. The effect of temperature on the reproductive rate also has a major effect on the predictions of SACSIM. At temperatures below 10°C, SACSIM predicts larger reproductive rates than SAM7 because reproduction is assumed not to occur at temperatures below 10°C in SAM7. However, when temperatures are in the range 10°C to 20 °C, then SAM7 predicts higher reproductive rates than SACSIM, because it is assumed in SAM7 that reproduction always occurs at the maximum rate and is altered only by the number

of hour degrees available for reproduction.

Since temperatures in the summer are often in the range 10°C to 20°C, SAM7 would be expected to predict larger numbers than SACSIM because of its larger assumed reproductive rate.

The effect of temperature on reproductive and development rates can be used to explain the timing of the maximum numbers of the individual morphs shown in Figures 2.7 to 2.14. Early in the season, the aphids are mainly apterous, and a slow reproductive rate will probably lead to a slow build up of numbers, which means that the maximum numbers occurs later. Later in the season, when the alate aphids are produced, temperatures are likely to be in the range 18°C to 25°C, and reproductive rate will no longer be limiting. The timing of the maximum will be determined principally by the development rate used in SACSIM, which will be larger than that used by SAM7, and hence the maximum numbers of alatae in SACSIM occur earlier than in SAM7.

The comparison of the output of SACSIM and SAM7 with field collected data has reinforced the fact that SACSIM predicts lower numbers than SAM7. It has also shown that field to field variation can have a major effect on whether SACSIM provides a reasonable fit to field-collected data.

It is necessary to recognise that the data used for this comparison were collected from individual fields, and that the majority of the inputs into the model, especially in relation to aphid numbers, are representative of a wide area. The suction trap counts used to initialize the model are representative of an area with radius of 80 kilometres (Taylor, 1973). The model will therefore not be able to account for the characteristics of an individual field, but the changes made to SAM7 appear acceptable; SACSIM produces a reasonable representation of the aphid population dynamics in a field.

3.1 REVIEW OF PREDATION MODELS

Examination of the coccinellid submodel included in SAM7 highlighted the need for a coccinellid submodel that could predict the population dynamics of coccinellids in the field, and for a more detailed model of the predation interaction between *S. avenae* and *C. septempunctata*. Whereas the predation model used in SAM7 had a fixed predation rate for each instar, the true predation rate varies with temperature and the hunger and activity of the coccinellids.

The coccinellid predation models in the literature were reviewed to select a reasonable model of the predation of *S. avenae* by *C. septempunctata*. This chapter describes the main models available, their advantages and their disadvantages, before describing which of the models was chosen, and the reasons for this choice.

3.1.1 The main coccinellid models

The three main coccinellid predation models in the literature are those of Mack and Smilowitz (1982), Gutierrez *et al.* (1981), and, Frazer and Gilbert (1976). The model of Mack and Smilowitz (1982) describes the interaction between the coccinellid, *Coleomegilla maculata* (DeGeer) and the peach potato aphid, *Myzus persicae* (Sulzer). The model uses both day degrees (D°) and hours as time steps in a dynamic and deterministic temperature-dependent model. The D° are based on a half-day sine wave calculated from daily maximum and minimum temperatures. Mack and Smilowitz assumed that the aphid population grew exponentially, with an intrinsic rate dependent on temperature. The coccinellid population was described using difference equations. Cannibalism was included as a Holling type II functional response. Thresholds of aphid density were used to determine the timing of coccinellid emigration and oviposition. The biomass of aphids eaten per time step was calculated from a temperature-mediated functional response (Mack and Smilowitz 1982):

$$n = \frac{\frac{1}{T_h}AP}{\frac{1}{T_h}a + A}$$

where: n = Biomass of aphids eaten; T_h = Handling time (time taken to consume an aphid (h)); A = Density of aphids; P = Density of coccinellids and a = Searching rate of coccinellids (area searched per hour).

The model proposed by Gutierrez *et al.* (1981) described the biology of the coccinellid *Hippodamia convergens* (G.-M.) in an alfalfa system. The model, based on the metabolic pool model (Gutierrez and Wang, 1976), dealt with the energetics of coccinellids rather than the interaction between the coccinellid and its aphid prey. The model had three main submodels, which described hunger, assimilation and the metabolic pool. The hunger model considered the hunger of the coccinellids via the processes of ingestion, digestion and excretion. The assimilation submodel assigned different fractions of the energy obtained from the prey to the processes of growth, excretion, reproduction and metabolism. Prey consumption was based on the functional response of Frazer and Gilbert (1976), described below. The metabolic pool submodel was a priority scheme for the allocation of assimilated prey.

Frazer and Gilbert (1976) constructed a model to examine the effect of predation by *Coccinella trifasciata* (Mulsant) on *Acyrtosiphum pisum* (Harris). The model was unique among aphid-coccinellid studies, in that it was based on experimental data from both laboratory and field. The model used physiological time, updated every quarter of an instar period or QUIP, which was calculated by fitting a sine curve to the daily maximum and minimum temperatures and integrating above a threshold of 4°C. Initially, the model used a simple predation function, based on the voracity of the beetle, but this proved to be inadequate and a more complex equation describing the predation interaction was derived:

$$n = N_o(1 - \exp[-\frac{bT_rP}{N_o}][1 - \exp-\frac{-aN_o}{b}]]$$

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where: n = number of prey attacked; N_0 = Initial density of prey; b = the maximum possible consumption; T_i = temperature; a = attack rate and P = density of predators.

The model also included coccinellid hunger, which, with the time since the last aphid contact, determined the attack rate. The spatial distribution of the aphids was incorporated into the model, which provided a more realistic simulation of the field situation, but there were some discrepancies in the required number of coccinellids predicted by the model to control aphid numbers and observed data.

In addition to the three models described above, there are also several other relevant models which deal with aphid-syrphid predation or multiple predation of aphids. The first of these is the model of Tamaki *et al.* (1974), which used the Bombosch equation:

$$A_n = A_0 q^n - kq((q^{n-1})/(q-1))$$

where: A_n = pest population on day n ; A_0 = initial pest population; q = potential rate of increase of pest population and k = number of aphids consumed by predators. This model was aimed at calculating the efficacy and power of a predator complex.

Gilbert and Hughes (1976) modelled the effect of syrphids on *Brevicoryne brassicae* (L.). The model used physiological time to describe aphid development, with a time step of one instar. Syrphid eggs were laid when a threshold of aphid density was exceeded, and the voracity and number of predators was related to the aphid density four instar periods earlier. This allowed for both a functional response to aphid density and an increase in larval voracity with aphid density. The probability that an aphid escaped predation was calculated as the zero term of a Poisson distribution.

The final model examined was that of Barlow and Dixon (1980). This model consists of sets of difference equations built from component processes, assumed linearly related to temperature. The model uses a multi-predator, multi-prey functional

response as shown below.

$$n_{ii} = N_i (1 - e^{-\sum_j a_{ij} P_j S_j})$$

where: $S_j = V_j / \sum_i a_{ij} N_i W_i$; $S \leq 1$; n_{ii} = the number of prey, i , attacked by all predators per 100 cm²; N_i = the number of prey, i , per 10 cm²; a_{ij} = attack coefficient of predator, j , on prey, i ; P_j = the number of predators per 100 cm²; S_j = correction factor for saturation of predator, j ; W_i = weight of prey, i and V_j = maximum weight of prey killed by predator, j , per day.

3.1.2 Disadvantages and advantages of each model

The model of Gutierrez *et al.* (1981) was the most complex model reviewed. It provided a realistic simulation of the processes involved for an individual coccinellid, due to being based at the metabolic level. However, this individualistic approach made it unsuitable for use at the population level. Also, since the model aimed to describe the growth of a coccinellid, it did not include the processes involved in the predation of aphids by the coccinellid, the element of coccinellid biology of primary interest in this project. The complexity of the model also precluded its use in this work, since it would be extremely difficult to obtain values for all the parameters required without extensive experimentation.

Frazer and Gilbert's (1976) model was aimed specifically at representing the aphid-coccinellid interaction, and had a similar aim to the present work. However, it required data for the spatial distribution of the aphids and coccinellids, which is difficult to measure at field level. Also, incorporation of spatial data requires a great deal of computing time, and its inclusion here would be futile, due to the coarse resolution of SAM7. Also, the model used by Frazer and Gilbert (1976) was only able to calculate the number of aphids eaten by one coccinellid at a time, which could be a problem were a similar approach to be used in SAM7, since there might be a large number of coccinellids in the cereal field modelled.

Estimation of the parameters required by the model of Frazer and Gilbert (1976) to describe coccinellid and aphid movement would require a large experimental study, as there is very little data available. The predation equation used by Frazer and Gilbert (1976) calculates the interaction between each of the coccinellid and aphid instars separately, and if this approach were used in SAM7, it would require the estimation of parameters for 25 predator-prey interactions.

The approach used by Mack and Smilowitz (1982) is arguably not as realistic as the approaches described so far, but does include the majority of the important details. The model is also temperature-dependant, which is useful for the present work, since climate change was to be considered later. The model is also fairly simple; it requires relatively few parameters to be estimated, and is therefore adaptable for other predator species.

The combination of simplicity and realism is important to produce a generalized model with reliable output. The incorporation of temperature into the functional response provides a useful technique for determining the effect of temperature on the interaction between aphids and coccinellids.

The main problem with this model lies in its estimation of the effect of temperature on searching rate and handling rate of the coccinellids, which could prove difficult depending on the amount of data available in the literature.

Barlow and Dixon (1980) produced a simple model designed to incorporate a maximum of biological reality with a minimum of computing time, an aim shared by this project. Their multi-predator, multi-prey, functional response could possibly be adapted for use for different coccinellid and aphid instars. The facility of this approach would depend on the availability of further data describing the predation of the coccinellid instars on the aphid instars.

The other models, e.g. Tamaki *et al.* (1974), Gilbert and Hughes (1971) are overly simple, and would not be suitable for predictions.

After weighing up the advantages and disadvantages, it was decided to use the approach of Mack and Smilowitz (1982) because of its simplicity and adaptability.

3.2 FORMULATION OF EQUATIONS TO BE USED IN THE COCCINELLID SUBMODEL

Having chosen the equation to describe the predation of aphids by coccinellids, the next step was to gather the data required to describe the biology of *C. septempunctata*, and to formulate the equations used in the submodel.

The development rate of *C. septempunctata* was related to temperature through a set of equations, one for each instar (Hodek 1973). A sigmoid curve was fitted to Hodek's (1973) data in the temperature range 0°C and 35°C, and a linear relationship in the temperature range 35°C and 50°C (Fig. 3.1). The equations describing these relationships are shown below, with the estimated parameters in Table 3.1:

$D = 0.0$	$t \leq 0.0$
$D = a_i / (1 + \exp (-x_j (m_i + t)))$	$0.0 < t \leq 35.0$
$D = c_i - b_j t$	$35.0 < t \leq 50.0$
$D = 0.0$	$t > 50.0$

where: D = development rate (1/time); a = constant (lower asymptote of logistic equation); b = constant (slope of linear relationship); c = constant (intercept); m = constant (upper asymptote of logistic equation); x = constant (slope parameter of logistic equation); i = instar of coccinellid and t = temperature (°C). The standard errors of the parameters of the logistic equation are given in Table 3.1. The parameters describing the relationship between development rate and temperature in the range 35°C to 50°C were obtained by linear interpolation, and hence, the standard errors of these parameters could not be estimated

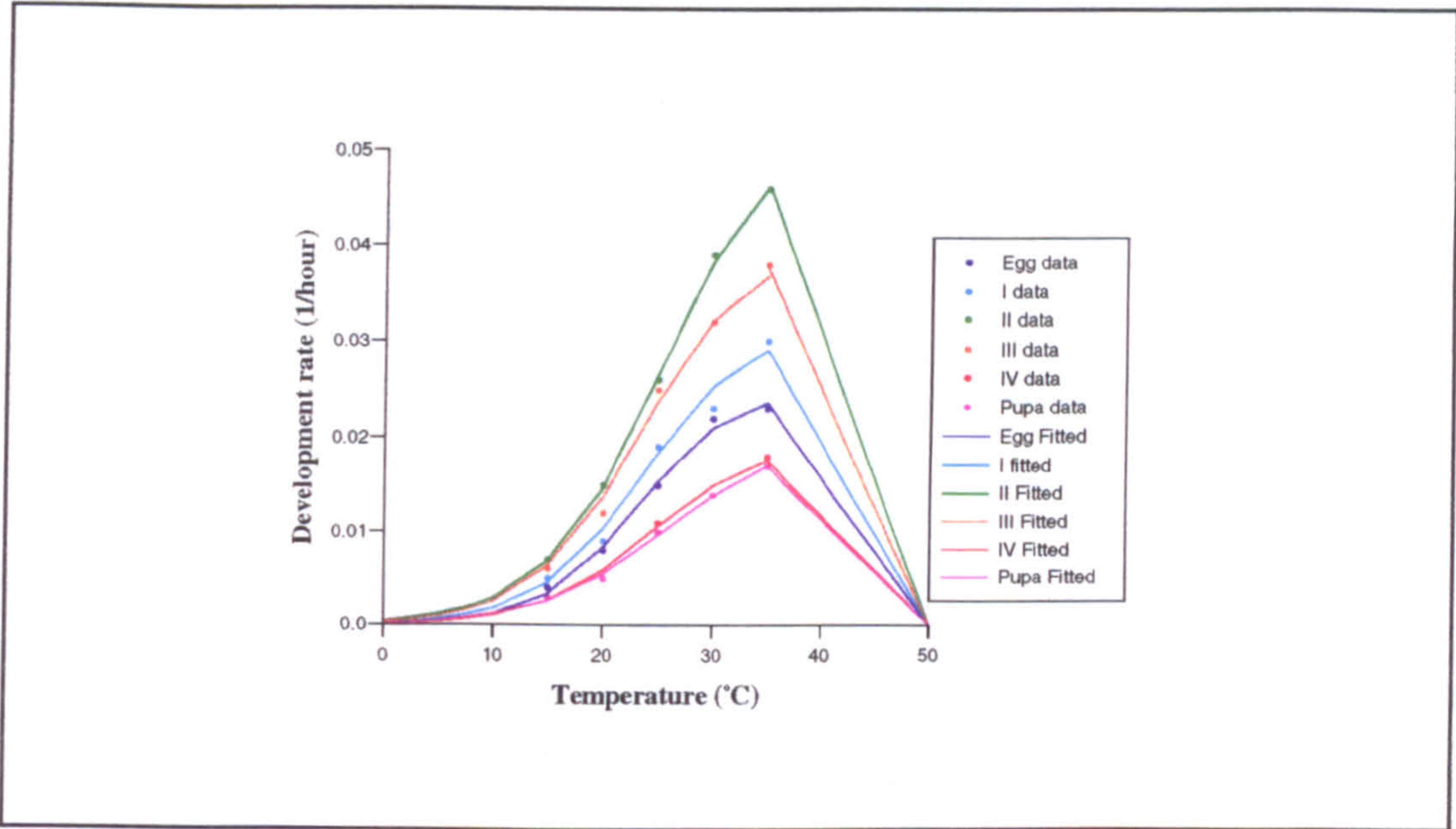


Figure 3.1: Relationship between temperature and development rate for coccinellid instars from egg through to pupa.

Instar, i	b_i	c_i	a_i	x_i	m_i
Egg	0.078615	0.001723	0.02497 ± 0.0017	2.350 ± 0.0393	22.94 ± 0.920
1	0.09695	0.001939	0.03162 ± 0.0035	0.2109 ± 0.0501	23.43 ± 1.44
2	0.154235	0.001939	0.05316 ± 0.00048	0.1905 ± 0.00269	25.0 ± 0.122
3	0.125155	0.0025031	0.04004 ± 0.0017	0.2289 ± 0.0207	23.15 ± 0.548
4	0.05876	0.0011752	0.01955 ± 0.0014	0.2043 ± 0.0240	24.15 ± 0.880
Pupa	0.05681	0.0011362	0.02005 ± 0.00089	0.1812 ± 0.0176	25.43 ± 0.611

Table 3.1: The parameter estimates for the equations describing the relationship between temperature and development rate in the six coccinellid instars.

Having determined the relationship between temperature and development, attention was then focused on reproduction. The literature contained a large amount of data on the reproduction of *C. septempunctata*, but there appeared to be great geographic variation in the number of eggs laid. Data from Ruzicka (1980) suggested that the longevity of adults was constant and that females died after having laid their eggs. With these assumptions, the process of modelling reproduction and adult longevity was simplified.

Mills (1981) showed that egg-laying, for the two-spot ladybird, *Adalia bipunctata*, was linearly related to temperature, increasing in the range 0°C to 20°C, and decreasing subsequently. Dixon and Guo (1994) suggested that egg production in *C. septempunctata* was linearly related to temperature, and also to aphid consumption by the coccinellid. They showed that the maximum reproductive rate occurred at 20°C. Reproduction ceased at 40°C (Sethi and Atwal 1964). It was assumed that reproduction commenced when the temperature exceeded 0°C.

Using the data of Ghanim, Freier and Wetzel (1984), a relationship between reproduction and aphid consumption was determined, with egg laying assumed zero at a consumption of 10mg of aphids per day, increasing to a plateau at 20.94mg of aphids per day.

These two relationships were combined to produce a surface (Fig. 3.2) which was described by the equations shown below:

$$\begin{aligned}
 R &= 0.0 & t \leq 0.0, 10.0 \leq C \leq 20.94 \\
 R &= 0.00037Ct - 0.0037t & 0.0 < t \leq 20, 10.0 \leq C \leq 20.94 \\
 R &= 0.00148C - 0.0148 - 0.00037Ct + 0.0037t & 20.0 < t \leq 40.0, 10.0 \leq C \leq 20.94 \\
 R &= 0.0 & t > 0.0, 10.0 \leq C \leq 20.94
 \end{aligned}$$

where: R = reproductive rate (eggs/female/H°); t = temperature (°C); C = aphid consumption by coccinellids (mg). Since linear interpolation was used to determine

the parameters describing the above relationship, the standard errors of the parameters could not be estimated.

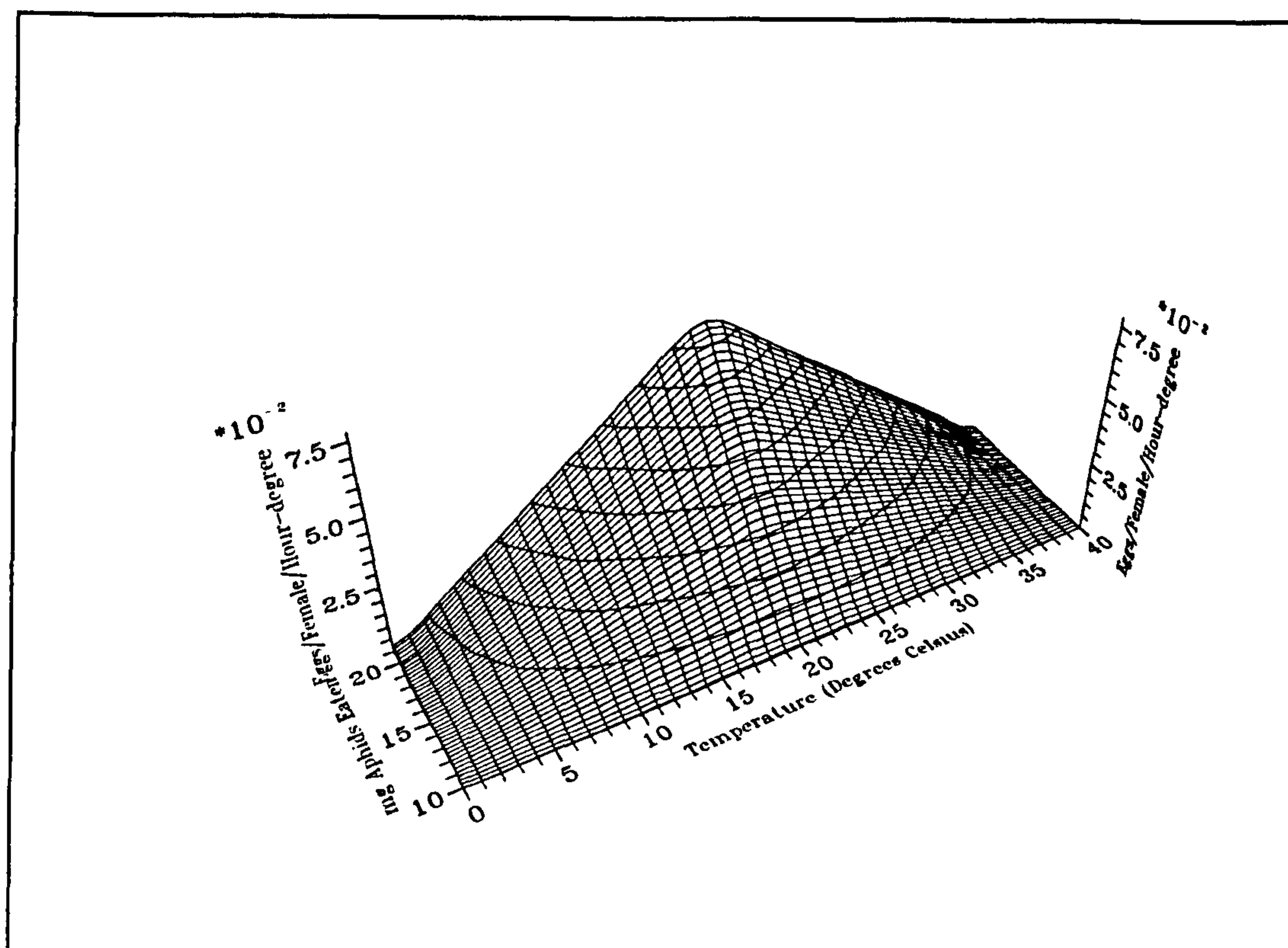


Figure 3.2: Relationship between the reproductive rate (Eggs/female/H^o), temperature and aphid consumption in female *C. septempunctata*.

The next stage in the mathematical representation of the coccinellid biology was to determine the factors involved in the predation equation. The values for aphid biomass and predator density were available, as state variables, from the model itself. The equations for the searching rate and handling rate, assumed to be functions of temperature, needed to be formulated.

There was only a limited amount of data describing the effect of temperature on the searching rate of coccinellids in general, but a study on *Adalia bipunctata* (Mills, 1981) suggested that the relationship was possibly sigmoid in nature. For *C. septempunctata*, a sigmoid curve was fitted to the data of McLean (1980) in the temperature range 0°C to 35°C; at temperatures above 35°C, the searching rate was decreased linearly to zero at 50°C (Fig 3.3). The equations describing the effect of

temperature on searching rate are shown below, with the parameter estimates for each instar shown in Table 3.2:

$a = 0.0$	$t \leq 0.0$
$a = b_{1i} + c_{1i} / (1 + \exp (m_i - x_i t))$	$0.0 < t \leq 35.0$
$a = c_{2i} - b_{2i} t$	$35.0 < t \leq 50.0$
$a = 0.0$	$t > 50.0$

where: a = searching rate of coccinellids (m²/hour/predator); b = constant (lower asymptote of logistic equation); c = constant (difference between upper and lower asymptotes of logistic equation); x = constant (slope parameter of logistic equation); m = constant (inflexion point of logistic equation multiplied by the slope parameter) and t = temperature (°C). Since there were insufficient data to perform a regression, the fitted curve was forced through the data, and hence standard errors of the parameters used could not be estimated.

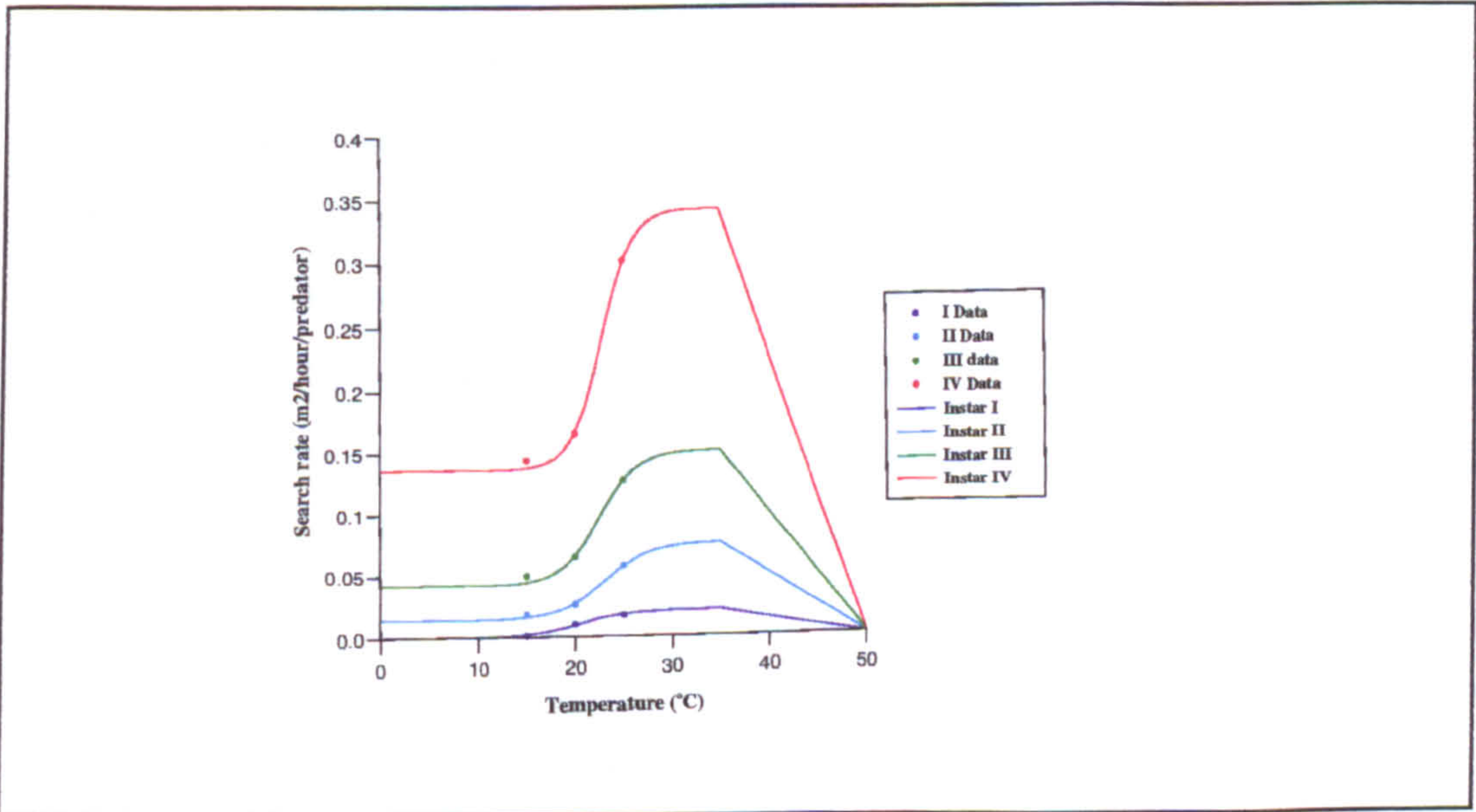


Figure 3.3: The effect of temperature on the searching rate (m²/predator/hour) of coccinellid larval instars.

Instar, i	b_1	c_1	x	m	b_2	c_2
1	0.0	0.0206	0.407	8.20512	0.0013697	0.068485
2	0.01486	0.06021	0.438	10.0994	0.0049823	0.249116
3	0.04125	0.1080	0.5025	11.3027	0.0099972	0.49986
4	0.1360	0.20405	0.6323	14.3994	0.0226653	1.133265

Table 3.2: Parameter estimates for the equations describing the searching rate of coccinellid larval instars.

Adult coccinellids were assumed to have a searching rate equivalent to that of the second instar larvae because they are less voracious than the third and fourth instar larvae (McLean, 1980), and their handling rate is similar to that of second instar larvae.

Having determined the effect of temperature on searching rate, a similar set of equations was required to describe the effect of temperature on the handling rate. This proved difficult since there were few data available in the literature. Sigmoid curves were formulated based on the data of Olszak (1988), who measured the number of *Acyrtosiphum pisum* eaten per day by *C. septempunctata* at 20°C. Using this value, and assuming that handling rate was zero at 0°C, reached a maximum at 35°C, and that the sigmoid curve was symmetrical with an inflexion point at 17.5°C, a set of equations was formulated. As with development and reproduction, the handling rate was assumed to decline linearly to zero at 50°C from the maximum at 35°C.

The equations formulated are shown below, with the parameter estimates in Table 3.3, and a graphical representation being shown in Figure 3.4.

$S = 0.0$	$t \leq 0.0$
$S = b_{1i} / (1 + \exp (m_{1i} - x_{1i} t))$	$0.0 < t \leq 35.0$
$S = c_i - b_{2i} t$	$35.0 < t \leq 50.0$
$S = 0.0$	$t > 50.0$

where: S = handling rate (mg of aphids/coccinellid/hour); b_1 = constant (upper asymptote of logistic equation); b_2 = constant (slope of regression line) ; c = constant (intercept of regression line); m = constant (inflexion point of logistic equation multiplied by slope parameter); x = constant (slope parameter of logistic equation); t = temperature (°C) and i = instar of coccinellid. As with the searching rate, the fitted curve had to be forced through the limited data available, which means that the standard errors of the parameters could not be estimated

Instar, i	b_1	m	x	c	b_2
1	0.05	9.70375	0.5545	0.1667	0.00333
2	0.12	9.70375	0.5545	0.40	0.0080
3	1.6	12.159	0.6948	5.33	0.1067
4	1.76	12.9203	0.7383	5.867	0.1173
Adult	0.95	13.419	0.7668	3.25	0.0011362

Table 3.3: Parameter estimates for the equations describing the effect of temperature on coccinellid handling rate.

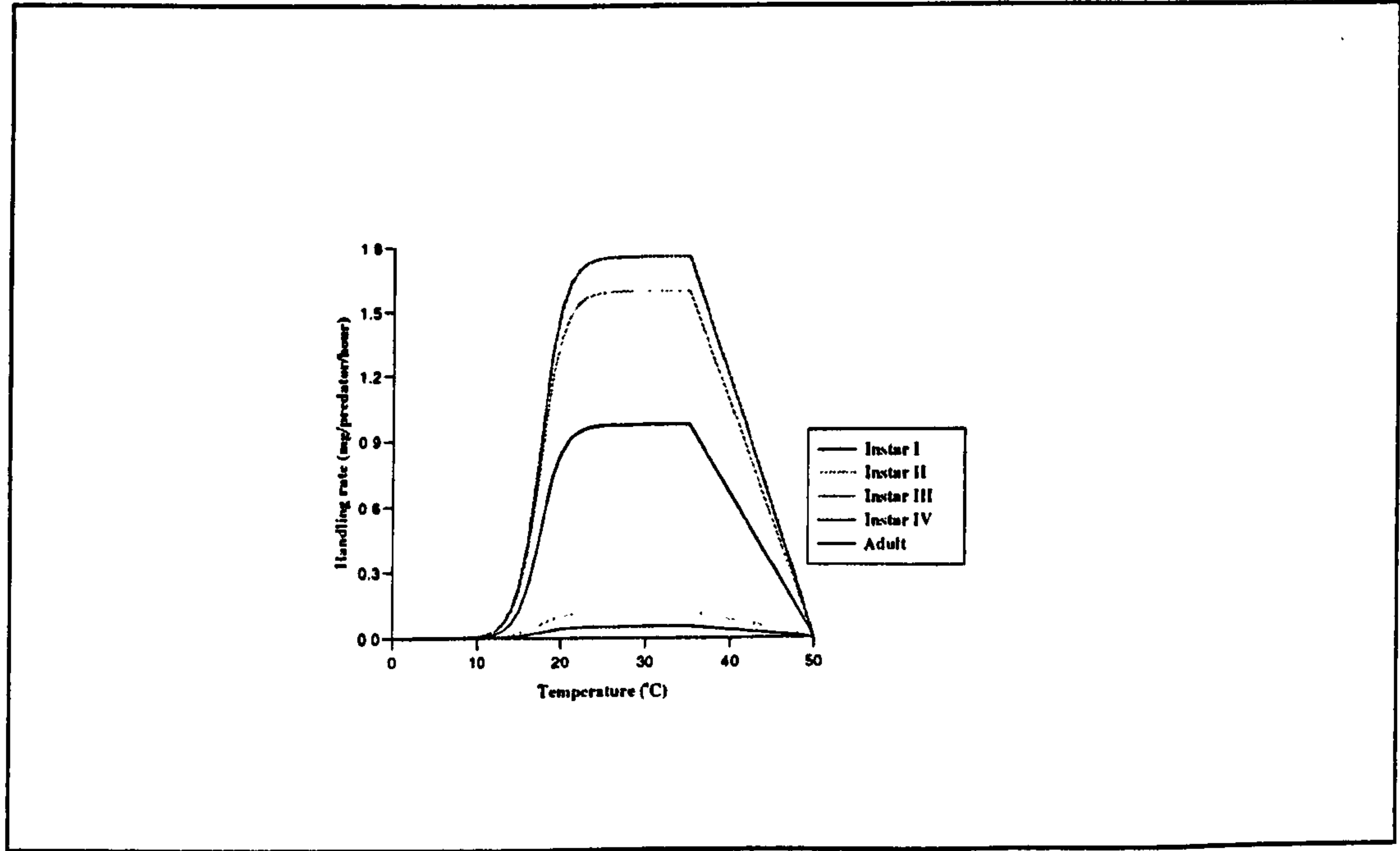


Figure 3.4: The effect of temperature on the handling rate (mg/predator/hour) of *C. septempunctata* larval instars and adults.

These equations must be considered as approximate, and may need to be modified in the light of more detailed studies on the effect of temperature on the handling rate of *C. septempunctata*. They are however, probably the best set of equations that can be formulated using the available data.

As was mentioned in the introduction, coccinellids spend a great deal of time basking, and therefore, not searching actively for food. It was therefore necessary to formulate an equation to describe the proportion of coccinellids active during any simulated time-step.

Hodek (1985) studied the effect of temperature and satiation on the activity of adult *C. septempunctata*, and his data was used to construct a surface (Fig. 3.5 The colours in the graph represent the relative level of activity from blue representing low activity through to yellow representing high activity) which described the combined effects of temperature and satiation on the activity of the adult coccinellids in the model. In constructing the surface, the following assumptions were made: coccinellids were assumed to be 100% satiated if well fed, and hungry (0% satiated) if the aphid supply was restricted, in terms of there being few aphid available for the coccinellids to eat. The equations describing the surface are shown below:

$$\begin{array}{ll}
 A = 0 & t \leq 11.7 - 4.3S \\
 A = 3.86t + 27.15S - 1.43tS - 45.24 & 11.7 - 4.3S < t \leq 37.6 + 11.0S \\
 A = 100 & t > 37.6 + 11.0S
 \end{array}$$

where: A = percentage activity; S = percentage satiation (0% being equivalent to hungry and 100% being fully satiated). As with reproduction, the fitted relationship was determined using linear interpolation and, therefore, the standard errors of the parameters could not be estimated.

The model assumes that only coccinellids which actively move around search for food, and therefore the amount of aphids eaten by all the coccinellids is adjusted according to those active.

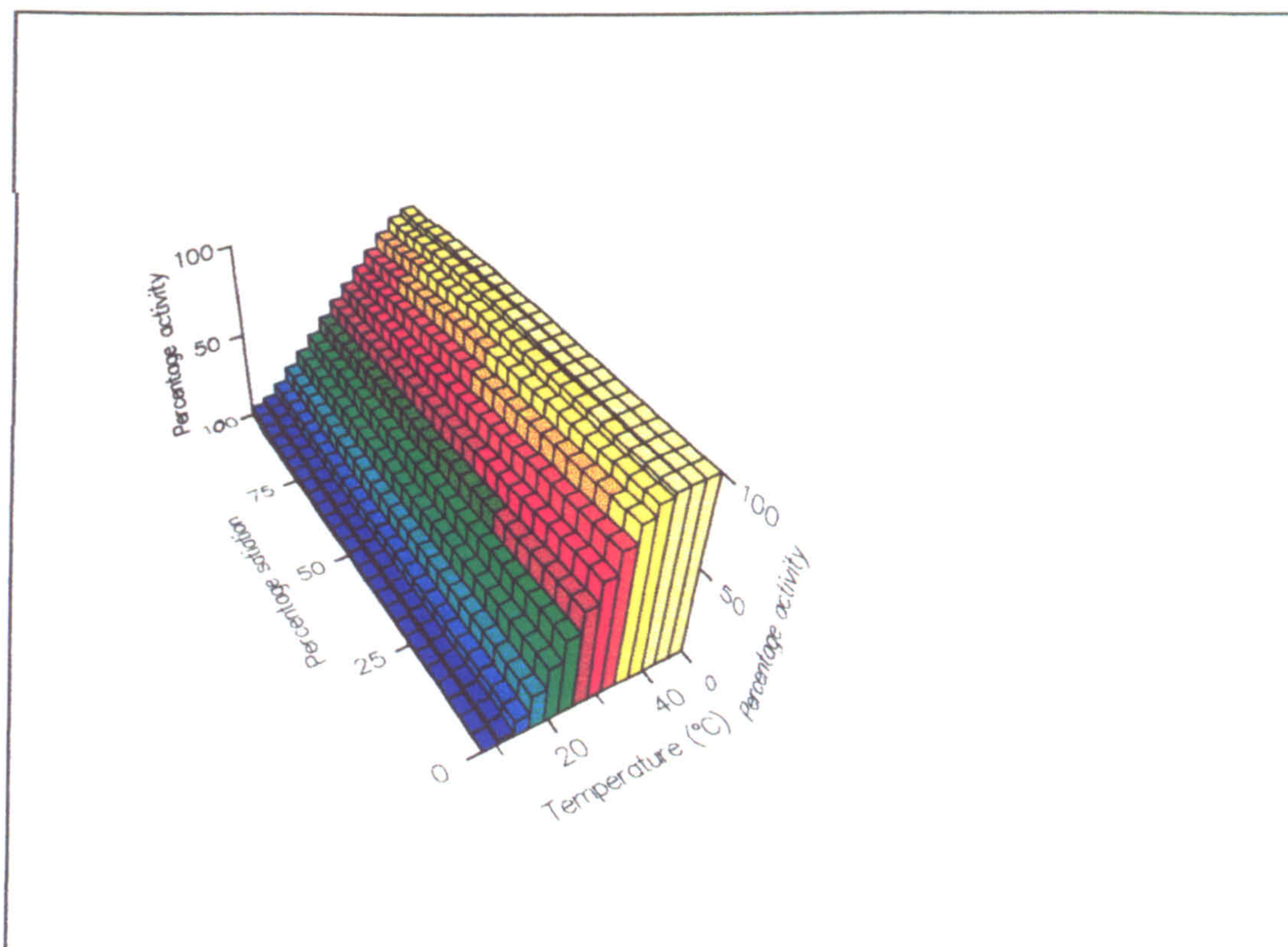


Figure 3.5: Surface describing the effect of temperature and satiation on the activity of adult *C. septempunctata*. The colours represent the relative values of activity.

The equations described above were concatenated, to build the coccinellid submodel, described in the next section.

3.3 DESCRIPTION OF THE COCCINELLID SUB-MODEL

This section brings together all of the equations detailed in the previous section and also shows how these equations link together to form the coccinellid sub-model. A flow diagram of the submodel is shown in Figure 3.6.

3.3.1 Initialisation

The coccinellid submodel has a similar time structure to the aphid submodel, so initially all arrays are declared, with the inputs required read from an input file.

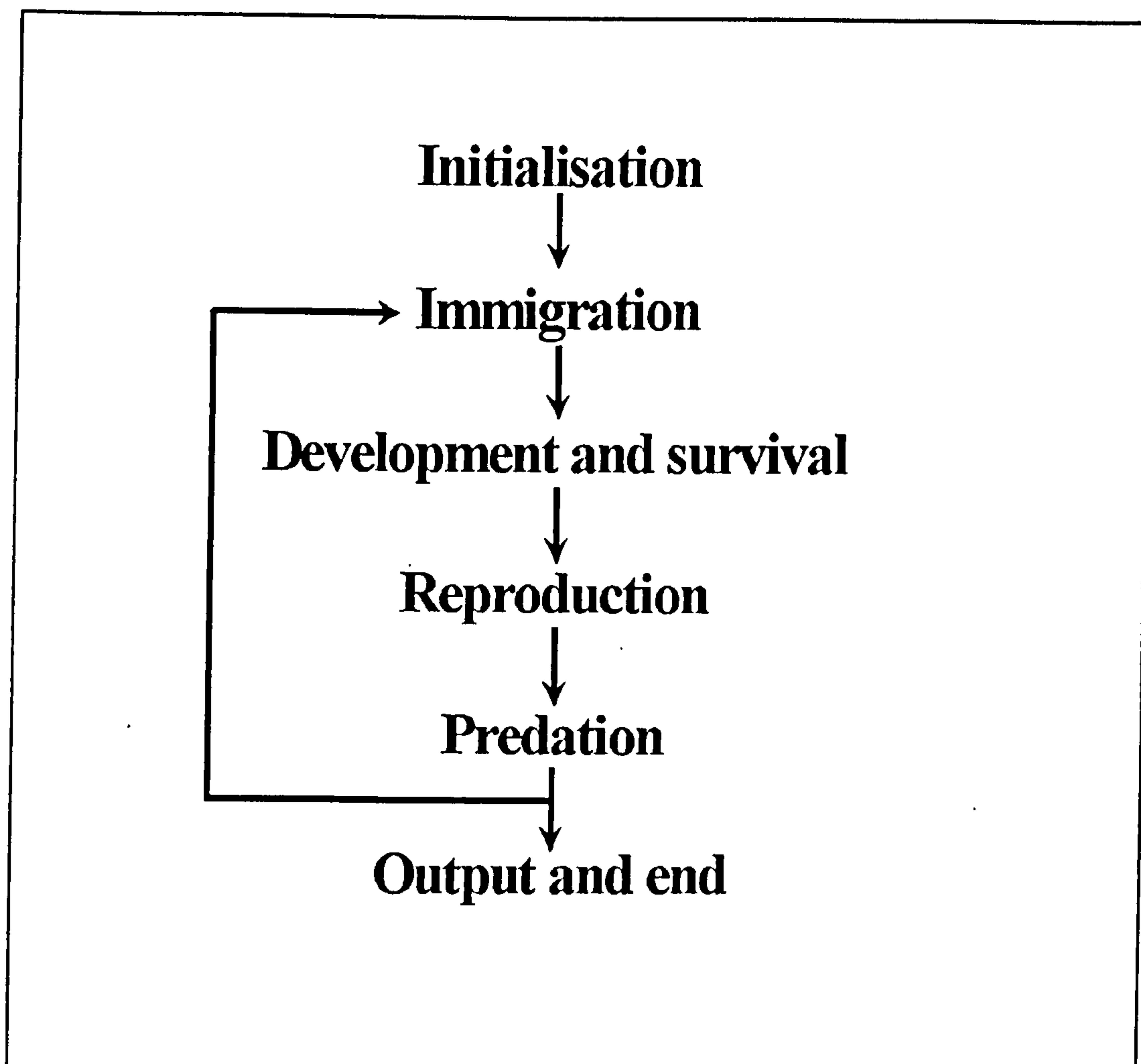


Figure 3.6: Flow diagram describing the processes involved in the coccinellid submodel.

3.3.2 Immigration

Before immigration takes place, the model checks that the density of aphids is above a threshold of 10 aphids per m^2 (Adams, 1984). This threshold complies with the observation (Adams, 1984; Honek, 1980) that coccinellids do not enter the field unless the aphid density is greater than this minimum. Honek (1980) observed that this threshold is constant between years. If this threshold is not exceeded, then the submodel continues, but assuming that coccinellid immigration has not occurred. However, if the threshold is exceeded then the number of adult coccinellids recorded in the field count, on the day being simulated, is used as the number of coccinellids immigrating into the field on that day. The sex ratio is assumed to be 1:1.

3.3.3 Development

The hourly development of each coccinellid instar is calculated from the hourly temperature using the equations listed in the previous section. The array containing the development of the coccinellid instars is updated iteratively.

The first generation adult coccinellids, which have overwintered in hibernation sites, are treated separately from the nymphs, and are assumed to accumulate developmental time (hour-degrees) towards a total of $9975H^{\circ}$, based upon their longevity after hibernation (Ruzicka *et al.*, 1981; Sethi and Atwal, 1964). Upon reaching this total, they are assumed to die. The second generation coccinellid adults, which immigrate into the field near the end of the season, are assumed not to reproduce and are assumed to accumulate H° towards a total of $3300H^{\circ}$. They are assumed to remain in the field for no more than 7 days (Honek, 1990).

Coccinellids that develop from eggs within the simulated field, are assumed to emigrate after 40 hours (Honek, 1990). Newly emerged adult coccinellids are restless and fly between 40 and 60 hours after emerging from the pupa (Honek, 1990).

3.3.4 Survival

The survival subroutine used in the coccinellid submodel is similar to that used in the aphid model. The proportion of coccinellids surviving the hourly time-step is calculated as a proportion of the coccinellids that survive to complete the whole instar, using the equation shown below:

$$\log_{10} s = (hh/hl)\log_{10}(sv)$$

where: s = proportion of coccinellids surviving the hourly time-step; sv = proportion of coccinellids that survive to complete the instar; hl = Total towards which development is accumulated (H°) and hh = development for the hour being simulated (H°).

The survival of each instar is calculated separately, and the percentage of coccinellids that survive to complete each instar (Sethi and Atwal, 1964) is shown in Table 3.4 below.

Instar	Percentage survival for instar
Egg	88.1
I - IV	94.4
Pupa	94.1
Adult	92.3

Table 3.4: Percentage survival of coccinellid instars.

Once the survival for the hour has been calculated, an iterative technique is used to adjust the number of coccinellids stored in the arrays containing the numbers of coccinellids in each instar. Once the arrays have been adjusted, the total number of coccinellids in each instar is calculated by totalling up the array entries.

3.3.5 Reproduction

This section of the submodel begins by calculating the density of the aphids to see if it is greater than the assumed threshold of 0.1 aphids/tiller (Adams, 1984). This threshold allows for the observation (Adams, 1984; Honek, 1980) that the female coccinellids require a minimum density of prey to allow the completion of ovariole maturation. If this threshold is not exceeded then reproduction does not occur and the sub-model proceeds assuming that no eggs have been laid.

However, if the threshold is exceeded, the number of eggs laid by a female coccinellid per H° is calculated from the equations described above. The total number of eggs laid in the hour is then calculated by multiplying the value derived from these equations by the number of H° for the hour and the proportion of coccinellids that are active.

It is assumed that only coccinellids which are actively moving will lay eggs. The array containing the age and number of eggs is then updated.

3.3.6 Predation

This largest section of the submodel calculates the number of aphids eaten by the coccinellids. Initially, the subroutine converts the number of aphids per tiller in each aphid instar into the biomass per m^2 , by multiplying the numbers per tiller by the number of tillers per m^2 and the average weight of an aphid in that instar. The average weight of an aphid in a given instar (Vereijken, 1979) is shown in Table 3.5 below.

Aphid instar	Weight (mg)
I	0.1
II	0.2
III	0.4
IV	0.8
Adult	1.6

Table 3.5: The average weight (mg) of an aphid instar (Vereijken, 1979)

The ratio of alatae to apterae is calculated for each of the aphid instars. The ratio of aphid instars eaten by each coccinellid instar is then calculated, assuming that first instar coccinellids eat only first instar aphids, second instar coccinellids eat both first and second instar aphids, third instar coccinellids eat first, second and third instar aphids and that fourth instar and adult coccinellids eat all aphid instars.

The searching rate and the handling rate are calculated using the equations described earlier. The model then calculates the proportion of coccinellids that are active using the equations described earlier.

The model then calculates the biomass of aphids eaten by each coccinellid instar using the temperature-mediated functional response described above. The biomass of aphids

eaten is truncated if necessary to ensure that it does not exceed the maximum hourly consumption of the coccinellids.

The biomass of aphids eaten in each aphid instar is then calculated by multiplying the consumption of each coccinellid by the proportion that the aphid instar contributes to the total diet of the coccinellid. The biomass of each aphid instar consumed is then converted to give the number of aphids per tiller consumed in each instar and then the aphid arrays are adjusted accordingly. Having completed the predation routine, the coccinellid sub-model reiterates for the next time-step.

3.4 SENSITIVITY ANALYSIS

3.4.1 Aims of the sensitivity analysis

A sensitivity analysis was performed to see if there were any weaknesses in the model, and whether any of the parameters in the model had an unreasonably large effect on the model output.

3.4.2 Description of technique used

A fine sensitivity analysis (Carter, 1980) was performed, where each parameter was increased or decreased by 20%, except for survival where an increase of 20% would have meant a survival greater than 100%, for which the upper value was set at 100%.

Each parameter was altered individually, and then parameters were altered in pairs. Further combinations of parameters were omitted as it was felt that the cause of any changes to the output would have been difficult to determine.

3.4.3 Results of the analysis

Graphical summaries of the effects of changing a single parameter are shown in Figures 3.7, 3.8 and 3.9.

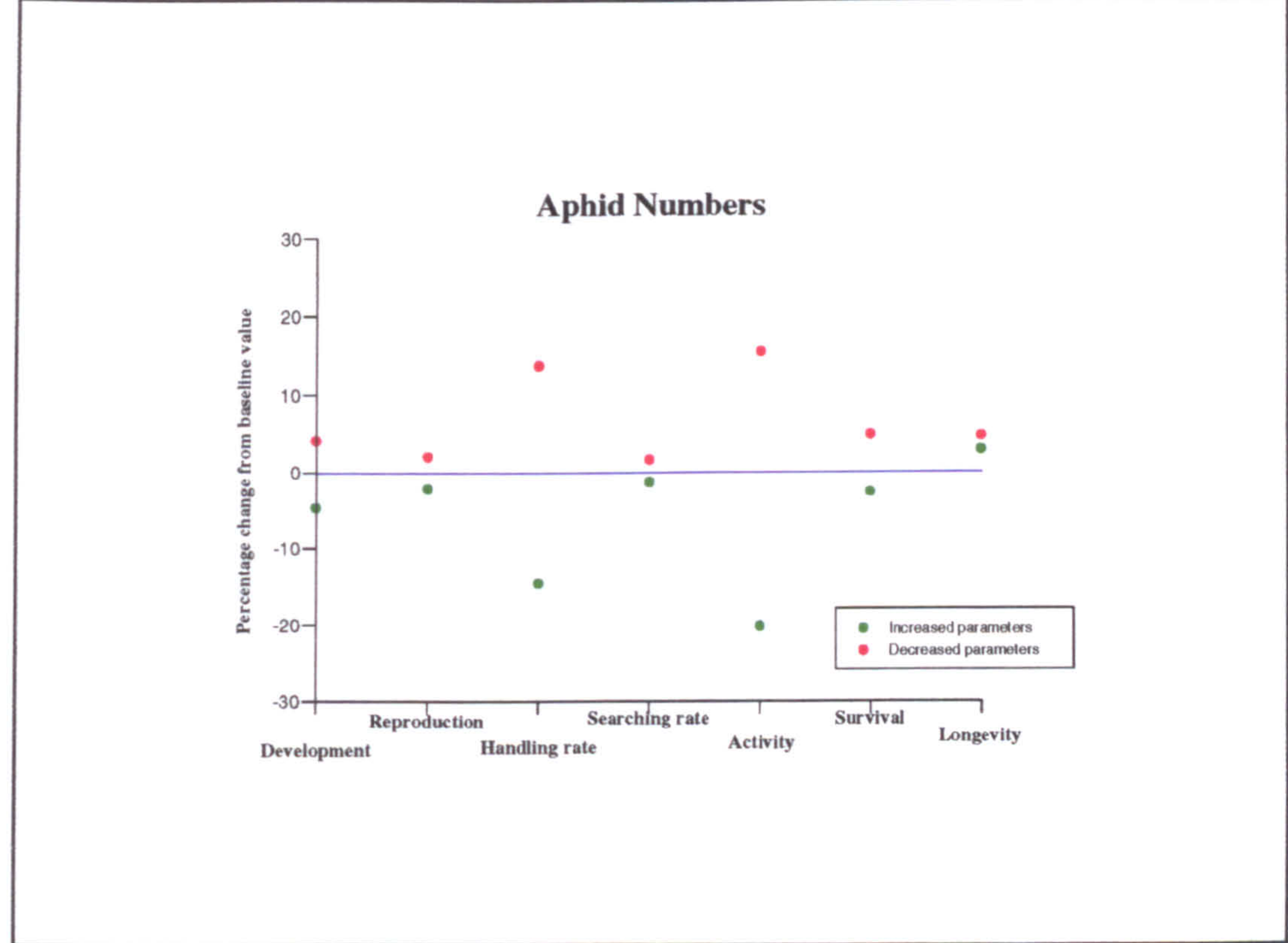


Figure 3.7: Effect of changing the parameters of the coccinellid submodel on the maximum number of aphids.

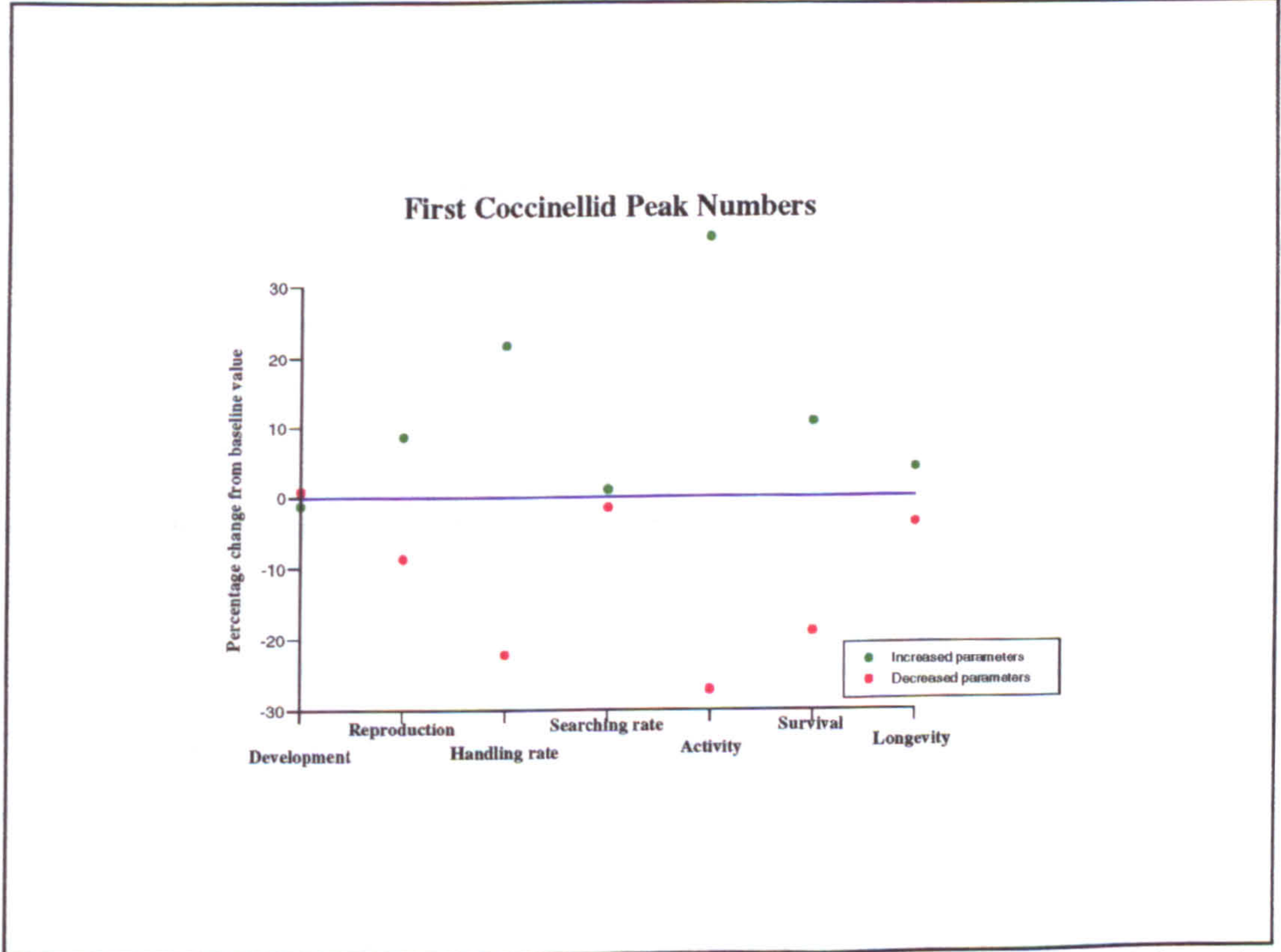


Figure 3.8: Effect of changing the parameters of the coccinellid submodel on the number of coccinellids in the first peak.

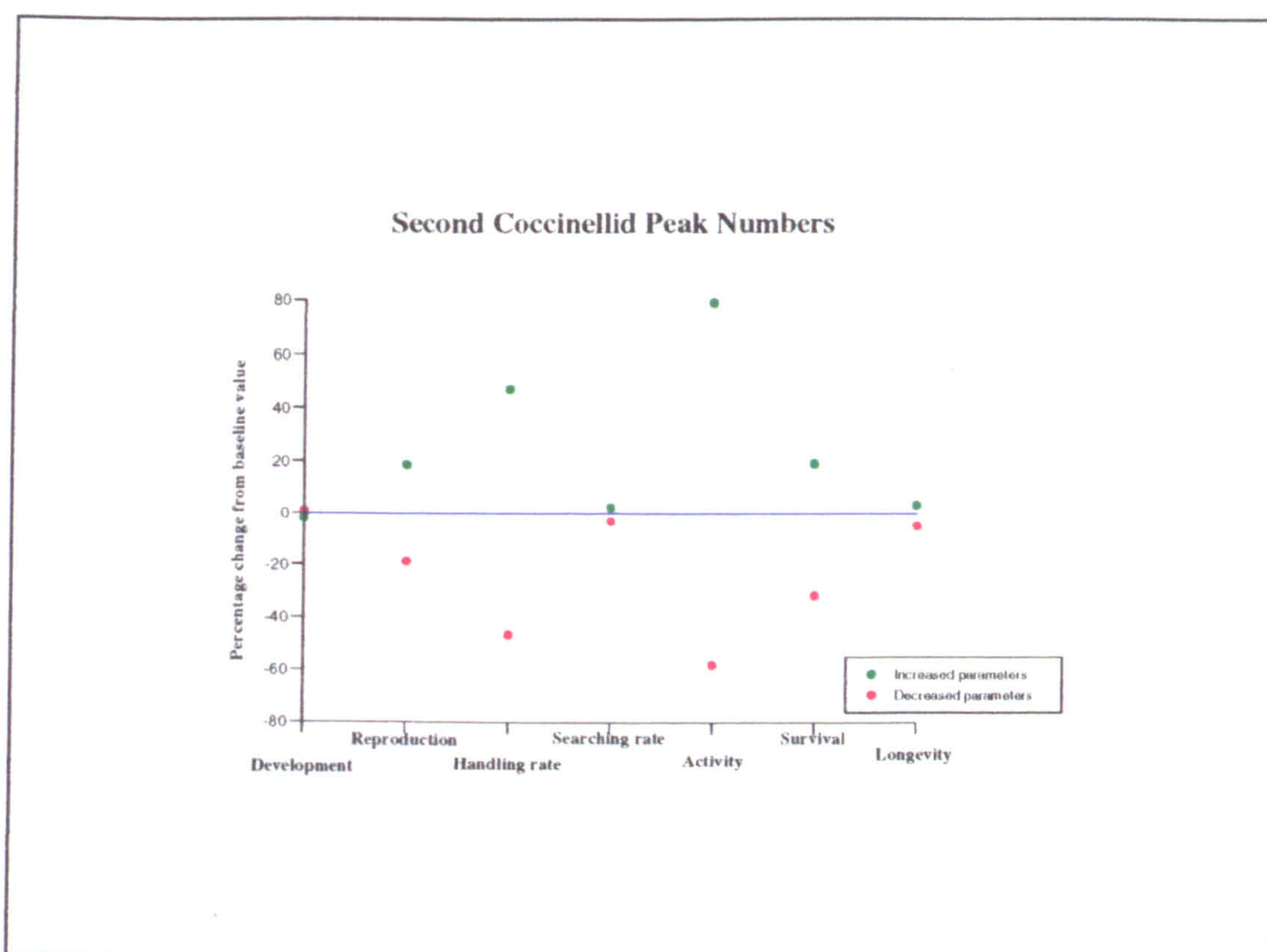


Figure 3.9: Effect of changing the parameters of the coccinellid submodel on the number of coccinellids in the second peak.

3.4.3.1 *Changing parameters individually*

The results of the sensitivity analysis showed that altering the values of the main parameters used in the coccinellid sub-model did not affect the timing of the aphid or coccinellid peaks predicted by the model. However, the changes did affect the numbers predicted at these peaks.

The figures show that changing the parameters had little effect on the output, except for those of handling rate and activity. It is interesting to note that these are the two parameters about which the least is known and there were few data available for the formulation of their equations. The results therefore suggest that more data may be necessary to describe accurately the effects of temperature on these two parameters.

The effects of increasing and decreasing the parameters were reasonably symmetrical,

except in the case of survival, which has a greater effect when decreased. However, it must be remembered that survival could not be increased by 20%, as a survival of over 100% would have resulted. This may well account for the fact that the effect is not symmetrical. However, it is also possible that decreasing survival has a far greater effect on the numbers of coccinellids than increasing survival. This is because a cascade is formed, whereby once the numbers in one instar have been decreased, they are then decreased further in the next instar, and so on through further instars.

3.4.3.2 Changing pairs of parameters

There was no interaction between any pair of parameters, and therefore the effects on the predicted peak numbers of aphids and coccinellids were a multiplicative combination of the effects of the parameters when used singly.

3.4.4 Changing the day of coccinellid immigration

The effect of altering the timing of coccinellid immigration, by increasing or decreasing the dates on which coccinellids immigrated into the simulated field, was also investigated. The date of immigration was increased or decreased by one to seven Julian days.

3.4.4.1 Decreasing the day of immigration

A decrease in the Julian day of immigration of between one and seven days, caused the date on which the first coccinellid peak occurred to be earlier by just one Julian day in all cases. This was probably due to temperatures early in the simulated season being unsuitable for coccinellid development and reproduction and represents a limit to the date of the first coccinellid peak, which cannot be earlier than Julian day 180.

The number of coccinellids predicted for the first peak increased as the date of immigration became earlier. This was probably due to there being more time for the coccinellids to develop, although the difference was not great, again suggesting that

the temperatures earlier in the simulated season were relatively unfavourable for development and reproduction.

The second coccinellid peak, which comprised much larger numbers than the first, occurred earlier by the same number of Julian days that immigration was advanced. This is because in the latter part of the season, immigrants are assumed not to reproduce and so the numbers counted in the field are input directly into the model.

The number of coccinellids predicted for the second peak also increased as immigration became earlier. Most likely, this was due to the increase in the first peak, since the coccinellids immigrating into the field late in the season do not reproduce, but just increase the overall numbers in the field by their presence.

The aphid peak was not affected by changing the date of immigration of the coccinellids. The peak number of aphids predicted decreased as the date of coccinellid immigration was advanced. This was expected, since the coccinellids had a longer time in the simulated field and therefore had a longer time during which they were eating aphids, causing a decrease in the aphid numbers.

3.4.4.2 *Increasing the day of immigration*

Retarding the date of immigration caused both the first and second coccinellid peaks to be retarded by the same number of Julian days by which the date of immigration was retarded. This was expected since if immigration occurred later then the coccinellids would be expected to peak later as they were experiencing similar temperatures to those in the baseline condition.

The retardation in immigration date caused the predicted number of coccinellids at each of the two peaks to decrease, probably due to there being less time for them to develop and reproduce.

As above, for advanced immigration, the date of the aphid peak was unaffected.

However, the number of aphids predicted at the peak increased as the date of coccinellid immigration was retarded. This was expected since the later that the coccinellids entered the field, the less time they had to eat aphids and decrease aphid numbers.

3.5 SUMMARY AND DISCUSSION

A description of how a predation model for the coccinellid aphid system was chosen from the available models has been presented. This was followed by a description of how the equations used in the coccinellid sub-model were formulated and a description of the coccinellid sub-model itself. Finally, the results of a sensitivity analysis of the main components of the coccinellid sub-model were presented.

The results of the sensitivity analysis were very encouraging since the majority of changes to the parameters used in the coccinellid model had only small effects on the model output. The sensitivity analysis was very important in highlighting the areas within the model where future research should be focussed, such as activity and handling rate.

The approximately symmetrical response obtained from changing the parameters was also encouraging, since it suggests that the components are unlikely to have a complex effect on the output of the model. Survival did not show an approximately symmetrical response, but the reasons for this have been discussed above. It may have been better to use probits transformation of percentage survival, as this would have allowed an increase or decrease of 20% on the probit scale, without causing the value for survival to be greater than 100%. The lack of interactions between parameters, as shown by the additive response when changing pairs of parameters, was most helpful, since the reasons for any changes in the model output can be easily identified.

The effect of changing the date of immigration on the output of the model are interesting, especially the fact that advancing the date of coccinellid immigration only causes the date of the first peak to occur one day earlier. As discussed above, this is

most likely due to the conditions at the time of immigration being unsuitable for coccinellid development and reproduction, such that the date predicted by the model, when immigration is advanced, is the earliest date that a peak can occur.

The effects on the second peak were expected, since the second peak is caused by coccinellids immigrating into the field late in the season, and their number is taken directly from the number recorded in the field.

The effects of changing the date of coccinellid immigration on the predicted peak numbers of coccinellids and aphids are more interesting, since they emphasise that the effect of the coccinellids on the number of aphids is related to when the coccinellids immigrate into the field. The earlier that they immigrate, the more likely they are to reduce the aphid numbers; this result may seem intuitively obvious, but it emphasises the importance of synchronisation between the pest and predator species.

There are a few problems with the coccinellid sub-model. The main one is the lack of data available for the formulation of some of the equations, as highlighted by the sensitivity analysis. Also, certain areas of coccinellid ecology could not be incorporated, such as larval cannibalism. This, again, was due to the lack of appropriate data, although on a field scale cannibalism is unlikely to affect significantly coccinellid numbers.

In spite of these problems, the sub-model provides, overall, a reasonable simulation of the general biology of *C. septempunctata*, since all the main processes involved in coccinellid ecology, such as reproduction, development, survival and predation, have been included.

Chapter 4 FIELDWORK

4.1 INTRODUCTION AND AIMS

Field counts of aphids and coccinellids were made at Rothamsted between 20/4/94 and 2/8/94 to obtain an independent dataset which could be used in the validation of the model. For a full validation of the model, much more field data would be required, but due to time constraints, 1994 was the only year in which data could be obtained for the complete field season from April through to August.

4.2 MATERIALS AND METHODS

4.2.1 The field sites

Two field sites were selected at Rothamsted Experimental Station, the first being a triangular section of Delharding field, sown with winter wheat cultivar Genesis at 380 seeds per m² on 22/10/93 and 23/10/93. This site was approximately 400 metres north of a Rothamsted Insect Survey 12.2m suction trap.

The field was bordered on one side by Rothamsted Park, and on the other two sides by a track and a path through the field respectively. The park and field margins contained several clumps of stinging nettles, which are known to act as refuges for *C. septempunctata* (Majerus and Kearns, 1989; Perrin, 1975).

The second site was a 15m by 2m plot contained within a larger field, Garden Plots, adjacent to a Rothamsted Insect survey 12.2m suction trap. The field was sown with winter wheat cultivar Genesis at 380 seeds per m² on 2/11/93.

4.2.2 Sampling methods

The fields were sampled for aphids and coccinellids by counting the number found in 20 randomly selected rows, each 30cm long. The rows were selected randomly on

each sampling occasion. Random number tables were used to provide the number of paces taken across the rows, and then the number of paces taken along a row to reach the sampling position. The number of aphids, the number of coccinellid larvae, adults and pupae and the number of tillers of wheat within each 30cm row were recorded. The average numbers of tillers per row, aphids per tiller, and coccinellids per m² were calculated from the recorded data.

It was also decided to investigate whether coccinellids were using the nettle patches around Delharding as refuges. A map was made to show the relative positions and sizes of the nettle patches. It was assumed that the coccinellids would be randomly distributed within and between the nettle patches, and the number of samples (out of a total of twenty) to be made in any given patch was to be proportional to size.

Samples within the nettle patches were done using a 25cm by 25cm quadrat, and the number of coccinellid adults, larvae and pupae within the quadrat was recorded. A count was also made of the total number of coccinellid adults, larvae and pupae seen while walking round the nettle patches.

Rothamsted Insect Survey suction traps sample at a height of 12.2 metres (Taylor 1973), and use a nine inch diameter fan to draw air down into the trap and through a conical net of metal gauze that filters the insects out of the air stream (Taylor 1962). These insects are then preserved in a buffer, which is held at the base of the conical net, and collected daily, before being counted by the Rothamsted Insect Survey.

4.3 RESULTS

Unfortunately, not all the results can be presented in this thesis, due to a misclassification of the aphids between 20/4/94 and 23/6/94. However as the peak number of aphids occurred during July, the numbers just before and after the peak can be presented.

4.3.1 Aphid counts from the field sites

Aphids were first recorded in both Delharding and Garden Plots on 11/5/94, but the peak numbers were not recorded until 4/7/94 for Delharding, and 6/7/94 for Garden plots. The mean counts (and standard errors) made from 23/6/94 onwards are shown in Table 4.1.

Delharding			Garden Plots		
Date	Average number of tillers per 30cm row	Average number of aphids per tiller	Date	Average number of tillers per 30cm row	Average number of aphids per tiller
23/6/94	19.6 ±5.23	0.28 ±0.317	23/6/94	15.1 ±4.56	0.225 ±0.424
4/7/94	22.2 ±6.33	1.397 ±0.929	6/7/94	21.1 ±4.86	0.751 ±0.668
11/7/94	17.85 ±3.34	0.377 ±0.418	12/7/94	22.8 ±4.63	0.323 ±0.539
14/7/94	21.65 ±5.32	0.336 ±0.497	21/7/94	22.7 ±6.30	0.0163 ±0.0296
18/7/94	24.55 ±5.98	0.295 ±0.302	27/7/94	21.3 ±4.17	0.0
21/7/94	22.15 ±4.51	0.251 ±0.229	2/8/94	22.0 ±4.99	0.0
27/7/94	23.35 ±6.17	0.026 ±0.041			
2/8/94	22.4 ±3.17	0.0			

Table 4.1: The number of tillers per row and the number of aphids per tiller in both field sites (Mean of 20 samples, with standard error).

4.3.2 Coccinellid counts from the field sites

The coccinellids first appeared in Delharding on 16/6/94 and reached a peak on 11/7/94, declining after that, although they were still being observed in mid-August, despite the fact that aphids were no longer being recorded in the field.

In Garden Plots, coccinellids were not observed until 6/7/94. They reached a peak on 21/7/94, and then remained in the field until mid-August, despite the fact that aphids were not recorded in the field after 21/7/94. The numbers recorded in each of the fields is shown in Table 4.2.

Delharding		Garden Plots	
Date	Number of coccinellid adults and larvae per m ²	Date	Number of coccinellid adults and larvae per m ²
16/6/94	1.27 ±5.66	14/6/94	0.0
20/6/94	0.00	23/6/94	0.00
23/6/94	0.00	6/7/94	0.66 ±2.93
4/7/94	3.37 ±9.50	12/7/94	0.00
11/7/94	2.18 ±6.76	21/7/94	2.65 ±6.84
14/7/94	6.83 ±9.80	27/7/94	0.76 ±3.40
18/7/94	9.45 ±11.75	2/8/94	0.70 ±3.15
21/7/94	3.19 ± 8.65		
27/7/94	1.73 ±5.34		
2/8/94	1.27 ±5.66		

Table 4.2: The number of adult and larval *C. septempunctata* per m² recorded in both field sites (Mean of 20 samples, with standard error).

4.3.3 Counts of coccinellids in nettle patches

Coccinellids were present in the nettle patches from 26/4/94 through to 27/7/94, when the patches were cut. Coccinellids were absent between 27/5/94 and 11/6/94, probably because the adult coccinellids of the overwintering generation either died or emigrated after laying eggs. The coccinellids recorded after this absence were most likely to be the adults of the second generation, that had developed from eggs laid in the nettle patches. This hypothesis is supported by the fact that only adults were observed between 26/4/94 and 25/5/94, but larvae and pupae, and later adults, were present in the observations from 11/7/94 to 27/7/94.

The mean number of coccinellid adults, larvae and pupae per m² recorded in the nettle patches are presented in Table 4.3.

The counts of coccinellids observed while walking round the nettle patches showed that there were large numbers of coccinellids in the nettles, despite there being few or none in the fields. This observation seemed to support the observation of Perrin (1975) that *C. septempunctata* adults often migrate large distances from refuges to fields, and that the presence of coccinellids in a refuge next to a field is no guarantee that they will enter that field.

Date	Number of adults per m ²	Number of larvae per m ²	Number of pupae per m ²
26/4/94	3.2 ±8.37	0.0	0.0
3/5/94	1.6 ±4.92	0.0	0.0
11/5/94	3.2 ±6.57	0.0	0.0
18/5/94	1.6 ±4.92	0.0	0.0
19/5/94	2.4 ±7.83	0.0	0.0
25/5/94	0.8 ±3.58	0.0	0.0
27/5/94 - 4/7/94	No adults, larvae or pupae recorded		
11/7/94	0.0	8.8 ±14.19	8.8 ±19.75
14/7/94	7.6 ±4.92	0.8 ±3.58	2.4 ±5.86
18/7/94	7.2 ±10.98	1.6 ±7.16	5.6 ±8.80
21/7/94	4.8 ±7.52	0	7.2 ±17.58
27/7/94	Nettle patches cut		

Table 4.3: The number of adult, larval and pupal *C. septempunctata* recorded in the nettle patches bordering Delharding (Mean of 20 samples, with standard error).

4.4 USING THE FIELD COUNTS TO VALIDATE THE MODEL

As mentioned earlier, the aim of the fieldwork was to provide an independent dataset for the validation of the model. Before the counts could be used, they had to be converted into the format required by the model. Coccinellid counts had to be entered as numbers per m². The number of coccinellids was converted from numbers per tiller to numbers per m² by multiplying by the number of tillers per m², which was taken to be the same as the number of seeds sown per m², since row counts do not provide an accurate estimate of the number of tillers per m².

The suction trap records for the 1994 summer season were obtained, and used as the initialising input for aphid numbers in the model. The daily maximum and minimum temperatures, obtained from the Rothamsted meteorological station, completed the inputs required by the model. The model was then run, and the output compared graphically with the field counts of both coccinellids and aphids (Figs. 4.1 and 4.2).

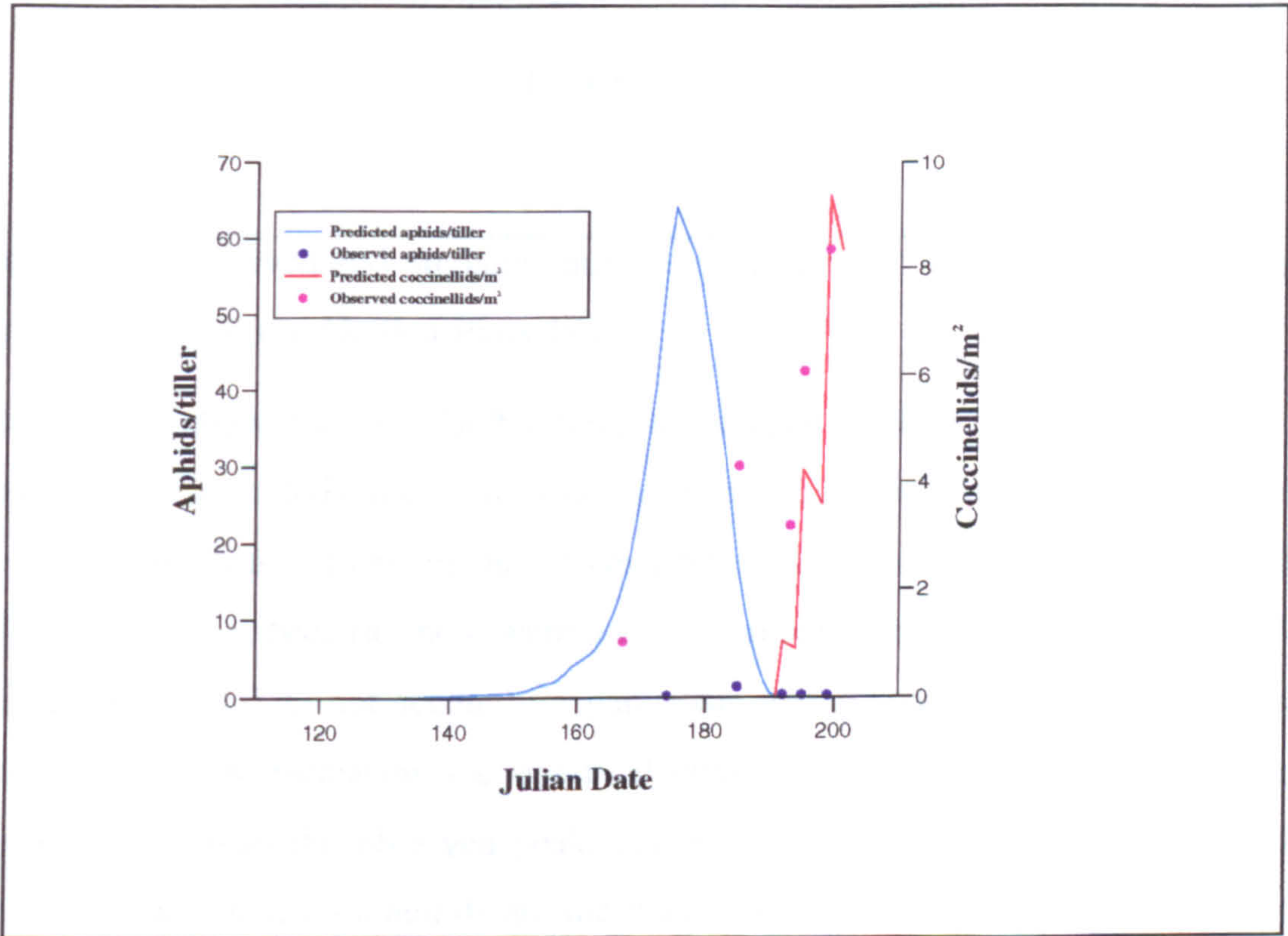


Figure 4.1: Observed and predicted number of aphids and active coccinellid stages (adults and larvae) in Delharding 1994.

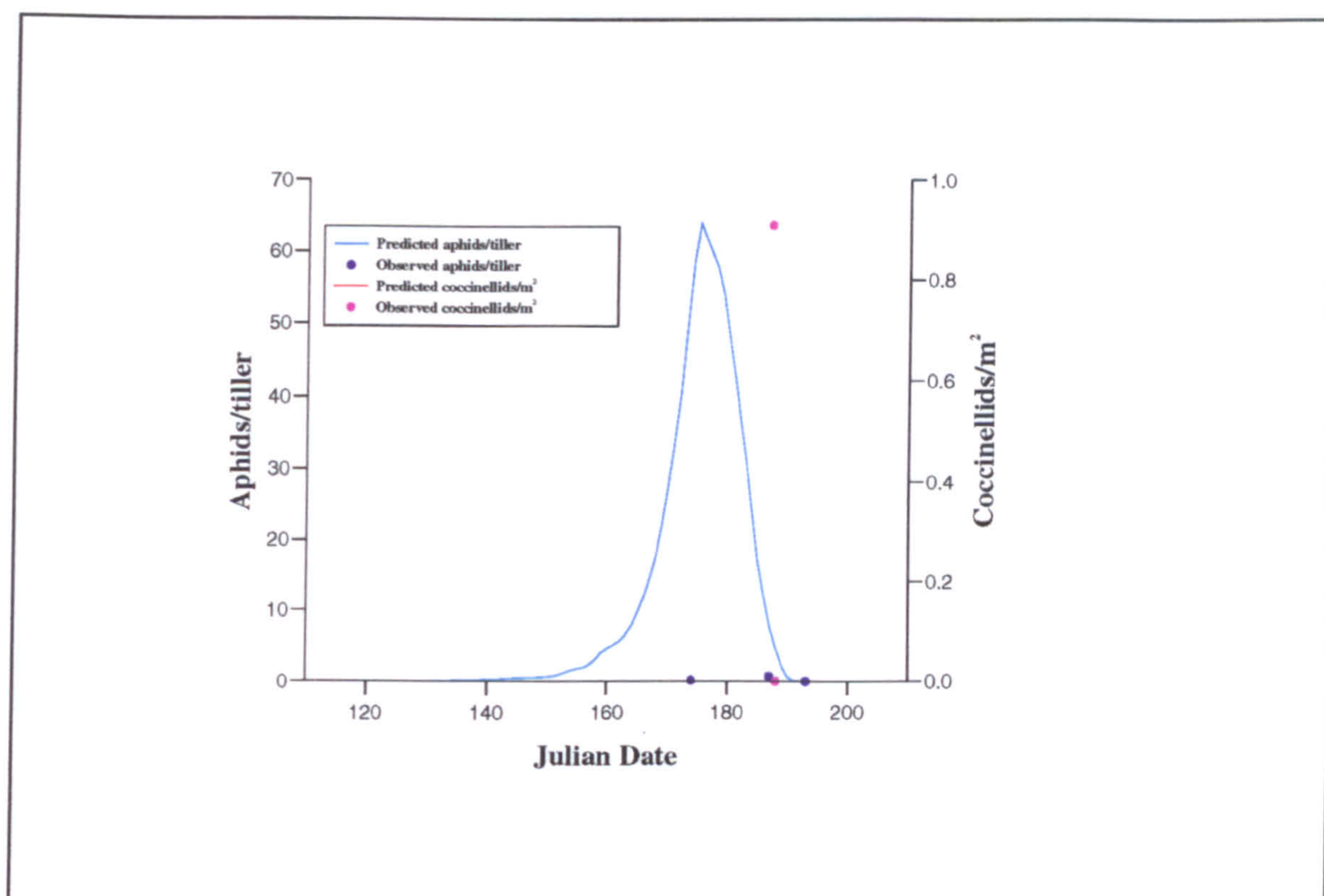


Figure 4.2: Observed and predicted number of aphids and active coccinellid stages (adults and larvae) in Garden Plots 1994.

The graphs show that for Delharding, the model predicts nearly two orders of magnitude more aphids than were actually observed in the field. This could be due to the fact that suction traps are not necessarily representative of an individual field (Taylor 1973), or because there were a large number of syrphid larvae in the fields. Also, the model does not account for parasitism of the aphids, which may also have had an effect on decreasing the observed numbers. The predicted aphid peak also occurs earlier than the observed peak, but this is probably due to the fact that the model assumes that coccinellids are the only natural enemies, and the timing of the peak number of aphids may have been delayed in the field by predation and parasitism by other natural enemies.

The model predicts the coccinellid peak reasonably well, although it must be remembered that the observed numbers of coccinellids also form an input to the model.

For Garden Plots, the predicted numbers of aphids are much higher than the observed

values, probably due also to the reasons mentioned above. Also, the model does not predict the presence of any coccinellids, this is due to the fact that the field observations showed that there were no coccinellids in the field early in the season (before Julian day 173), and therefore the model runs assuming that there is no coccinellid immigration.

4.5 SUMMARY AND DISCUSSION

This chapter has described and presented the results of fieldwork carried out in the summer of 1994. A description of how the results were compared to predictions by the model was also presented.

The attempted validation has highlighted the need for a greater range of data, and also the limitation of using a deterministic model, in that there is only one outcome. There are several reasons for the lack of fit of the model predictions to the aphid numbers which have been discussed above.

Although the predicted number of coccinellids in Delharding was similar to the observed number, as pointed out earlier, the observations act as both input and validation data. When models use a variable as both input and output, the fit to field data may be improved spuriously, and caution is then required in interpretation.

The prediction of zero coccinellids for Garden Plots was caused by the fact that coccinellids were not observed in the field early in the season, and, therefore the model could not simulate the presence of coccinellids in the field.

These problems stem from the fact that the model is deterministic, and only gives a single output for a given set of inputs. In order to rectify this situation, it was decided to incorporate stochastic elements into the model, which are described in the next chapter.

Chapter 5: INCORPORATION OF STOCHASTIC ELEMENTS AND RESULTS

Having constructed a deterministic model which simulates the population dynamics of both *C. septeimpunctata* and *S. avenae*, the next step was to incorporate the different temperature regimes into the model, and also to remove the reliance of the model on inputs based on field observations. This chapter describes this process and then presents the results obtained by running the model.

5.1 INCLUSION OF STOCHASTIC ELEMENTS

5.1.1 Formulation of temperature regimes

In order to allow the simulation of increased temperatures on the population dynamics of the aphid and coccinellid, it was necessary to allow the model to simulate a range of temperature scenarios. It was decided to simulate temperatures based on observations within current experience, assuming that what we presently perceive as unusually warm years would become the norm in the future (Harrington and Woiwod, 1995).

Using data collected from the Rothamsted meteorological station, the mean monthly temperatures from April through to August were examined. An analysis of variance showed that there was significant between-year variation in temperature, and the years were ranked according to their difference from the mean temperature over the five months examined. The years were then classified into three distinct groups, labelled hot, moderate and cold (Table 5.1). A Bartlett test (Bartlett 1937) showed that the mean temperatures of each of the three groups, or regimes, were significantly different.

Cold Regime (Temperature (°C))	Moderate Regime (Temperature (°C))	Hot Regime (Temperature (°C))
1972 (12.16)	1965 (12.28)	1969 (12.96)
1977 (11.84)	1966 (12.52)	1970 (13.16)
1978 (12.00)	1967 (12.80)	1973 (13.12)
1986 (12.16)	1968 (12.44)	1975 (13.56)
	1971 (12.68)	1982 (13.38)
	1974 (12.5)	1983 (13.62)
	1979 (12.44)	1984 (12.92)
	1980 (12.50)	1989 (13.68)
	1981 (12.50)	1990 (13.50)
	1985 (12.34)	
	1987 (12.62)	
	1988 (12.54)	
	1991 (12.64)	

Table 5.1: Table showing the categorization of years into regimes based on mean temperatures between April and August

Following the method of Kocabas *et al.* (1992), a double Fourier curve was fitted to the daily mean temperatures, in each regime, from 1 April through to 31 August. The equations describing the mean daily temperatures for each regime are shown in the equations below:

Cold regime $t = 5.709 - 1.639A - 9.83B + 1.202C - 1.173D + e_t$

Moderate regime $t = 11.44 - 3.448A - 2.26B - 0.045C + 0.973D + e_t$

Hot regime $t = 5.709 - 1.98A - 13.14B + 1.195C - 2.371D + e_t$;

where $A = \sin((2\pi k)/365)$; $B = \cos((2\pi k)/365)$; $C = \sin((4\pi k)/365)$; $D = \cos((4\pi k)/365)$; k = Julian date and e_i is a normal random variable with zero mean and a standard deviation ϕ_i (Table 5.2).

Having calculated each mean daily temperature, it was necessary to calculate the daily maximum and minimum temperature since these were the temperature inputs required by the model. The data on the daily maximum and minimum temperatures between 1 April and 31 August for each year were obtained from the Rothamsted meteorological station archives. The difference between the daily maximum and minimum temperatures was calculated for each day being simulated and a lognormal distribution was then fitted to the data for each regime. Assuming that the difference between the maximum and minimum temperatures was symmetrical, the daily maximum, D_{max} , and minimum, D_{min} , temperatures were obtained from:

$$D_{max} = t + 0.5d ; D_{min} = t - 0.5d ,$$

where d represents the difference between D_{max} and D_{min} and was sampled from a lognormal distribution with mean, μ , and standard deviation, ϕ_2 (Table 5.2).

Regime	ϕ_1	μ	ϕ_2
Hot	2.63	1.94 \pm 0.0123	0.701 \pm 0.0087
Moderate	2.40	1.88 \pm 0.0094	0.647 \pm 0.0066
Cold	2.19	1.90 \pm 0.0146	0.557 \pm 0.0103

Table 5.2: Parameters used to simulate daily maximum and minimum temperatures.

The model was amended so that the daily maximum and minimum temperatures were obtained from the above equations, which meant that a separate model was required for each of the three regimes.

5.1.2 Simulation of aphid immigration

Data on aphid immigration were obtained from the Rothamsted Insect Survey 12.2m suction trap, at Rothamsted, from 1966 to 1993 (Woiwod and Harrington, 1994). The data were plotted in order to distinguish immigration of aphids during the early part of the summer growing season from movements later in the season.

The start and end dates of aphid immigration during the early part of the summer growing season were determined from the graphs for each regime. The start date was determined as the day upon which the first aphid was caught in the suction trap. The end date was more difficult to determine, and a subjective judgement as to the end of the immigration period had to be made based on a visual inspection of the daily suction trap counts. An end date was assumed to occur when there was a period during which no aphids were caught, which lasted for more than 3 days, and also when the daily catches after this period showed a rise to a peak which exceeded 10 aphids per day. The start and end dates were then plotted to determine whether there was a relationship between the start and end dates of immigration. The graph showed that there was a significant linear relationship between the start and end dates of immigration. The data from the moderate and cold regimes had similar relationships to each other, and were combined to form a single dataset. A regression analysis was performed on the data to quantify the relationship between start and end dates for the hot regime and the combined cold and moderate regime. The equations fitted to the data (Figure 5.1.) are shown below:

$$\text{Hot regime:} \quad D_e = 10.8 + 1.084D_s + e_s ,$$

$$\text{Cold and Moderate regime:} \quad D_e = 52.0 + 0.840D_s + e_s ,$$

where D_e = end date, D_s = start date and e_s is a normal random variable with mean zero and standard deviation, ϕ_s , being estimated as the square root of the residual mean square term in the regression analysis (Table 5.3). The normal random variable allows for the scatter within the data.

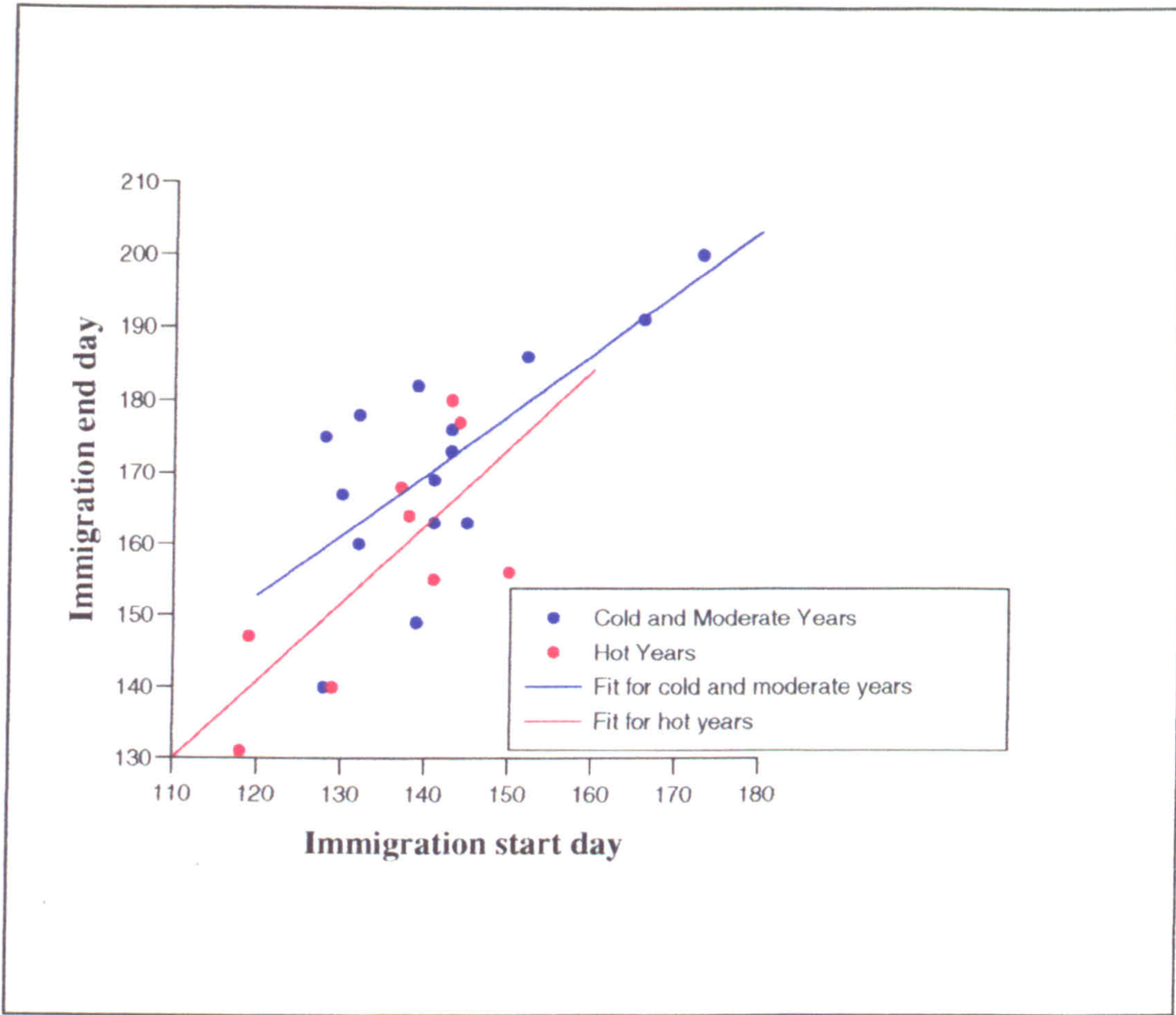


Figure 5.1: The regression line fitted to the data for start and end dates of immigration.

Regime	ϕ_3	v_I	ϕ_4
Hot	11.9	135.44 ± 3.51	10.53 ± 2.31
Cold and Moderate	11.4	142.13 ± 3.27	12.66 ± 2.31

Table 5.3: Parameters used to simulate the start and end dates of aphid immigration

In order to predict the end data using the equations above, a start date was required. The start date is obtained by sampling from a normal distribution, fitted to the data for the hot regime or the combined cold and moderate regimes. The mean, v_I , and the standard deviation, ϕ_4 , of these distributions is shown in Table 5.3.

Having obtained the start and end dates of immigration, the next step was to simulate the number of aphids caught in the suction trap on each day of the immigration period. The number of aphids caught per day was sampled from a negative binomial distribution with mean, v_2 , and standard deviation, ϕ_5 , (Table 5.4) estimated from the suction trap data, for each of the three regimes.

Regime	v_2	ϕ_5
Hot	1.22 \pm 0.144	0.487 \pm 0.087
Moderate	1.55 \pm 0.177	0.241 \pm 0.028
Cold	0.583 \pm 0.122	0.293 \pm 0.089

Table 5.4: Parameters used to simulate the aphid suction trap count

The model code was amended to include the equations and distributions described above, so that aphid immigration could be simulated.

5.1.3 Simulation of coccinellid immigration

This was the most difficult part of the model to construct, due to the lack of appropriate data. However, using sticky trap data (Zhou *et al.* 1994) from 1991 and 1992 it was possible to build a submodel of coccinellid immigration. Coccinellid immigration was assumed to occur in two waves, each lasting 29 days. The first wave simulates the immigration of those coccinellids that overwintered and moved into the simulated field in spring from hibernation sites. The start date of this first wave, C_{s1} , and the end date, C_{e1} , are obtained from:

$$C_{s1} = C_{p1} - 14 ; C_{e1} = C_{p1} + 14 ,$$

where C_{p1} is sampled randomly from a normal distribution, derived from Zhou *et al.* (1994), with mean 140 and standard deviation 5. The mean of the normal distribution was obtained by examining the data (Zhou *et al.* 1994), and choosing the average day on which the largest number of coccinellids moved into the field in the first wave of immigration. Zhou *et al.* (1994) estimated the average weekly coccinellid catch as 1.0,

and the proportion of the daily catches that were zero as 0.80. Therefore, the number of coccinellids assumed to enter the field each day during the first wave of immigration, W , was sampled randomly from a uniform distribution in the range -6.0 to 1.5, any negative value of W being truncated to zero. The resulting values of W agree closely with Zhou *et al.*'s data, in terms of the number of day when coccinellid immigration did not occur, and in the general shape of the immigration distributions.

The second wave of immigration simulates the immigration of the second generation adult coccinellids which move from field to field on their way back to the hibernation sites. The start date, C_{s2} , and end date, C_{e2} , of the second wave were simulated in a similar way to the first wave, except that the median date, C_{p2} , was sampled from a normal distribution with mean 180 and standard deviation 5. The phenological data (Zhou *et al.* 1994) indicated that the daily number of coccinellids in the second wave of immigration followed approximately a normal curve in time. Therefore, the number of coccinellids assumed to enter the field between dates C_{s2} and C_{e2} are distributed as a normal about C_{p2} with standard deviation of unity. The maximum daily number of coccinellids in the second wave can be up to five times as large as the maximum daily number in the first (Honek 1989). If the factor by which the maximum number in the second wave is larger than the first is denoted as P , then P is sampled from a normal distribution with mean 5, and standard deviation 5. The number of coccinellids entering the simulated field on each day of the second wave of immigration is taken to be a proportion, given by the area under the normal curve, of the maximum number that occurs on day C_{p2} .

Having incorporated all the equations described above into the model, it was now possible to simulate the effect of increased temperature on the population dynamics of *S. avenae* and *C. septempunctata*, without the use of field observation as inputs.

5.2 OUTPUT

Having made the changes described above to SACSIM, it was now possible to use the output from the model to predict how increased temperatures would affect the

population dynamics of both *S. avenae* and *C. septempunctata*, and also the interaction between the two species.

Due to the incorporation of stochastic elements into SACSIM, it was necessary to run SACSIM several times in order to gain a representative sample of the range of output that was possible. SACSIM was run 100 times for each of the three regimes, both with and without the immigration of coccinellids into the simulated field, so that it was possible to see how the inclusion of coccinellids within the model affected the numbers of aphids, and to obtain an estimate of the precision of these predictions.

The model was also run with the base temperature of each regime increased by 1°C or 2°C. This enabled the effect of an increase in temperature on the population dynamics and interaction between the two species to be determined, without a major alteration in the immigration behaviour of the aphids and coccinellids.

Three output variables were used for the aphids; the maximum number of aphid per tiller, the date on which the maximum number of aphids occurred, and the total number of aphid days per tiller over the simulate season, which was calculated by summing the number of aphids per tiller predicted each day by the model (Henderson and Perry 1978). Similar output variables were used for the coccinellids; the maximum number of coccinellids per m², the date on which these maximum numbers occurred, and the total number of coccinellid days per m² over the simulated season.

Output from the model was analysed separately for each regime using analysis of variance. The output variables for the aphid were examined to see whether increasing the temperature within a regime, or the presence of coccinellids affected the predictions of the model; the coccinellid output variables were examined to assess the effect of increasing the temperature within a regime. An analysis of variance of the output for all three regimes identified any between-regime differences.

5.3 RESULTS

A representative graph of the output produced by the model for each of the regimes is shown in Figures 5.2, 5.3 and 5.4, and a summary of the output for all three regimes is presented in Table 5.5.

Regime: Temperature	Maximum number of aphids per tiller		Date of maximum aphid abundance		Total number of aphid days in a season (/tiller)		Maximum number of active coccinellid stages (/m ²)	Date of maximum coccinellid abundance	Total number of coccinellid days in a season (/m ²)
Cold: base	10.2 ±0.77	17.9 ±1.08	188.5 ±1.99	194.5 ±2.03	192.9 ±14.6	352.4 ±19.3	31.8 ±1.77	195.0 ±2.03	327.7 ±15.3
Cold: base plus 1°C	7.9 ±0.54	15.6 ±0.78	189.7 ±0.52	190.9 ±1.97	143.3 ±10.7	295.5 ±15.0	26.9 ±1.11	197.5 ±0.49	228.0 ±9.88
Cold: base plus 2°C	6.8 ±0.46	13.9 ±0.81	183.8 ±2.67	186.9 ±1.92	112.7 ±8.41	244.2 ±15.2	24.5 ±1.13	192.5 ±2.81	175.6 ±7.98
Moderate: base	20.2 ±1.96	34.2 ±2.54	184.2 ±0.48	189.9 ±0.59	331.3 ±27.6	569.5 ±29.6	33.6 ±1.31	191.3 ±0.57	384.0 ±16.6
Moderate: base plus 1°C	14.1 ±1.20	31.1 ±1.98	182.4 ±0.56	185.4 ±0.50	240.3 ±19.4	512.5 ±23.9	29.8 ±1.51	189.9 ±0.56	315.5 ±14.0
Moderate: base plus 2°C	14.7 ±1.26	24.2 ±1.18	181.4 ±0.47	184.0 ±0.45	241.9 ±19.5	463.0 ±17.9	30.3 ±1.14	190.6 ±0.52	300.6 ±13.8
Hot: base	11.7 ±0.93	36.3 ±1.56	181.4 ±0.57	184.0 ±1.86	199.8 ±15.9	594.5 ±18.6	28.9 ±1.12	183.1 ±0.59	321.7 ±13.7
Hot: base plus 1°C	8.8 ±0.85	31.4 ±1.45	174.5 ±0.57	178.2 ±0.55	144.7 ±14.4	507.3 ±17.3	25.5 ±1.27	182.0 ±0.57	292.3 ±15.3
Hot: base plus 2°C	7.35 ±0.61	24.4 ±0.92	172.0 ±1.83	173.5 ±2.53	118.5 ±10.5	400.6 ±13.6	26.1 ±1.31	179.0 ±1.88	286.6 ±15.0

Table 5.5: Mean values and standard errors (from 100 runs) of the output from all three regimes, the two values in the aphid columns represent the values with and without coccinellids. Coccinellid numbers include only larvae and adults.

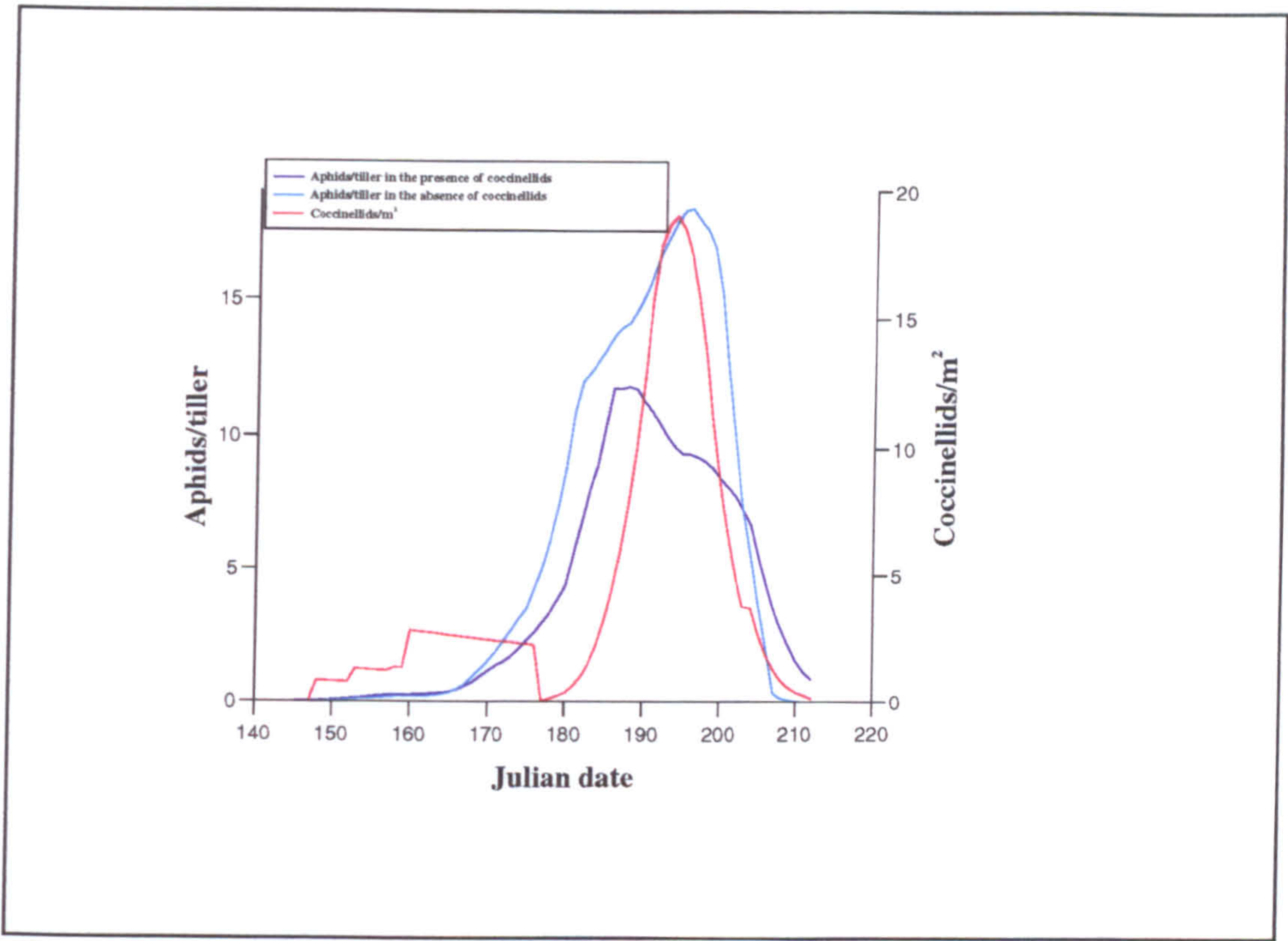


Figure 5.2: Graph showing representative output from the cold regime.

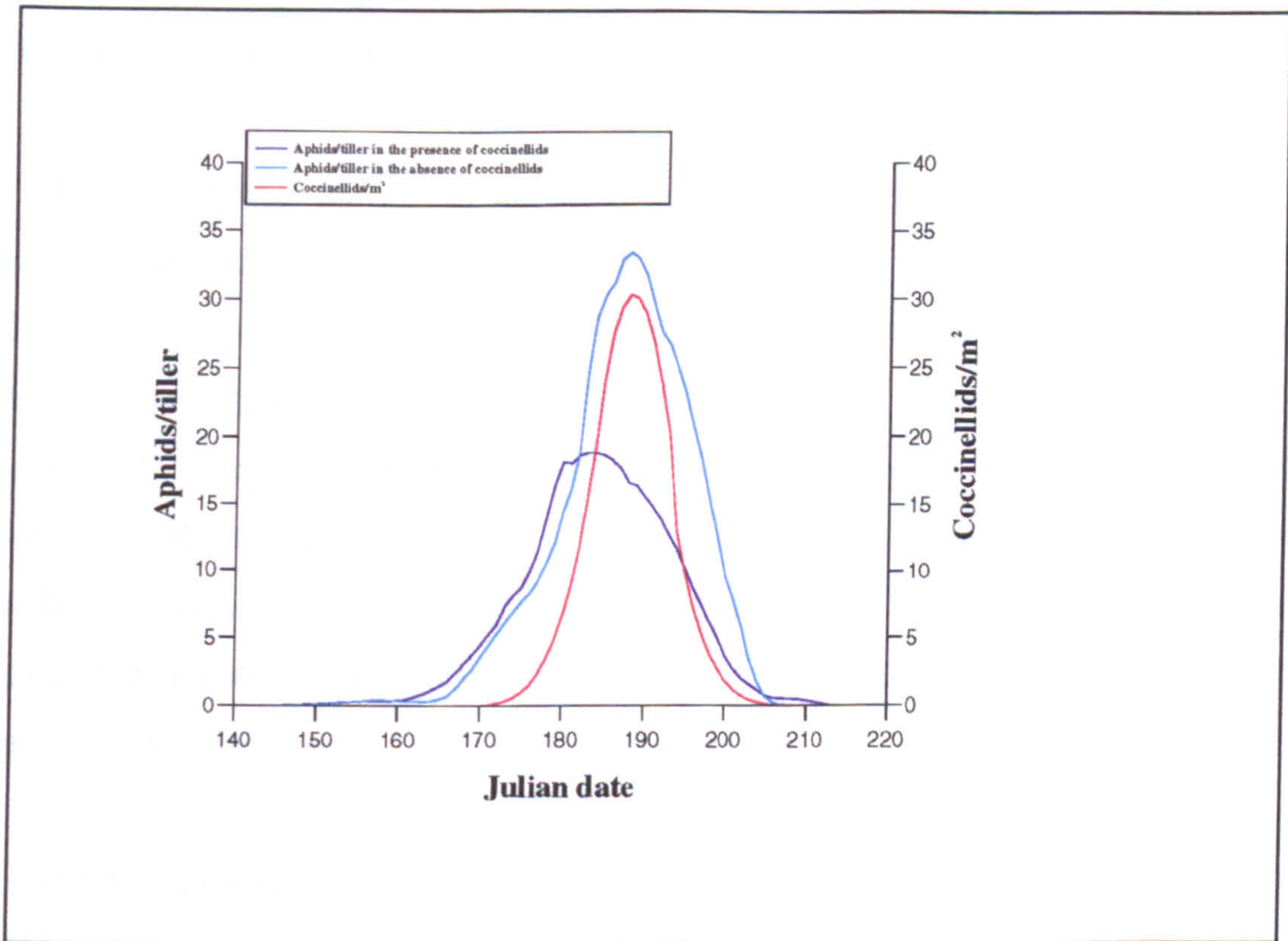


Figure 5.3: Graph showing representative output from the moderate regime.

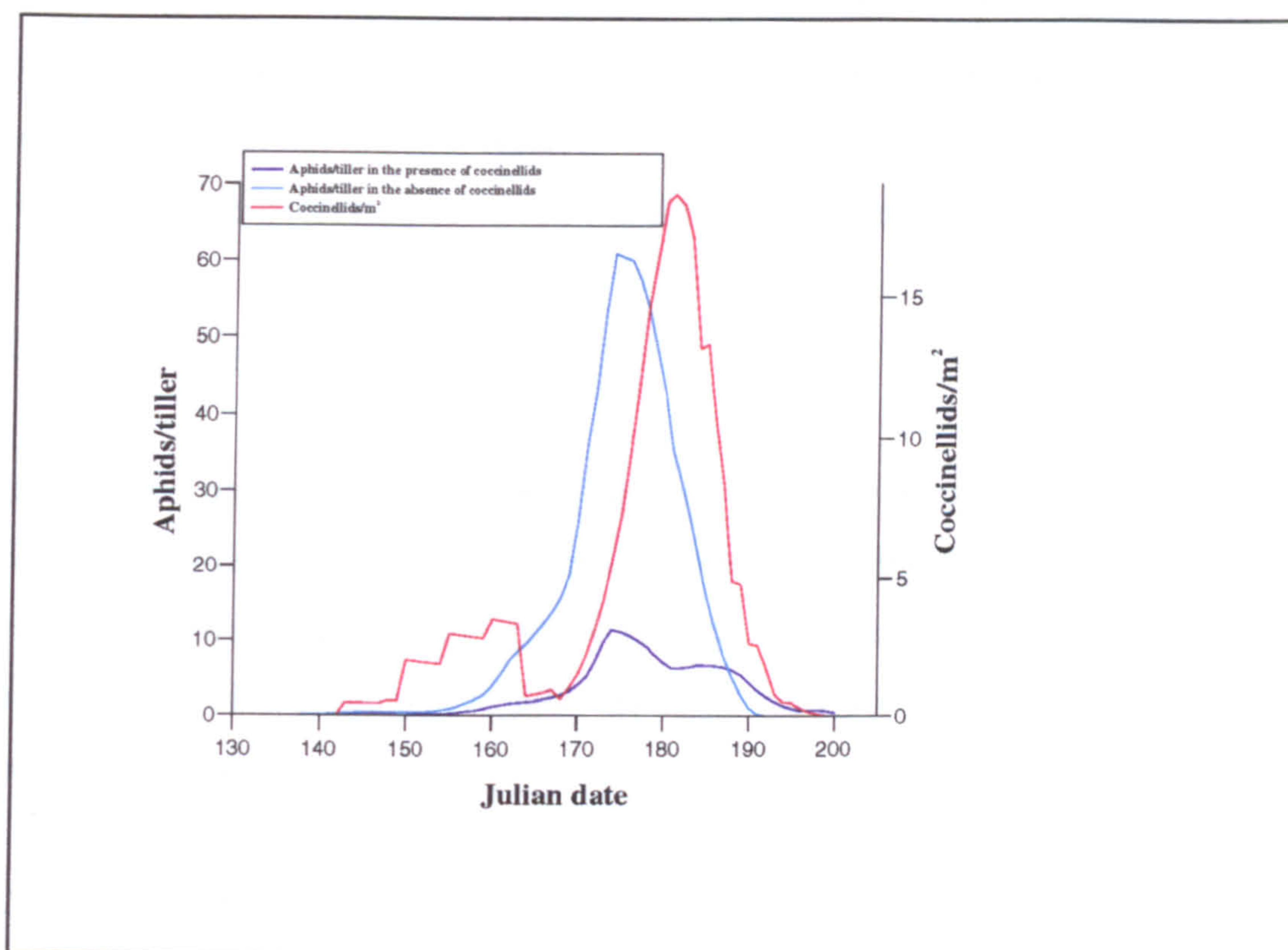


Figure 5.4: Graph showing representative output from the hot regime.

5.3.1 Model output and analyses of variance

In all three regimes, the presence of coccinellids resulted in a significant decrease in both the maximum number of aphids and total number of aphid days ($P < 0.05$) (Table 5.5). As temperature within a regime increased, the maximum number of aphids and total number of aphid days decreased ($P < 0.05$), both in the presence and absence of coccinellids. However only the total number of coccinellid days decreased significantly ($P < 0.05$) as the temperature within a regime increased. The date of maximum aphid numbers occurs earlier in the presence of coccinellids ($P < 0.05$), and also as the regime changed from cold through to hot ($P < 0.05$), as does the date of maximum coccinellid numbers ($P < 0.05$).

The results show that the moderate regime appears to be the most suitable regime for aphids. The greatest values for maximum number of aphids and total number of aphid days were reached in this regime, both in the presence and absence of coccinellids. This observation was highlighted by the significantly large ($P < 0.05$) interaction

between regime and presence of coccinellids on both these two variables. Coccinellids also achieve their greatest maximum numbers and total number of coccinellid days in the moderate regime; the total number of coccinellid days were significantly affected ($P < 0.01$) by the interaction between regime and temperature.

5.3.1.1 *Cold regime*

Although the date of maximum aphid numbers generally occurs earlier as temperature within a regime increases the relationship appears quadratic, and the date was latest for the base temperature plus 1°C. A similar relationship occurred for the date of maximum coccinellid numbers, although these were not significantly affected by an increase in temperature within a regime.

5.3.1.2 *Moderate regime*

The numbers of aphids followed the general trend to decrease with increasing temperature, except that the model predicted slightly higher numbers for the base plus 2°C than for base plus 1°C, in the presence of coccinellids. The effect of temperature on the date of maximum aphid numbers was less apparent, in the presence of coccinellids, than in the other regimes.

5.3.1.3 *Hot regime*

The maximum number of coccinellids followed the general trend to decrease with increasing temperature, although the model predicted higher numbers for the base temperature plus 2°C, than for the base temperature plus 1°C. The date of occurrence of maximum aphid numbers was advanced by the presence of coccinellids, but not significantly so.

5.3.2 **Determination of Control**

The accepted threshold for an aphid outbreak is 5 aphids per ear when the crop is

flowering (Oakley and Walters, 1994). The number of runs of the model where the maximum number of aphids exceeds 5 aphids per tiller is shown in Table 5.6. The use of aphids per tiller for this analysis instead of aphids per ear is acceptable since *S. avenae* feeds on the ears of wheat as soon as they have developed, and is only found on the leaves of wheat when the ears are not present (Kolbe, 1969; Rabbinge *et al.*, 1979; Vereijken, 1979; Vickerman and Wratten, 1979; Watson and Dixon, 1984)

Regime: Temperature	Coccinellids: present or absent	Number of runs (Maximum aphid numbers > 5/tiller)
Cold: base	present	6
	absent	46
Cold: base plus 1°C	present	9
	absent	54
Cold: Base plus 2°C	present	17
	absent	61
Moderate: base	present	0
	absent	35
Moderate: base plus 1°C	present	2
	absent	29
Moderate: base plus 2°C	present	2
	absent	36
Hot : base	present	1
	absent	47
Hot: base plus 1°C	present	0
	absent	48
Hot: base plus 2°C	present	3
	absent	55

Table 5.6: Number of runs from each regime where the maximum number of aphids exceeds 5 aphids per tiller.

In an attempt to determine the mechanism that caused aphids to remain below the

threshold in the model, plots of the numbers of aphids and coccinellids over time, and the growth rate of the aphids against the numbers of the coccinellids were examined.

The examination revealed that it is not always the presence of coccinellids that keeps the aphid numbers below the threshold. However, when coccinellids do restrict aphid numbers it seems to be related to how soon after the initial aphid immigration that the coccinellids enter the field. For control, the difference must usually be less than 10 days, although there were several occasions when coccinellids did not control aphids when they did arrive within 10 days from the initial aphid immigration. Therefore, there seem to be factors other than the relative timing of the immigrations of the coccinellids and aphids, but these have proved difficult to identify using the model in its present format, since it does not output the crop growth stage and average daily temperature, which may be having an effect on the control of aphids. In order to determine whether temperature and crop growth stage were affecting aphid control, a large amount of output would be required, and the analysis of such output would be both time consuming and difficult, since the precise relationship of these factors is not known. It is possible, that there could be purely random factors determining whether control of aphids by coccinellids occurs. It may prove more enlightening to output the number of aphids every hour instead of every day, as this would possibly show the more subtle effects which may affect the control of aphids by coccinellids.

5.4 SUMMARY AND DISCUSSION

This chapter describes the incorporation of stochastic elements into the model, which enabled the model to simulate a range of possible outcomes, when it was run. This description was followed by a presentation and analysis of the model predictions.

The model predicted that the presence of coccinellids reduced the number of aphids and brought forward the date of occurrence of maximum aphid numbers. These predictions are as expected because of the effect of reducing the prey abundance, especially that of reproducing adults, so that fewer nymphs are produced, which leads in turn to a earlier peak in the numbers of aphids.

The model also predicted that an increase in temperature within a regime, which simulates a change in temperature without an alteration of the aphids' immigration behaviour, resulted in a lower number of aphids, which peaked earlier both in the presence and absence of coccinellids. Whilst this prediction seems strange, it is probably due to the fact that enhancing temperature within a regime aided the growth of the crop more than aphid development. The increase in temperature caused the crop to develop faster, and even though aphid development and reproduction was enhanced, the crop was probably unsuitable for the aphids at an earlier date. Since aphid immigration was still being simulated, as for the base temperature, the initial numbers were as low as at the base level, and immigration occurred at the same time as for the base level, instead of reacting to the change in temperature, leading to a shorter time period in which the crop is suitable for aphid development and reproduction, hence leading to lower numbers of aphids.

In the absence of coccinellids, the model predicted that as the average yearly temperature (regime) increased from cold through to hot, conditions became more favourable for aphids and their numbers increased. However, in the presence of coccinellids, aphids in the UK were predicted to fare best in a moderate regime. The reason for this lies in the contrasting biology of the two species. Whilst the reproductive rates of both aphids and coccinellids peak at 20°C, the reproductive rate of the aphids declines more sharply at high temperatures. Coccinellids can also continue to develop at high temperatures, while aphid development is restricted. This ability of the coccinellids to develop and reproduce at higher temperatures than their prey gave the coccinellids a distinct advantage in the hot regime, where the maximum daily temperatures may reach 30°C to 35°C.

The predicted maximum number of coccinellids did not seem greatly affected by temperature, probably because of its dependence on the second wave of immigrants which do not develop in the field and at present in the model, the timing of this immigration is independent of temperature, as is the number of coccinellids assumed to immigrated during this wave. The expected total number of coccinellid days in a simulated season increased with increased average yearly temperature (cold to hot

regime), but decreased with increased temperature within a regime. These total numbers appear to depend on the regime, in that they are maximal at the moderate regime. This is caused by two factors, first the aphid numbers are also maximal for the moderate regime and can therefore support higher numbers of coccinellids. Secondly, the temperatures early in the season (before day 100) in the moderate regime are warmer than for the other two regimes (Figure 5.5), allowing a longer period for development and reproduction.

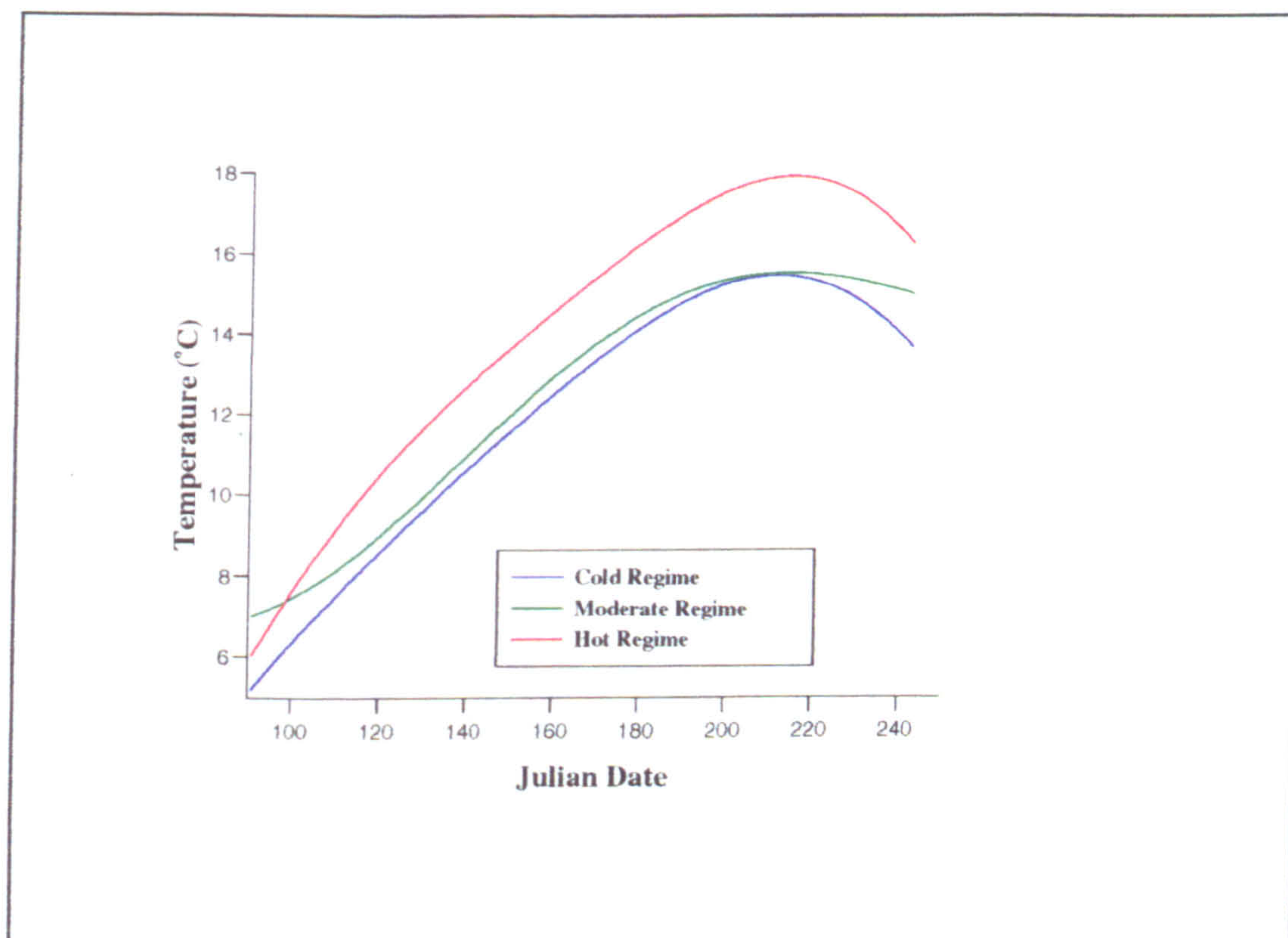


Figure 5.5: Graph showing the predicted mean daily temperatures for each of the three regimes.

The decline in the numbers of coccinellids as temperature within a regime increases was probably related to a decrease in the number of aphids. When fewer prey were available, correspondingly fewer coccinellids were produced, since reproduction depends on prey consumption.

The model predictions suggest that although coccinellids do regulate aphid numbers, economic control, defined as the maximum number of aphids not exceeding 5 aphid per tiller, is not always caused by predation. In fact, it appears that temperature plays

a large part in determining whether coccinellids can keep aphids below the threshold for economic damage. The earlier that coccinellids arrive the better chance they have of controlling aphids, but temperature regulates this in a way which cannot be fully determined from the model output. The coccinellids were rarely able to keep aphid numbers in check if they arrived more than 10 days after the initial aphid immigration because the aphids were able to reproduce faster, being parthenogenetic. If coccinellids arrived within 10 days of the initial aphid immigration, then the coccinellids could slow, but did not usually prevent the build up of aphid numbers. If the second wave of coccinellid immigrants occurred soon after the initial immigration of aphids, then they could prevent aphid numbers exceeding the threshold for economic damage by hastening the crash in the aphid population or sometimes causing the aphid numbers to crash.

Temperature affected the speed of the increase in aphid numbers, and in some cases where aphids remained below the threshold for economic damage, low temperatures caused this by preventing the aphids from increasing their numbers quickly.

It is certain that the timing of the two coccinellid immigrations had greatest impact on whether coccinellids can control aphids. If the two immigrations were widely separated, then the aphids were able to build up their numbers to damaging levels after the initial control by the first wave, before the second wave was able to reduce aphid numbers. If the two waves were close together, then they could act in concert with the first wave slowing the build up, the second wave then causing an early crash in the aphid numbers.

The model has not been validated, since there is not enough independent data which includes field counts of both aphids and coccinellids available for this. However, the large variation in the output of the stochastic model means that it provides a wide range of outputs, which encompasses the existing field data. If more time had been available for examination of the model, it would have been informative to have compared the output of the stochastic model with field data. It was felt that a comparison between the deterministic model output and the output of the stochastic

model would not provide much useful information since the output of the deterministic model is highly dependent upon the input to the model, whereas the output of the stochastic model is not dependent upon the inputs to the model. This is because the main inputs to the deterministic model; aphid and coccinellid immigration, and daily temperatures; are those that are simulated in the stochastic model.

Chapter 6 GENERAL SUMMARY AND DISCUSSION

6.1 THE MODEL

The work presented in this thesis has described the development and testing of a computer model which is able to predict the effects of increased temperature on the population dynamics of *S. avenae* and *C. septempunctata*.

The model integrates the results of several studies on the population dynamics of both the aphid and coccinellid, and has enabled a greater understanding of the two species and their interaction to be developed. The model of Carter *et al.* (1982), SAM7, has been improved by the use of more accurate representations of aphid biology and by the inclusion of a submodel describing the biology of *C. septempunctata*. Also, the use of field counts as inputs has been superseded by the incorporation of stochastic elements that allow the model to simulate a range of possible scenarios, in particular the response of this prey-predator system to potential long-term temperature changes associated with global warming. Furthermore the model simulates more realistically natural field-to-field variation. However, the stochastic model is more difficult to validate, due to the need for long-term data from a large number of field sites.

The incorporation of aphid immigration into the model, through the use of distributions based on suction trap counts, is a novel approach used in this model. It is probably the most suitable approach for a simulation model tackling the effects of increased temperature on the population dynamics of aphids because, it allows the model to be predictive rather than retrospective, as when field counts are used. Sampling randomly from distributions fitted to actual aphid immigration data mimics the actual suction trap counts, leading to a more realistic simulation of aphid immigration.

The splitting and ranking of temperatures into regimes is also a novel method for simulating climate change in a population dynamics model. It is probably more accurate than using temperature data obtained from a global circulation model, since

the data is specific to a small area, and all the temperatures simulated are within current experience.

The use of a simulation model could be criticised because the complexity of the model makes it difficult to interpret its predictions. However, I feel that the use of a simulation modelling approach, rather than a more analytical approach, was justified by the nature of the problem being addressed. To investigate the effects of climate change on aphids and coccinellids, we must understand how temperature affects the biology of the two species. Since the interactions between temperature and the various components of aphid and coccinellid biology are complex and subtle, this is most easily done through the use of a multi-parameter, mechanistic simulation model. Indeed the majority of models describing aphid and coccinellid biology use a simulation approach (Barlow and Dixon, 1980; Frazer and Gilbert, 1976; Gilbert and Hughes, 1971; Gutierrez *et al.*, 1984; Mack and Smilowitz, 1982). The use of a simulation model has highlighted some subtle effects of temperature on aphids and coccinellids, such as the effect of increased temperature within a regime on the maximum coccinellid numbers, and the fact that the moderate regime is most suitable for aphids. These interactions would probably not have been discovered if an analytical approach had been used.

The approach taken in constructing this model, SACSIM, is similar to that of Barlow and Dixon (1980), Frazer and Gilbert (1976) and Mack and Smilowitz (1982), but here, the components of aphid and coccinellid biology were treated as non-linear functions of temperature, rather than the strictly linear measures implied by the use of physiological time such as hour-degrees or day-degrees.

Throughout its production, the model has been regarded not as a means to an end, but more as a tool to enhance the understanding of the complex relationships between temperature and the biology of the two species modelled. By contrast the simple Bombosch model (Chambers, 1988) does not allow for the effect of temperature on either aphids or coccinellids. Gilbert and Gutierrez (1973) cautioned against the uncritical use of simulation models: "A simulation has no intrinsic value. It is useful

only when it exposes our ignorance, or answers biological questions." SACSIM fits both of these criteria since it is based on accurate representations of aphid and coccinellid biology, and has highlighted several areas where future research needs to be focused, such as the activity, immigration and handling rates of coccinellids.

6.2 LIMITATIONS OF THE MODEL

Before discussing the predictions of the model, it is necessary to understand its limitations. First of all, the model concentrates on only one aphid species, instead of the three species common to cereal fields, and only one natural enemy. The reasons for this have been given in Chapter 1 of the thesis. However, it is likely that, in the field, *C. septempunctata* would not prey solely on *S. avenae*, and so caution needs to be exercised in examining the predictions of the model.

6.2.1 Limitations due to aphid biology

The limitations due to aphid biology stem from the lack of adequate data regarding the effect of low and high temperatures on the aphids' development and reproductive rates. As mentioned in Chapter 2, extreme high and low temperatures are not often encountered in the model nor in the field, so it is unlikely that there would be any major effect on the predictions of the model. However, the data used to determine the equations for the developmental rates of the aphid nymphs comes from work done on barley (Dean 1974b), rather than winter wheat. However, it is felt that the work of Dean (1974b) was the best data available in the literature, due to the wide range of temperatures used and the frequent monitoring of the aphids. There is very little difference in the development rates of aphids on barley compared to wheat (Lykouressis 1984, Dean 1973), therefore it is unlikely that the use of such data from studies on barley will have a major impact on the model predictions.

The data used for reproduction (Dean 1974b) also came from studies performed on barley since this study again provided the most comprehensive data. Work on winter wheat (Chaudhury *et al.*, 1969; Dean, 1973; Ferreres *et al.*, 1989; Kieckhefer and

Gellner, 1988; Lykouressis, 1984; Southerton and Van Emden, 1982) showed that the variety of wheat can have a large effect on the reproductive rate of the aphids, due to differences in cultivar resistance to aphid feeding. It was felt that the equations used were adequate and as long as the use of studies from barley is recognised, the predictions should provide a reasonable guide to the possible effects of climate change.

Finally, aphid survival rate was considered to be constant, which is unlikely to be the case in the field. It was difficult to incorporate variable survival rates of aphids into the model, since some of the principal factors which may alter survival, such as humidity and rainfall, were not included in the model. Use of a constant survival provided a reasonable measure of aphid mortality for the purpose of predicting the effects of temperature on the population dynamics of aphids.

6.2.2 Limitations due to coccinellid biology

The biology of *C. septempunctata*, although well studied in countries such as Czechoslovakia (Hodek, 1973), has not been studied in detail in Britain. Therefore it is possible that the equations used to describe the biology of *C. septempunctata* may not accurately reflect the biology of coccinellids in the fields at Rothamsted. It is possible that British coccinellids may be adapted to the lower temperatures experienced in Britain, compared to those in Czechoslovakia. For example, the development data (Hodek, 1973) suggested that peak development occurred around 35°C, which may not be the case in Britain. Indeed, observations on the two-spot ladybird, *Adalia bipunctata* (Mills, 1982), suggest that this species reaches its maximum development rate between 20°C and 25°C. However, this species is smaller than *C. septempunctata* and so is likely to be more greatly affected by high temperatures. If *C. septempunctata* did reach its maximum development rate at lower temperatures in Britain, then it is possible that the model predictions would be slightly erroneous, however, as mentioned before, the temperatures simulated in the model do not often reach 30°C, so it is unlikely that this would have a great affect on the model predictions.

The model assumes that female coccinellids reproduce throughout all of their reproductive life. Recent work (Thieme, T. personal communication) has shown that female coccinellids have bouts of reproduction, interspersed by periods where no eggs are laid. This observations means that it is possible that the model overpredicts the numbers of coccinellid eggs laid, although this is taken into account, to some extent, by the assumption that only active females are laying eggs,. Females that are inactive will not lay eggs, leading to a break in reproduction.

Recent work on the searching behaviour of *Adalia bipunctata* (Hemptinne and Dixon, 1994) has shown that male coccinellids do not show a functional response to an increase in aphid abundance, and also that they consume markedly fewer aphids than females. This observation has important consequences for the model, since it assumes that males and females eat equal amounts of aphids. Also, it means that it is now important to distinguish between males and females in experiments on handling and searching rates, as an experiment using females would lead to a higher prediction for coccinellid searching rate than one performed on males. However, since most of the data from previous studies used here to derive the equations of the model included observations on both male and female beetles (approximately in a 1:1 ratio) any differences in searching rate between males and females would be averaged out, and therefore the model predictions should not be affected.

As mentioned in Chapter 3, the equations describing handling rate and activity were based on sparse data, and several assumptions were made in determining these equations. It is possible, therefore, that the equations may not be a true reflection of the behaviour of *C. septempunctata* in the field situation. However, since there is no other data to contradict these equations, they will have to be assumed to be adequate at present.

As with aphids, the model assumes that the survival rate of the coccinellids is constant, so the same problems apply.

The model assumes that the maximum possible daily consumption of aphids is the

same for all instars, since there was no evidence to the contrary. However, it is possible that this assumption may lead to over-consumption by young larvae, and under-consumption by older larvae, which are more voracious (McLean, 1980). However, this is unlikely to be a major problem, since in the model coccinellids rarely attain the maximum consumption level allowed. This is largely due to the constraints invariably imposed on prey searching and handling rates in the coccinellid sub-model, by a limited availability of prey (number of aphids) and/or less than optimum temperature for coccinellid activity.

Finally, the observation that larvae of coccinellids can be cannibalistic (Banks, 1956; Hagen, 1962; Hodek, 1973) was not included within the model since there were no data on the relative frequency with which coccinellid larvae encounter and eat other coccinellid larvae in the field. It was felt that cannibalism was unlikely to have a major effect on the numbers of coccinellids in the field situation, since cannibalism usually occurs only when aphids are extremely scarce.

6.2.3 Other limitations

The distributions used to describe aphid and coccinellid immigration also impose limitations on the output of the model. The distributions are specific to Rothamsted, and therefore the model predictions cannot be extrapolated to other areas of the country, although it would be reasonably easy to formulate distributions for other areas of the country from the suction trap counts for those areas.

The coccinellid immigration distributions may not be representative of coccinellid immigration in the field since they are derived from just two years' sticky trap data, and more data is required to produce accurate distribution, especially since it is likely that coccinellid immigration is highly variable from year to year. However, the distribution used mimicked the sticky trap observations reasonably well, and so are at least representative of the observed data currently available.

6.3 MODEL PREDICTIONS

The model predicts that as the average yearly temperature increases, aphid outbreaks are less likely, and control of aphids by coccinellids is more likely. This prediction appears to contradict the observations that several aphid outbreaks occurred during unusually hot years in the 1970s (Carter, 1994; Carter *et al.*, 1980). However, on closer inspection of these observations, it can be seen that during the 1970s the aphid outbreaks are spread through the range of temperature regimes simulated by the model. Also, some outbreaks were actually outbreaks of *Metopolophium dirhodum* as opposed to *S. avenae*.

What these observations did not show was the population dynamics of *C. septempunctata* during those years, which would perhaps be more revealing, especially since the model predicts that the relationship between aphid and coccinellid immigration, in other words, the synchronisation between the two populations, is important in determining whether *C. septempunctata* can control *S. avenae*. Observations in the field have shown that coccinellids do not always enter the field early in the season, a situation which the model is unable to simulate because it relies on the presence of the first wave of coccinellid immigration to determine the numbers for the second wave. Therefore, it is possible that, in future, outbreaks may occur just as often as they do at present if coccinellids do not enter the cereal fields early in the growing season.

If the model predictions are correct, then it is possible that changes in the practice of prophylactic spraying may occur. Oakley and Walters (1994) suggested that although prophylactic spraying leads to a great crop yield, it is not cost-effective in years when aphids do not overwinter in the cereal fields. It is possible that aphid outbreaks may only occur if aphids are able to overwinter in cereal fields, but unfortunately the model does not include any overwintering of aphids. However, the presence of aphids in the field early in the season, would be more likely to attract coccinellids into the field then, a situation which is simulated by the model.

6.4 FUTURE WORK

There are many possible avenues of further research indicated by this work. The most urgent would be a validation of the model or its components. Validation of the model itself would require data covering several sites near Rothamsted over several years, which is perhaps an unrealistic aim in the current research climate. However, validation of the individual equations used in the model should be possible using a series of laboratory and field experiments, although care must be taken in extrapolating laboratory results to the field situation. The laboratory experiments would need to be performed over a range of temperatures from 0°C to 50°C, in order to investigate the effects of temperature on each of the components of aphid and coccinellid biology.

A second avenue is improvement of the model. This could be attempted in several ways. Firstly experiments on British coccinellids could be performed to determine whether the equations used in the model from Czechoslovakian data (Hodek, 1973) are appropriate. Also, the other two species of cereal aphid, *Metopolophium dirhodum* and *Rhopalosiphum padi*, could be included in the model. This would require much work to determine the effects of temperature on the biology of these two species, as only a few studies have been performed on these species (Cannon, 1984; Dean, 1973, 1974a; Dixon and Glen, 1971; Elliott and Kieckhefer, 1989; Kuroli, 1984; Simon *et al.*, 1991; Vereijken, 1979). The inclusion of sub-models describing the biology of these two species would also require alteration of the coccinellid sub-model to account for the preference of *C. septempunctata* for each of the three species, and the relative abundance of each species. However, overall this would allow the model to give more accurate predictions of the possibility of aphid outbreaks, since it would allow for an outbreak by any of the three cereal aphid species.

In the same vein, it would be useful to incorporate the effects of other natural enemies into the model, especially since *C. septempunctata* is only one of a whole complex of natural enemies of aphids that occur in a cereal field, as mentioned in Chapter 1. The

inclusion of other natural enemy species could prove difficult due to the scarcity of data relating to the predation or parasitization of aphids. However, it should prove reasonably easy to include the syrphid, *Episyrphus balteatus* (Deg.), for which sufficient studies have been performed (Ankersmit *et al.*, 1986; Geusen-Pfister, 1987; Honek and Koucourek, 1988; Ito and Iwao, 1977; Medvey, 1987).

As mentioned earlier in the discussion, data on the movement of *C. septempunctata* into cereal fields were scarce, and further research could be undertaken to investigate the mechanisms and factors involved in determining how early coccinellids immigrate into cereal fields. This would enable more accurate immigration distributions to be included in the model, leading to more accurate predictions.

The model could also benefit from research on the overwintering of aphids and coccinellids. It has been suggested (Parry *et al.*, 1989; Porter *et al.*, 1991) that mild winters may allow more aphids to overwinter, leading to an increased likelihood of an outbreak. However, this would depend on how natural enemies responded to aphids being present in the field earlier in the season, relating back to the research into coccinellid movement suggested earlier. This area of research may prove to be more fruitful, especially since the model predictions suggest that synchronisation between *C. septempunctata* and *S. avenae* is important in determining whether or not control occurs. The inclusion of overwintering in the model would allow the model to be incorporated into current work on forecasting the spread and incidence of barley yellow dwarf virus (Harrington *et al.*, 1994).

Finally, the effects of pesticide spraying could be included in the model. This could follow the method of Zhou and Carter (1989), which used a simulation model to predict when spraying would be most effective for *Metopolophium dirhodum*. Alternatively the model could be used as part of a decision system following Waller (1994), to provide information on when pesticide should be applied to fields.

6.5 OVERALL SUMMARY

The aim of this project was to produce a model that enabled qualitative estimates to be made of the effect of predicted increases in temperature on the outcome of the interaction between *S. avenae* and *C. septempunctata*. This aim has been achieved, the model produced being based on an accurate representation of aphid and coccinellid biology, using equations derived from published data. The predictions obtained from the model give reasonable forecasts of the aphid and coccinellid population dynamics in the field within known ranges. The model has integrated current knowledge on *S. avenae* and *C. septempunctata*, as well as highlighting several areas where knowledge or understanding needs to be enhanced.

The model provides a firm grounding on which to base future studies, to examine the effect of increasing global temperatures on the interaction between pests and natural enemies in economically important crops.

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Appendix LISTING OF THE MODEL FOR THE MODERATE REGIME

Brief details about the model

Programming language

The model, SACSIM, is written in Fortran and runs on a VAX/VMS system. Fortran was used as the programming language for two main reasons. Firstly, the model, SAM7, upon which SACSIM is based was written in Fortran 77, and it would have been a laborious task to rewrite the model in another language. Also Fortran 77 on a VAX/VMS system can be easily linked to the NAG mathematical library which provides many routines for the generation of random numbers. Since SACSIM requires several random numbers, the use of the NAG libraries saved time in the construction of the program.

Model structure

The model structure is very similar to that of SAM7 and consists of a main block of code which has several parts, each of which describes an area of aphid and coccinellid biology, and six subroutines, which are used to perform array updates and repeated calculations. A brief description of the main parts of the code and the subroutines is given below.

Main code

- | | |
|---------------------|--|
| Initialisation | - The arrays and variables to be used in the model are declared and zeroed |
| Data input | - Data required by the model to run is read from file. The immigration arrays for the coccinellids and aphids are calculated. The daily temperatures and the time of sunrise are calculated. Overwintered aphids are sorted into instars and assigned ages |
| Hourly temperatures | - The hourly temperatures for each day are calculated, along with the hour degrees for development, reproduction and predation. Hourly development rates are also calculated |
| Immigration | - The number of immigrant coccinellids and aphids arriving on the simulated day are assigned to the appropriate array |

Development and survival	- The percentage survival of each coccinellid and aphid instar is calculated. Development for the hour is then accumulated. Parasitism of the aphids and coccinellids is also simulated.
Reproduction	- The number of aphid nymphs and coccinellid eggs produced are calculated.
Predation	- The aphid numbers/tiller are converted to mg/m ² , ratios of instars and morphs are also calculated, before the biomass of aphids eaten is calculated. The aphid arrays are then updated accordingly
Output	- The main output variables are written to file
Crop development model	- The number of day-degrees above 6°C are calculated, and the crop growth stage updated.
Input variables printed	- The input variables read in at the beginning of the model are printed and the model then ends
Subroutines	
PARDIS	- Calculates the number of aphids killed by parasitism per hour
DEVSUR	- Updates the arrays containing the number and age of the aphids according to accumulated development and percentage survival.
PREDTR	- Calculates the biomass per m ² of aphids eaten by the coccinellids
CIMDVSR	- Updates the arrays containing the age and number of immigrant coccinellids
COCDVSR	- Updates the arrays containing the age and number of coccinellid instars that develop within the simulated field
NB	- Generates a random number sampled from a negative binomial distribution.

System requirements of model

The model is 1628 lines long, and takes six hours of cpu time to complete 100 runs on a

VAX/VMS system. The model is run using a small command file which contains the input data required by the model, although these inputs can be entered interactively, or read directly from an input file.

The model is the property of the Ministry of Agriculture, Fisheries and Food. The model is currently stored on a tape archive at IACR-Rothamsted, and also on a DAT-tape help by the author, and a copy of the model can be obtained by contacting the author.

Differences between the models for the Hot, Moderate and Cold regimes

The main differences between the regimes have been documented in the thesis, but below is a summary of the changes to variables that are required to convert the listing of the model for the moderate regime given, to a model for the cold or hot regimes.

Changes required to use the model for the cold regime

For the equations determining the daily temperature:

$$\begin{aligned}
 A1 &= -1.639 \sin((2 \cdot \pi \cdot KT)/365) \\
 B1 &= -9.83 \cos((2 \cdot \pi \cdot KT)/365) \\
 A2 &= 1.202 \sin((4 \cdot \pi \cdot KT)/365) \\
 B2 &= -1.173 \cos((4 \cdot \pi \cdot KT)/365) \\
 YT &= 5.709 + A1 + B1 + A2 + B2 \\
 E &= G05DDF(0.0, 2.19) \\
 Z &= G05DEF(1.90, 0.557)
 \end{aligned}$$

For the equations describing aphid immigration:

$$\begin{aligned}
 IMSTAR &= NINT(G05DDF(142.13, 12.66)) \\
 IMFINI &= NINT(52.0 + (0.840 \cdot IMSTAR)) \\
 ERR &= NINT(G05DDF(0.0, 11.42))
 \end{aligned}$$

For the equations describing coccinellid immigration:

$$\begin{aligned}
 INITMN &= NINT(G05DDF(147.0, 5.0)) \\
 MAINMN &= NINT(G05DDF(194.0, 5.0))
 \end{aligned}$$

For the subroutine NB

$$K = 0.243$$

$$MU = 0.583$$

Changes required to use the model for the hot regime

For the equations determining the daily temperature:

$$A1 = -1.98 \sin((2 \cdot \pi \cdot KT)/365)$$

$$B1 = -13.14 \cos((2 \cdot \pi \cdot KT)/365)$$

$$A2 = 1.195 \sin((4 \cdot \pi \cdot KT)/365)$$

$$B2 = -2.371 \cos((4 \cdot \pi \cdot KT)/365)$$

$$YT = 5.709 + A1 + B1 + A2 + B2$$

$$E = G05DDF(0.0, 2.63)$$

$$Z = G05DEF(1.94, 0.701)$$

For the equations describing aphid immigration:

$$IMSTAR = NINT(G05DDF(135.44, 10.53))$$

$$IMFINI = NINT(10.8 + (1.084 \cdot IMSTAR))$$

$$ERR = NINT(G05DDF(0.0, 11.90))$$

For the equations describing coccinellid immigration:

$$INITMN = NINT(G05DDF(133.0, 5.0))$$

$$MAINMN = NINT(G05DDF(180.0, 5.0))$$

For the subroutine NB

$$K = 0.487$$

$$MU = 1.22$$

List of variables and arrays used in the model

A1	=	Constant used in the double-Fourier curve describing mean temperature
A2	=	Constant used in the double-Fourier curve describing mean temperature
ACTIV	=	The proportion of coccinellids that are actively searching for food
ADULTS	=	Number of adult aphids (apterae) per tiller
ALATAD	=	Number of adult aphids (alatae) per tiller
ALATE	=	Proportion of new nymphs that are alate
ALATED	=	Number of alate aphids per tiller emigrating during time step
ALATIM	=	Number of alate immigrants per million tillers
ALFEC	=	Number of nymphs produced per female aphid per hour degree for alatae
ALFN	=	Number of fourth instar aphids (alatae) per tiller
ALLOW	=	Highest number of aphids per tiller reached after each time step
ALLOWAF	=	Threshold for low aphid densities
ALPN	=	Number of first instar aphids (alatae) per tiller
ALSN	=	Number of second instar aphids (alatae) per tiller
ALTIM	=	Number of alate immigrants per tiller
ALTN	=	Number of third instar aphids (alatae) per tiller
AMTEMP	=	Average temperature for each time step
APTTL	=	Total number of aphids per tiller
AS	=	Constant used in the calculation of the time of sunrise
AVHDRP	=	Number of hour-degrees for reproduction in the time step
AVHPRD	=	Number of hour-degrees for predation in the time step
AVHRDG	=	Number of hour-degrees in the time step
AVTEMP	=	Number of hour-degrees for development in the time step
B	=	Variable used in regression describing number of day-degrees above 6°C
B1	=	Constant used in the double_Fourier curve describing mean temperature

B2	=	Constant used in the double_Fourier curve describing mean temperature
CCOS	=	Constant used in the calculation of the time of sunrise
CCTTL	=	Total number of coccinellids per m ²
CEGLONG	=	Longevity of coccinellid eggs
CIIKILL	=	Milligrams of aphids eaten by third instar coccinellid larvae
CIIILONG	=	Longevity of third instar coccinellid larvae
CIKILL	=	Milligrams of aphids eaten by second instar coccinellid larvae
CIILONG	=	Longevity of second instar coccinellid larvae
CIKILL	=	Milligrams of aphids eaten by first instar coccinellid larvae
CILONG	=	Longevity of first instar coccinellid larvae
CIMLON	=	Longevity of immigrated coccinellid adults
CIVKILL	=	Milligrams of aphids eaten by fourth instar coccinellid larvae
CIVLONG	=	Longevity of fourth instar coccinellid larvae
CLONAD	=	Longevity of coccinellid adults after emerging from pupae in the field
CLOW	=	Highest number of coccinellids per m ² reached during all time steps
CNI	=	Number of first instar aphids killed by the coccinellids (/m ² or /tiller)
CNII	=	Number of second instar aphids killed by the coccinellids (/m ² or /tiller)
CNIII	=	Number of third instar aphids killed by the coccinellids (/m ² or /tiller)
CNIV	=	Number of fourth instar aphids killed by the coccinellids (/m ² or /tiller)
CNV	=	Number of adult aphids killed by the coccinellids (/m ² or /tiller)
COCCIM	=	Number of coccinellid adults per m ² that have immigrated into the field
COCCIMAGE	=	Age of coccinellid adults that have immigrated into the field
COCEGG	=	Number of eggs laid per female coccinellid per hour-degree
CONSUME	=	Milligrams of aphids consumed by coccinellid adults

CONV	=	Conversion factor for latitude of field site
CPARASURV	=	Proportion of coccinellid adults surviving parasitism
CPLONG	=	Longevity of coccinellid pupae
CSURADS	=	Survival of coccinellid adults that have emerged from pupae in the field
CSUREGS	=	Survival of coccinellid eggs
CSURIM	=	Survival of immigrated adult coccinellids
CSURINS	=	Survival of coccinellid larvae
CSURPUP	=	Survival of coccinellid pupae
CVKILL	=	Milligrams of aphids eaten by coccinellid adults
CVLONG	=	Total longevity of coccinellid larvae
DAYCON	=	Total number of aphids per tiller consumed per day
DAYL	=	Daylength in hours
DD	=	Number of day-degrees above 6°C
DEC	=	Constant used in the calculation of the time of sunrise
DIFF	=	Factor by which the maximum daily number of coccinellids per m ² in the first wave is multiplied by to give the maximum daily number of coccinellids per m ² in the second wave
E	=	Error term (Normal random deviate)
ERR	=	Error term used in determining the end date of aphid immigration
FCNT	=	Number of coccinellids per m ² immigrating on a single day
FEC	=	Number of nymphs produced per female aphid per hour degree by apterous female aphids
FIAL	=	Number of overwintered first instar alates (/tiller)
FIAP	=	Number of overwintered first instar apterae (/tiller)
FILONG	=	Longevity of first instar aphids
FIRAU	=	Number of aphid units made up of first instar aphids
FLLONG	=	Longevity of fourth instar alate aphids
FNYMPH	=	The number of fourth instar apterae per tiller
FORAU	=	Number of aphid units made up of fourth instar aphids
FPLONG	=	Longevity of the fourth instar apterous aphids
GSTAGE	=	Crop growth stage on the decimal scale (Zadoks 1974)

HIGH	=	Maximum daily number of coccinellids per m ² in the first wave
HRATE	=	Coccinellid handling rate (mg of aphids/predator/hour)
HRCEG	=	Development rate for coccinellid eggs
HRCIG	=	Development rate for first instar coccinellids
HRCIIG	=	Development rate for second instar coccinellids
HRCIIIG	=	Development rate for third instar coccinellids
HRCIVG	=	Development rate for fourth instar coccinellids
HRCPG	=	Development rate for coccinellid pupae
HRCVG	=	Average development rate for all coccinellid larvae
HRDDG	=	Hour degrees for development for each hour
HRDEG	=	Hour degrees for each hour
HRDIG	=	Development rate of first instar aphids
HRDIIG	=	Development rate of second instar aphids
HRDIIG	=	Development rate of third instar aphids
HRDIVG	=	Development rate of fourth instar aphids
HRDPG	=	Hour degrees accumulated towards the total for the pre-reproductive delay
HRDVG	=	Average development rate for all aphid nymphal instars
HRREP	=	Hour degrees for reproduction for each hour
HRDPRD	=	Hour degrees for predation for each hour
IMM	=	Total number of immigrant aphids per tiller
IRISE	=	Hour of sunrise
IADSTP	=	Array size for adult apterous aphids
IALSTP	=	Array size for adult alate aphids
ICOCSTP	=	Array size for all coccinellid instars
IDAYY	=	Day number
IFINIS	=	End day of the simulation
IFOSTP	=	Array size for fourth instar aphids
II	=	Number of time step completed by the model
IIJ	=	Length of time step
IJ	=	Hour number
IMSTAR	=	Start date of aphid immigration

IMFINI	=	End date of aphid immigration
IMMLEN	=	Length of aphid immigration (days)
INCONF	=	Concentration factor for aphid immigration
INIFIN	=	End date of the first wave of coccinellid immigration
INISTAR	=	Start date of the first wave of coccinellid immigration
INITMN	=	Median day of the first wave of coccinellid immigration
INYSTP	=	Array size for first, second and third aphid instars
IPAFIN	=	End date of aphid parasitism
IPARA	=	Start date of parasitism
ISTART	=	Day on which simulation begins
KT	=	Day count variable used in the simulation of daily temperatures
LAT	=	Latitude of simulated field
M	=	Day number for totalling of aphids
MAINFIN	=	End date of the second wave of coccinellid immigration
MAINMN	=	Median day of the second wave of coccinellid immigration
MAINSTAR	=	Start date of the second wave of coccinellid immigration
MNTT	=	Minimum daily temperature (°C)
MXTT	=	Maximum daily temperature (°C)
N	=	Day number for totalling of coccinellids
NEWNY	=	Number of first instar apterous nymphs produced by aphid reproduction
NWNY	=	Number of first instar alate nymphs produced by aphid reproduction
OALNY	=	Number of overwintered fourth instar alate aphids (/tiller)
ONYMPH	=	Number of overwintered fourth instar apterous aphids (/tiller)
PADAY	=	Day of maximum aphid numbers
PARA	=	Hourly parasitism of aphids
PARNO	=	Skip value
PCDAY	=	Day of maximum coccinellids
PEAKAPH	=	Maximum daily number of aphids (/tiller)
PEAKCOC	=	Maximum daily number of coccinellids (/m ²)
PI	=	Pi
PKA	=	Number of aphid peaks

PKC	=	Number of coccinellid peaks
PNYMPH	=	Number of first instar apterous aphids per tiller
PRD	=	Pre-reproductive delay (H°)
PRED	=	Number of each coccinellid instar per m^2
PREDAGE	=	Age of coccinellid instars (H° for adults)
PREDNO	=	Skip value
PRIIL	=	Proportion of third instar alatae killed by coccinellids
PRIIP	=	Proportion of third instar apterae killed by coccinellids
PRIL	=	Proportion of second instar alatae killed by coccinellids
PRIIP	=	Proportion of second instar apterae killed by coccinellids
PRIL	=	Proportion of first instar alatae killed by coccinellids
PRIP	=	Proportion of first instar apterae killed by coccinellids
PRIVL	=	Proportion of fourth instar alatae killed by coccinellids
PRIVP	=	Proportion of fourth instar apterae killed by coccinellids
PROP	=	Area under a normal curve
PRVL	=	Proportion of adult alatae killed by coccinellids
PRVP	=	Proportion of adult apterae killed by coccinellids
RAD	=	Conversion value from degrees to radians
RALTI	=	Proportion of first instar aphids that are alate
RALTII	=	Proportion of second instar aphids that are alate
RALTIII	=	Proportion of third instar aphids that are alate
RALTIV	=	Proportion of fourth instar aphids that are alate
RALTV	=	Proportion of adult aphids that are alate
RAPTI	=	Proportion of first instar aphids that are apterous
RAPTII	=	Proportion of second instar aphids that are apterous
RAPTIII	=	Proportion of third instar aphids that are apterous
RAPTIV	=	Proportion of fourth instar aphids that are apterous
RAPTV	=	Proportion of adult aphids that are apterous
RAT1	=	Ratio of the number of apterae in the fourth instar to the total number of apterous nymphs
RAT2	=	Ratio of the number of alatae in the fourth instar to the total number of alate nymphs

RATIO	=	Proportion of fourth instar apterous aphids to the total number of nymphs
RHGR	=	Relative hunger of the coccinellid adults
RICII	=	Ratio of the biomass of first instar aphids to the biomass of first and second instar aphids
RICIII	=	Ratio of the biomass of first instar aphids to the biomass of first, second and third instar aphids
RICV	=	Ratio of the biomass of first instar aphids to the total biomass of aphids
RIICII	=	Ratio of the biomass of second instar aphids to the biomass of first and second instar aphids
RIICIII	=	Ratio of the biomass of second instar aphids to the biomass of first, second and third instar aphids
RIICV	=	Ratio of the biomass of second instar aphids to the total biomass of aphids
RIIICIII	=	Ratio of the biomass of third instar aphids to the biomass of first second and third instar aphids
RIICV	=	Ratio of the biomass of third instar aphids to the total biomass of aphids
RISE	=	Hour of sunrise
RIVCV	=	Ratio of the biomass of fourth instar aphids to the total biomass of aphids
RNIMM	=	Threshold aphid density for coccinellid immigration (/tiller)
RVCV	=	Ratio of the biomass of adult aphids to the total biomass of aphids
SARTA	=	Survival of adult alatae
SEAL	=	Number of overwintered second instar alatae (/tiller)
SEAP	=	Number of overwintered second instar apterae (/tiller)
SEN1-SEN9	=	Sensitivity analysis parameters
SLONG	=	Longevity of second instar aphids
SNYMPH	=	Number of second instar apterae per tiller
SRATE	=	Searching rate of coccinellids (m ² /predator/hour)
SSIN	=	Constant used in calculating the time of sunrise

SURALIV	=	Survival of alate nymphs
SURNIV	=	Survival of apterous nymphs
SURT	=	Longevity of adult apterous aphids (H°)
SURTA	=	Survival of adult apterae
SURTAL	=	Longevity of alate adult aphids (H°)
SV	=	Coccinellid survival
T	=	Variable used in the regression describing the number of day-degrees above 6°C
TAYPAL	=	Conversion factor for converting the number of alates in the suction trap to the number landing per tiller
TEMP	=	Temperature for each hour calculated from fitted sine curve
TH1, TH2	=	Aphid density threshold (number/tiller)
THAL	=	Number of overwintered third instar alatae (/tiller)
THAP	=	Number of overwintered third instar apterae (/tiller)
THLONG	=	Longevity of third instar aphids
THRESH	=	Threshold for crop growth ($^{\circ}\text{C}$)
TILERS	=	Number of tillers per m^2
TOT	=	Accumulated day-degrees above 6°C
TOTAD	=	Total number of apterous adult aphids (/tiller)
TOTADR	=	Total of reproductive aphids (/tiller)
TOTALA	=	Total number of alate adult aphids (/tiller)
TOTALE	=	Total number of alate emigrants (/tiller)
TOTALF	=	Total number of alate fourth instar aphids (/tiller)
TOTALP	=	Total number of alate first instar aphids (/tiller)
TOTALS	=	Total number of alate second instar aphids (/tiller)
TOTALT	=	Total number of third instar alate aphids (/tiller)
TOTCIM	=	Total number of immigrant coccinellids per m^2
TOTCOC	=	Total number of coccinellids per m^2
TOTCON	=	Total number of aphids per tiller consumed per hour
TOTDEN	=	Total density of aphids (/tiller)
TOTFIR	=	Total number of first instar apterae (/tiller)
TOTFOR	=	Total number of fourth instar apterae (/tiller)

TOTPAR	=	Total number of aphids per tiller parasitised
TOTPNY	=	Total longevity of all apterous aphid nymphal instars
TOTLNY	=	Total longevity of all alate aphid nymphal instars
TOTSEC	=	Total number of apterous second instar aphids (/tiller)
TOTTHI	=	Total number of third instar apterae (/tiller)
TOTYAL	=	Total number of alatae per tiller in the first, second and third instars
TOTYNY	=	Total number of apterae per tiller in the first, second and third instars
TT	=	Constant used in the calculation of the time of sunrise
XMAX	=	Maximum daily temperature (°C)
XMIN	=	Minimum daily temperature (°C)
Y	=	Variable used in the regression describing the number of day-degrees above 6°C
YALNY	=	Number of overwintered alate first, second and third instar aphids
YAPNY	=	Number of overwintered apterous first, second and third instar aphids
YNYMPH	=	Number of overwintered first, second and third instar aphids
YT	=	Simulated daily mean temperature (°C)
YT1	=	Simulated daily maximum temperature (°C)
YT2	=	Simulated daily minimum temperature (°C)
Z	=	Difference between daily maximum and minimum temperature (°C)
ZMGCON	=	Weights of aphid instars (mg)
ZMGDII	=	Biomass of first and second instar aphids (mg/m ²)
ZMGDIII	=	Biomass of first, second and thirds instar aphids (mg/m ²)
ZMGI	=	Biomass of first instar aphids (mg/m ²)
ZMGII	=	Biomass of second instar aphids (mg/m ²)
ZMGIII	=	Biomass of third instar aphids (mg/m ²)
ZMGIV	=	Biomass of fourth instar aphids (mg/m ²)
ZMGTOT	=	Total biomass of all aphids (mg/m ²)
ZMGV	=	Biomass of adult aphids (mg/m ²)

Listing of the model for the moderate regime

```
      PROGRAM THEBIZ
C
C A POPULATION MODEL FOR THE SIMULATION OF SITOBION AVENAE
C POPULATIONS
C TAKING INTO ACCOUNT THE EFFECT OF PREDATORS, PARASITES AND THE HOST
C
C
C*****1.....INITIALISATION.....*****
C
C
      REAL NEWNY,NWNY,LAT,MXTT,MNTT,COCEGG,RNIMM
      REAL G05DEF
      REAL G05DDF
      REAL G05CAF
      EXTERNAL G05CAF
      EXTERNAL G05DDF
      EXTERNAL G05DEF
      EXTERNAL G05CCF
      DIMENSION PRED(7,2000),PARA(250),ALATAD(2,400),ADULTS(2,750),
      *FNYMPH(2,300),ALFN(2,300),TNYMPH(2,250),ALTN(2,250),SNYMPH(2,250),
      *ALSN(2,250),PNYMPH(2,250),ALPN(2,250),IMM(365),MNTT(250),MXTT(250)
      *,DAYL(250),IRISE(250),RISE(250),TEMP(24),AMTEMP(24),HRDEG(24),
      *AVTEMP(24),HRDDG(24),AVHRDG(24),HRREP(24),AVHDRP(24),HRDPRD(24),
      *AVHPRD(24),HRDIG(24),HRDIIG(24),HRDIIG(24),HRDIVG(24),HRDPG(24),
      *HRDVG(24),HRCEG(24),HRCIG(24),HRCIIG(24),HRCIIG(24),HRCIVG(24),
      *HRCPG(24),HRCVG(24),COCCIM(2,2000),PREDAGE(7,2000),COCCIMAG(2,2000
      *),TOTCOC(7),TOTCIM(2),CIMLON(2),CSURIM(2),FCNT(400),ZMGCON(5),SR
      *ATE(5),HRATE(5),SV(4),PROP(29),PEAKAPH(200),PADAY(200),
      *PEAKCOC(200),PCDAY(200)

C
C INPUT ARRAY SIZES
      DATA IADSTP,IALSTP,IFOSTP,INYSTP/750,400,300,250/
      DATA ICOCSTP/2000/
C ZERO ARRAYS AND VARIABLES
C
309  TOTADR=0.0
      TOTAD=0.0
      TOTALA=0.0
      TOTFOR=0.0
      TOTALF=0.0
      TOTTHI=0.0
      TOTALT=0.0
      TOTSEC=0.0
      TOTALS=0.0
      TOTFIR=0.0
```



```

TOTALP=0.0
TOTALE=0.0
ALATED=0.0
TOTDEN=0.0
CNI=0.0
CNII=0.0
CNIII=0.0
CNIV=0.0
CNV=0.0
PI=3.1415927
YT=0.0
Y1T=0.0
Y2T=0.0
A1=0.0
A2=0.0
B1=0.0
B2=0.0
Z=0
E=0
PKA=1
PKC=1
DO 400 I=1,250
DO 401 J=1,2
ALTN(J,I)=0.0
TNYMPH(J,I)=0.0
ALSN(J,I)=0.0
SNYMPH(J,I)=0.0
ALPN(J,I)=0.0
PNYMPH(J,I)=0.0
401 CONTINUE
400 CONTINUE
DO 402 I=1,300
DO 403 J=1,2
ALATAD(J,I)=0.0
403 CONTINUE
402 CONTINUE
DO 404 I=750
DO 405 J=1,2
ADULTS(J,I)=0.0
405 CONTINUE
404 CONTINUE
DO 406 I=1,300
DO 407 J=1,2
ALFN(J,I)=0.0
FNYMPH(J,I)=0.0
407 CONTINUE
406 CONTINUE
DO 408 I=1,2000

```

```

      DO 409 J=1,7
      PRED(J,I)=0.0
      PREDAGE(J,I)=0.0
409  CONTINUE
      DO 444 J=1,2
      COCCIM(J,I)=0.0
      COCCIMAG(J,I)=0.0
444  CONTINUE
408  CONTINUE
      DO 445 I=1,4
      SV(I)=0.0
445  CONTINUE
      DO 410 I=1,250
      PARA(I)=0.0
      MNTT(I)=0.0
      MXTT(I)=0.0
      IRISE(I)=0.0
      RISE(I)=0.0
410  CONTINUE
      DO 411 I=1,24
      AVTEMP(I)=0.0
      AVHRDG(I)=0.0
      AVHPRD(I)=0.0
      AVHDRP(I)=0.0
      HRDDG(I)=0.0
      HRREP(I)=0.0
      TEMP(I)=0.0
      AMTEMP(I)=0.0
      HRDEG(I)=0.0
      HRDIG(I)=0.0
      HRDIIG(I)=0.0
      HRDIIIG(I)=0.0
      HRDIVG(I)=0.0
      HRDPG(I)=0.0
      HRDVG(I)=0.0
      HRCEG(I)=0.0
      HRCIG(I)=0.0
      HRCIIG(I)=0.0
      HRCIIIG(I)=0.0
      HRCIVG(I)=0.0
      HRCVG(I)=0.0
      HRCPG(I)=0.0
411  CONTINUE
      DO 412 I=1,2
      TOTCIM(I)=0.0
      CIMLON(I)=0.0
      CSURIM(I)=0.0
412  CONTINUE

```



```

      DO 413 I=1,7
      TOTCOC(I)=0.0
413  CONTINUE
      DO 414 I=1,400
      FCNT(I)=0.0
415  CONTINUE
414  CONTINUE
      DO 416 I=1,200
      EFF(I)=0.0
      PEAKAPH(I)=0.0
      PEAKCOC(I)=0.0
      PADAY(I)=0.0
      PCDAY(I)=0.0
416  CONTINUE
      DO 418 I=1,300
      IMM(I)=0.0
418  CONTINUE
C
C
C*****2.....DATA INPUT.....*****
C
C
C THE FIRST TWO NUMBERS ARE THE START AND FINISH DAYS (JAN 1ST=1),NEXT
C SKIP VALUE FOR APHID INSTAR INPUT, THEN STEP LENGTH IN HOURS
C
      READ*,ISKIP,IJJ
      IF (ISKIP.EQ.100) GOTO 310
      IFINIS=243
C
C
C NOW TO INPUT APHID NUMBERS, IF ISKIP EQUALS 1.0 THEN THIS SECTION IS
C MISSED
      IF(ISKIP.NE.1)THEN
      READ*,YNYMPH,ONYMPH,OALNY,TOTAD,TOTALA
C NOS OF 1-3,4AP,4AL,5AP AND 5AL/TILLER
      END IF
C
C
      READ*,SEN1,SEN2,SEN3,SEN4,SEN5,SEN6,SEN7,SEN8,SEN9
C
C INSTAR LENGTHS
      PRD=411.06
      FPLONG=1.0
      FLLONG=1.5
      THLONG=1.0
      SLONG=1.0
      FILONG=1.0
      TOTPNY=FILONG+SLONG+THLONG+FPLONG

```

```

      TOTLNY=FI LONG+SLONG+THLONG+FL LONG
C
C -----
C
C COCCINELLID INSTAR LENGTHS
C
      CEGLONG=1.0*SEN7
      CILONG=1.0*SEN7
      CIILONG=1.0*SEN7
      CIIILONG=1.0*SEN7
      CIVLONG=1.0*SEN7
      CPLONG=1.0*SEN7
      CVLONG=CILONG+CIILONG+CIIILONG+CIVLONG
C
C -----
C
C NOW THREE VARIABLES, LATITUDE OF SITE, INITIAL CROP DEVELOPMENT
C STAGE
C AND NUMBER OF TILLERS/SQ M.
C
      READ*,LAT,TILERS
C
C NOW TO CALCULATE THE NUMBER OF ALATES LANDING PER TILLER FOR EACH
C ALATE CAUGHT IN THE SUCTION TRAP, ASSUMING RANDOM DEPOSITION
C
      TAYPAL=(9600/(0.4047*TILERS))
C
C NOW THE IMMIGRATION DATA - DAILY SUCTION TRAP CATCHES, FIRST THE
C START
C AND FINISH DAYS OF MIGRATION AND THE CONCENTRATION FACTOR,
C NORMALLY 40
C
      CALL G05CCF
      IMSTAR=NINT(G05DDF(142.13,12.66))
      IMFINI=NINT(52.0+(0.84*IMSTAR))
      ERR=NINT(G05DDF(0,11.42))
      IMFINI=IMFINI+ERR
      IF(IMFINI.LE.IMSTAR)IMFINI=IMSTAR+7
      IMMLN=((IMFINI-IMSTAR)+1)
      CALL NB(IMM,IMMLN,IMSTAR,IMFINI)
C
C
      ISTART=IMSTAR
C
C CALCULATE GROWTH STAGE BASED ON IMSTAR
C
      GSTAGE=26.71+54.79/(1+EXP(-0.0921*(IMSTAR-152.86)))

```


TOT=(((-0.173224+(SQRT((0.173224*0.173224)-(4*(-0.000125)*(26.338-G
*STAGE)))))/(-0.00025))

C

C NOW THE NATURAL ENEMIES

C THE FIRST TWO NUMBERS IF EQUAL TO ONE WILL SKIP ROUND THE PREDATOR
AND

C PARASITE SUBROUTINES RESPECTIVELY, WHILE IF THE THIRD NUMBER IS
EQUAL

C TO ONE WILL REDUCE PREDATION AT LOW APHID DENSITIES

C

READ*,PREDNO,PARNO,ALLOWAF

IF(PREDNO.NE.1.0)THEN

C

CALL G05CCF

INITMN=NINT(G05DDF(140.0,5.0))

INISTAR=INITMN-14

INIFIN=INITMN+14

MAINMN=NINT(G05DDF(187.0,5.0))

MAINSTAR=MAINMN-14

MAINFIN=MAINMN+14

C

C

PROP(1)=0.01

PROP(2)=0.02

PROP(3)=0.03

PROP(4)=0.04

PROP(5)=0.07

PROP(6)=0.1

PROP(7)=0.14

PROP(8)=0.2

PROP(9)=0.27

PROP(10)=0.36

PROP(11)=0.45

PROP(12)=0.59

PROP(13)=0.71

PROP(14)=0.85

PROP(15)=1.0

PROP(16)=PROP(14)

PROP(17)=PROP(13)

PROP(18)=PROP(12)

PROP(19)=PROP(11)

PROP(20)=PROP(10)

PROP(21)=PROP(9)

PROP(22)=PROP(8)

PROP(23)=PROP(7)

PROP(24)=PROP(6)

PROP(25)=PROP(5)

PROP(26)=PROP(4)

```

      PROP(27)=PROP(3)
      PROP(28)=PROP(2)
      PROP(29)=PROP(1)
C
C
      DO 18 I=INISTAR,INIFIN
      CALL G05CCF
      FCNT(I)=G05CAF(0.0,1.0)
      FCNT(I)=(7.5*FCNT(I))-6.0
      IF (FCNT(I).LT.0.0)FCNT(I)=0.0
      IF (FCNT(I).GT.HIGH)HIGH=FCNT(I)
18 CONTINUE
818 DIFF=G05DDF(5.0,5.0)
      IF (DIFF.LE.0.0) GOTO 818
      MAINPK=DIFF*HIGH
      DO 19 J=MAINSTAR,MAINFIN
      FCNT(J)=PROP((J+1)-MAINSTAR)*MAINPK
19 CONTINUE
      END IF
C NOW FOR THE PARASITES AND DISEASE AGAIN THE SKIP STEP FIRST
C
      IF(PARNO.NE.1.0)THEN
C
C FIRST READ IN START AND FINISH DAYS
      READ*,IPARA,IPAFIN
C
C NOW HOURLY PARASITISM AND DISEASE MORTALITIES, CALCULATED
DIRECTLY
C FROM FIELD MUMMY COUNTS AND DEAD APHIDS MULTIPLIED BY 2.0, DIVIDED
BY
C THE APHID TOTAL (LIVING AND DEAD), THEN DIVIDED BY 7.0 AND 24.0
C
      READ (*,14)(PARA(I),I=IPARA,IPAFIN)
14 FORMAT(5F10.5)
      END IF
C
C Now proportions of savenae in the field
C
C
C THIS FINISHES DATA INPUT
C
C
C -----
C
C NOW SET UP TEMPERATURE ARRAY - SIMULATED FROM DOUBLE FOURRIER
CURVE
C
      CALL G05CCF

```



```

DO 10 KT=91,243
YT=0.0
A1=-3.448*SIN((2*PI*KT)/365)
B1=-2.26*COS((2*PI*KT)/365)
A2=-0.045*SIN((4*PI*KT)/365)
B2=0.973*COS((4*PI*KT)/365)
YT=11.44+A1+B1+A2+B2
E=G05DDF(0.0,2.402)
YT=YT+E
CALL G05CCF
Z=G05DEF(1.8825,0.6471)
Y1T=YT+Z/2
Y2T=YT-Z/2
MXTT(KT)=Y1T
MNTT(KT)=Y2T
Y1T=0.0
Y2T=0.0
YT=0.0
10 CONTINUE
C
C AS THE MODEL IS UPDATED HOURLY TEMPS HAVE TO BE CALCULATED
HOURLY
C BUT FIRST THE TIME OF SUNRISE (IRISE) IS CALCULATED
C
PI=3.1415927
RAD=PI/180.0
CONV=RAD*LAT
C
DO 15 IDAYY=ISTART,IFINIS+1
DEC=-23.4*COS(PI*(IDAYY+10.173)/182.621)
SSIN=SIN(CONV)*SIN(RAD*DEC)
CCOS=COS(CONV)*COS(RAD*DEC)
TT=SSIN/CCOS
AS=ASIN(TT)
DAYL(IDAYY)=12.0*(PI+2.0*AS)/PI
RISE(IDAYY)=12.0-(DAYL(IDAYY)/2.0)+0.5
IRISE(IDAYY)=RISE(IDAYY)
15 CONTINUE
C
C HEADINGS ARE PRINTED
C
WRITE(2,600)
600 FORMAT(1H1,115HIDAYY I-APT II-APT III-APT IV-APT V-AP
*T I-ALT II-ALT III-ALT IV-ALT V-ALT TOTYN//
*)
WRITE(3,601)
601 FORMAT(1H0,111H GSTAGE REP-AD ALTIM TOTALE TOTAL DEN
*SITY TOTPAR DAILY CON PRDFAC PRDADC AFIDUN TOTDDG//)

```

```

C
C SKIP STATEMENT, NOS IN EACH AGE CLASS OF EACH INSTAR ARE CALCULATED
C
  IF(ISKIP.NE.1)THEN
C
C CALCULATION IN FIRST THREE INSTARS
C RATIO OF APTEROUS FOURTHS TO TOTAL
C
  RATIO=(ONYMPH*1.5)/(ONYMPH*1.5+OALNY)
C NOW CALCULATE PROPORTION OF APTEROUS 1-3, THEN ALATIFORM 1-3
  YAPNY=YNYPH*RATIO
  YALNY=YNYPH-YAPNY
C CALCULATION IN INDIVIDUAL INSTARS
  RAT1=(YAPNY+ONYMPH)/YAPNY
  THAP=ONYMPH*RAT1
  SEAP=THAP*RAT1
  FIAP=SEAP*RAT1
  TOTYNY=FIAP+SEAP+THAP
C NOW CHECK TO SEE THAT TOTYNY=YAPNY, AND TO MAKE NECESSARY
ADJUSTMENTS
  TOTTHI=THAP*YAPNY/TOTYNY
  TOTSEC=SEAP*YAPNY/TOTYNY
  TOTFIR=FIAP*YAPNY/TOTYNY
C NOW THE SAME PROCEDURE FOR THE ALATIFORM NYMPHS
  RAT2=(YALNY+OALNY)/YALNY
  THAL=OALNY*RAT2
  SEAL=THAL*RAT2
  FIAL=SEAL*RAT2
  TOTYAL=THAL+SEAL+FIAL
  TOTALT=THAL*YALNY/TOTYAL
  TOTALS=SEAL*YALNY/TOTYAL
  TOTALP=FIAL*YALNY/TOTYAL
C
C NOW TO PUT THE APHIDS INTO AGE CLASSES WITHIN EACH INSTAR
C
  TOTFOR=ONYMPH
  TOTALF=OALNY
  DO 304 I=1,100
  PNYMPH(1,I)=TOTFIR/100.0
  SNYPH(1,I)=TOTSEC/100.0
  TNYMPH(1,I)=TOTTHI/100.0
  ALPN(1,I)=TOTALP/100.0
  ALSN(1,I)=TOTALS/100.0
  ALTN(1,I)=TOTALT/100.0
  FNYMPH(1,I)=ONYMPH/100.0
  ALFN(1,I)=OALNY/100.0
C NOW FOR THE AGES
  IF(I.NE.1)THEN

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```

PNYMPH(2,I)=PNYMPH(2,I-1)+0.0099675
SNYMPH(2,I)=SNYMPH(2,I-1)+0.0099148
TNYMPH(2,I)=TNYMPH(2,I-1)+0.0099275
FNYMPH(2,I)=FNYMPH(2,I-1)+0.0099953
ALPN(2,I)=ALPN(2,I-1)+0.0099675
ALSN(2,I)=ALSN(2,I-1)+0.0099148
ALTN(2,I)=ALTN(2,I-1)+0.0099275
ALFN(2,I)=ALFN(2,I-1)+0.0099953
END IF
304 CONTINUE
C
C NOW FOR THE ADULTS
C
  ADD=28.3
  IF(GSTAGE.GT.59.0)ADD=42.4
  IF(GSTAGE.GT.73.0)ADD=14.1
  DO 307 I=1,200
    ADULTS(1,I)=TOTAD/200.0
    ALATAD(1,I)=TOTALA/200.0
    IF(I.NE.1)THEN
      ADULTS(2,I)=ADULTS(2,I-1)+ADD
      ALATAD(2,I)=ALATAD(2,I-1)+14.1
    END IF
    IF(ADULTS(2,I).GT.481.75)TOTADR=TOTADR+ADULTS(1,I)
  307 CONTINUE
  END IF
C
C
C MODEL NOW STARTS*****
C
  DO 107 IDAYY=ISTART,IFINIS
C
C
C
C*****3.....HOURLY TEMPERATURES ARE CALCULATED
C
C
  DO 4320 IT=1,24
    IF(IDAYY.EQ.ISTART.AND.IT.EQ.1)TEMP(24)=((MXTT(IDAYY-1)-MNTT(IDAYY
    *))*(COS(PI*(-10)/(10+IRISE(IDAYY)))))/2.0+(MXTT(IDAYY-1)+MNTT(IDAY
    *Y))/2.0
C
    IF(IT.LT.IRISE(IDAYY))TEMP(IT)=((MXTT(IDAYY-1)-MNTT(IDAYY))*(COS(P
    *I*(-(IT+10))/(10+IRISE(IDAYY)))))/2.0+(MXTT(IDAYY-1)+MNTT(IDAYY))/
    *2.0
C
    IF(IT.EQ.IRISE(IDAYY))TEMP(IT)=MNTT(IDAYY)
C

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IF(IT.GT.IRISE(IDAYY).AND.IT.LT.14)TEMP(IT)=((MXTT(IDAYY)-MNTT(IDA
*YY))*(-COS(PI*(IT-IRISE(IDAYY))/(14-IRISE(IDAYY)))))/2.0+(MXTT(IDA
*YY)+MNTT(IDAYY))/2.0
C
IF(IT.EQ.14)TEMP(IT)=MXTT(IDAYY)
C
IF(IT.GT.14)TEMP(IT)=((MXTT(IDAYY)-MNTT(IDAYY+1))*(COS((PI*(14-IT)
*)/(10+IRISE(IDAYY+1)))))/2.0+(MXTT(IDAYY)+MNTT(IDAYY+1))/2.0
C
IF(IT.EQ.1)AMTEMP(IT)=(TEMP(IT)+TEMP(24))/2.0
IF(IT.GT.1)AMTEMP(IT)=(TEMP(IT)+TEMP(IT-1))/2.0
C
C HOUR DEGREES FOR DEVELOPMENT, SURVIVAL, REPRODUCTION AND
PREDATION
C
HRDEG(IT)=AMTEMP(IT)
C NOW SURVIVAL
HRDDG(IT)=HRDEG(IT)
C NOW REPRODUCTION
HRREP(IT)=HRDEG(IT)
IF(AMTEMP(IT).LT.0.0)HRREP(IT)=0.0
IF(AMTEMP(IT).GE.30.0)HRREP(IT)=0.0

C NOW PREDATION
HRDPRD(IT)=AMTEMP(IT)-13.1
IF(HRDPRD(IT).LT.0.0)HRDPRD(IT)=0.0
C FINALLY DEVELOPMENT
IF(AMTEMP(IT).LT.0.0) THEN
HRDIG(IT)=0.0
HRDIIG(IT)=0.0
HRDIIIG(IT)=0.0
HRDIVG(IT)=0.0
HRDPG(IT)=0.0
ENDIF
IF ((AMTEMP(IT).GE.0.0).AND.(AMTEMP(IT).LE.13.45))HRDIG(IT)=0.0010
*104*AMTEMP(IT)
IF ((AMTEMP(IT).GT.13.45).AND.(AMTEMP(IT).LE.25.0))HRDIG(IT)=0.027
*18/(1+EXP((-0.1602*AMTEMP(IT))+2.15469))
IF ((AMTEMP(IT).GT.25.0).AND.(AMTEMP(IT).LE.41.0))HRDIG(IT)=0.0600
*41-(0.0014618*AMTEMP(IT))
IF (AMTEMP(IT).GT.41.0)HRDIG(IT)=0.0
IF ((AMTEMP(IT).GE.0.0).AND.(AMTEMP(IT).LE.13.00))HRDIIG(IT)=0.001
*1165*AMTEMP(IT)
IF ((AMTEMP(IT).GT.13.00).AND.(AMTEMP(IT).LE.25.0))HRDIIG(IT)=0.02
*903/(1+EXP((-0.1423*AMTEMP(IT))+1.8499))
IF ((AMTEMP(IT).GT.25.0).AND.(AMTEMP(IT).LE.41.3))HRDIIG(IT)=0.061
*995-(0.0014968*AMTEMP(IT))
IF (AMTEMP(IT).GT.41.4)HRDIIG(IT)=0.0

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IF ((AMTEMP(IT).GE.0.0).AND.(AMTEMP(IT).LE.12.67))HRDIIIG(IT)=0.00
*11243*AMTEMP(IT)
IF ((AMTEMP(IT).GT.12.67).AND.(AMTEMP(IT).LE.25.00))HRDIIIG(IT)=0.
*02849/(1+EXP((-0.1709*AMTEMP(IT))+2.1653))
IF ((AMTEMP(IT).GT.25.0).AND.(AMTEMP(IT).LE.39.0))HRDIIIG(IT)=0.07
*02173-(0.0017926*AMTEMP(IT))
IF (AMTEMP(IT).GT.36.6)HRDIIIG(IT)=0.0
IF ((AMTEMP(IT).GT.0.0).AND.(AMTEMP(IT).LE.12.07))HRDIVG(IT)=0.001
*0194*AMTEMP(IT)
IF ((AMTEMP(IT).GT.12.07).AND.(AMTEMP(IT).LE.25.0))HRDIVG(IT)=0.02
*461/(1+EXP((-0.1326*AMTEMP(IT))+1.6005))
IF ((AMTEMP(IT).GT.25.0).AND.(AMTEMP(IT).LE.42.0))HRDIVG(IT)=0.051
*6745-(0.00123278*AMTEMP(IT))
IF (AMTEMP(IT).GT.46.4)HRDIVG(IT)=0.0
CONTINUE
HRDVG(IT)=((HRDIVG(IT)+HRDIIIG(IT)+HRDIIG(IT)+HRDIG(IT))/4)
IF (HRDVG(IT).EQ.0.0)HRDVG(IT)=0.000001

```

C -----

C ***** COCCINELLID DEVELOPMENT *****

C

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IF ((AMTEMP(IT).GT.0.0).AND.(AMTEMP(IT).LE.35.0))HRCEG(IT)=0.02497
*/(1+EXP((-0.2350*AMTEMP(IT))+5.390))*SEN1
IF ((AMTEMP(IT).GT.0.0).AND.(AMTEMP(IT).LE.35.0))HRCIG(IT)=0.03162
*/(1+EXP((-0.2109*AMTEMP(IT))+4.941))*SEN1
IF ((AMTEMP(IT).GT.0.0).AND.(AMTEMP(IT).LE.35.0))HRCIIG(IT)=0.0531
*6/(1+EXP((-0.1905*AMTEMP(IT))+4.763))*SEN1
IF ((AMTEMP(IT).GT.0.0).AND.(AMTEMP(IT).LE.35.0))HRCIIIG(IT)=0.040
*04/(1+EXP((-0.2289*AMTEMP(IT))+5.299))*SEN1
IF ((AMTEMP(IT).GT.0.0).AND.(AMTEMP(IT).LE.35.0))HRCIVG(IT)=0.0195
*5/(1+EXP((-0.2043*AMTEMP(IT))+4.934))*SEN1
IF ((AMTEMP(IT).GT.0.0).AND.(AMTEMP(IT).LE.35.0))HRCPG(IT)=0.02005
*/(1+EXP((-0.1812*AMTEMP(IT))+4.607))*SEN1
IF ((AMTEMP(IT).LE.50.0).AND.(AMTEMP(IT).GT.35.0))HRCEG(IT)=0.0786
*15-(AMTEMP(IT)*0.0015723)*SEN1
IF ((AMTEMP(IT).LT.50.0).AND.(AMTEMP(IT).GT.35.0))HRCIG(IT)=0.0969
*5-(0.001939*AMTEMP(IT))*SEN1
IF ((AMTEMP(IT).LT.50.0).AND.(AMTEMP(IT).GT.35.0))HRCIIG(IT)=0.154
*235-(AMTEMP(IT)*0.0030847)*SEN1
IF ((AMTEMP(IT).LT.50.0).AND.(AMTEMP(IT).GT.35.0))HRCIIIG(IT)=0.12
*5155-(0.0025031*AMTEMP(IT))*SEN1
IF ((AMTEMP(IT).LT.50.0).AND.(AMTEMP(IT).GT.35.0))HRCIVG(IT)=0.058
*76-(AMTEMP(IT)*0.0011752)*SEN1
IF ((AMTEMP(IT).LT.50.0).AND.(AMTEMP(IT).GT.35.0))HRCPG(IT)=0.0568
*1-(AMTEMP(IT)*0.0011362)*SEN1
IF ((AMTEMP(IT).LE.0.0).OR.(AMTEMP(IT).GE.50.0)) THEN
HRCIG(IT)=0.0
HRCIIG(IT)=0.0
HRCIIIG(IT)=0.0

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    HRCIVG(IT)=0.0
    HRCPG(IT)=0.0
    END IF
    CONTINUE
    HRCVG(IT)=((HRCIG(IT)+HRCIIG(IT)+HRCIIG(IT)+HRCIVG(IT))/4)
    IF(HRCVG(IT).EQ.0.0)HRCVG(IT)=0.000001
    IF(HRCPG(IT).EQ.0.0)HRCPG(IT)=0.000001
    IF(HRCEG(IT).EQ.0.0)HRCEG(IT)=0.000001
C -----
4320 CONTINUE
C NOW ACCUMULATION OF HOUR DEGREES OVER THE STEP LENGTH
    II=1
    IJ=IIJ
    IF(IJ.NE.1)THEN
    DO 60 I=1,24
    AVTEMP(I)=0.0
    AVHPRD(I)=0.0
    AVHRDG(I)=0.0
    AVHDRP(I)=0.0
60 CONTINUE
    DO 22 J=1,24/IIJ
    DO 23 I=II,IJ
C DEVELOPMENT
    AVHRDG(J)=AVHRDG(J)+HRDEG(I)
C SURVIVAL
    AVTEMP(J)=AVTEMP(J)+HRDDG(I)
C REPRODUCTION
    AVHDRP(J)=AVHDRP(J)+HRREP(I)
C PREDATION
    AVHPRD(J)=AVHPRD(J)+HRDPRD(I)
23 CONTINUE
    II=II+IIJ
    IJ=IJ+IIJ
    HRDDG(J)=AVTEMP(J)
    HRDEG(J)=AVHRDG(J)
    HRREP(J)=AVHDRP(J)
    HRDPRD(J)=AVHPRD(J)
22 CONTINUE
    END IF
C
C
C*****4.....IMMIGRATION.....*****
C
    INCONF=40
C
C THE BASIC DATA HAS ALREADY BEEN INPUT. FIRST THE SKIP STATEMENTS
    IF(IDAYY.GE.IMSTAR.AND.IDAYY.LE.IMFINI.AND.IMM(IDAYY).NE.0)THEN
C

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```

    ALTIM=IMM(IDAYY)*INCONF*TAYPAL
    ELSE
    ALTIM=0.0
    END IF
    ALATIM=ALTIM/1000000.0
    ALATAD(1,1)=ALATIM
    TOTALA=TOTALA+ALATAD(1,1)
C
C
C
C -----
C   COCCINELLID IMMIGRATION
C
    RNIMM=10/TILERS
C
C
    IF (TOTDEN.GT.RNIMM) THEN
    COCCIM(1,1)=FCNT(IDAYY)/2
    ELSE
    COCCIM(1,1)=0.0
    END IF
C -----
    COCCIM(2,1)=COCCIM(1,1)
    TOTCIM(1)=TOTCIM(1)+COCCIM(1,1)
    TOTCIM(2)=TOTCIM(2)+COCCIM(2,1)
C
C*****5.....DEVELOPMENT AND SURVIVAL.....*****
    ITT=1
    IF(IDAYY.EQ.ISTART.AND.ISKIP.NE.1)ITT=12/IIJ
    DO 1000 IT=ITT,24/IIJ
C
C SET LONGEVITIES, IN HOUR DEGREES, ARE INPUT FOR ALATE AND APTEROUS
C ADULTS AT DIFFERENT CROP DEVELOPMENT STAGES
C
    IF(GSTAGE.LE.59.0)THEN
    SURTAL=2416.44
    SURT=4832.89
    ELSE IF(GSTAGE.GT.59.0.AND.GSTAGE.LE.73.0)THEN
    SURTAL=2416.44
    SURT=7249.33
    ELSE
    SURTAL=2416.44
    SURT=2416.44
    END IF
C
C -----
C
C *****COCCINELLID LONGEVITIES*****

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```

C
  CIMLON(1)=9975*SEN7
  CIMLON(2)=9975*SEN7
  IF (IDAYY.GE.MAINSTAR) THEN
    CIMLON(1)=3000*SEN7
    CIMLON(2)=3000*SEN7
  END IF
  CLONAD=60*SEN7
C
C -----
C
C NOW THE HOURLY SURVIVAL RATES DEPENDENT ON GROWTH STAGE, ALATES,
C APTEROUS ADULTS, ALATIFORM NYMPHS AND APTERIFORM NYMPHS
C
  IF (HRDDG(IT).LT.0.0)HRDDG(IT)=0.0000001
  SARTA=10.0**(LOG10(0.9)/(SURTAL/HRDDG(IT)))
  SURTA=10.0**(LOG10(0.9)/(SURT/HRDDG(IT)))
  SURALIV=10.0**(LOG10(0.93)/(TOTLNY/HRDVG(IT)))
  SURNIV=10.0**(LOG10(0.938)/(TOTPNY/HRDVG(IT)))
  IF(GSTAGE.GT.73.0)THEN
    SARTA=10.0**(LOG10(0.6)/(SURTAL/HRDDG(IT)))
    SURTA=10.0**(LOG10(0.6)/(SURT/HRDDG(IT)))
    SURALIV=10.0**(LOG10(0.374)/(TOTLNY/HRDVG(IT)))
    SURNIV=10.0**(LOG10(0.45)/(TOTPNY/HRDVG(IT)))
  END IF
C
C
C NOW TO CALL UP THE DEVELOPMENT AND SURVIVAL SUBROUTINE
C
  IF(ADULTS(1,IADSTP).NE.0.0)GO TO 1001
  ADSKIP=1.0
  IF(TOTAD.NE.0.0)CALL DEVSUR(ADULTS,IADSTP,TOTAD,ADSKIP,TOTADR,OLDA
*PH,SURTA,HRDEG(IT),SURT,PRD)
  ADSKIP=0.0
  IF(ALATAD(1,IALSTP).NE.0.0)GO TO 1001
  IF(TOTALA.NE.0.0)CALL DEVSUR(ALATAD,IALSTP,TOTALA,ADSKIP,TOTADR,OL
*DAPH,SARTA,HRDEG(IT),SURTAL,PRD)
  IF(FNYMPH(1,IFOSTP).NE.0.0)GO TO 1001
  IF(TOTFOR.NE.0.0)CALL DEVSUR(FNYMPH,IFOSTP,TOTFOR,ADSKIP,TOTADR,AD
*ULTS(1,1),SURNIV,HRDIVG(IT),FPLONG,PRD)
  IF(ALFN(1,IFOSTP).NE.0.0)GO TO 1001
  IF(TOTALF.NE.0.0)CALL DEVSUR(ALFN,IFOSTP,TOTALF,ADSKIP,TOTADR,ALAT
*ED,SURALIV,HRDIVG(IT),FLLONG,PRD)
C
C THIS FINISHES THE ADULTS AND FOURTHS, NEXT THE PARASITISM AND
DISEASE
C SUBROUTINE IS CALLED, PRIOR TO UPDATING THE YOUNG NYMPHS
C

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        IF(PARNO.NE.1.0)CALL PARDIS(ALATED,ADULTS(1,1),IDAYY,IPARA,IPAFIN,
        *TOTDEN,PARA(IDAYY),IT,IJJ,TOTPAR)
C
C NOW EMIGRATION, ALL NEWLY MOULTED ALATE ADULTS WHICH SURVIVE
PARASITES
C AND DISEASE EMIGRATE IMMEDIATELY
C
        IF(IT.EQ.12/IJJ+1)TOTALE=0.0
        TOTALE=TOTALE+ALATED
C
C
C NOW BACK TO THE YOUNG NYMPHS
C
        IF(TNYMPH(1,INYSTP).NE.0.0)GO TO 1001
        IF(TOTTHI.NE.0.0)CALL DEVSUR(TNYMPH,INYSTP,TOTTHI,ADSKIP,TOTADR,FN
        *YMPH(1,1),SURNIV,HRDIIG(IT),THLONG,PRD)
C
        IF(ALTN(1,INYSTP).NE.0.0)GO TO 1001
        IF(TOTALT.NE.0.0)CALL DEVSUR(ALTN,INYSTP,TOTALT,ADSKIP,TOTADR,ALFN
        *(1,1),SURALIV,HRDIIG(IT),THLONG,PRD)
C
        IF(SNYMPH(1,INYSTP).NE.0.0)GO TO 1001
        IF(TOTSEC.NE.0.0)CALL DEVSUR(SNYMPH,INYSTP,TOTSEC,ADSKIP,TOTADR,TN
        *YMPH(1,1),SURNIV,HRDIIG(IT),SLONG,PRD)
C
        IF(ALSN(1,INYSTP).NE.0.0)GO TO 1001
        IF(TOTALS.NE.0.0)CALL DEVSUR(ALSN,INYSTP,TOTALS,ADSKIP,TOTADR,ALTN
        *(1,1),SURALIV,HRDIIG(IT),SLONG,PRD)
C
        IF(PNYMPH(1,INYSTP).NE.0.0)GO TO 1001
        IF(TOTFIR.NE.0.0)CALL DEVSUR(PNYMPH,INYSTP,TOTFIR,ADSKIP,TOTADR,SN
        *YMPH(1,1),SURNIV,HRDIG(IT),FILONG,PRD)
C
        IF(ALPN(1,INYSTP).NE.0.0)GO TO 1001
        IF(TOTALP.NE.0.0)CALL DEVSUR(ALPN,INYSTP,TOTALP,ADSKIP,TOTADR,ALSN
        *(1,1),SURALIV,HRDIG(IT),FILONG,PRD)
C
C
C THIS FINISHES DEVELOPMENT AND SURVIVAL
C
C
C TOTAL UP THE INSTARS
C
        TOTAD=TOTAD+ADULTS(1,1)
        TOTALA=TOTALA+ALATAD(1,1)
        TOTFOR=TOTFOR+FNYMPH(1,1)
        TOTALF=TOTALF+ALFN(1,1)

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TOTTHI=TOTTHI+TNYMPH(1,1)
TOTALT=TOTALT+ALTN(1,1)
TOTSEC=TOTSEC+SNYMPH(1,1)
TOTALS=TOTALS+ALSN(1,1)
C
C
C -----
C
C ***** COCCINELLID SURVIVAL *****
C
SV(1)=0.881*SEN6
SV(2)=0.944*SEN6
SV(3)=0.941*SEN6
SV(4)=0.923*SEN6
DO 961 I=1,4
IF (SV(I).GT.1.0) SV(I)=1.0
961 CONTINUE
IF (TOTDEN.LE.RNIMM) THEN
DO 966 I=1,4
SV(I)=0.1
966 CONTINUE
SV(3)=0.941
END IF
C
CSUREGG=10**(LOG10(SV(1))/(CEGLONG/HRCEG(IT)))
CSURINS=10**(LOG10(SV(2))/(CVLONG/HRCVG(IT)))
CSURPUP=10**(LOG10(SV(3))/(CPLONG/HRCPG(IT)))
CSURADS=10**(LOG10(SV(4))/(CLONAD/1))
CSURIM(1)=10**(LOG10(SV(4))/(CIMLON(1)/HRDEG(IT)))
CSURIM(2)=10**(LOG10(SV(4))/(CIMLON(2)/HRDEG(IT)))
C
IF (TOTDEN.LE.RNIMM) THEN
CSURADS=0.0
CSURIM(1)=0.0
CSURIM(2)=0.0
END IF
C
C -----
C -----
C
C COCCINELLID DEVELOPMENT AND SURVIVAL
C
C IMMIGRANT COCCINELLIDS
C
DO 9221 INS=1,2
C
VMSKIP=1.0
IF(COCCIM(INS,ICOCTP).NE.0.0)GO TO 1101

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        IF(TOTCIM(INS).NE.0.0)CALL CIMDVSR(COCCIM,COCCIMAG,ICOCSTP,TOTCIM(
        *INS),OLDCOC,CSURIM(INS),HRDEG(IT),CIMLON(INS),VMSKIP,INS)
C
9221  CONTINUE
C
C    NOW FOR THE DEVELOPING POPULATION
C
        VMSKIP=0.0
        IF(PRED(7,ICOCSTP).NE.0.0)GO TO 1101
        IF(TOTCOC(7).NE.0.0)CALL COCDVSR(PRED,PREDAGE,ICOCSTP,TOTCOC(7),OL
        *DCOC,CSURADS,1,CLONAD,VMSKIP,7)
        IF(PRED(6,ICOCSTP).NE.0.0)GO TO 1101
        IF(TOTCOC(6).NE.0.0)CALL COCDVSR(PRED,PREDAGE,ICOCSTP,TOTCOC(6),PR
        *ED(7,1),CSURPUP,HRCPG(IT),CPLONG,VMSKIP,6)
        IF(PRED(5,ICOCSTP).NE.0.0)GO TO 1101
        IF(TOTCOC(5).NE.0.0)CALL COCDVSR(PRED,PREDAGE,ICOCSTP,TOTCOC(5),PR
        *ED(6,1),CSURINS,HRCIVG(IT),CIVLONG,VMSKIP,5)
        IF(PRED(4,ICOCSTP).NE.0.0)GO TO 1101
        IF(TOTCOC(4).NE.0.0)CALL COCDVSR(PRED,PREDAGE,ICOCSTP,TOTCOC(4),PR
        *ED(5,1),CSURINS,HRCIIG(IT),CIILONG,VMSKIP,4)
        IF(PRED(3,ICOCSTP).NE.0.0)GO TO 1101
        IF(TOTCOC(3).NE.0.0)CALL COCDVSR(PRED,PREDAGE,ICOCSTP,TOTCOC(3),PR
        *ED(4,1),CSURINS,HRCIIG(IT),CIILONG,VMSKIP,3)
        IF(PRED(2,ICOCSTP).NE.0.0)GO TO 1101
        IF(TOTCOC(2).NE.0.0)CALL COCDVSR(PRED,PREDAGE,ICOCSTP,TOTCOC(2),PR
        *ED(3,1),CSURINS,HRCIG(IT),CILONG,VMSKIP,2)
        IF(PRED(1,ICOCSTP).NE.0.0)GO TO 1101
        IF(TOTCOC(1).NE.0.0)CALL COCDVSR(PRED,PREDAGE,ICOCSTP,TOTCOC(1),PR
        *ED(2,1),CSUREGG,HRCEG(IT),CEGLONG,VMSKIP,1)
C
C    NOW TO ADD UP THE TOTALS
C
        TOTCIM(1)=0.0
        TOTCIM(2)=0.0
        TOTCOC(1)=0.0
        TOTCOC(2)=0.0
        TOTCOC(3)=0.0
        TOTCOC(4)=0.0
        TOTCOC(5)=0.0
        TOTCOC(6)=0.0
        TOTCOC(7)=0.0
C
C parasitism of immigrant coccinellids at 30-50%
        CPARASURV=10**((LOG10(0.7)/(CIMLON(1)/HRDEG(IT)))
        DO 1199 I=1,ICOCSTP
        COCCIM(1,I)=COCCIM(1,I)*CPARASURV
        COCCIM(2,I)=COCCIM(1,I)*CPARASURV
1199  CONTINUE

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C
  DO 9222 XYZ=1,ICOCSTP
    TOTCIM(1)=TOTCIM(1)+COCCIM(1,XYZ)
    TOTCIM(2)=TOTCIM(2)+COCCIM(2,XYZ)
    TOTCOC(1)=TOTCOC(1)+PRED(1,XYZ)
    TOTCOC(2)=TOTCOC(2)+PRED(2,XYZ)
    TOTCOC(3)=TOTCOC(3)+PRED(3,XYZ)
    TOTCOC(4)=TOTCOC(4)+PRED(4,XYZ)
    TOTCOC(5)=TOTCOC(5)+PRED(5,XYZ)
    TOTCOC(6)=TOTCOC(6)+PRED(6,XYZ)
    TOTCOC(7)=TOTCOC(7)+PRED(7,XYZ)+COCCIM(1,XYZ)+COCCIM(2,XYZ)
  9222 CONTINUE
C
C
C -----
C
C*****6.....REPRODUCTION.....*****
C*****.....AND MORPH DETERMINATION.....*****
C
C FIRST REPRODUCTION, APTEROUS ADULTS AND THEN ALATES, DEPENDENT
C ON CROP DEVELOPMENT STAGE
C
  IF (AMTEMP(IT).LE.20)FEC=0.000366*AMTEMP(IT)
  IF (AMTEMP(IT).GT.20)FEC=0.0220-(0.000732*AMTEMP(IT))
  IF (AMTEMP(IT).LE.0.0.OR.AMTEMP(IT).GE.30)FEC=0.0
  IF(GSTAGE.GT.59.0.AND.GSTAGE.LE.73.0)FEC=FEC*1.6
  IF(GSTAGE.GT.83.0)FEC=0.0
C
C NYMPHS LAID BY THE APTERAE
C
  NEWNY=TOTADR*(HRREP(IT)*FEC)
C
  IF (AMTEMP(IT).LE.20)ALFEC=0.000283*AMTEMP(IT)
  IF (AMTEMP(IT).GT.20)ALFEC=0.0170-(0.000566*AMTEMP(IT))
  IF (AMTEMP(IT).LE.0.0.OR.AMTEMP(IT).GE.30)ALFEC=0.0
  IF(GSTAGE.GT.59.0.AND.GSTAGE.LE.73.0)ALFEC=ALFEC*1.6
  IF(GSTAGE.GT.83.0)ALFEC=0.0
  NWNV=TOTALA*(HRREP(IT)*ALFEC)
C
C APHIDS ARE TOTALLED UP
C
  TOTDEN=TOTAD+TOTALA+TOTFOR+TOTALF+TOTTHI+TOTALT+TOTSEC+TOTALS
  *+TOTFIR+TOTALP
C
C NOW TO DECIDE THE PROPORTION OF NYMPHS WHICH WILL BE ALATIFORM
C
  ALATE=((2.603*TOTDEN+0.847208*GSTAGE-27.18896)/100.0)
  IF(ALATE.GT.1.0)ALATE=1.0

```



```

    ALPN(1,1)=(NWNKY+NEWNY)*ALATE
    IF(ALPN(1,1).LT.0.0)ALPN(1,1)=0.0
C NOW THE NUMBER OF APTERAE
    PNYMPH(1,1)=NEWNY+NWNKY-ALPN(1,1)
    IF(PNYMPH(1,1).LT.0.0)PNYMPH(1,1)=0.0
C
C NOW THE TOTALS ARE CALCULATED, AND AGES SET
C
    TOTFIR=TOTFIR+PNYMPH(1,1)
    TOTALP=TOTALP+ALPN(1,1)
    ALPN(2,1)=0.0
    PNYMPH(2,1)=0.0
    TOTDEN=TOTDEN+ALPN(1,1)+PNYMPH(1,1)
C
C -----
C
C ***** COCCINELLID REPRODUCTION *****
C
C
C
C Reproduction only if aphid density high enough
C
    IF (TOTDEN.GE.0.1)THEN
C
C
C
C First two statements are main equations for temperature
C
    IF (CONSUME.GT.20.94)CONSUME=20.94
    IF (AMTEMP(IT).LE.20)COCEGG=((0.00037*CONSUME)-0.0037)*AMTEMP(IT)
    IF (AMTEMP(IT).GT.20)COCEGG=(0.0148*CONSUME)-0.148-(0.00037*AMTEM
    *P(IT)*CONSUME)+(0.0037*AMTEMP(IT))
C
C
C
    IF (CONSUME.LE.10)COCEGG=0.0
C
    IF (IDAYY.GE.MAINSTAR)COCEGG=0.0
C Now put eggs into array
C
    PRED(1,1)=COCEGG*SEN2*HRREP(IT)*TOTCIM(2)*ACTIV
C
C
C
C Now adjust the totals
C
C
    TOTCOC(1)=TOTCOC(1)+PRED(1,1)
C

```

```

      END IF
C -----
C -----
C COCCINELLID PREDATION
C
      IF (PREDNO.NE.0.0) GOTO 7777
C
C SET UP CONVERSION VALUES
      ZMGCON(1)=0.1
      ZMGCON(2)=0.2
      ZMGCON(3)=0.4
      ZMGCON(4)=0.8
      ZMGCON(5)=1.6
C
C*****7.....PREDATION.....*****
C
C ALL INSTARS ARE CONVERTED TO MG/M2
C
C
      ZMGI=((TOTFIR+TOTALP)*ZMGCON(1)*TILERS)
      ZMGII=((TOTSEC+TOTALS)*ZMGCON(2)*TILERS)
      ZMGIII=((TOTTHI+TOTALT)*ZMGCON(3)*TILERS)
      ZMGIV=((TOTFOR+TOTALF)*ZMGCON(4)*TILERS)
      ZMGV=((TOTAD+TOTALA)*ZMGCON(5)*TILERS)
      ZMGTOT=ZMGI+ZMGII+ZMGIII+ZMGIV+ZMGV
      ZMGDII=ZMGI+ZMGII
      ZMGDIII=ZMGI+ZMGII+ZMGIII
C
C
C CALCULATE ALATE TO APTERAE RATIOS FOR EACH INSTAR
C
C
      IF ((TOTFIR+TOTALP).EQ.0.0) GOTO 7111
      RAPTI=TOTFIR/(TOTFIR+TOTALP)
      RALTI=1-RAPTI
7111 IF ((TOTSEC+TOTALS).EQ.0.0) GOTO 7112
      RAPTII=TOTSEC/(TOTSEC+TOTALS)
      RALTII=1-RAPTII
7112 IF ((TOTTHI+TOTALT).EQ.0.0) GOTO 7113
      RAPTIII=TOTTHI/(TOTTHI+TOTALT)
      RALTIII=1-RAPTIII
7113 IF ((TOTFOR+TOTALF).EQ.0.0) GOTO 7114
      RAPTIV=TOTFOR/(TOTFOR+TOTALF)
      RALTIV=1-RAPTIV
7114 IF ((TOTAD+TOTALA).EQ.0.0) GOTO 7115
      RAPTV=TOTAD/(TOTAD+TOTALA)
      RALTV=1-RAPTV
7115 CONTINUE

```



```

C
C
C ASSUME CI ONLY EATS AI, CII EATS AI&AII, CIII=AI,AII & AIII
C CIV AND CAD EAT AI-AV
C
C NOW CALCULATE RATIOS OF APHIDS THAT ARE EATEN BY EACH COCINELLID
INSTAR
C
C
    IF (ZMGDI.EQ.0.0) GOTO 7211
    RICII=ZMGI/ZMGDI
    RIICII=1-RICII
7211 IF (ZMGDIIE.EQ.0.0) GOTO 7212
    RICIII=ZMGI/ZMGDIIE
    RIICIII=ZMGII/ZMGDIIE
    RIICIII=1-(RICIII+RIICIII)
7212 IF (ZMGTOE.EQ.0.0) GOTO 7213
    RICV=ZMGI/ZMGTOE
    RIICV=ZMGII/ZMGTOE
    RIICV=ZMGIII/ZMGTOE
    RIVCV=ZMGIV/ZMGTOE
    RVCV=ZMGV/ZMGTOE
7213 CONTINUE
C
C
C Now to calculate the search rate of the coccinellids
C
C
C
C
    IF((AMTEMP(IT).GT.0.0).AND.(AMTEMP(IT).LE.35)) THEN
    SRATE(1)=0.020605/(1+EXP(-0.4070*(AMTEMP(IT)-20.158)))
    SRATE(2)=0.01485+0.06021/(1+EXP(-0.4381*(AMTEMP(IT)-23.088)))
    SRATE(3)=0.04215+0.10801/(1+EXP(-0.5025*(AMTEMP(IT)-22.493)))
    SRATE(4)=0.13602+0.20405/(1+EXP(-0.6323*(AMTEMP(IT)-22.773)))
    SRATE(5)=SRATE(2)
    ELSE IF ((AMTEMP(IT).GT.35.0).AND.(AMTEMP(IT).LE.50.0)) THEN
    SRATE(1)=0.06868-0.001374*AMTEMP(IT)
    SRATE(2)=0.02007-0.004014*AMTEMP(IT)
    SRATE(3)=0.36-0.0072*AMTEMP(IT)
    SRATE(4)=0.68-0.0136*AMTEMP(IT)
    SRATE(5)=SRATE(2)
    ELSE
    DO 888 I=1,5
    SRATE(I)=0.0
888 CONTINUE
    END IF
    DO 886 I=1,5
    SRATE(I)=SRATE(I)*SEN4

```

```

      886 CONTINUE
C
C
C
C
C
      IF(AMTEMP(IT).LE.50.0) THEN
      HRATE(1)=0.1667-0.00333*AMTEMP(IT)
      HRATE(2)=0.4-0.008*AMTEMP(IT)
      HRATE(3)=5.33-0.1067*AMTEMP(IT)
      HRATE(4)=5.867-0.1173*AMTEMP(IT)
      HRATE(5)=3.25-0.065*AMTEMP(IT)
      ELSE IF(AMTEMP(IT).LE.35.0) THEN
      HRATE(1)=0.05/(1+EXP(-0.5545*(AMTEMP(IT)-17.5)))
      HRATE(2)=0.12/(1+EXP(-0.5545*(AMTEMP(IT)-17.5)))
      HRATE(3)=1.6/(1+EXP(-0.6938*(AMTEMP(IT)-17.5)))
      HRATE(4)=1.76/(1+EXP(-0.7668*(AMTEMP(IT)-17.5)))
      HRATE(5)=0.975/(1+EXP(-0.7668*(AMTEMP(IT)-17.5)))
      ELSE IF(AMTEMP(IT).LE.0.0) THEN
      DO 887 I=1,5
      HRATE(I)=0.0
887 CONTINUE
      END IF
      DO 885 I=1,5
      HRATE(I)=HRATE(I)*SEN3
885 CONTINUE
C
C
C Now to calculate the percentage of coccinellids that are active
C
C
C First calculate the relative hunger
      IF (TOTCOC(7).LE.0.0) GOTO 7911
      RHGR=(CVKILL/TOTCOC(7))/0.875
C
7911 CONTINUE
      IF ((TOTCOC(7).LE.0.0).AND.(CVKILL.LE.0.0)) RHGR=0.0
C
C
      ACTIV=-45.24+(3.86*AMTEMP(IT))+(27.15*RHGR)-(1.43*AMTEMP(IT)*RHGR)
      ACTIV=ACTIV*SEN5
      IF (ACTIV.LE.0.0) ACTIV=0.0
      IF (ACTIV.GE.100.0) ACTIV=100.0
      ACTIV=ACTIV/100
7913 CONTINUE
C
C NOW CALL UP PREDATOR SUBROUTINE
C

```



```

C First set kills to zero
C
  CIKILL=0.0
  CIIKILL=0.0
  CIIIKILL=0.0
  CIVKILL=0.0
  CVKILL=0.0
C
  IF ((SRATE(1).LE.0.0).OR.(HRATE(1).LE.0.0)) GOTO 3133
  CALL PREDTR(TOTCOC(2),ZMGI,SRATE(1),HRATE(1),ACTIV,CIKILL)
3133 IF ((SRATE(2).LE.0.0).OR.(HRATE(2).LE.0.0)) GOTO 3134
  CALL PREDTR(TOTCOC(3),ZMGDI,SRATE(2),HRATE(2),ACTIV,CIIKILL)
3134 IF ((SRATE(3).LE.0.0).OR.(HRATE(3).LE.0.0)) GOTO 3135
  CALL PREDTR(TOTCOC(4),ZMGDII,SRATE(3),HRATE(3),ACTIV,CIIIKILL)
3135 IF((SRATE(4).LE.0.0).OR.(HRATE(4).LE.0.0)) GOTO 3136
  CALL PREDTR(TOTCOC(5),ZMGDTOT,SRATE(4),HRATE(4),ACTIV,CIVKILL)
C
C  TOTAL ADULTS
C
3136 IF ((SRATE(5).LE.0.0).OR.(HRATE(5).LE.0.0))GOTO 3137
  CALL PREDTR(TOTCOC(7),ZMGDTOT,SRATE(5),HRATE(5),ACTIV,CVKILL)
3137 CONTINUE
C
C
  IF(CVKILL.GT.(0.875*TOTCOC(7)))CVKILL=0.875*TOTCOC(7)
  IF(CIVKILL.GT.(0.555*TOTCOC(5)))CIVKILL=0.555*TOTCOC(5)
  IF(CIIIKILL.GT.(0.324*TOTCOC(4)))CIIIKILL=0.324*TOTCOC(4)
  IF(CIIKILL.GT.(0.200*TOTCOC(3)))CIIKILL=0.200*TOTCOC(3)
  IF(CIKILL.GT.(0.062*TOTCOC(2)))CIKILL=0.062*TOTCOC(2)
C
C
C
C
C
C  Calculate the number of aphids killed in each instar
C
C
  CNI=(CIKILL+(CIIKILL*RICII)+(CIIIKILL*RICIII)+((CIVKILL+CVKILL)*RI
*CV))
  CNII=((CIIKILL*RIICII)+(CIIIKILL*RIICIII)+((CIVKILL+CVKILL)*RIICV)
*)
  CNIII=((CIIIKILL*RIIICIII)+((CIVKILL+CVKILL)*RIIICV))
  CNIV=(((CIVKILL+CVKILL)*RIVCV))
  CNV=(((CIVKILL+CVKILL)*RVCV))
C
C
C ENSURE KILL NEVER GREATER THAN APHIDS AVAILABLE
C
  IF (CNI.GT.ZMGI)CNI=ZMGI

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```

      IF (CNII.GT.ZMGII)CNII=ZMGII
      IF (CNIII.GT.ZMGIII)CNIII=ZMGIII
      IF (CNIV.GT.ZMGIV)CNIV=ZMGIV
      IF (CNV.GT.ZMGV)CNV=ZMGV
C
C Now convert mg aphid consumedper m2 back to aph/tiller
C
      CNI=CNI/(ZMGCON(1)*TILERS)
      CNII=CNII/(ZMGCON(2)*TILERS)
      CNIII=CNIII/(ZMGCON(3)*TILERS)
      CNIV=CNIV/(ZMGCON(4)*TILERS)
      CNV=CNV/(ZMGCON(5)*TILERS)
      TOTCON=CNI+CNII+CNIII+CNIV+CNV
C
C
C Now calculate the proportion of aphids killed in each instar and morph
C
C
      IF ((TOTFIR.LE.0.0).OR.(CNI.LE.0.0).OR.(RAPTI.LE.0.0))THEN
      PRIP=0.0
      ELSE
      PRIP=(CNI*RAPTI)/TOTFIR
      END IF
      IF ((TOTALP.LE.0.0).OR.(CNI.LE.0.0).OR.(RALTI.LE.0.0))THEN
      PRIL=0.0
      ELSE
      PRIL=(CNI*RALTI)/TOTALP
      END IF
      IF ((TOTSEC.LE.0.0).OR.(CNII.LE.0.0).OR.(RAPTII.LE.0.0))THEN
      PRIIP=0.0
      ELSE
      PRIIP=(CNII*RAPTII)/TOTSEC
      END IF
      IF ((TOTALS.LE.0.0).OR.(CNII.LE.0.0).OR.(RALTII.LE.0.0))THEN
      PRIIL=0.0
      ELSE
      PRIIL=(CNII*RALTII)/TOTALS
      END IF
      IF ((TOTTHI.LE.0.0).OR.(CNIII.LE.0.0).OR.(RAPTIII.LE.0.0))THEN
      PRIIP=0.0
      ELSE
      PRIIP=(CNIII*RAPTIII)/TOTTHI
      END IF
      IF ((TOTALT.LE.0.0).OR.(CNIII.LE.0.0).OR.(RALTIII.LE.0.0))THEN
      PRIIL=0.0
      ELSE
      PRIIL=(CNIII*RALTIII)/TOTALT
      END IF

```



```

IF ((TOTFOR.LE.0.0).OR.(CNIV.LE.0.0).OR.(RAPTIV.LE.0.0))THEN
PRIVP=0.0
ELSE
PRIVP=(CNIV*RAPTIV)/TOTFOR
END IF
IF ((TOTALF.LE.0.0).OR.(CNIV.LE.0.0).OR.(RALTIV.LE.0.0))THEN
PRIVL=0.0
ELSE
PRIVL=(CNIV*RALTIV)/TOTALF
END IF
IF ((TOTAD.LE.0.0).OR.(CNV.LE.0.0).OR.(RAPTV.LE.0.0))THEN
PRVP=0.0
ELSE
PRVP=(CNV*RAPTV)/TOTAD
END IF
IF ((TOTALA.LE.0.0).OR.(CNV.LE.0.0).OR.(RAPLTV.LE.0.0))THEN
PRVL=0.0
ELSE
PRVL=(CNV*RAPLTV)/TOTALA
END IF

```

C
C
C
C
C

C NOW TO REDUCE NOS IN EACH INSTAR DUE TO PREDATION

C

C First set totals to zero

C

```

TOTFOR=0.0
TOTALF=0.0
TOTTHI=0.0
TOTALT=0.0
TOTSEC=0.0
TOTALS=0.0
TOTFIR=0.0
TOTALP=0.0
TOTAD=0.0
TOTALA=0.0
TOTADR=0.0

```

C
C

```

DO 717 I=1,IFOSTP
FNYMPH(1,I)=FNYMPH(1,I)-(FNYMPH(1,I)*PRIVP)
ALFN(1,I)=ALFN(1,I)-(ALFN(1,I)*PRIVL)
IF(FNYMPH(1,I).LE.0.0)FNYMPH(1,I)=0.0
IF(ALFN(1,I).LE.0.0)ALFN(1,I)=0.0
TOTFOR=TOTFOR+FNYMPH(1,I)
TOTALF=TOTALF+ALFN(1,I)

```

717 CONTINUE

DO 719 I=1,INYSTP

TNYMPH(1,I)=TNYMPH(1,I)-(TNYMPH(1,I)*PRIIP)

SNYMPH(1,I)=SNYMPH(1,I)-(SNYMPH(1,I)*PRIIP)

PNYMPH(1,I)=PNYMPH(1,I)-(PNYMPH(1,I)*PRIP)

IF (TNYMPH(1,I).LE.0.0)TNYMPH(1,I)=0.0

IF (SNYMPH(1,I).LE.0.0)SNYMPH(1,I)=0.0

IF (PNYMPH(1,I).LE.0.0)PNYMPH(1,I)=0.0

C

ALTN(1,I)=ALTN(1,I)-(ALTN(1,I)*PRIIL)

ALSN(1,I)=ALSN(1,I)-(ALSN(1,I)*PRIIL)

ALPN(1,I)=ALPN(1,I)-(ALPN(1,I)*PRIL)

IF(ALTN(1,I).LE.0.0)ALTN(1,I)=0.0

IF(ALSN(1,I).LE.0.0)ALSN(1,I)=0.0

IF(ALPN(1,I).LE.0.0)ALPN(1,I)=0.0

C

TOTTHI=TOTTHI+TNYMPH(1,I)

TOTSEC=TOTSEC+SNYMPH(1,I)

TOTFIR=TOTFIR+PNYMPH(1,I)

TOTALT=TOTALT+ALTN(1,I)

TOTALS=TOTALS+ALSN(1,I)

TOTALP=TOTALP+ALPN(1,I)

719 CONTINUE

DO 718 I=1,IADSTP

ADULTS(1,I)=ADULTS(1,I)-(ADULTS(1,I)*PRVP)

IF (ADULTS(1,I).LE.0.0)ADULTS(1,I)=0.0

TOTAD=TOTAD+ADULTS(1,I)

IF (ADULTS(2,I).GT.PRD) TOTADR=TOTADR+ADULTS(1,I)

718 CONTINUE

DO 720 I=1,IALSTP

ALATAD(1,I)=ALATAD(1,I)-(ALATAD(1,I)*PRVL)

IF(ALATAD(1,I).LE.0.0)ALATAD(1,I)=0.0

TOTALA=TOTALA+ALATAD(1,I)

720 CONTINUE

C

C NOW TO ADD UP DAILY CONSUMPTION

C

IF(IT.EQ.12/IIJ+1)DAYCON=0.0

DAYCON=DAYCON+TOTCON

C

C

C Now to set up the mg aphids consumed by reproductive females

C

C

IF ((TOTCOC(7).GT.0.0).AND.(TOTCIM(2).GT.0.0))CONSUME=
((CVKILL(TOTCIM(2)/TOTCOC(7)))/TOTCIM(2))*24

C

7777 CONTINUE


```

C
C
C
C*****8.....OUTPUT.....*****
C
C
    IF(IT.EQ.12/IIJ)THEN
    TOTYN=TOTFIR+TOTSEC+TOTTHI+TOTALP+TOTALS+TOTALT
    WRITE(2,132)IDAYY,TOTFIR,TOTSEC,TOTTHI,TOTFOR,TOTAD,
    *TOTALP,TOTALS,TOTALT,TOTALF,TOTALA,TOTYN
132 FORMAT(I4,11F10.4)
    WRITE(3,39)GSTAGE,TOTADR,ALATIM,TOTALE,TOTDEN,TOTPAR,DAYCON,
    *PRDFAC,PRDADC,AFIDUN,TOT
39 FORMAT(11F10.4)
    WRITE(12,939)TOTCOC(1),TOTCOC(2),TOTCOC(3),TOTCOC(4),TOTCOC(5
    *),TOTCOC(6),TOTCOC(7),totcim(1),idayy,it
939 FORMAT(8F10.4,i4,i4)
    WRITE(14,9839)APTTL,CCTTL,IDAYY
9839 FORMAT(2F10.4,I4)
    END IF
C -----DERIVE SUMMARY DATA-----
C
    IF (IT.EQ.12/IIJ) THEN
    APTTL=TOTYN+TOTAD+TOTALA
    CCTTL=TOTCOC(2)+TOTCOC(3)+TOTCOC(4)+TOTCOC(5)+TOTCOC(6)+TOTCO
    *C(7)
    IF ((N.GT.PKA).AND.(APTTL.GT.ALLOW))PKA=PKA+1
    IF ((M.GT.PKC).AND.(CCTTL.GT.CLOW))PKC=PKC+1
    IF (APTTL.GT.PEAKAPH(PKA)) THEN
    PEAKAPH(PKA)=APTTL
    PADAY(PKA)=IDAYY
    ALLOW=PEAKAPH(PKA)
    END IF
    IF(CCTTL.GT.PEAKCOC(PKC))THEN
    PEAKCOC(PKC)=CCTTL
    PCDAY(PKC)=IDAYY
    CLOW=PEAKCOC(PKC)
    END IF
C
    IF (APTTL.LT.PEAKAPH(PKA))N=PKA+1
    IF (CCTTL.LT.PEAKCOC(PKC))M=PKC+1
    IF (APTTL.LT.ALLOW) ALLOW=APTTL
    IF (CCTTL.LT.CLOW) CLOW=CCTTL
C
    END IF
1000 CONTINUE
C
C

```

```

C*****9.....CROP DEVELOPMENT MODEL.....*****
C
C THIS IS THE END OF THE DAY AND THE DEVELOPMENT STAGE OF THE CROP
C IS UPDATED
C
    THRESH=6.0
    XMAX=MXTT(IDAYY)
    XMIN=MNTT(IDAYY)
    DD=0.0
    DO 8011 I=1,2
    Y=XMAX+XMIN-2.0*THRESH
    IF(XMIN.LT.THRESH)GO TO 6006
    B=0.25*Y
    GO TO 8010
6006 IF(XMAX.GT.THRESH)GO TO 8008
    B=0.0
    GO TO 8010
8008 T=ASIN(Y/(XMIN-XMAX))
    B=0.125*Y*(1.0-0.63661977*T)+0.079577472*(XMAX-XMIN)*COS(T)
    IF(B.LT.0.0)B=0.0
8010 CONTINUE
    DD=DD+B
    XMIN=MNTT(IDAYY+1)
8011 CONTINUE
C DAY DEGREES ARE SUMMED
    TOT=TOT+DD
    GSTAGE=0.173224*TOT-0.000125*TOT*TOT+26.33648
    IF(GSTAGE.GT.86.3)GO TO 1004
107 CONTINUE
    GO TO 1003
C
C WARNING MESSAGE WHEN AN ARRAY OVERFLOWS, PROGRAM STOPS
C
1001 WRITE(2,1002)
1002 FORMAT(1H1, 15H ARRAY EXCEEDED)
1101 WRITE(12,1102)
1102 FORMAT(1H1, 15H ARRAY EXCEEDED)
1003 CONTINUE
C
C
C*****10.....INPUT VARIABLES ARE PRINTED.....*****
C
C
1004 CONTINUE
    WRITE(42,1010)
1010 FORMAT(1H0,35H CONC FACTORS AND SUCTION TRAP DATA/)
    WRITE(4,1012)INCONF,IMSTAR,IMFINI
1012 FORMAT(3I4)

```



```

        WRITE(4,1013)(IMM(I),I=IMSTAR,IMFINI)
1013 FORMAT(10I4)
        WRITE(4,1019)
1019 FORMAT(1H0,'SENSITIVITY ANALYSIS FACTORS ARE')
        WRITE(4,1114)SEN1,SEN2,SEN3,SEN4,SEN5,SEN6,SEN7,SEN8,SEN9
1114 FORMAT(1H0,9F5.2)
        WRITE(4,1020)IIJ
1020 FORMAT(1H0,'STEP LENGTH IS',I2,' HOURS')
        WRITE(4,1021)FIRAU,SECAU,THIAU,FORAU
1021 FORMAT(1H0,'FIRST=',F4.2,' SECOND=',F4.2,' THIRD=',F4.2,' FOURTH='
*,F4.2)
        WRITE(4,1022)LAT,TILERS,TAYPAL
1022 FORMAT(1H0,' LATITUDE=',F8.2,' TILLERS PER SQM=',F8.2,
*' ALATES PER TILLER PER SUCTION TRAP APHID=',F10.6)
        IF(PREDNO.NE.1.0)THEN
            WRITE(4,1023)PREDNO,ALOWAF,TH1,TH2
1023 FORMAT(1H0,'PREDNO=',F3.1,' ALOWAF=',F3.1,' TH1=',F3.1,
*' TH2=',F3.1)
            WRITE(4,1014)
1014 FORMAT(1H0,16H PREDATOR MATRIX/)
            WRITE(4,7780)INISTAR,INIFIN,MAINSTAR,MAINFIN
7780 FORMAT(4I4)
            DO 1016 I=INISTAR,IFINIS
                WRITE(4,1015)(PRED(J,I),J=1,7)
1015 FORMAT(5F10.4)
1016 CONTINUE
            END IF
            WRITE(4,1024)PARNO
1024 FORMAT(1H0,'PARNO=',F3.1)
            IF (PARNO.NE.1.0)THEN
                WRITE(4,7781)IPARA,IPAFIN
7781 FORMAT(2I4)
                WRITE(4,1017)
1017 FORMAT(1H0,18H PARASITISM MATRIX/)
                WRITE(4,1018)(PARA(I),I=IPARA,IPAFIN)
1018 FORMAT(5F10.4)
                END IF
                WRITE(4,9996)
9996 FORMAT(1H0,10H MAX TEMPS/)
                WRITE(4,9995)(MXTT(I),I=ISTART-1,IFINIS)
9995 FORMAT(15F7.2)
                WRITE(4,9994)
9994 FORMAT(1H0,10H MIN TEMPS/)
                WRITE(4,9993)(MNTT(I),I=ISTART,IFINIS+1)
9993 FORMAT(15F7.2)
                IF (PKA.GE.PKC)ZZZ=PKA
                IF (PKC.GE.PKA)ZZZ=PKC
                DO 9841 ZZ=1,ZZZ

```

```

        WRITE(15,9840),PEAKAPH(ZZ),PADAY(ZZ),PEAKCOC(ZZ),PCDAY(ZZ)
9840 FORMAT(4F10.4)
9841 CONTINUE
        GO TO 309
310 CONTINUE
C
C
C*****..... THE END.....*****
        STOP
        END
        SUBROUTINE PARDIS(ALATED,ADULTS,IDAYY,IPARA,IPAFIN,TOTDEN,PARA,IT,
        *IIJ,TOTPAR)
C
C FIRST THE NUMBER IN THE FIRST AGE CLASS OF ALATE AND APTEROUS
ADULTS
C ARE SUMMED
C
        TOTFAD=ALATED+ADULTS
        IF(TOTFAD.NE.0.0.AND.IDAYY.GE.IPARA.AND.IDAYY.LE.IPAFIN)THEN
C
C THE NUMBER DYING ARE CALCULATED AS A PROPORTION OF THE TOTAL
DENSITY
        PARSIT=TOTDEN*PARA*IIJ
        IF(PARSIT.GT.TOTFAD)PARSIT=TOTFAD
        PARALD=ADULTS*PARSIT/TOTFAD
        PARAL=PARSIT-PARALD
        ELSE
        PARAL=0.0
        PARALD=0.0
        END IF
        ALATED=ALATED-PARAL
        ADULTS=ADULTS-PARALD
        IF(IT.EQ.12/IIJ+1)TOTPAR=0.0
        TOTPAR=TOTPAR+PARAL+PARALD
        RETURN
        END
C
C
        SUBROUTINE DEVSUR(APHIDS,ISTEP,TOTAL,ADSKIP,TOTADR,TNWAPH,SURVIV,
        *HRDEG,ALONG,PRD)
        DIMENSION APHIDS(2,ISTEP)
        TOTAL=0.0
        IF(ADSKIP.EQ.1.0)TOTADR=0.0
        TNWAPH=0.0
C
C NOW THE UPDATING STARTING WITH THE OLDEST AGE CLASS
        DO 109 I=ISTEP,2,-1
C ANOTHER SKIP STATEMENT IF ELEMENT IS EMPTY

```



```

      IF(APHIDS(1,I-1).NE.0.0)THEN
C NOS IN OLD AGE CLASS I-1 ARE MOVED INTO I AND SOME DIE
      APHIDS(1,I)=APHIDS(1,I-1)*SURVIV
C AGE IS UPDATED
      APHIDS(2,I)=APHIDS(2,I-1)+HRDEG
C THE TWO ELEMENTS IN I-1 ARE ZEROED
      APHIDS(1,I-1)=0.0
      APHIDS(2,I-1)=0.0
C THE AGE FOR ELEMENT I IS CHECKED FOR LONGEVITY
      IF(APHIDS(2,I).GT.ALONG)THEN
      TNWAPH=TNWAPH+APHIDS(1,I)
      APHIDS(1,I)=0.0
      APHIDS(2,I)=0.0
      END IF
C NOW TOTAL UP APHIDS
      TOTAL=TOTAL+APHIDS(1,I)
      IF(ADSKIP.EQ.1.0.AND.APHIDS(2,I).GT.PRD)TOTADR=TOTADR+APHIDS(1,I)
      END IF
109 CONTINUE
      RETURN
      END
C
C
      SUBROUTINE PREDTR(CDEN,ZMGAPH,RATSER,RATHAN,ACT,EATEN)
C
C   Calculate the biomass of aphids eaten
C
      EATEN=((RATHAN*ZMGAPH*CDEN)/((RATHAN*(1/RATSER))+ZMGAPH))*ACT
C
      RETURN
      END
C
C
      S      U      B      R      O      U      T      I      N      E
CIMDVSR(COCS,PRDGE,ISTP,TOTAL,TNCOCC,SURVCO,HRC DG,CLONG
*,ZMSKIP,INS)
      DIMENSION COCS(2,ISTP),PRDGE(2,ISTP)
      DO 111 I=ISTP,2,-1
      IF(COCS(INS,I-1).NE.0.0)THEN
      COCS(INS,I)=COCS(INS,I-1)*SURVCO
      PRDGE(INS,I)=PRDGE(INS,I-1)+HRC DG
      COCS(INS,I-1)=0.0
      PRDGE(INS,I-1)=0.0
      IF(PRDGE(INS,I).GT.CLONG)THEN
      TNCOCC=TNCOCC+COCS(INS,I)
      COCS(INS,I)=0.0
      PRDGE(INS,I)=0.0
      END IF

```

```

TOTAL=0.0
END IF
111 CONTINUE
RETURN
END

```

C

S U B R O U T I N E

```

COCDVSR(COCS,PRDGE,ISTP,TOTAL,TNCOCC,SURVCO,HRCDDG,CLONG

```

```

*,MSKIP,INS)
DIMENSION COCS(7,ISTP),PRDGE(7,ISTP)
DO 110 I=ISTP,2,-1
IF(COCS(INS,I-1).NE.0.0)THEN
COCS(INS,I)=COCS(INS,I-1)*SURVCO
PRDGE(INS,I)=PRDGE(INS,I-1)+HRCDDG
COCS(INS,I-1)=0.0
PRDGE(INS,I-1)=0.0
IF(PRDGE(INS,I).GT.CLONG)THEN
TNCOCC=TNCOCC+COCS(INS,I)
COCS(INS,I)=0.0
PRDGE(INS,I)=0.0
END IF
TOTAL=0.0
END IF

```

```

110 CONTINUE
RETURN
END

```

C

C

```

SUBROUTINE NB(IMM,IMMLEN,IMSTAR,IMFINI)
DIMENSION IMM(300)
INTEGER*4 II,N,URNLP,S,COUNTLT,COUNTGT,COUNTEQ,VALSZERO,VALUEQ
INTEGER*4 XX(8300)
REAL*8 RANDNB(8300),FXX(8300)
REAL*8 MOMP,K,PXEI,K,MU
REAL*8 XXBAR
REAL*8 VARX
REAL*8 X,G05CAF

```

```

C READ IN N (LENGTH OF CUMULATIVE PROBABILITIES ARRAY), URNLP
C (NO. OF NEG.BIN. RAND. NO.S TO BE FOUND), S (NO. OF SETS OF
C URNLP RANDOM NO.S TO BE USED)

```

```

N=8300
URNLP=IMMLEN
S=1

```

```

C K AND MU
K=0.2410
MU=1.5452
NM1=N-1
DO 410 J=1,N

```



```

      FXX(J)=0.0
410  CONTINUE
C    SET ARRAY X TO HAVE VALUES OF 0 TO NM1 FOR PROBABILITIES
      DO 411 I=1,N
      XX(I)=I-1
411  CONTINUE
      MOMPCK=MU/(MU+K)
C    PROBABILITY X=0
      PXEI=(K/(MU+K))**K
C    FIRST ELEMENT OF CUMULATIVE PROBABILITIES ARRAY FXX SET TO
C    PROB X=0
      FXX(1)=PXEI
C    CALCULATE THE CUMULATIVE PROBABILITIES UP TO X IS LESS THAN
C    OR EQUAL TO NM1 AND PUT INTO FXX
      DO 412 I=1,NM1
      PXEI=PXEI*MOMPCK*((K+I-1.)/(I))
      II=I+1
      FXX(II)=FXX(I)+PXEI
412  CONTINUE
C    SET SEVERAL COUNTERS TO ZERO
C    COUNT-NO. OF TIMES VARX.EQ/LT/GT.XXBAR
      COUNTSQ=0
      COUNTLT=0
      COUNTGT=0
      VALSEQ=0
      VALSZERO=0
49   DO 50 M=1,S
C    CALL NAG LIBRARY ROUTINE TO GENERATE UNIFORM RANDOM NUMBERS
C    FROM A CONTINUOUS DISTRIBUTION BETWEEN 0 AND 1 - PRODUCES
C    DIFFERENT NUMBERS FOR EACH CALL OF THE ROUTINE
      CALL G05CCF
C
C    SET X(1...URNLP) TO BE THE GENERATED UNIFORM RANDOM NUMBERS
      DO 408 I=1,URNLP
      X=G05CAF(X)
      DO 409 J=1,N
C    CHECK WHICH VALUES OF FXX THE RANDOM NUMBER FALLS BETWEEN
C    FIND THE CORRESPONDING VALUES OF X AND PUT THE LOWEST INTO
C    AN ARRAY RANDNB
      IF(X.GT.FXX(J))GOTO 409
      RANDNB(I)=XX(J)
      GOTO 408
409  CONTINUE
408  CONTINUE
50   CONTINUE
      DO 999 I=IMSTAR,IMFINI
      Z=((I-IMSTAR)+1)
      IMM(I)=RANDNB(Z)

```

999 CONTINUE
RETURN
END