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## DOCTOR OF PHILOSOPHY

### Modelling the spatio-temporal dynamics of aphid-parasitoid interactions

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# Modelling the spatio-temporal dynamics of aphid-parasitoid interactions

By

Ananthi Anandanadesan

A Thesis submitted for the degree of Doctor of Philosophy

Division of Mathematics

University of Dundee

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# **Declaration**

I declare that the following thesis is my own composition and that it has not been submitted before in application for a higher degree.

Ananthi Anandanadesan

# Certification

This is to certify that Ananthi Anandanadesan has complied with all the requirements for the submission of this Doctor of Philosophy thesis to the University of Dundee.

Prof. Mark Chaplain

Dr. Alison Karley

# Chapter 1

## Introduction

Aphids are pests that are harmful to plants both as consumers and as vectors of disease. In agriculture they are a significant threat, causing millions of pounds of damage globally per annum (Tatchell, 1989). Although there are various strategies used to control aphid populations, they are not fool-proof. One such strategy is the use of biological control agents such as parasitoid wasps.

This thesis explores the spatio-temporal dynamics of an aphid-parasitoid system using an individual-based model. The focus is on a system comprised of the host *Macrosiphum euphorbiae* (potato aphid) and the parasitoid wasp *Aphidius ervi*, although this model can be applied to other aphid-parasitoid systems and more generally to host-parasitoid systems with overlapping generations. More complexity is added to the model by incorporating two competing parasitoids parasitising one aphid host and also by modelling the original aphid-parasitoid system, but on multiple patches that are either adjacent or apart.

The structure of the thesis is as follows: chapter 2) biology of aphid-host parasitoid systems, chapter 3) mathematical modelling of host-parasitoid systems, chapter 4) the

individual-based mathematical model, chapter 5) modelling the dynamics of the aphid-parasitoid system, chapter 6) modelling additional complexity in the aphid-parasitoid system and chapter 7) discussion and future work.

## **Chapter 2**

# **Biology of Aphid-Host-Parasitoid Systems**

### **2.1 Aphid biology**

#### **Effect on plants**

Aphids can cause serious harm to plants through feeding and disease transmission which has resulted in millions of pounds of damage per annum in agricultural systems (Tatchell, 1989). Aphids feeding on plants inflict injury by removing resources by phloem feeding and via salivary secretions containing toxins (Williams and Dixon, 2007). Injury resulting from feeding may be asymptomatic (not apparent) or symptomatic (apparent). Aphid species that trigger a symptomatic response in plants can cause among other things chlorosis, stunting, necrosis and the production of abnormal looking fruit in plants (Quisenberry and Ni, 2007). Asymptomatic aphid species induce plant responses that are not as obvious such as a decrease in plant biomass (Quisenberry and Ni, 2007).

Aphids are also effective vectors of plant disease. The number of virus species that they have been reported to spread is about 275, several of which lead to the onset of plant diseases that are economically significant in agriculture. Virus transmission can range from being a very quick process in the case of non-persistent transmission, which requires brief contact between the aphid stylet (or mouthpart) and the plant, to a longer process in the case of persistent transmission, which requires a longer period of contact between plant and aphid vector (Katis et al., 2007). Virus transmission can also be either circulative (which is the case for viruses spread persistently) where the virus is transported through the gut and salivary gland membranes in the aphid prior to being transmitted to the plant or non-circulative (which is the case for viruses spread non-persistently) where the virus inhabits the aphid stylets and foregut (Katis et al., 2007). Besides feeding and disease transmission, aphids can also damage plants by excreting body wax and honeydew onto plant surfaces (Quisenberry and Ni, 2007). High densities of aphids can produce large quantities of honeydew which can become a breeding ground for fungi and bacteria (correspondence with Dr. A. Karley).

## **Life history**

Aphids are insects that belong to the sub-order *Homoptera*, otherwise known as plant-sucking bugs (Dixon, 1998), an apt description for this group of insects, many species of which feed on plants by imbibing phloem sap through their stylets. Most species of aphids are polymorphic, existing as asexual morphs during the spring and summer months and as sexual morphs during the autumn (Dixon, 1998). After the sexual morphs mate, the oviparous females lay overwintering eggs. The eggs hatch the following spring as the availability and growth of plant material increases, producing female morphs that initiate subsequent parthenogenetic generations (Blackman, 1974). During the spring and summer months, aphid populations are predominantly female

and reproduce through parthenogenesis (a form of asexual reproduction), giving birth to live young (viviparous). The embryos developing inside an asexual mother contain embryos as well, a phenomenon that is known as telescoping of generations (Dixon, 1973). Both parthenogenesis and telescoping of generations and the lack of a metamorphosis phase enable aphids to proliferate quickly. This type of life cycle where aphids have a period of parthenogenetic reproduction followed by a period of sexual reproduction which gives rise to eggs is called holocyclic. Some aphids do not reproduce via sexual reproduction and reproduce entirely via parthenogenesis during the year (Williams and Dixon, 2007). This type of life cycle is anholocyclic. There are aphid species that exhibit both holocyclic and anholocyclic (Williams and Dixon, 2007).

Parthenogenetic morphs can either be wingless (apterous) or winged (alate) (Dixon, 1973). They develop through four juvenile stages (1st, 2nd, 3rd, and 4th instars) before a final moult to become adults. For apterous aphids, there is often a lag of 12-24 hours between the final moult and the start of reproduction, although there is variation in the duration of this delay (correspondence with Dr. A. Karley). Nymphs destined to be alate exhibit wing buds in the 3rd-4th instar. Typically for alate individuals after becoming adult, flight exercise is required before they can reproduce, although this is also subject to variation, and some alate individuals can reproduce without flying (Kring, 1972, and references therein). Several factors can induce wing formation in aphids, and in most species, these causation factors appear to be a combination of maternal effects (conditions experienced by the mother that induces her to produce alate offspring) and conditions experienced by the juvenile aphid in early nymphal stages. Studies have shown that wing production can be induced by poor host quality, overcrowding, exposure to predators and the presence of parasitoids (Sutherland, 1969; Dixon, 1998; Lees, 1967; Muller et al., 2001; Sloggett and Weisser, 2002). The ability to produce winged morphs enables aphids to colonise more than one plant and spread over greater distances, as well as to escape poor quality plants, disturbance and natural

enemies. This adaptation, however, comes at a cost. Aphids that have wings tend to be less fecund than wingless aphids and also take longer to develop (Wratten, 1977; Hughes, 1963). The progeny of wingless aphids also are larger in size than those of winged aphids (Dixon, 1998). Aphid fecundity and development are also affected by fluctuations in temperature and the degree of crowding that they experience. Different species have different temperatures at which fecundity and development are maximised (Dixon, 1973). Crowded environments tend to give rise to adults that weigh less and produce fewer offspring (Dixon, 1973).

## **Life cycle**

Aphids undergo various life cycles. Two of the main life cycles observed in aphids are heteroecious (or host alternating) and autoecious (or non-host alternating) life cycles (Williams and Dixon, 2007). Aphids that undergo a heteroecious life cycle typically inhabit a single species of plant during the winter known as the primary host. In the summer they move to plants of an entirely different and wider range of species, known as the secondary hosts, and in the autumn they move back to the original primary host plant species (Williams and Dixon, 2007). Host alternating aphids are of particular significance because their secondary host often includes crop species. Aphids that undergo an autoecious life cycle inhabit one species of plant or switch between related plant species throughout the year (Williams and Dixon, 2007).

## **Dispersal**

Aphids, including alate aphids spend little time moving over their lifetime. Juveniles for the most part are immobile, although older instar juveniles may show a greater propensity to move by walking (not flight) (Irwin et al., 2007, and references therein).



For most heteroecious species, winged aphids cease to fly after their flight muscles autolyse which occurs a few days after becoming adult (although they still retain the ability to walk). Nevertheless, as a result of their ability to move and disperse, aphids feeding on crop plants have attained the status of a super pest. The pest status of aphids is largely due to their capacity to transmit plant diseases (Irwin et al., 2007). Alate aphids are crucial in the spread of disease and the spread of aphid infestations because they can traverse vast distances and colonise new areas. By contrast, apterous adults traverse shorter distances (via walking) in comparison with their alate counterparts, but their role is just as important. Apterous individuals are more fecund, are generally bigger and require a shorter development time than alatae, attributes that are vital for an aphid population to proliferate and expand in numbers, if not in space. Furthermore, aphid flight is very risky and most alatae that fly die before finding a host (Irwin et al., 2007).

In experiments conducted by Hodgson (1991) to study the dispersal of apterae of three different aphid species from their natal plant, there was a greater tendency for apterous dispersal away from the natal plant when plant growth declined or stopped (a causal factor being increasing pressure from aphids), although apterous dispersal did take place to a small extent at low population densities. Most dispersing apterae were either fourth instar or prereproductive adults, the aphid stages with the largest potential to produce offspring (Hodgson, 1991). Hodgson (1991) argued that apterous dispersal allows aphids to take full advantage of resources in the vicinity of the natal plant, whereas alate dispersal from the natal plant entails the risk of missing good-quality host plants near the natal plant. In contrast to Hodgson (1991), Boiteau (1997) observed little movement of 4th instar juveniles between adjacent leaves by walking in three different potato-colonising aphid species, with greatest activity from reproductive adults. In all three aphid species, dispersal was most significant in the first half

(or approximately first 10 days) of the aphid's reproductive life, after which movement diminished (Boiteau, 1997). The first 10 days of the aphids' reproductive period was also when all three species were most fecund (MacGillivray and Anderson, 1958), thus the aphids' dispersal was optimised so that their offspring could be spread over a favourable host or cluster of host plants (Boiteau, 1997, and references therein). Among potato aphids, apterous adult dispersal between plants can also be induced by environmental perturbations such as rain, wind and mechanical raking (Narayandas and Alyokhin, 2006). Apterous potato aphids, if they happen to land on bare soil, can survive on the ground for a limited time and are capable of walking directly on soil to locate a plant (Alyokhin and Sewell, 2003).

Before alate aphids can fly, they go through a teneral period which begins just after the last moult, and ends when aphids take off (Kring, 1972, and references therein). There is intra- and interspecific variation in the duration of this period (Kring, 1972). For the summer morphs of the potato aphid, a period of 24-48h has been observed at 22-24°C (Boiteau, 1986a).

Aphid pests move long distances and colonise crops via migratory flight. Migratory flight is a continuous flight in which aphid dispersal is also assisted by atmospheric currents (Irwin et al., 2007, and references therein). Migratory flight is seasonal, occurring during spring when aphids disperse from a primary to a secondary host and during the autumn when aphids disperse back to the primary host (Irwin et al., 2007, and references therein). During migration, aphids fly uninterrupted in the direction of an ultraviolet light source, disregarding any alighting cues such as potential hosts. The act of migration consists of events triggering take-off, actual take-off followed by active flight high into the atmosphere where the aphids are displaced horizontally by air currents, and lastly followed by events that result in descent and landing (Irwin et al., 2007). Events that physiologically prime aphids to take-off may include deteriorating host quality, crowding and exposure to natural enemies. The opportunity for aphids

to take-off and begin their migratory flight is limited to a small span of time that begins 12 hours after eclosion and ends about 4 days after eclosion (Irwin et al., 2007, and references therein). Aphids that ascend and reach the planetary boundary layer can be transported vast distances by the horizontal air currents in this stratum (Irwin et al., 2007). Without the assistance of air currents, aphids would not be able to cover such long distances as their flight speed is quite low, less than  $1m/s^2$ , and they are not equipped for flying such long distances using their own resources (Irwin et al., 2007, and references therein). Several crop-feeding aphid species engage in migratory flight during their maiden flight (Hardie, 1993). Flights following the maiden flight tend to be of shorter duration (Kennedy and Booth, 1963).

Aphids will postpone flights if conditions are very windy (Irwin et al., 2007, and references therein). Aphids will not take-off if the temperature is not optimal (Wiktelius, 1981) and most species will not take-off at all when there is little or no light (Irwin et al., 2007).

The urge to engage in migratory flight is turned off at some point during the flight and the aphid responds to cues that lead it towards resources (Irwin et al., 2007). Subsequent flights are not as long and are characterised by 'appetitive dispersal' or for the purposes of finding resources or escape (Irwin et al., 2007, and references therein). Appetitive dispersal is characteristic of the dispersal of summer morphs (correspondence with Dr. A. Karley). Appetitive dispersal can range from moving by walking from one part of a plant to another part, or by moving from one field to another field through walking or flight (Irwin et al., 2007). This type of dispersal can be triggered by changes in host quality (which can be due to plant injury, disease or dense aphid infestations, for example), being displaced by external factors (for example by farm machinery) or the presence of natural enemies (Irwin et al., 2007, and references therein).

Flight termination of aphids is typically under the control of the aphid (Irwin et al., 2007). Cues governing landing behaviour and subsequent host selection are mostly visual (Irwin et al., 2007, and references therein). Several aphid species are attracted to the colour yellow (Irwin et al., 2007, and references therein). The landing site of an aphid may not be a suitable host (Irwin et al., 2007). If a host is unsuitable then the aphid may fly off in search of a better host. If a host is of good quality, then the aphid may stay and deposit offspring (correspondence with Dr. A. Karley). In addition, landing is affected by ground cover (Irwin et al., 2007, and references therein). Several aphid pest species have higher landing rates when there is less ground cover (Irwin et al., 2007).

### **Host selection and nutrition**

Locating a host plant of suitable quality and plant species involves response to visual, chemical and tactile stimuli (Pettersson et al., 2007). Although newly-colonising aphids tend to be winged, many winged aphids do not find a host because the orientation of their long-distance flight tends to be controlled by air movements (Dixon, 1998; Ward et al., 1998). Aphids mainly use visual stimuli to track down a suitable host which gives an indication of plant quality. Many species of aphids are tempted to alight on yellower leaves because these tend to be more nutritious (Dixon, 1973, and references therein). Prior to landing, aphids may also use olfactory cues to locate hosts, although cues such as taste become more important after aphids land (Pettersson et al., 2007).

After landing, aphids quickly determine a host's suitability through physical contact with the plant's surface and sometimes by penetrating the surface using its stylet. This allows them to gather information on the plant's physical and chemical attributes which they use to determine whether to continue probing or to stop. If they choose to remain

on the plant, they penetrate their stylet more deeply into plant tissue until they reach a phloem vessel from which they feed as phloem sap is forced up the stylet under pressure (Dixon, 1998).

Nitrogen availability is the major nutritional limitation on growth in insect herbivores (Mattson, 1980). Aphids obtain nitrogen in the form of amino acids in phloem sap (Mittler, 1958). The quality of phloem sap, in terms of amino acid composition, can vary among plants and in different parts of the plant (Dixon, 1998), and during plant development. As plants mature, they become less attractive as sources of food because the nitrogen content in the phloem sap decreases in comparison to younger and senescent plants (Dixon, 1998). An aphid will most likely stop feeding and relocate elsewhere to find food that is more nutritious if the quality of the sap is poor. This is supported by the results of Karley et al. (2002) who showed that aphids on potato plants exhibited lower feeding rates on 'old' diets that had a similar amino acid composition to the phloem of mature plants in comparison to 'young' diets that had a similar amino acid composition to the phloem of young plants.

Once aphids have fed on the phloem sap, it must be processed. Phloem sap is a solution containing mostly simple sugars and small quantities of amino acids (Dixon, 1998). The sugars provide aphids with a carbon source for respiration and growth (Douglas and van Emden, 2007). However, essential nutrients, particularly the essential amino acids, are often at low concentrations in phloem sap (Douglas and van Emden, 2007; Dixon, 1998) and aphids must digest large amounts of phloem sap to meet their dietary needs (Dixon, 1998). Additionally, aphids harbour the obligate bacterial endosymbiont, *Buchnera aphidicola*, which produces essential amino acids that are lacking in the phloem sap diet. *Buchnera* is also suspected to recycle nitrogen from ammonia, which would otherwise be excreted as a waste product of aphid metabolism, to be reused by the host (Douglas and van Emden, 2007).

## **Microbial Endosymbionts**

A symbiotic relationship is ‘an intimate association between individuals of different species, in which one lives on or in the other’ (Townsend et al., 2000). Most aphids harbour bacterial symbionts which can be categorised as either primary or secondary. Primary symbionts have arisen from a host infection that took place 150-250 million years ago and their presence is necessary for the survival of the aphid (‘obligate’). These symbionts are passed on vertically from mother to offspring (Sandstrom et al., 2001). Most aphids harbour the primary endosymbiont *Buchnera aphidicola* (Munson et al., 1991) whose essential role in supplementing the nutrition of the aphid diet was described previously. They exhibit congruent phylogeny with the aphid host, suggesting evolution from an ancient infection and cospeciation afterwards (Martinez-Torres et al., 2001). The bacteria are located in bacteriocytes, specialist aphid cells (Buchner, 1965). The *Buchnera* genome is highly reduced (450 to 642 Mb) compared to free-living bacteria and cells carry a number of replicates of the genome that changes as aphids mature (Baumann, 2005, and references therein).

By contrast, secondary bacterial symbionts reflect a more recent evolutionary interaction and are facultative, i.e. not necessary for the aphid host to survive (Baumann, 2005, and references therein). Similarly to primary symbionts, they are transmitted vertically, but occasionally they can be transmitted horizontally (Sandstrom et al., 2001). Some secondary symbionts enhance the fitness of the host which may favour their transmission in the aphid population (Dion et al., 2011a). Dissimilar phylogeny between secondary symbionts compared to the aphid host and primary symbionts suggests that repeated infection events have occurred over time (Baumann, 2005). Many aphids harbour secondary symbionts that tend to live in syncytial cells located next to bacteriocytes, although they may reside elsewhere in aphid tissues as well (Griffiths and Beck, 1973; Fukatsu et al., 2000). Secondary symbionts can have a range of

effects on aphid fitness, for example by influencing host plant specialisation, conferring protection against parasitoid wasps and pathogens and protecting aphids from heat stress (Tsuchida et al., 2004; Clark et al., 2010, and references therein). The presence of secondary symbionts in individuals can vary within and between aphid populations (Darby and Douglas, 2003; Frantz et al., 2009). In addition, the effect of a secondary symbiont on the aphid host can differ among individuals (Dion et al., 2011b; Guay et al., 2009; Russell and Moran, 2006) possibly because of variation in aphid genotype or between strains of the same bacterial symbiont (Dion et al., 2011b; Oliver et al., 2010).

Considerable research has been conducted on interactions between the pea aphid *Acyrtosiphon pisum* and its secondary bacterial symbionts. Secondary symbionts characterised in pea aphids include *Serratia symbiotica*, *Regiella insecticola* and *Hamiltonella defensa* (Moran et al., 2005). *Serratia symbiotica* can protect the aphid against heat stress (Burke et al., 2009; Russell and Moran, 2006). In *Acyrtosiphon pisum*, heat stress lowers fecundity and general aphid fitness mainly by reducing the titre of the primary symbiont *Buchnera aphidicola* (Ohtaka and Ishikawa, 1991; Douglas, 1998; Guay et al., 2009). *Serratia symbiotica* appears to protect aphids from heat stress by maintaining the integrity of bacteriocytes containing *Buchnera aphidicola* (Burke et al., 2009; Russell and Moran, 2006).

*Regiella insecticola* protects pea aphids from a fungal pathogen (Scarborough et al., 2005) and can influence aphid-plant interactions (Tsuchida et al., 2004). *Pandora (Erynia) neoaphidis* is a fungal pathogen that kills aphids within days, leaving spores on the carcass to germinate and potentially infect other nearby aphids (Scarborough et al., 2005). Through this mechanism it can easily eliminate an entire aphid population. *R. insecticola* protects aphids from this pathogen by decreasing the likelihood of spores forming on the aphid carcass. While this does not prevent the attacked aphid from being killed, it does increase the chances of survival of the aphid population as a whole

(Scarborough et al., 2005). As well as conferring resistance to a fungal pathogen, *R. insecticola* has also been shown to enhance pea aphid performance on white clover in Japan, compared to other legume host plants (Tsuchida et al., 2004).

*Hamiltonella defensa* protects pea aphids from the parasitoid wasp *Aphidius ervi* (Oliver et al., 2003). Wasp eggs laid in pea aphids harbouring *H. defensa* fail to develop, allowing the aphid to live and produce offspring (Oliver et al., 2003, 2006). This resistance is associated with a bacteriophage that infects *H. defensa* known as *Acyrtosiphon pisum* secondary endosymbiont (APSE). APSE encodes toxins which may prevent wasp development (Oliver et al., 2009). In a study conducted by Oliver et al. (2009), absence of the phage left aphids harbouring *H. defensa* more vulnerable to parasitoid attack. Degree of protection provided by *H. defensa* can range from partial to complete resistance depending on the strain of *H. defensa*/APSE (Oliver et al., 2010).

Dion et al. (2011b) showed that over several generations parasitoids can develop increased virulence towards aphids harbouring *H. defensa*, becoming as successful at infecting aphids as parasitoids attacking aphids without *H. defensa*. This virulence, however, may come at the cost of a reduction in wasp size (Dion et al., 2011b) which is also associated with a reduction in reproductive output (Godfray, 1994). Infection with *H. defensa* can also lead to changes in behaviour of the aphid. Pea aphids harbouring *H. defensa* were less likely to exhibit defensive behaviour (i.e. dropped off plants less and were less combative) than pea aphids without *H. defensa* (Dion et al., 2011b). Defensive behaviours, while decreasing the likelihood of aphids succumbing to parasitoid attack, can also decrease its chances of survival and its feeding time, resulting in reduced fitness (Nelson, 2007). Therefore, it would seem that aphids harbouring *H. defensa* would have the advantage of being able to resist parasitoid wasps while not suffering the fitness decrements that result from defensive behaviours (Dion et al., 2011b). However, aphids also fend off other natural enemies with behavioural



defences (Gross, 1993). Therefore, although aphids harbouring *H. defensa* are resistant to attack from parasitoid wasps, their lack of defensive behaviours means that they are potentially more vulnerable to predators (Dion et al., 2011b).

## **Aphid Mortality and Biological Control**

Aphids can suffer mortality through natural enemy attack, resource limitation, exposure to extreme weather (for example being knocked off plants in very windy or rainy conditions) or during dispersal.

Natural enemies of aphids include predators, parasitoids and pathogens which as a group can be called Aphidophaga. Predators of aphids include ladybirds (Coccinellidae), hoverflies (Syrphidae), lacewings (Chrysopoidea) and midges (Itonididae) and these insects instantly kill aphids by consumption. For some predators, not all individuals are predacious. For instance, only the larval stages of Syrphidae, Chrysopoidea and Itonididae consume aphids and not the adult stage. In other predators such as Coccinellidae, both larvae and adults consume aphids (Völkl et al., 2007).

In contrast to predators, parasitoids do not immediately kill the host. Some aphid parasitoids (those in the subfamily Aphidiinae (Hymenoptera: Braconidae) and certain genera in the family Aphelinidae) are endoparasitoids (Völkl et al., 2007), i.e. they develop within the host. The females insert eggs into the aphid body, from which larvae emerge that survive and grow by eating the aphid from the inside out, eventually killing it. In contrast to the larval stages, parasitoid adults are free-living (Völkl et al., 2007).

Parasitoids are thought to be effective at limiting aphid populations because they are prey-specific, have a generation time similar to that of their host and have the capacity to produce a large number of offspring (Snyder and Ives, 2003). The parasitoids that attack *M. euphorbiae* most commonly are *Aphidius ervi* and to a lesser extent, *Praon vulgare* (correspondence with Professor S. Hubbard).

Pathogens of aphids include fungi which produce infectious spores that germinate on the aphid cuticle, killing the aphid within days (Völkl et al., 2007). Fungal pathogens thrive in moist conditions and when host density is high (Snyder and Ives, 2003). It is not unusual for aphids to be attacked by fungal pathogens and in some cases they can be the sole cause of an aphid population crash.

Under optimal conditions, natural enemies have the potential capacity to limit aphid populations to a level at which they cannot cause serious economic harm. Yet this is rarely achieved in field conditions due to abiotic factors that disrupt or limit searching efficiency or success of predators, parasitoids and pathogens. The effect of natural enemies is also diminished by intraguild predation, where different species of natural enemies share the same prey, but also natural enemy species feed on other natural enemy species. Nevertheless, natural enemies can significantly reduce the density of aphids in crops and have been used in biological control programmes (Völkl et al., 2007).

## **Defence against natural enemies**

Aphids are not completely defenceless against natural enemies. For instance, they can escape predators and parasitoid wasps either by walking away, flying or dropping off plants entirely or they can defend themselves by kicking (Sloggett and Weisser, 2002; He, 2008) or covering their attacker in a waxy substance also known as waxing (Irwin

et al., 2007). The latter usually occurs with the excretion of an alarm pheromone that communicates the danger to other aphids (Pickett and Glinwood, 2007). In studies of pea aphids, upon exposure to predators and parasitoids, pea aphids tend to produce winged offspring, a delayed form of defence (Minoretti and Weisser, 2000; Sloggett and Weisser, 2002). However, there are fitness trade-offs between defence mechanisms and the risks associated with escaping. Winged individuals are often less fit than wingless individuals and flying itself is life-risking. Also, dropping off plants does not ensure that aphids will necessarily land in safer territory.

## **Chemical ecology**

The interactions between aphids and the interspecific interactions between aphids and parasitoids and aphids and plants are mediated by semiochemicals. Aphids emit sex pheromones to enhance chances of mating (in the case of sexual morphs), and other semiochemicals to signal danger and alert other aphids to danger and to mediate aggregation and competition. Aphids use semiochemicals emitted from plants to locate a suitable host (Pickett and Glinwood, 2007). Parasitoids use chemical cues emitted directly by aphids in honeydew (Gardner and Dixon, 1985; Budenberg et al., 1992), aphid sex pheromones (Glinwood et al., 1999; Hardie et al., 1991) and volatile signals emitted from aphid-infested plants to locate an aphid host (Du et al., 1996, 1998).

### ***Macrosiphum euphorbiae***

*Macrosiphum euphorbiae* is a host alternating species of aphid (Williams and Dixon, 2007) that is of particular interest because it is a pest species that is problematic in Scotland. *M. euphorbiae*, commonly known as the potato aphid, seldom produces

overwintering eggs on *Rosa* spp.<sup>1,2</sup>. Instead, it mostly exists as mobile forms on weeds, potato sprouts in stores and lettuce below glass during winter<sup>1</sup>. During May/June alate individuals form and disperse to crops including potato<sup>1</sup>. *M. euphorbiae* is extremely polyphagous, utilising more than 200 different species of plants that encompass greater than 20 different families as secondary hosts (Blackman and Eastop, 2007). The potato aphid favours *Solanaceae*, in particular potato as its summer host<sup>1</sup>. If aphid infestations become very dense, another migration event can occur in July<sup>1</sup>. During autumn, a much smaller scale dispersal event takes place<sup>1</sup>.

According to a field study conducted by Davis et al. (2007), potato aphids became reproductively mature from as young as 9.8 to 17.7 days old. Potato aphids reproduce quickly and asexual morphs tend to produce between 30 and 50 nymphs each during adulthood<sup>3</sup>. In experimental work from the studies of Karley et al. (2002, 2003), the average lifespan of potato aphids was measured as 40.5 days. However, this value is probably not realistic as the aphids were monitored in clip cages, and thus were sheltered from natural enemies and external risk factors that they would have otherwise been exposed to (Karley et al., 2002, 2003, Dr. A. Karley, pers. comm.).

As a vector of disease, the potato aphid is not as dangerous as other species (such as *Myzus persicae*), but nevertheless can spread diseases such as Potato leaf roll virus, Beet mild yellowing virus, Beet yellows virus (BYV) and Lettuce mosaic virus<sup>1</sup>. Also, at high densities, potato aphids can cause false top roll or curling of leaves, which can reduce crop yields (Evans, 2000).

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<sup>1</sup> [http://www.rothamsted.ac.uk/insect-survey/STMacrosiphum\\_euphorbiae.php](http://www.rothamsted.ac.uk/insect-survey/STMacrosiphum_euphorbiae.php)

<sup>2</sup> Information from [http://www.rothamsted.ac.uk/insect-survey/STMacrosiphum\\_euphorbiae.php](http://www.rothamsted.ac.uk/insect-survey/STMacrosiphum_euphorbiae.php) applies mainly to UK *M. euphorbiae*

<sup>3</sup> <http://www.inra.fr/hyppz/RAVAGEUR/6maceup.htm>

## 2.2 Aphid and Aphid-Natural Enemy Models

The dynamics of many summer aphid populations on agricultural plants in temperate regions tend to consist of an exponential increase in abundance to a midsummer peak, followed by a dramatic decline in numbers. The reduction of aphid numbers from peak counts to almost nonexistence, otherwise known as the mid-season crash, occurs over a few days and tends to occur shortly after mid-summer (Karley et al., 2004). Studies suggest that the mid-season crash occurs in aphid populations on natural vegetation as well (Karley et al., 2004, and references within). Aphid populations tend to peak a second time in the autumn when sexual morphs are produced, but this was not captured in the model developed here because the second peak is not always observed in aphid populations and involves multiple underlying factors, among them effects of photoperiod and weather and reduced natural enemy pressure (correspondence with Dr. A. Karley).

Mathematical modelling can be a useful tool for understanding the dynamics of an aphid outbreak and the underlying biological processes that cause the mid-summer population crash. However, many modelling studies of aphid dynamics have concentrated on tree aphid species that are not usually significant crop pests (Dixon, 1998; Kindlmann et al., 2007) or tend to focus on aphid population dynamics outwith the asexual summer phase. Regardless, they provide insight into aphid population dynamics in general and inform us about key biological features of aphids that should be taken into account in aphid models. This section first covers models that describe aphid population dynamics followed by a section on models that describe aphid-natural enemy dynamics.

## **Aphid Models**

Studies suggest that many aphid populations are regulated by density-dependent feedback (Dixon, 1985; Alyokhin et al., 2005; Woiwod and Hanski, 1992; Maudsley et al., 1996). A few aphid models developed around the assumption that density-dependent feedback in aphid populations is dependent on cumulative population size (Prajneshu, 1998; Matis et al., 2007, 2008a,b, 2009). These models are derived from the aphid model of Kindlmann (1985), which is essentially a generalised logistic growth model that includes cumulative-size dependence. For this model and other cumulative-size based models described here, the accumulated damage of resources by aphids (due to feeding, excretion of honeydew, inviting predators etc.) is assumed to be proportional to the cumulative-density of previous populations. The survival of future generations of aphids is affected by the past destruction and therefore per-capita death rate is assumed to be dependent on cumulative population density (Matis et al., 2008a). Prajneshu (1998) solved the model in Kindlmann (1985) analytically, deriving a non-linear regression model that was later reparameterised by Matis et al. (2007). Characteristic of the models described in Kindlmann (1985); Prajneshu (1998); Matis et al. (2007) is their symmetry. The non-linear regression model of Matis et al. (2007) has been fitted to population data for aphid pests such as the mustard aphid and cotton aphid (Matis et al., 2007, 2008b) and provides reasonably accurate simulations of the population dynamics of these species.

Since some aphid data sets indicate the occurrence of immigration, Matis et al. (2008a) developed cumulative-size based models with immigration, one with continuous immigration and another with restricted immigration. The models with immigration provided a better fit to mustard aphid population data than the Matis et al. (2007) model (without immigration) (Matis et al., 2008a). In Matis et al. (2009), Kindlmann's model is generalised to include power-law kinetics producing a skewed population abundance

curve since many empirical aphid population abundance curves are slightly left-skewed and not symmetric. The model was fitted to observed data for the soybean aphid, and while the model provided a superior fit to data than Kindlmann's symmetric model, its parameter estimates lacked precision (Matis et al., 2009).

Williams et al. (1999) constructed an exponential growth model with decreasing intrinsic rate of growth ( $r$ ) to describe the population growth of aphids *Myzus persicae* and *Aphis fabae* feeding on sugar beet. An assumption of the model is that the intrinsic growth of both types of aphid decreases with declining host quality as plants age (Williams et al., 1999). Reduced host plant quality as plants mature is also believed to be a contributing factor to the decline in summer aphid populations (Williams et al., 1999; Karley et al., 2004). In Costamagna et al. (2007) the decreasing  $r$  model was fitted to soybean aphid data and, in addition to providing a favourable representation of the data, it made reasonable forecasts.

Simulation models have also been used to capture the dynamics of aphid populations. For example, Lombaert et al. (2006) developed an individual-based simulation model of the population dynamics and movement of the melon aphid in a melon field in order to assess how dispersal strategy affects fitness. The model is not explicitly spatial, but does have a spatial component. Optimal dispersal parameters from the model were evaluated in relation to dispersal rate parameters obtained from experiments. Results indicated that dispersal parameters for rates at which walking and flying aphids are generated on leaves largely influences aphid fitness and the extent to which dispersal parameters affect aphid fitness is influenced by plant traits (Lombaert et al., 2006).

Morgan (2000) used simulation modelling to capture the population dynamics of the bird cherry-oat aphid in barley during autumn and winter. Their model was used to gauge the impact of different population processes on aphid dynamics. Results from the model were compared to field data from aphid outbreaks on barley. The model

described the outbreaks quite well, estimating peak aphid density within 20% of the empirical data and the timing of peak density within 14 days of empirical data in most instances. Varying mortality of apterous nymphs and temperature were both shown to have a significant effect on the dynamics of the system (Morgan, 2000).

Unlike the models described above, which do not explicitly represent space, the individual-based simulation model presented by Parry et al. (2006) does. Their model describes the dynamics of aphid populations in agricultural landscapes and takes into account how the characteristics of the landscape affect individuals. The model was used to explore the population dynamics of the bird cherry-oat aphid on winter cereals in Hertfordshire under different pesticide regimes. Data input into the model included habitat data (divided up into regions of favourable, marginal and unfavourable habitat), temperature, wind speed and wind direction. Validation of the model without pesticide with field data suggests that the model adequately estimates aphid population size. Output from the model indicates that wind affects aphid distribution considerably and varying temperature has important temporal and spatial implications. Raising mortality resulted in decreased aphid movement and sparsely populated low quality habitat. Also, the results indicated that the timing of pesticide spray relative to aphid immigration waves strongly influenced the capacity of pesticides to decrease aphid numbers (Parry et al., 2006).

The models described above reveal some of the aspects of aphid biology and abiotic factors that have been used to capture aphid dynamics. In a review by Karley et al. (2004), reduced plant quality and natural enemy pressure were mentioned as factors contributing to the mid-season crash in aphid populations, but there was no hard evidence to show that either factor alone could cause the population crash. Rather, Karley et al. (2004) suggest that more likely more than one factor plays a role in the



mid-season population crash. While the model of Williams et al. (1999) represents the effect of declining plant quality on population growth, this model and the other aphid models do not address the effect of natural enemies explicitly.

### **Aphid-Natural Enemy Models**

The mid-season population crash has been attributed to the following factors in the literature: growing effect of natural enemies, changes in plant quality and weather (Karley et al., 2004, and references within). Declining quality of host plants as they mature has been reported as a contributing factor to the decrease in summer aphid field populations (Williams et al., 1999; Karley et al., 2003, 2004). In a study done by Karley et al. (2003) changes in the amino acid composition of phloem sap (in particular a decline in the concentration of glutamine) in potato crops were noted in the weeks leading up to the mid-season aphid population crash. These changes occur in parallel with a decline in aphid fecundity by 25-45% (in the absence of natural enemies) suggesting that changes in plant quality is a causal factor of the mid-summer population crash (Karley et al., 2003).

The onset of the mid-summer crash is also associated with an increase in the abundance of natural enemies. Natural enemy exclusion experiments performed on potato and cereal plants showed that aphid numbers declined by 10-70% and 30-100% respectively in the presence of natural enemies (Boiteau, 1986b; Karley et al., 2003; Jones, 1979; Holland and Thomas, 1997; Sigsgaard, 2002). Therefore, increasing pressure from natural enemies could also be a causal factor.

The evidence suggesting that weather conditions may be a causal factor as well is not very strong. Though severe weather conditions can wipe out entire aphid populations and aphids are sensitive to changes in temperature, weather has not been identified as a consistent causal factor of the aphid population crash (Karley et al., 2004).

Various models have been developed which consider one or more of the above factors. For example, Karley et al. (2003) developed an excitable medium model representing summer aphid population dynamics in which aphid reproduction changes in response to developmental changes in plants and influence of natural enemies changes over time using experimental data. In the model, small initial populations of aphids and natural enemies coexist, but as plant material increases aphids experience higher levels of reproduction, which enables the aphid population to grow quickly to a maximum. After some time has lapsed during which the aphid population is still at its peak, the population undergoes a steep decline due to growing pressure from natural enemies. The model provided a good representation of the population dynamics of *Macrosiphum euphorbiae* and its natural enemies in the field during summer. As well, it was able to capture the variation in population dynamics between years that was reported in field experiments (Karley et al., 2003).

Unlike Karley et al. (2003), the model of Ro and Long (1999) factor in how climate affects aphid population processes. Ro and Long (1999) constructed a model of the summer population dynamics and phenology of the green peach aphid on potato. The model captures the interaction among aphids, predators and temperature. Time was modelled in developmental degree days (Ro and Long, 1999). The model provided a good description of field data (Ro and Long, 1999).

In contrast to the model in Karley et al. (2003) which lumps natural enemies into one complex, Snyder and Ives (2003) consider the effects of parasitoids and predators on aphids separately in their stage-structured aphid-natural enemy model. The results

from the model agreed with experimental data; both of which indicated that during a harvest cycle the effects of generalist predators (comprising mainly *Nabis* and *Orius* bugs, coccinellid and carabid beetles, and spiders) and specialist parasitoids (*Aphidius ervi*) on the pea aphid in alfalfa are additive. The model does imply, however, that running experiments for a longer period than the harvest cycle would probably show nonadditive effects due to intraguild predation on parasitoids whose effect on aphid numbers is delayed (Snyder and Ives, 2003). The model shows that even when predator and parasitoid effects are nonadditive, the natural enemy complex as a whole is more successful in regulating the pea aphid population than either just parasitoids or just predators, that is unless the level of mummy predation is high (Snyder and Ives, 2003).

Ekbom et al. (1992) combined predator foraging simulations with an aphid population growth model that also describes aphid phenology. The resulting spatial, nonlinear model showed that varying predator density affects peak aphid density and under certain conditions predators can inhibit an outbreak of *Rhopalosiphum padi* (Ekbom et al., 1992).

Lopes et al. (2007) modelled the interactions between aphids and parasitoids in a (spatially heterogeneous) greenhouse using a spatially implicit approach. The flux-based model consists of a partial differential equation that describes changes in plant infestation coupled to an ordinary differential equation that captures parasitised aphid dynamics and a delay-differential equation that captures parasitoid dynamics. The model was used to simulate the aphid-parasitoid system comprising *Aphis gossypii* and *Lysiphellus testaceipes*, on melon plants (Lopes et al., 2007). Results indicated that the initial host distribution and initial parasitoid density were important in determining the population dynamics of the system. Also, the model was sensitive to changes in the time delay in the parasitoid equation and the rate of aphid population increase (Lopes et al., 2007). Lopes et al. (2010) compared the modelling approach in Lopes et al. (2007) to a spatially explicit approach and found that the population dynamics generated from

both models were in agreement most of the time, although the behaviour of the models became more dissimilar when there was a lot of local movement in the spatially explicit model. However, the spatially implicit model is seen as an acceptable compromise which captures enough detail to make forecasts (Lopes et al., 2010).

Wolfgang et al. (1997) showed using a simulation model that rain and wind altered parasitisation patterns of *Aphidius rosae* on aphids in rose bushes (in agreement with results from a field study) and the reproductive success of *A. rosae* which have ramifications at the population level.

Although there are spatial aphid and aphid-natural enemy models in the literature, the research in this area of study is limited and furthermore, there are relatively few aphid related models that explore the spatial heterogeneity of these systems. In addition, there is a lack theoretical study that specifically is aimed towards understanding the mid-summer crash in aphid populations. The work presented here investigates some of these gaps in the study of aphid dynamics by exploring the spatial dynamics of an aphid-parasitoid system and modelling spatial heterogeneity, although at the level of two patches. Also, the aphid-parasitoid model here has been analysed for its behaviour during the peak season and how varying certain model parameters affects this behaviour.

## **2.3 Parasitoid biology**

Since parasitoid wasps are one of the more effective biological control agents among aphids natural enemies, knowledge of their biology may be useful for finding ways to control an aphid outbreak. Parasitoids are insects whose larvae require a host to survive. While adults are free living, larvae survive by feeding on an arthropod host and in the process killing their host. Larvae need only one host to grow and develop

and sometimes several larvae develop on one host (Godfray, 1994). The adult female typically locates the host and lays its eggs on or near the host. These eggs hatch, developing into larvae and then pupae before emerging as adults (Godfray, 1994).

Parasitoids can be either solitary or gregarious, with either one or more feeding on an individual host, respectively. Most parasitoids can be categorised as either endoparasitoids or ectoparasitoids (Godfray, 1994). Endoparasitoids grow inside the host while ectoparasitoids survive outside the host (Godfray, 1994). Parasitoids that do not impede host development post-parasitism are known as koinobionts, whereas, parasitoids that do are known as idiobionts (Godfray, 1994, and references therein). Many aphid parasitoids belong to the order *Hymenoptera* (Völkl et al., 2007) and several are species that also belong to the subfamily Aphidiinae (Mackauer and Starý, 1967).

## **Aphidiinae**

Species that fall under this category are solitary endoparasitoids and most have short generation times. While larvae require a host to survive, the adults' diet consists of aphid honeydew and extrafloral nectaries (Völkl et al., 2007). Aphidiinae females are highly fecund; females can carry 200-400 mature eggs in their ovaries at any given time. For the most part, females tend to give birth to males or females depending on whether the egg is unfertilised or fertilised, respectively (Völkl et al., 2007, and references therein). Usually, females lay one egg per aphid host (Völkl et al., 2007, and references therein), however, superparasitism (when more than one egg is laid on an individual host by the same species) is possible particularly if hosts that are not already parasitised are few (Godfray, 1994; Völkl et al., 2007, and references therein). However, only a single larva from each host emerges as a parasitoid due to larval competition or physiological suppression (Völkl et al., 2007, and references therein). *Aphidius ervi* is an Aphidiinae species that is of particular relevance to the study conducted here.

## *Aphidius ervi*

*Aphidius ervi* is a koinobiont parasitoid wasp that is prey-specific and has a similar generation time to that of its host, qualities that are ideal in a biological control agent (He, 2008; Snyder and Ives, 2003). When foraging, *A. ervi* appears to use olfactory cues to locate the habitat of its aphid host from afar. Wind tunnel studies conducted on *A. ervi*'s behavioural response to odours from sources that include its host *Acyrtosiphon pisum* and broad bean plants suggest that *A. ervi* may locate the host's habitat using plant volatiles emitted in response to aphid infestation (Du et al., 1996; Guerrieri et al., 1993). *A. ervi* may also be able to improve its capacity to forage through experience and previous exposure to aphid-infested plants according to wind tunnel studies conducted on *A. ervi* and its host *A. pisum* on bean plants (Du et al., 1997; Guerrieri et al., 1997).

Host location by *A. ervi* appears to be governed by both visual and semiochemical cues at short distances. Studies have shown that green pea aphid colour can generate an oviposition attack response in *A. ervi* (Battaglia et al., 1995, 2000). Studies have also demonstrated that semiochemical cues such as pea aphid cornicle secretion, exuviae and honeydew can trigger an oviposition attack response by *A. ervi* (Battaglia et al., 2000; Du et al., 1997).

Experimental studies showed that *A. ervi* has a preference for 2nd and 3rd instar pea aphid hosts (Ives et al., 1999; He, 2008) over younger aphids because of their greater size and over older aphids which are better at fending off attackers (He, 2008). Once the parasitoid locates a suitable aphid host according to preference and availability, *A. ervi* attacks the aphid by stinging it with its ovipositor, paralyzing the aphid. The parasitoid wasp then deposits the egg into the host using its ovipositor (Godfray, 1994). It must be noted that not all attacks by parasitoids result in an egg being laid. After it is laid, the egg takes 3 days to hatch and develops into a larva. The larval stage takes ~8

days (He, 2008). Seven days post parasitism, aphids become mummified and are dead (He, 2008). The parasitoid larva pupates inside the aphid mummy and after 5-6 days ecloses (He, 2008; Snyder and Ives, 2003). Adults can live anywhere from 10-20 days (He, 2008, correspondence with Professor S. Hubbard). After eclosion, females mature eggs for 1-2 days before they can lay (correspondence with Professor S. Hubbard).

## **Chapter 3**

# **Mathematical Modelling of Host-Parasitoid Systems**

### **3.1 Literature Review**

The study of host-parasitoid systems has a long and rich history. Many attempts have been made to understand the dynamic behaviour of these systems using mathematical models. Most of the non-spatial models are based on the Nicholson-Bailey model (1933; 1935) (in discrete time) or the Lotka-Volterra predator-prey model (1920; 1926) (in continuous time) (Briggs and Hoopes, 2004). (Predator-prey is also a metaphor for host-parasitoid interactions.) A fundamental difference between the Nicholson-Bailey and Lotka-Volterra models is that the Lotka-Volterra model assumes that generations are overlapping, i.e. the Nicholson-Bailey model uses a discrete-time approach with nonlinear difference equations while the Lotka-Volterra model uses a continuous time approach with ordinary differential equations.



Lotka and Volterra's predator-prey model captures the dynamics of a predator-prey system using the following system of ordinary differential equations:

$$\frac{dV}{dt} = rV - aPV, \quad (3.1)$$

$$\frac{dP}{dt} = caPV - dP, \quad (3.2)$$

where  $V$  is the number of prey,  $r$  is the intrinsic growth rate,  $a$  is the predator attack rate,  $P$  is the number of predators,  $c$  is the conversion efficiency at which prey are converted into new predators and  $d$  is the death rate of predators. Non-dimensionalising the system by substituting the following variables

$$V = \frac{d\tilde{V}}{ac}, \quad P = \frac{r\tilde{P}}{a}, \quad t = \frac{\tilde{t}}{r}, \quad \gamma = \frac{d}{r}$$

and dropping the tildes gives the following system of equations:

$$\frac{dV}{dt} = V(1 - P), \quad (3.3)$$

$$\frac{dP}{dt} = \gamma P(V - 1), \quad (3.4)$$

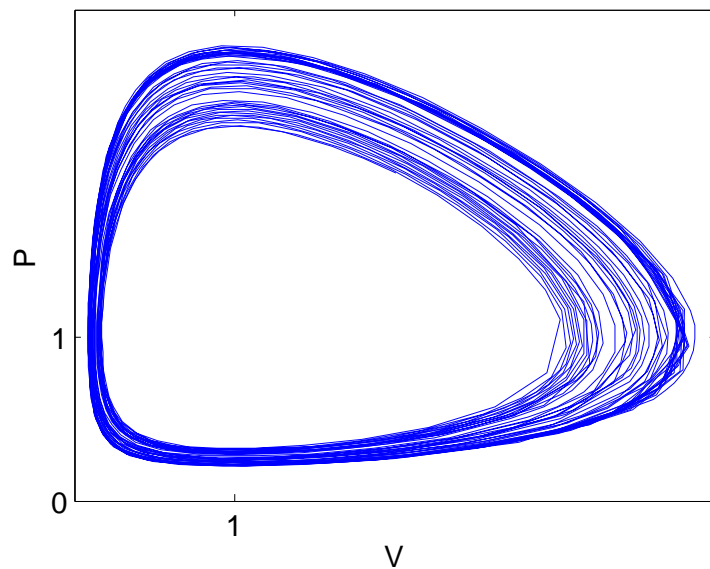
which has equilibrium points at  $(V^*, P^*) = (0, 0)$  and  $(V^*, P^*) = (1, 1)$ . Phase plane analysis can be used to determine the qualitative behaviour of the system described in equations 3.3, 3.4 (Murray, 1993). If this system is considered in the  $V$ - $P$  phase plane, the following equation is obtained:

$$\frac{dP}{dV} = \gamma \frac{P(V - 1)}{V(1 - P)}. \quad (3.5)$$

Solving 3.5 gives the phase trajectories

$$\gamma V + P - \ln V^\gamma P = K, \quad (3.6)$$

where  $K > 1 + \gamma$  is a constant (Murray, 1993). Figure 3.1 shows the family of closed trajectories generated from plotting equation 3.6 for  $K > 1 + \gamma$  in the  $V$ - $P$  phase plane.



**Figure 3.1:** Phase curves described by equation 3.6 for different values of  $K$ .

The closed phase curves suggest  $P$  (predator) and  $V$  (prey) have oscillatory solutions in  $t$  and figure 3.1 suggests that the Lotka-Volterra model is structurally unstable. That is, two orbits initially close together are not continually close together (Murray, 1993). Given its qualitative behaviour, the Lotka-Volterra model is not very useful for describing natural predator-prey or host-parasitoid populations because it predicts that these interactions verge on being unstable when in reality they have persisted for years.

If the system is linearised about its equilibrium points  $(V^*, N^*)$ , information on the stability of the equilibria can be obtained as well as the types of dynamics that emerge in

the neighbourhood of these equilibria. Using  $x$  and  $y$  to represent deviations from equilibrium and letting  $\dot{V} = F(V, P)$  and  $\dot{P} = G(V, P)$ , linearisation about the equilibrium gives

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} \approx \begin{pmatrix} F_V & F_P \\ G_V & G_P \end{pmatrix}_{(V^*, P^*)} \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} 1 - P^* & -V^* \\ \gamma P^* & \gamma(V^* - 1) \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = A \begin{pmatrix} x \\ y \end{pmatrix} \quad (3.7)$$

where  $A$  is referred to as the Jacobian matrix (Murray, 1993; Kot, 2001). Substituting the trivial equilibrium  $(V^*, P^*) = (0, 0)$  into equation 3.7 gives

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} \approx \begin{pmatrix} 1 & 0 \\ 0 & -\gamma \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix} = A \begin{pmatrix} x \\ y \end{pmatrix} \quad (3.8)$$

for which the general solution is

$$x(t) = B_1 \exp(\lambda_1 t), \quad y(t) = B_2 \exp(\lambda_2 t) \quad (3.9)$$

where  $B_1$  and  $B_2$  are constants. The equilibrium is locally stable if the eigenvalues  $\lambda_i$  of the Jacobian matrix are less than 0. The Jacobian matrix in equation 3.8 has eigenvalues  $\lambda_1 = 1$  and  $\lambda_2 = -\gamma$  which indicates that  $(V^*, P^*) = (0, 0)$  is unstable and the opposite signs of  $\lambda_i$  indicate that the equilibrium is a saddle point.

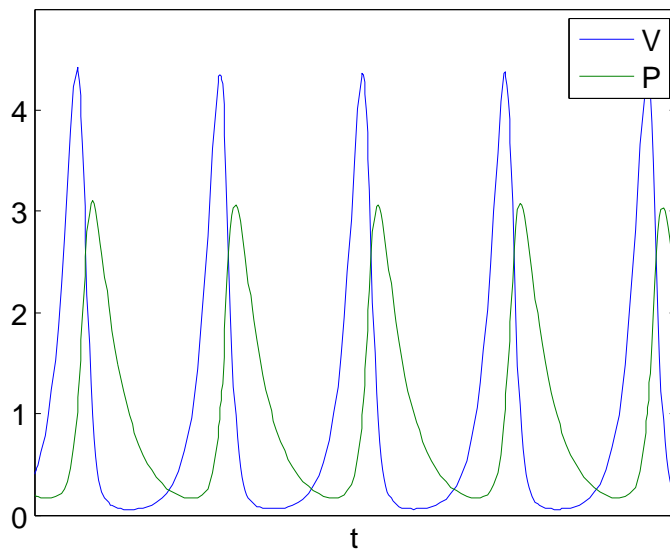
Considering the equilibrium point  $(P^*, V^*) = (1, 1)$  and substituting this into equation 3.7 gives

$$\begin{pmatrix} \dot{x} \\ \dot{y} \end{pmatrix} \approx \begin{pmatrix} 0 & -1 \\ \gamma & 0 \end{pmatrix} \begin{pmatrix} x \\ y \end{pmatrix}. \quad (3.10)$$

The eigenvalues of the Jacobian matrix are  $\lambda_1 = i\sqrt{\gamma}$  and  $\lambda_2 = -i\sqrt{\gamma}$ . As  $\lambda_i$  are purely imaginary, the equilibrium is a centre and is neutrally stable. Equation 3.10 has solution

$$\begin{pmatrix} x(t) \\ y(t) \end{pmatrix} = C_1 \underline{u} \exp(i\sqrt{\gamma}t) + C_2 \underline{v} \exp(-i\sqrt{\gamma}t), \quad (3.11)$$

in which  $\underline{u}$  and  $\underline{v}$  are eigenvectors and  $C_1$  and  $C_2$  are constants. Near the equilibrium  $(P^*, V^*) = (1, 1)$ , the solutions are therefore oscillatory in nature. Figure 3.2 shows predator-prey cycles generated from the Lotka-Volterra model.



**Figure 3.2:** *Oscillatory solutions to the Lotka-Volterra model over  $t$ .*

The Lotka-Volterra model can be extended by considering a more general version of the model in which there are  $n$  predators each of which prey on all  $n$  species of prey in the system though at various intensities.

This 'modified' Lotka-Volterra system is given by

$$\frac{dV_i}{dt} = V_i \left[ r_i - \sum_{j=1}^n a_{ij}P_j \right], \quad (3.12)$$

$$\frac{dP_i}{dt} = P_i \left[ \sum_{j=1}^n c_{ij}a_{ij}V_j - d_i \right], \quad (3.13)$$

for  $i = 1, \dots, n$  and  $r_i, a_{ij}, c_{ij}, d_i > 0$ .

This system has a trivial equilibrium at  $V_i^* = P_i^* = 0$  (for all  $i$ ) with corresponding Jacobian matrix

$$A = \begin{pmatrix} r_1 & & & & \\ & \ddots & & & \\ & & r_n & & \\ & & & -d_1 & \\ 0 & & & & \ddots \\ & & & & & -d_n \end{pmatrix}. \quad (3.14)$$

The eigenvalues of the Jacobian are  $\lambda_i = r_i > 0$ ,  $\lambda_{n+i} = -d_i < 0$  for  $i = 1, \dots, n$  which indicates that this equilibrium is unstable. The system in equations 3.12, 3.13 also has a non-trivial equilibrium given by the vectors  $\underline{V}^*, \underline{P}^*$ . Linearising about this equilibrium gives a  $2n \times 2n$  Jacobian matrix

$$A = \left( \begin{array}{c|c} 0 & B \\ \hline C & 0 \end{array} \right) \quad (3.15)$$

in which the top left and lower right blocks represent zero matrices of dimension  $n$ ,  $B$  is an  $n \times n$  matrix with coefficients  $-a_{ij}V_i^*$  and  $C$  represents the  $n \times n$  matrix with coefficients  $c_{ij}a_{ij}P_i^*$ . The eigenvalues of the Jacobian either consist entirely of purely imaginary numbers or do not. The equilibrium is neutrally stable if  $\text{Re}\lambda_i = 0$  for all

$i$  otherwise if  $Re\lambda_i \neq 0$  for any  $i$ , then the equilibrium is unstable (Murray, 1993). Perturbations to this equilibrium give rise to a Hopf bifurcation or change of state from a stable focus to an unstable focus which results when eigenvalues in the complex plane cross the imaginary axis from left to right (de Roos, 2011).

There are some more recent continuous non-spatial host-parasitoid models, but these are few in comparison to the number of discrete non-spatial host-parasitoid models. Ives (1992) and Murdoch and Stewart-Oaten (1989), for example, developed continuous models of host-parasitoid systems and studied the effect of parasitoid aggregation and spatial heterogeneity on the dynamics. Ives (1992) analysed and compared three different continuous models and concluded that the effect of spatial heterogeneity and parasitoid aggregation varies from model to model and advised against making any general conclusions about their effect on the dynamics of continuous models (Ives, 1992). Murdoch and Stewart-Oaten (1989) developed an ordinary differential equation model to study the effect of parasitoid aggregation on host-parasitoid dynamics. They found that parasitoid aggregation tends to be destabilising rather than stabilising as it is in discrete systems (Murdoch and Stewart-Oaten, 1989).

Křivan and Sirot (1997) took a slightly different approach to modelling a host-parasitoid system in continuous time. They developed a host-parasitoid model consisting of ordinary differential equations that includes a parameter which describes how parasitoids allocate their time between searching for host and non-host food. The parameter value is chosen so that individual parasitoid fitness is maximised. Křivan and Sirot (1997) concluded from their model that optimising time sharing between searching for host and non-host food in order to maximise individual fitness can stabilise the dynamics of a host-parasitoid system.

There also are quite a few studies that use delayed-differential equations to model host-parasitoid systems. Some of these models (Murdoch et al., 1987; Godfray and Hassell, 1989; Gordon et al., 1991; Murdoch et al., 1997, 1992; Briggs et al., 1999) show that when stage structure is incorporated, different types of oscillations can emerge such as generation cycles (which have a period equal to the generation time of the host), longer period cycles and delayed feedback cycles which can result when older juvenile hosts are more profitable to the female parasitoid. In most of these models the time delay is fixed which corresponds to a fixed development time. (Xu et al., 2010), in contrast, consider continuous-time models of host-parasitoid interactions with distributed development times in the host and parasitoid to find out how this variation affects the stability of these interactions. They considered two types of age-structured models, one where parasitoid search is random and there is an invulnerable host stage and another where parasitoid search is described by a negative binomial distribution and that gives rise to generation cycles. Variation in development times is represented by a shifted gamma distribution. In the random parasitism model distributed development in the host confers stability, whereas in the negative binomial model both distributed development in the host and parasitoid confer stability. Hosts with different development times are not equally susceptible to parasitoid attack and this skewed distribution of risk may be an underlying stabilising mechanism (Xu et al., 2010).

A disadvantage of using the Lotka-Volterra or Lotka-Volterra-based models is that they represent generations as being continuous, whereas in many (but not all) insect populations generations evolve in a discrete manner (Royama, 1973). Nicholson and Bailey (1933; 1935), in contrast to Lotka and Volterra, modelled host-parasitoid systems in discrete time using the following difference equations:

$$N_{t+1} = rN_t \exp(-aP_t), \quad (3.16)$$

$$P_{t+1} = N_t(1 - \exp(-aP_t)), \quad (3.17)$$

where  $N_t$  is the number of hosts at time  $t$ ,  $r$  is the rate at which the host population increases,  $a$  is the area that a parasitoid forages within on average during its entire life and  $P_t$  is the number of parasitoids at time  $t$  (Nicholson, 1933; Nicholson and Bailey, 1935).

Dynamically, the model has a trivial equilibrium at  $(N^*, P^*) = (0, 0)$  when both species become extinct and an equilibrium at  $(N^*, P^*) = \left(\frac{r \ln r}{(r-1)a}, \frac{\ln r}{a}\right)$  when both species co-exist (Kot, 2001). The Jacobian matrix for the system is

$$A = \begin{pmatrix} r \exp(-aP_t) & -arN_t \exp(-aP_t) \\ 1 - \exp(-aP_t) & aN_t \exp(-aP_t) \end{pmatrix}. \quad (3.18)$$

Substituting in the trivial equilibrium values gives a diagonal matrix with eigenvalues  $\lambda_1 = r$  and  $\lambda_2 = 0$ . Since the system is discrete,  $|\lambda_i| < 1$  in order for the equilibrium to be stable. If  $r > 1$  the equilibrium is therefore unstable and is a saddle point.



Substituting in the values of the nontrivial equilibrium gives the Jacobian matrix

$$A = \begin{bmatrix} 1 & -\frac{r \ln r}{r-1} \\ 1 - \frac{1}{r} & \frac{\ln r}{r-1} \end{bmatrix}, \quad (3.19)$$

which has characteristic polynomial

$$P(\lambda) = \lambda^2 - \left[1 + \frac{\ln r}{r-1}\right]\lambda + \frac{r \ln r}{r-1} = 0. \quad (3.20)$$

In order for the equilibrium to be asymptotically stable, the magnitude of the roots of the characteristic polynomial must be less than 1. This is true if the following Jury conditions are satisfied for  $r > 1$ :

$$P(1) > 0, \quad (3.21)$$

$$P(-1) > 0, \quad (3.22)$$

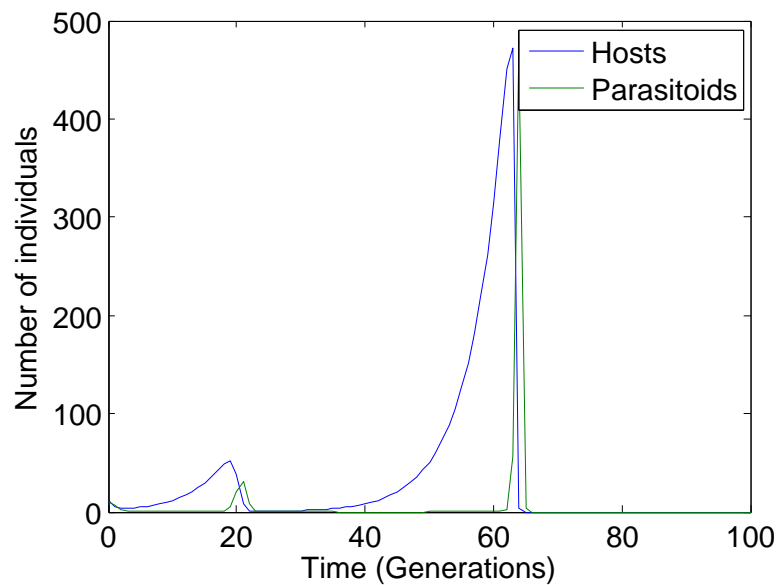
$$\lambda \bar{\lambda} < 1, \quad (3.23)$$

or the above condition can be rewritten as

$$\frac{r \ln r}{r-1} < 1. \quad (3.24)$$

$P(1) = \ln r > 0$ , therefore condition 3.21 is satisfied (Kot, 2001).  $P(-1) = 2 + \frac{r+1}{r-1} \ln r > 0$ , therefore condition 3.22 is satisfied. Rewriting condition 3.24 as  $S(r) = r - 1 - r \ln r > 0$  and allowing  $r = 1$  shows that this condition is not true and also the slope of  $S(r)$  is less than or equal to 0 and decreasing, therefore the steady state is not asymptotically stable

(Kot, 2001). Slight perturbations to this equilibrium give rise to oscillations of increasing amplitude that result in the extinction of one or both species (Kot, 2001). Figure 3.3 shows the oscillatory dynamics characteristic of the Nicholson-Bailey model. The unstable nature of the dynamics is not consistent with observations from nature where host-parasitoid interactions are comparatively more stable and persistent (Hassell and May, 1973). Also, the model makes the somewhat naive assumptions that parasitoids forage randomly and have a constant searching efficiency which is not representative of nature where parasitoids tend to respond to the density of hosts and parasitoids when making foraging decisions and, in some cases, also chemical cues in the environment (Hassell and May, 1973, correspondence with Professor S. Hubbard).



**Figure 3.3:** *Plot showing cyclic dynamics from the Nicholson-Bailey model.*

Since the work of Nicholson and Bailey (1933; 1935), there has been a proliferation of research on modelling host-parasitoid systems. Other models emerged based on the Nicholson-Bailey model with assumptions that were more realistic and/or could account for the relative stability of natural host-parasitoid populations. For example, some models included the more realistic assumption that parasitoids'/predators'

searching efficiency depends on host density rather than being constant (Holling, 1959; Royama, 1973; Rogers, 1972). Other models incorporated aspects of host-parasitoid biology that not only made these models more representative of actual host-parasitoid systems, but that could also stabilise an otherwise unstable Nicholson-Bailey model. For example, some models incorporated mechanisms which can be stabilising such as parasites'/predators' searching efficiency depending on parasite/predator density (Hassell and Varley, 1969; Hassell and Rogers, 1972), heterogeneity in risk of attack from parasitoids (Hassell and May, 1973; May, 1978), an invulnerable age class and a host carrying capacity (Briggs and Hoopes, 2004, and references therein).

Spatial heterogeneity in risk of attack from parasitoids has been acknowledged as a strong stabilising mechanism in host-parasitoid systems and has been given much attention to in theoretical studies (Holt and Hassell, 1993; Beddington et al., 1978; Chesson and Murdoch, 1986; Hassell and May, 1973). This type of spatial heterogeneity generates a more clumped distribution of parasitoid attacks across space (Hassell, 2000a). An example of how this spatial heterogeneity can be modelled in a host-parasitoid system is by varying the risk of parasitoid attack across patches in a patchy system. This was done by Hassell and May (1973).

Hassell and May (1973) modified the Nicholson-Bailey model by considering the spatial spread of populations. In their model they allocate a proportion of the host  $\alpha_i$  and parasite populations  $\beta_i$  to each of  $n$  areas such that

$$\left( \sum_{i=1}^n \alpha_i = 1; \sum_{i=1}^n \beta_i = 1 \right). \quad (3.25)$$

Hence the Nicholson-Bailey model becomes

$$N_{t+1} = FN_t \sum_{i=1}^n \alpha_i \exp(-a\beta_i P_t), \quad (3.26)$$

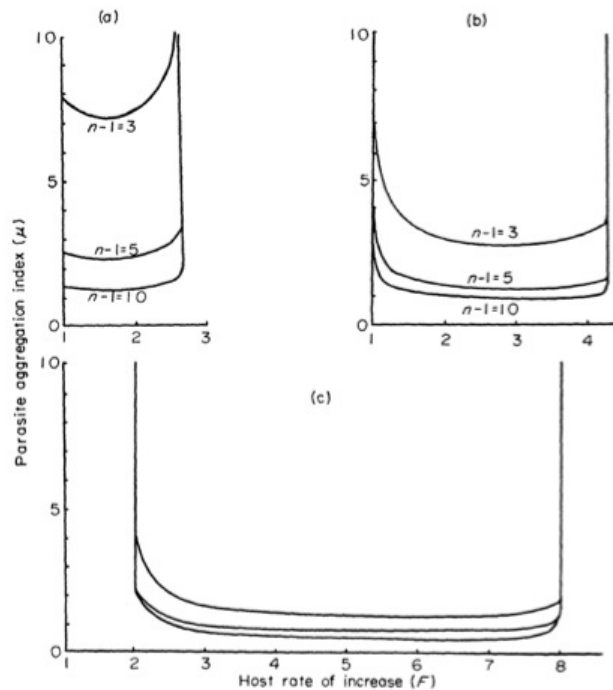
$$P_{t+1} = N_t \left(1 - \sum_{i=1}^n \alpha_i \exp(-a\beta_i P_t)\right), \quad (3.27)$$

where  $N_t$  is the number of hosts at time  $t$ ,  $F$  is the rate at which the host population increases,  $\alpha_i$  is the proportion of the host population  $N(t)$  in area  $i$ ,  $a$  is the searching efficiency,  $P_t$  is the number of parasitoids at time  $t$ ,  $\beta_i$  is the proportion of the parasitoid population  $P_t$  in area  $i$  and  $n$  is the number of unit areas over which the host and parasite populations are spread (Hassell and May, 1973).  $\mu$  is used to represent the population spread of the parasite in respect to the host distribution such that

$$\beta_i = c\alpha_i^\mu, \quad (3.28)$$

where  $c$  is a constant (Hassell and May, 1973).

The model of Hassell and May (1973), in contrast to the Nicholson-Bailey model, can be stable if the spatial distribution of hosts is skewed and there is a strong tendency for parasitoids to aggregate in areas where hosts are very abundant. They illustrated this by analysing a scenario with a population of parasites and a population of hosts which are allocated such that one area contains a high density of hosts and all other  $n - 1$  areas contain a low density of hosts. Parasites are distributed in relation to the host distribution according to  $\mu$  in equation 3.28 (Hassell and May, 1973). Figure 3.4 shows the results of their analysis. From this figure it can be inferred that parasite aggregation promotes stability and the degree of parasite aggregation needed to stabilise the system in this example is much higher when there are fewer areas of low host density (i.e. the host distribution is less skewed) for a given value of  $\alpha$ .



**Figure 3.4:** Plots showing stability regions in the  $\mu$  versus  $F$  parameter space as the number of areas containing a lower abundance of hosts ( $n - 1$ ) and the fraction of the host population in the area containing the largest abundance of hosts are varied. In (a), (b), (c)  $\alpha$  is 0.3, 0.5, 0.7, respectively. Reproduced with copyright permission from Hassell and May (1973).

While the study of Hassell and May (1973) and other early work on discrete-time host-parasitoid systems (Hassell and May, 1974; Murdoch and Oaten, 1975; Beddington et al., 1978) stress the importance of density-dependent parasitism on stability, more recent studies (for eg. Chesson and Murdoch (1986); Hassell et al. (1991); Hassell (1984)) suggest that host density-independent and inverse density-dependent patterns can be just as stabilising. Chesson and Murdoch (1986) studied and analysed several models including May's phenomenological model (1978), models with explicit parasitoid aggregation to host density and models with parasitoid aggregation independent of host density and studied how they are related. From their analysis they

were able to show that clumping of parasitoids that is not a consequence of host density stabilises Nicholson-Bailey based models and that this stabilising mechanism is more widespread than that of parasitoid aggregation to host density. They also showed that stability is equally likely to arise from inverse density dependence as it is from density dependence in space (Chesson and Murdoch, 1986). This recognition of the importance of density-independent and inverse density-dependent patterns to the stability of host-parasitoid systems is being given more attention to (see Hassell and Wilson (1997); Hassell (1984); Hassell and May (1988); Walde and Murdoch (1988); Pacala et al. (1990); Hassell et al. (1991)) and could account for the persistence of host-parasitoid systems under circumstances where density-dependent patterns may not.

Discrete-time models can also give rise to more complex dynamics such as chaos (Rohani and Miramontes, 1995; Beddington et al., 1975). For example, Beddington et al. (1975) showed that with the addition of density-dependent growth in the prey population, the Nicholson-Bailey model can exhibit high period limit cycles or chaos.

Some models of host-parasitoid systems have also explored the Allee effect whereby a population experiences negative growth at low densities, often dictated by a critical threshold (McCarthy, 1997; Liu et al., 2009). For example, Liu et al. (2009) studied a host-parasitoid model with an Allee effect for the host population and a clumping effect in the parasitoid population in discrete time. The inclusion of the Allee effect appears to decrease the complexity of dynamics that are generated in the model in the absence of the Allee effect.

Discrete-time models have an updating function which links the population densities on a specific day in the current year to the population densities on the same day of the past year. This function also accounts for the sum effect of all biological processes that occurred during the year (Singh and Nisbet, 2007). A problem with this approach

is that it does not account for the effects of continuous population change during the year due to various processes, some of which may be synchronous, and therefore the sum effect of all these processes on the updating function is not so clear (Singh and Nisbet, 2007). Using an alternative approach, Singh and Nisbet (2007) considered a hybrid model where the updating function represents biological processes occurring during the year as continuous and reproduction as a discrete process. This approach is known as semi-discrete (Pachepsky et al., 2008). Singh and Nisbet (2007) used this approach to study the effect of the type of functional response and density dependence on the stability of a host-parasitoid system. Their results from assessing the effect of functional response form on the stability of host-parasitoid interactions were very different from prior results produced from heuristically derived models suggesting further exploration of hybrid models may be useful.

In nature, it is usual for multiple parasitoid species to parasitise the same host species and for multiple host species to be parasitised by the same parasitoid (Hackett-Jones et al., 2008; Hassell, 2000b). There has been much work on multispecies systems that looks at smaller functional units of a multispecies web, for example a system consisting of a parasitoid/predator species attacking two different host/prey species (Hastings and Godfray, 1999; Holt, 1977; Comins and Hassell, 1976) or a host/prey species being attacked by two different parasitoid/predator species (May and Hassell, 1981; Briggs et al., 1993; Hassell and May, 1986) or a system consisting of a host, parasitoid and hyperparasitoid (Beddington and Hammond, 1977; May and Hassell, 1981; Hassell, 1979). These studies use models based on the Lotka-Volterra or Nicholson-Bailey formulation, but with an additional species. In a system with a parasitoid attacking two different species of hosts, the hosts may or may not compete with each other for resources (Hassell, 2000b). If the host species do compete, parasitoid 'switching' between hosts can promote coexistence. If there is no direct competition between hosts for resources, the hosts still may compete via apparent competition (Hassell, 2000b).

In basic models, apparent competition between two hosts with a shared natural enemy is an unstable interaction, but can be made stable through various mechanisms including ‘switching’ that is caused by parasitoid aggregation to host density. The introduction of a second parasitoid to a host-parasitoid system can lead to varying dynamics as a result of the stability of the constituent host-parasitoid interactions such as unsuccessful invasion of the parasitoid, exclusion of the other parasitoid species or persistence of all species in the system. These systems are typically more robust than similar systems with two hosts and one parasitoid as long as the separate host-parasitoid interactions are also stable. Systems with a host, parasitoid and a hyperparasitoid are typically more robust than systems with two primary parasitoids attacking a shared host. In a host-parasitoid system with the addition of a hyperparasitoid, density dependence affecting parasitoids and a greater searching efficiency in the hyperparasitoid compared to the primary parasitoid can promote persistence (Hassell, 2000b).

Preedy et al. (2010) developed an ordinary differential equation model of infection transmitted by contact to study the impact of incorporating a host infection vectored by parasitoids in a host-two-parasitoid system. The effects of horizontal and vertical transmission of infection on the system were analysed. Dynamics generated from the model are very complex. Horizontal transmission is stabilising whereas vertical transmission has the opposite effect and can lead to the onset of chaos (Preedy et al., 2010).

Hackett-Jones et al. (2008) developed a discrete-time host-multiple parasitoid model that captures the phenology of hosts and parasitoids to see whether this has any impact on the system’s dynamics. They found that differences in the timing of parasitism and emergence affect coexistence, but they believe these factors do not account for the ubiquity of host-multi-parasitoid systems. Similarly, Cobbold et al. (2009) studied the effect of parasitoid phenology (specifically parasitoid emergence time) on the



dynamics of a discrete-time host-parasitoid system, but rather than focus on competition between two parasitoid species, they focused primarily on competition between parasitised and non-parasitised hosts. The period of competition is influenced strongly by the parasitoid emergence time. They concluded that host competition diminishes the response of parasitoids to fluctuations in host density and decreases the likelihood of cyclic dynamics that tends to occur when the numerical response of parasitoids is stronger. They also concluded that parasitoids that emerge later tend to lead to more host outbreaks, though of lower intensity than parasitoids that emerge earlier.

Some models have used a metapopulation framework to study host-parasitoid systems (Rohani and Ruxton, 1999; Taylor, 1998; Reeve, 1988). A metapopulation is comprised of smaller subpopulations that exist in separate patches that are connected by dispersal (Levins, 1969). This approach is not explicitly spatial, but crudely accounts for spatial structure. Rohani and Ruxton (1999), for example, studied a host-parasitoid metapopulation model with dynamics described by nonlinear difference equations to assess how dispersal impacts stability. A significant difference in the fraction of individuals dispersing between each species may be destabilising. They show that density-dependent fecundity of the host and the existence of host refugia reduce the occurrence of instabilities driven by dispersal whereas positive-feedbacks due to thresholds in host reproduction or inverse density-dependent parasitism augment dispersal driven instability. Taylor (1998) also studied metapopulation host-parasitoid models in discrete time where dispersal is such that a constant fraction of the population in each patch leaves to be divided up among all patches. Within-patch dynamics were represented by either the Nicholson-Bailey model or the negative binomial model of May (1978). Variability was introduced through either spatio-temporal variability or spatial environmental variability in addition to altering rate of movement and the instability of individual patches (Taylor, 1998). Results from the study indicated that as movement increased, more environmental variability was necessary to prevent the system from

collapsing. This impact of environmental variability is weaker when individual patch dynamics become less stable. In certain cases, spatial variability was better at promoting persistence than spatio-temporal variability, although with more variation among trials. In the absence of environmental stability persistence happens within a more reduced set of movement rates.

In nature host-parasitoid dynamics evolve over time and space, and there has been a growing trend towards using spatial models to capture the dynamics of these systems. Tilman and Kareiva (1997) demonstrate the significance of space in ecological issues and show how it can shed light on answers to some ecological problems, for example the dynamics and end state in a host-parasite system. The non-spatial models mentioned above adopt a mean-field approach, whereby individuals experience the same environmental conditions and are equally likely to interact with all other individuals in the system. This is not representative of nature where interactions between individuals are affected by space and population processes depend on environmental conditions. Various approaches have been used to model the spatio-temporal dynamics of host-parasitoid/predator-prey systems including reaction-diffusion equations (Pearce et al., 2006; Preedy et al., 2007; Sherratt et al., 1995), patch models (Ives, 1992), individual-based systems (Keeling, 2000; Schofield et al., 2002, 2005a), coupled map lattices (Mistro et al., 2009; Sisterson and Averill, 2004; Savill et al., 1997) and integrodifference equations (Cobbold et al., 2005; Wright and Hastings, 2007). The dynamical behaviour of spatial models can differ significantly from that of a mean-field approach (Durrett and Levin, 1994a; Rand et al., 1995).

Reaction-diffusion equations represent time and space in a continuous manner. Unlike the mean-field approach, the reaction-diffusion model accounts for spatial inhomogeneity. However, it is not ideal for modelling small-scale interactions or local stochasticity (Durrett and Levin, 1994a, and references therein). Reaction-diffusion models can generate complex dynamics. For example, Pascual (1993) developed a

reaction-diffusion model of a predator-prey system whereby predators had a type II functional response and prey exhibited logistic growth. Without the spatial aspect, the model's dynamics are either stable or consist of limit cycles. The explicit modelling of space, however, can give rise to quasi-periodic dynamics or chaos. Chaotic dynamics have also been observed in other continuous systems when space is explicitly considered, without which the systems do not give rise to complex dynamics (Crutchfield and Kaneko, 1987; Vastano et al., 1990). Preedy et al. (2007) developed a reaction-diffusion model of a system consisting of a host, two parasitoid species and a pathogen. The underlying ordinary differential equation model indicates that the pathogen is required in order for the two parasitoid types to coexist and generates various dynamics such as chaos when the infection is added to the system. The spatial model, in which the host and parasitoids move by random diffusion, generates dynamics that include travelling waves and additional complex dynamics (Preedy et al., 2007). Output from the model indicates that the infection enables the less competitive parasitoid to persist by diminishing the impact of interspecific competition. The results also show initial transient dynamics, the duration of which can be prolonged (Preedy et al., 2007).

Pearce et al. (2006) studied a two host, two parasitoid reaction-diffusion model where one of the parasitoid species is a generalist and the other is a specialist. The model gives rise to spatio-temporal dynamics consisting of stable travelling waves when parasitoids invade. As certain parameter values are varied, these waves become irregular periodic travelling waves which generate spatio-temporal heterogeneity in the system. In another paper Pearce et al. (2007) developed a reaction-diffusion-chemotaxis model of a multi-species host-parasitoid system where parasitoids exhibit chemotactic movement (nonrandom search governed by response to changes in kairomone concentration). The model generates interesting dynamics including quasi-chaotic dynamic heterogeneous spatio-temporal patterns, quasi-stationary heterogeneous patterns and

destabilisation of equilibria. The authors show that chemotaxis causes the spatio-temporal heterogeneity and destabilisation of equilibria (Pearce et al., 2007).

Using an approach that combines experimental with theoretical study, Dwyer and Elkinton (1995) studied the impact of movement of the host and disease infectiousness on the spread of diseases. They conducted an experiment whereby they introduced a nuclear polyhedrosis virus (NPV) into populations of uninfected gypsy moth and measured the dispersal of ballooning first instar larvae, the stage of larvae that exhibits the most dispersal. They found that although larvae dispersal could explain the spread of infection in the first few weeks, it could not account for the spread of disease afterwards which was much greater than the larvae (Dwyer and Elkinton, 1995). Believing that a high rate of disease transmission as well as larvae dispersal could account for the spread of infection, they compared the experimental data to the results of a reaction-diffusion mathematical model describing the spread of insect pathogens which also factors in disease transmission and host movement. They used the model to predict the rate of virus spread, however, the results did not agree with the experimental data suggesting that the combination of disease transmission and host dispersal cannot account fully for the spatial spread of the virus.

Sherratt et al. (1995) showed that in a reaction-diffusion predator-prey model, spatio-temporal chaos can arise following a wave of invasion of predators if the underlying dynamics are periodic and predators and prey move via diffusion. Combining diffusion with predator-prey cycles may generate irregular dynamics that later can become chaotic, an example of diffusion-driven instability.

In another paper, Sherratt et al. (1997) investigated whether the wake of a predator invasion of prey is characterised by similar behaviour in various predator-prey models (reaction-diffusion equations, coupled map lattices, cellular automata and integrodifference equations) that have underlying cyclic dynamics and random dispersal of

predators and prey. In all models they found the behaviour following invasion was similar, characterised by irregular or regular spatiotemporal oscillations.

Schofield (2002) studied reaction-diffusion and integro-difference equation models of the disease *Wolbachia* transmission in dispersing insect *Drosophila simulans* populations. Cytoplasmic incompatibility is captured in the models as well as imperfect maternal transmission. For the same parameterisation, the various models generate dynamics that are not the same. Also, the outcome of *Wolbachia* invasion may hinge on the pattern of insect movement.

Patch models, in contrast to reaction-diffusion models, treat individuals as being discrete and are more amenable to looking at local, stochastic interactions. Patch models, as their name implies, organise space into patches whose arrangement and accessibility may or may not be otherwise indicated (Durrett and Levin, 1994a, and references therein). As an example, Comins et al. (1992) studied a 2-d patch model in which interactions between parasitoids and hosts are described by difference equations. Fractions of the hosts and parasitoids in each patch move locally during each generation, connecting locally unstable subpopulations and host reproduction rate is constant. They show that this mixing of subpopulations via movement can enable the system to persist. The model also gives rise to various complex spatial dynamics such as spiral waves, spatial chaos and ‘crystal lattice’ patterns or the system can collapse entirely. The fraction of hosts and parasitoids moving to other patches during each generation determines the resulting spatial dynamics.

Nguyen-Huu et al. (2006) also studied a patchy host-parasitoid model with underlying dynamics described by difference equations. Patches are connected via dispersal and the host exhibits logistic growth. Similarly to the model described in Comins et al. (1992), only a fraction of hosts and parasitoids disperse from each patch and these individuals can disperse to any of the 8 closest patches (Nguyen-Huu et al., 2006). Insects

move many times prior to laying offspring during each generation. The movement frequency of hosts and parasitoids was varied to see how this would influence spatial dynamics. Nguyen-Huu et al. (2006) found that the model can give rise to spatial structures such as spiral waves. They also concluded that when movement frequency is sufficiently increased, patches become spatially synchronised and spatial structure is lost.

Individual-based models, similarly to patch models, represent individuals as discrete, but the level of spatial detail is more refined. These models, rather than subdividing space into patches, typically divide space into cells which allows local stochasticity and spatial phenomena that are not local to be easily modelled (Rand et al., 1995; Durrett and Levin, 1994a,b). Although spatial individual-based models allow for an explicit treatment of individual interactions, space and stochasticity, this comes at a cost. These models are more difficult to analyse mathematically, requiring the use of numerical methods. This is in contrast to reaction-diffusion models which are more amenable to mathematical analysis. An example of an individual-based model is that of Schofield et al. (2005b) which captures host-parasitoid-microbe interactions and evolution of certain phenotypes including dispersal and movement. The model was used to study evolutionary dynamics in a spatially organised, stochastic setting. Initially, the distribution of characteristic values for a particular characteristic is even, but may change following selection (Schofield et al., 2005b). The model then incorporates *Wolbachia*, a bacterium that causes a bias in the sex ratio, to examine its spread via horizontal and vertical transmission while the degree of parasitoid superparasitism is varied. Model output indicates that reducing the refractory period after oviposition leads to a greater occurrence of superparasitism. The output also suggests that the relatively constant fraction of parasitoids infected with *Wolbachia* does not change when the degree of superparasitism is changed although the mechanism maintaining this differs for high

and low degrees of superparasitism. At low levels of superparasitism vertical transmission of *Wolbachia* is more prevalent and at high levels, horizontal transfer becomes important.

Coupled map lattice (CML) models are used to represent spatially structured populations on a two-dimensional patchy environment such that each patch is represented by a cell on a grid (Mistro et al., 2009). As an example, Mistro et al. (2009) used a CML approach to model a host-parasitoid system with underlying host-parasitoid dynamics described by the Nicholson-Bailey model and in an environment with partial refuge areas. Their aim was to see whether the spatial heterogeneity resulting from the refuges had any effect on the dynamics of the system. They found that refuges can either stabilise or destabilise the system and spatial patterns can arise due to the heterogeneity of the environment.

Savill et al. (1997) also studied a CML host-parasitoid model although this model included evolution in the aggregation strength of parasitoids. Using this model, they assessed the consequences of self-structuring spatial patterns on the ecological and evolutionary dynamics of the system. The spatial pattern can influence the direction of selection on aggregation strength and the resulting evolutionary consequences can in turn affect the self-structuring processes. As another example, White et al. (1996) developed a discrete CML host-pathogen model with movement between adjacent patches taking place in between generations. From their model they found that a diminished natural loss of pathogen particles can lead to a greater chance of the metapopulation becoming obsolete and they found that their model could generate radial wave patterns. In fact, the dynamics of the model can shift between two quasi-stable patterns, spirals and radial waves.

Integrodifference models are spatially continuous extensions of difference equations. They capture the lives of organisms that have a stationary and a mobile phase (Cobbold et al., 2005). This approach was used by Cobbold et al. (2005) and Wright and Hastings (2007) to model host-parasitoid systems. Cobbold et al. (2005) applied their model to a critical patch-size problem to glean how the required critical patch-size for parasitoid survival changes with parasitoid emergence time. They found that early emerging parasitoids require a smaller habitat for survival than late-emerging parasitoids and early emerging parasitoids give rise to more intense host outbreaks. Wright and Hastings (2007) used an integrodifference model to describe host-parasitoid interactions to see if they could account for stable spatial patterns that occur when parasitoids move much faster than their hosts (see Comins et al. (1992)). They found that their model can in fact account for these spatial patterns. Also they found that as in the field, the hosts are packed more closely to the edge of an outbreak, a pattern which occurs when there is a significant Allee effect in the host and unstable temporal dynamics.

Dynamics resulting from the different types of spatial models described above can vary significantly because the approach taken can affect the qualitative dynamics (Durrett and Levin, 1994a; Schofield et al., 2005a). This is especially apparent in the study done by Schofield et al. (2005a) who developed an individual-based stochastic model to capture the spatio-temporal dynamics of host-parasitoid interactions where host and parasitoid generations are synchronised. Individual movement parameters are obtained from a discretised partial differential equation host-parasitoid model which allows for comparison of the continuous and discrete models. In the model both within-generation and between-generation processes operate to control populations. Also, individuals are posed on a two-dimensional space and interactions between individuals are influenced by kairomones. When the hosts and parasitoids move at different rates,



the discrete and continuous models exhibit different dynamics. For a given set of parameters, the discrete model gives rise to spatio-temporal heterogeneity while the continuous model gives rise to a spatially homogeneous equilibrium. Though this study shows that different modelling approaches can give rise to entirely different dynamics, there are quite a few studies that have shown that spatio-temporal heterogeneity can emerge from spatial predator-prey and host-parasitoid models using both discrete and continuous approaches (Schofield et al., 2005a; Pearce et al., 2006; Preedy et al., 2007; Sherratt et al., 1995) suggesting that this is a general behaviour of these models. Spatial host-parasitoid models have also been shown to give rise to chaotic behaviour (Preedy et al., 2007; Sherratt et al., 1995).

The model studied here is based upon the work of Pearce et al. (2006) and Schofield et al. (2002, 2005a). Pearce et al. (2006) developed a reaction-diffusion 2-host-2-parasitoid model where hosts grow logistically. The model explored in this thesis similarly captures overlapping generations and describes a host with density-dependent growth using a PDE model similar to that of Pearce et al. (2006) to derive the probabilistic movement rules for individuals. Unlike the model of Pearce et al. (2006), the model here is stochastic and also individual-based. Schofield et al. (2002) developed an individual-based model to study a host-parasitoid system comprising a solitary, koinobiont parasitoid and a host that emits kairomones (or chemicals) at a certain rate which are used by the parasitoid to locate the host. The movement rules for their model are derived from discretised partial differential equations (PDEs) (see chapter 4 for details of the technique) shown here:

$$\frac{\partial h}{\partial t} = \delta_h \nabla^2 h, \quad (3.29)$$

$$\frac{\partial w}{\partial t} = \delta_w \nabla^2 w - \chi_w \nabla \cdot (w \nabla k), \quad (3.30)$$

$$\frac{\partial k}{\partial t} = \delta_k \nabla^2 k + \mu h - \rho k, \quad (3.31)$$

where equations 3.29 and 3.30 describe the movement of the host ( $h$ ) and parasitoid ( $w$ ), respectively and equation 3.31 describes the concentration of kairomone ( $k$ ).  $\delta_h$ ,  $\delta_w$  and  $\delta_k$  are the diffusion coefficients of the host, parasitoid and kairomone, respectively,  $\chi_w$  is the parasitoid's chemotaxis coefficient,  $\mu$  is the rate at which an individual host generates kairomone and  $\rho$  is the kairomone decay constant (Schofield et al., 2002). The equations represent the within-generation dynamics of the system, thus there are no births and deaths represented in the equations as these processes are assumed to take place at the end/beginning of each generation. Hosts move via random diffusion. Parasitoids can move via random diffusion and/or chemotaxis. Parasitoids also search for hosts using knowledge gained from prior experience or adopt a naive strategy. When a generation ends, the unparasitised hosts lay eggs which become the next generation of hosts. Those hosts that are parasitised in the current generation become the next generation of parasitoids. Schofield et al. (2002) demonstrated that the dynamics generated from the model were sensitive to changes in parameters that include diffusion rate of kairomones, parasitoid foraging behaviour and host egg load.

In contrast to the work of Schofield et al. (2002), the biological system that I am studying here includes a host with overlapping generations. Adult aphid hosts produce offspring for several consecutive days, so there is no clear distinction between generations. Despite this, the technique used by Schofield et al. (2002) to derive probabilistic movement rules can also be applied to the system studied here.

## Chapter 4

# The Individual-Based Mathematical Model

### 4.1 Introduction

The ecological focus of this thesis is on modelling the population dynamics of summer potato aphid populations in Scotland. Summer morphs predominate on potato plants from late May/ early/mid June to early/mid September (correspondence with Dr. A. Karley), otherwise known as the peak season. The model here is simulated typically for 210 days which is about twice the duration of the potato aphids' peak season. The system being modelled is initially made up of populations of parthenogenetic female potato aphids and parasitoid wasps distributed randomly on one or more  $5m \times 5m$  field plots that contain several potato plants. The initial aphid population is comprised of newly matured adults that later produce juveniles and the initial parasitoid wasp population is comprised of newly emerged parasitoids.

## 4.2 The Basic Mathematical Model

A spatial, individual-based model was developed to study the dynamics of the aphid-host-parasitoid system. State variables include the number of juvenile aphids, adult aphids and parasitoid wasps. Each individual aphid and parasitoid in the model has a set of movement and behavioural rules. Movement rules were obtained by discretising appropriate partial differential equations. Rules governing individual behaviour and interactions between individuals are based on data from the literature, observations and life histories of host and parasitoid individuals. In the model aphids are described by a set of parameters that includes lifespan, fecundity, diffusion coefficient, probability of not surviving to adulthood and fraction of adults migrating to another patch. Parasitoids similarly are described by a set of parameters that includes handling time, lifespan, diffusion coefficient, probability of discovering an aphid, success of parasitism, giving up time and fraction of parasitoids migrating to another patch. The model was solved computationally using C++. Individual simulations required anywhere from several minutes to a few days to run depending on the grid size used and number of grids being modelled, with larger grids and multiple grids requiring more computational time. What follows is a detailed description of the individual-based model beginning with the movement rules.

## I. Movement Rules

Adult aphids and parasitoids are assumed to move randomly on the domain whereas juvenile aphids are assumed to be stationary. Movement of adult aphids and parasitoids is described by the equations:

$$\frac{\partial A}{\partial t} = D_A \nabla^2 A, \quad (4.1)$$

$$\frac{\partial W}{\partial t} = D_W \nabla^2 W, \quad (4.2)$$

where  $A$  and  $W$  are the densities of the host and the wasp which have corresponding diffusion coefficients  $D_A$  and  $D_W$ . The domain on which the aphid-parasitoid system is posed has dimensions  $L \times L$  and zero flux boundary conditions. As a first step towards deriving the movement rules of the individuals, the system was non-dimensionalised with the length of the field plot ( $L = 5m$ ) and aphid generation time ( $T_0 = 12days$ ) as scaling variables. Since little species' activity occurs during nighttime, the hours passed during this part of the day are not accounted for in the model. This means that for each day that has passed in the model, two days have passed in real time. Non-dimensionalising the system of equations in 4.1 and 4.2 using the following substitutions:

$$x = L\tilde{x}, \quad t = T_0\tilde{t}, \quad A = A_0\tilde{A}, \quad W = W_0\tilde{W}$$

and removing the tildes yields a system with spatial domain of size  $[0, 1] \times [0, 1]$ :

$$\frac{\partial A}{\partial t} = \alpha_A \nabla^2 A, \quad (4.3)$$

$$\frac{\partial W}{\partial t} = \alpha_W \nabla^2 W, \quad (4.4)$$

where  $\alpha_A = \frac{D_A T_0}{L^2}$  and  $\alpha_W = \frac{D_W T_0}{L^2}$ .

A grid spacing of  $\Delta x = \Delta y = 0.01$  was then used to discretise the domain. This yields a grid with  $100 \times 100$  grid points, each of which can accommodate a number of individuals.

In the model an individual's tendency to move and direction of movement are determined by comparing a randomly generated number to prior calculated movement probabilities. Equations 4.3 and 4.4 were discretised to calculate the individual movement probabilities for the host and parasitoid, respectively. Using centred-differences, explicit time-step, the discretised host equation is:

$$A_{i,j}^{\tau+1} = P_0 A_{i,j}^{\tau} + P_1 A_{i+1,j}^{\tau} + P_2 A_{i-1,j}^{\tau} + P_3 A_{i,j+1}^{\tau} + P_4 A_{i,j-1}^{\tau}, \quad (4.5)$$

where the host density at grid point  $(i, j)$  at time  $\tau + 1$  is equal to the average of the densities of individuals in the four adjacent grid points at time  $\tau$ . Coefficients  $P_0 - P_4$  in equation 4.5 were used to calculate the movement probabilities for the model which are given as follows:

$$\begin{aligned} P_0 &= 1 - \frac{4\alpha_A \Delta t}{(\Delta h)^2} \\ P_1 &= \frac{\alpha_A \Delta t}{(\Delta h)^2} \\ P_2 &= \frac{\alpha_A \Delta t}{(\Delta h)^2} \\ P_3 &= \frac{\alpha_A \Delta t}{(\Delta h)^2} \\ P_4 &= \frac{\alpha_A \Delta t}{(\Delta h)^2} \end{aligned} \quad (4.6)$$

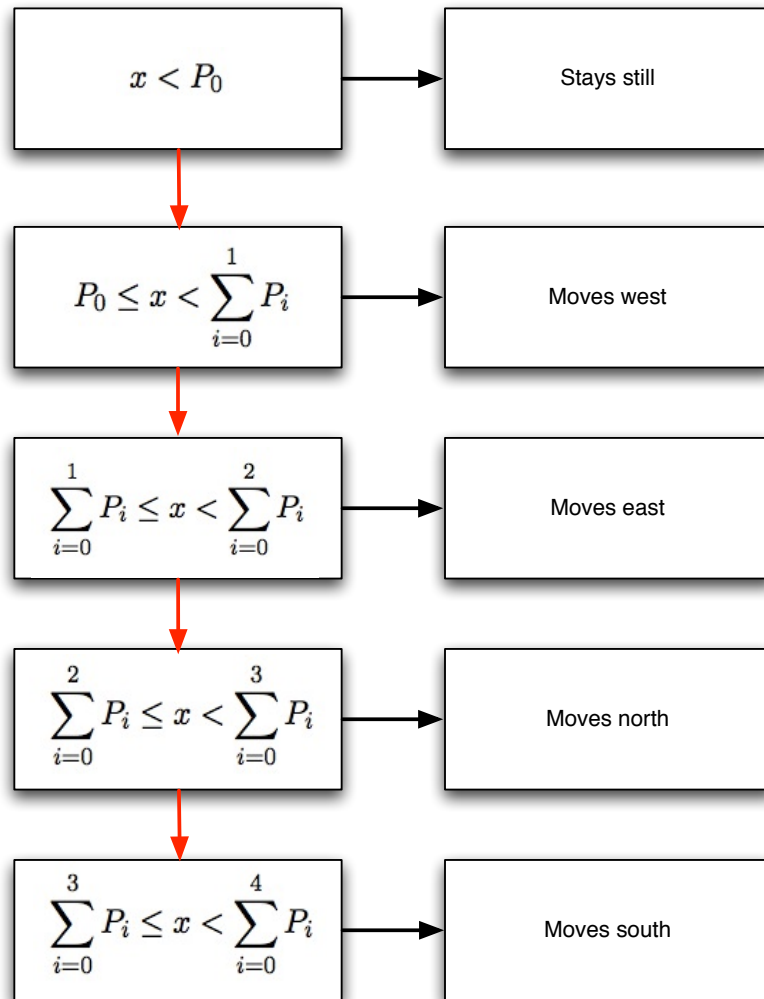
where  $\Delta h = \Delta x = \Delta y$  and  $P_0, P_1, P_2, P_3$  and  $P_4$  can be interpreted as the probability that an individual will stay still or move West, East, South or North, respectively.

In order for the system to be stable, the following condition must be satisfied:

$$\Delta t < \min \left[ \frac{\Delta x^2}{4\alpha_A}, \frac{\Delta x^2}{4\alpha_W} \right] \quad (4.7)$$

(Mitchell and Griffiths, 1980). For the system here, the host and parasitoid diffusion coefficients  $D_A$  and  $D_W$  are 0.00005 m<sup>2</sup>/s and 0.0005 m<sup>2</sup>/s (estimates based on parameter values used in a similar system (Pearce et al., 2007)), which when non-dimensionalised become  $\alpha_A \approx 1$  and  $\alpha_W \approx 10$ . Therefore given the values of the diffusion coefficients and the grid spacing, a time-step  $\Delta t = 0.000001$  was used.

Movement probabilities were calculated for each individual at every time-step and summed, producing five probability ranges,  $R_0 = 0 - P_0$  and  $R_j = \sum_{i=0}^{j-1} P_i - \sum_{i=0}^j P_i$  for  $j = 1 - 4$ . A number between 0 and 1 is randomly selected and the probability range which it falls in determines the individual's direction of movement. As shown in figure 4.1 an individual stays still or moves west, east, south or north if the number falls within the range  $R_0, R_1, R_2, R_3, R_4$ , respectively. Parasitoids' movement probabilities were also derived by using the method of discretising partial differential equations as described previously. Further information on the technique used here can be found in Anderson and Chaplain (1998).



**Figure 4.1:** Flow diagram describing the diffusion movement rules of individuals.  $x$  is a randomly generated number between 0 and 1.  $P_0, P_1, P_2, P_3$  and  $P_4$  approximate the probability that an individual will stay still or move West, East, South or North, respectively. Black arrows signify that the statement is true and red arrows signify that the statement is false.

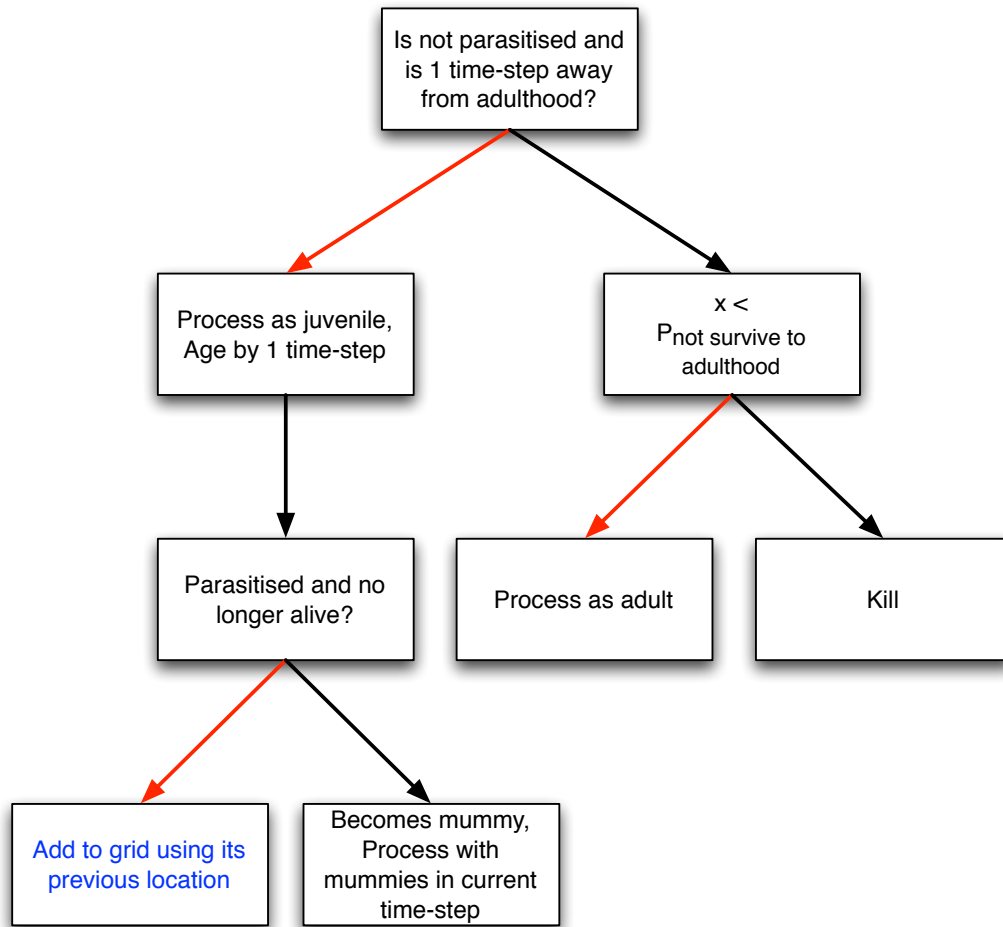


## II. Life history and interactions

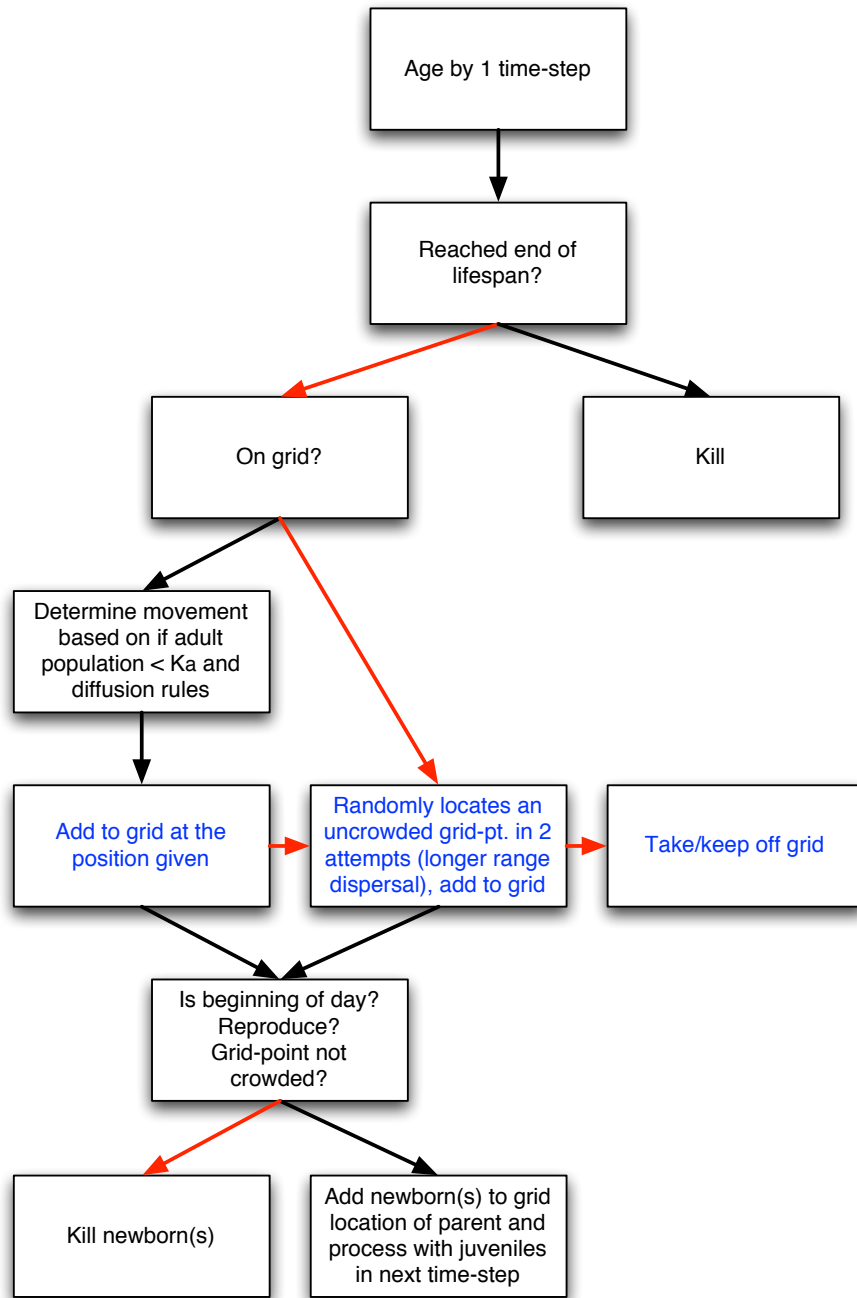
### A. Aphids

At each time-step, a sequence of events takes place for each individual aphid, the order of which is illustrated in figures 4.2 and 4.3 and also described here. Aphids age by one time-step after each time-step lapses. If the individual is a juvenile, it is immobile and develops and grows through four instar stages before becoming an adult at 12 days old. Otherwise, if the individual is an adult, it is given the option to move via random diffusion (according to the movement rules described previously) or via longer range dispersal (a reason for which may be flight). (As a simplification of the model, I do not distinguish aphids as being either alate or apterous.) Although when the adult aphid population has reached its carrying capacity, aphids are not allowed to move via random diffusion. In the model time to adulthood and reproductive maturity in aphids is assumed to be the same. In reality, not all aphids start to reproduce immediately upon becoming an adult. For simplicity though, I made the assumption that these events occur at the same time and doing so should not significantly change the outcome of the dynamics. Adults are assumed to reproduce at the beginning of each day with an average fecundity of  $2 \text{ day}^{-1}$  (value based on information from the literature) (Karley et al., 2002, 2003). In nature, aphids produce offspring throughout the day or continuously, but for the results that follow (with a few exceptions that will be identified in the text) I modelled fecundity as a process that occurs at one time in the day because this is more computationally efficient and does not significantly alter the overlapping generations assumption of the model. Offspring are laid at the current position of the adult and if this location is crowded, the newborn aphid is immediately killed (see section III). Adults continue to reproduce until the end of their lifespan (20 days), whereupon they die (Karley et al., 2002, 2003, correspondence with Dr. A. Karley).

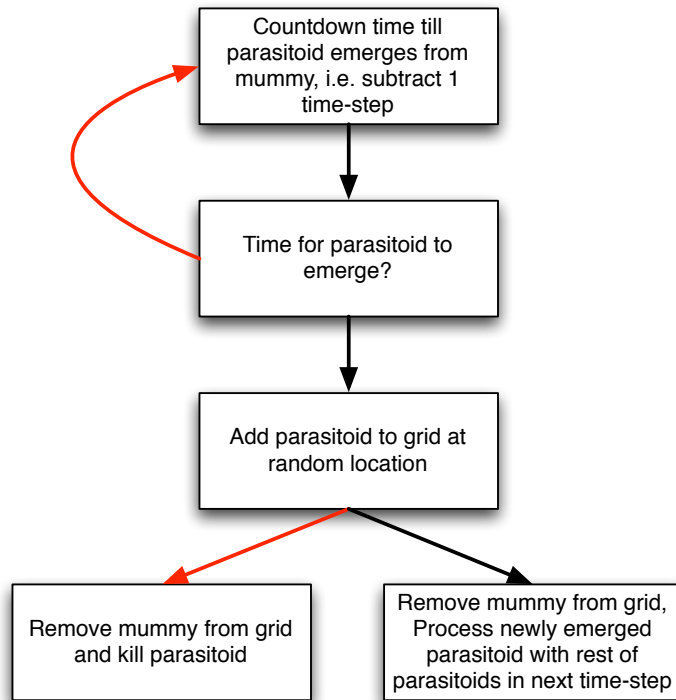
In nature, not all juvenile aphids necessarily survive to adulthood. Therefore, in the model juveniles are sometimes subject to a mortality rate whereby a proportion  $p$  of juveniles is killed. This is implemented by killing a proportion  $p$  of juvenile aphids born each day immediately before they become adults. When there is no juvenile mortality,  $p$  is 0. Juvenile aphids can also die from being parasitised. In the model, after parasitisation, the aphid's lifespan is curtailed to 7 days. A parasitised aphid is assumed not to grow or develop, but continues to utilise plant resources. Within the parasitised aphid is a developing wasp which continues to grow after the aphid has mummified and died. After 10 days a new parasitoid emerges from the aphid mummy and the mummy is removed from the grid (see figure 4.4 for an illustration of how aphid mummies are processed in the model).



**Figure 4.2:** Flow diagram showing the sequence of events juvenile aphids go through during each time-step in the model. Red arrows indicate that the statement is false and black arrows indicate that the statement is true. The text in blue refers to individuals that will go through the same sequence of events in the following time-step. Each  $x$  represents a different randomly generated number between 0 and 1.



**Figure 4.3:** Flow diagram showing the sequence of events adult aphids go through during each time-step in the model. See the description of figure 4.2 for an interpretation of the colour coding scheme used.



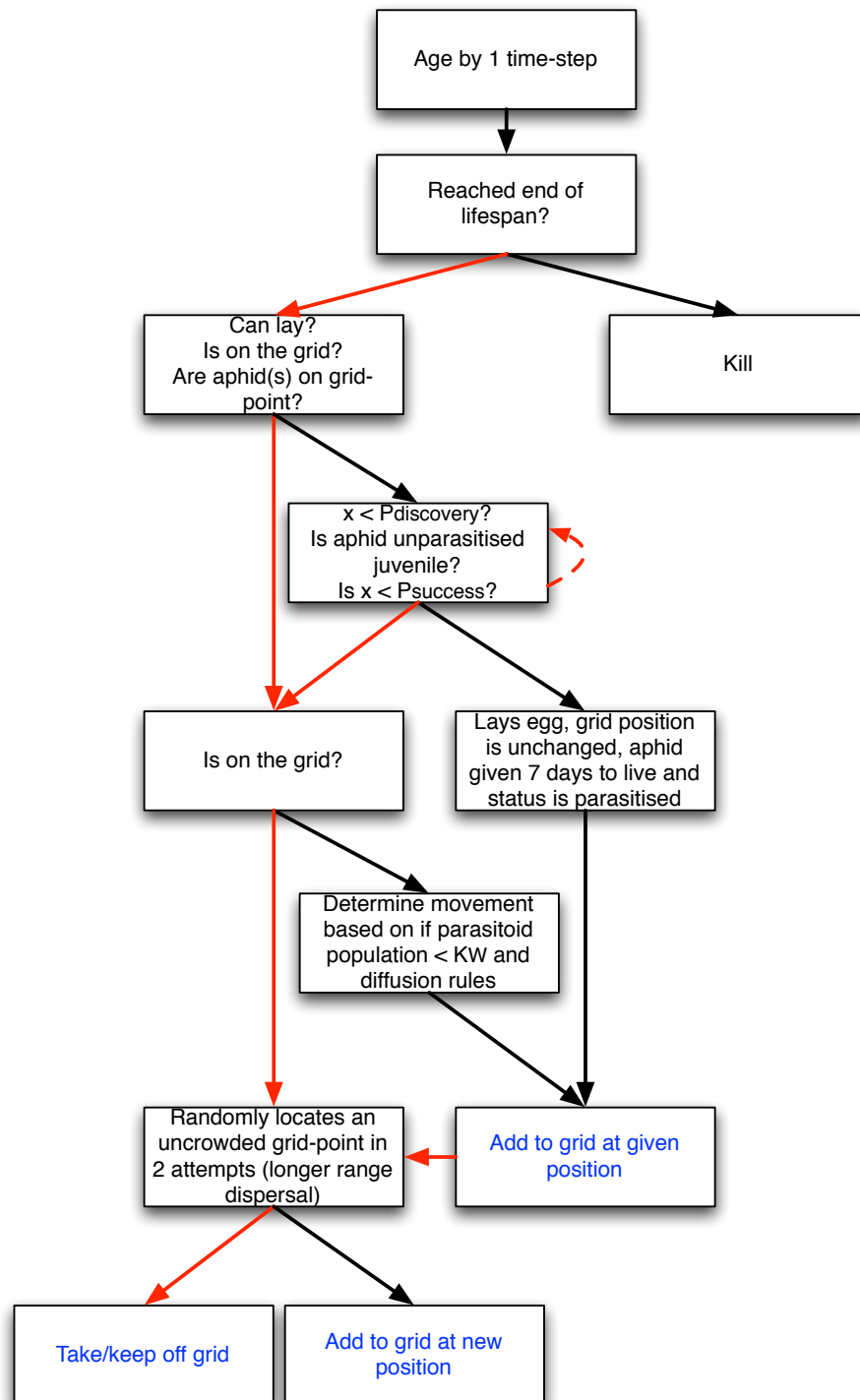
**Figure 4.4:** Flow diagram showing how aphid mummies are processed during each time-step in the model. See the description of figure 4.2 for an interpretation of the colour coding scheme used.

## B. Parasitoids

Similarly to aphids, parasitoids also undergo a sequence of events during each time-step as shown in figure 4.5 and described here. For every time-step that has elapsed, each parasitoid ages by one time-step. If the parasitoid is 2 days old, then it is considered reproductively mature and can parasitise juvenile aphids, provided they are on the same grid point as the parasitoid and have not already been parasitised. The success of an attack is determined by the parasitoid's probability of discovering an aphid and the probability of successful parasitism, factors which also determine parasitoid efficiency. Another factor influencing parasitoid efficiency is handling time. All parasitoids exhibit either of two types of handling behaviours: they can either handle one

aphid per time-step (analogous to a longer handling time) or handle more than one aphid per time-step on a given grid point if the previous host that they encountered was unsuitable and there are other aphids on the grid point (analogous to a shorter handling time). If a parasitoid does successfully attack an aphid, it subsequently lays an egg in the aphid which matures into a parasitoid after 17 days. The newly emerged parasitoid is assumed to fly soon after emergence after which it settles on a random location (in the model I made the simplifying assumption that this takes place over the course of one time-step).

Parasitoids that successfully lay in a given time-step do not move via diffusion (although they can move via longer range dispersal) in that particular time-step. Parasitoids that do not or cannot lay are given the option of moving via diffusion or longer range dispersal in each time-step (see movement rules previously) in order to find an unparasitised host elsewhere. (Although as with the adult aphids, parasitoids cannot move via diffusion when their population has reached its carrying capacity.) Individual parasitoids each have a lifespan of 10 days after which they die.



**Figure 4.5:** Flow diagram showing the sequence of events parasitoids go through during each time-step in the model. The loop represented by the dashed arrow is only considered when parasitoids have a short handling time and represents the handling of multiple aphids in a given time-step when parasitoids encounter unsuitable hosts on a grid-point. See the description of figure 4.2 for an interpretation of the colour coding scheme used.

In the model individuals are processed in each time-step in the following order, parasitoids, juvenile aphids, adult aphids followed by aphid mummies. This means that 1) if parasitism and juvenile mortality occur in the same time-step, a juvenile aphid will first face the possibility of being parasitised before the possibility of experiencing juvenile mortality (see figures 4.2 and 4.5) and 2) juvenile aphids experience the possibility of being parasitised before adult aphids produce offspring when these two events occur in the same time-step (see figures 4.3 and 4.5). This ordering of events is arbitrary, but justified as there is no biological evidence that suggests a particular ordering of these events over the course of 1 time-step. The same justification applies to modelling adult aphid movement before reproduction and the order of processing different types of individuals (parasitoids, juvenile aphids, adult aphids, aphid mummies) in a given time-step.

### III. Density Dependence

Density dependence was implemented in the model by assigning to each grid point a carrying capacity for the number of juvenile aphids (which includes non-parasitised and parasitised aphids), adult aphids and parasitoids:  $k_j = 3$ ,  $k_a = 2$  and  $k_w = 2$ . (Aphid mummies are not counted towards the carrying capacity of aphids because they do not utilise resources.) For the entire grid this means the total carrying capacity was 30,000 for juveniles ( $K_j$ ), 20,000 for adults ( $K_a$ ) and 20,000 for parasitoids ( $K_w$ ). Density-dependent limitation was modelled separately for adult and juvenile aphids in order to control for any skewness in the age class distribution of the population.

If an adult aphid or parasitoid found itself on a grid point already occupied by 2 adults or parasitoids respectively, rather than being eliminated from the population, it was given two chances in the same time-step to randomly locate a grid point that was not at capacity anywhere on the domain (i.e. longer range dispersal). If it was unsuccessful, it continued to remain off the grid. (Those aphids or parasitoids that do occupy a grid



point are labelled as 'on grid' in the graphs of the results while those that are not added to the grid are called 'flyers.'). In each subsequent time-step, aphids or parasitoids that were off the grid in the previous time-step were given two more chances to find a grid point that was not at capacity until they found an uncrowded grid point.

Newborn aphids or newly emerged parasitoids are added to the grid at the location of the parent or at a random location, respectively if that particular grid point is not already at capacity (i.e has 3 juveniles or 2 parasitoids). Otherwise, the aphid or parasitoid is immediately killed.

When the domain is completely full of aphids, the oldest aphids are killed to make way for the addition of younger adult aphids into the population. In this way, the population is revitalised with younger aphids that are reproductive for longer. This approach to density-dependent limitation is similar to what occurs in nature where younger, more agile aphids are more likely to outcompete older aphids for space and resources.

#### IV. Parasitoid Competition

A system comprising two parasitoid species parasitising the same host was also modelled. The assumptions made were the same as those used to model a single parasitoid species and an aphid host. Both parasitoid species have all parameters the same except for the probability of discovering an aphid.

## V. Patches

In addition to considering a spatially homogenous environment for the original host-parasitoid system, an environment consisting of two patches was considered where one patch is of good quality and the other is of low quality for the host. Quality was varied between patches by varying aphid performance. On the good quality patch, aphids experience less juvenile mortality than on the poor quality patch. The size of each patch was also varied to see how changes in the proportion of the domain that is of good/poor quality affects the dynamics of the system. Parasitoids and adult aphids were allowed to move between patches.

## VI. Multiple grids

The original host-parasitoid system was modelled on multiple non-adjacent grids. Each grid has a spatially homogenous environment. Parasitoids or adult aphids were allowed to migrate to another grid at certain intervals of time and the fraction of individuals migrating was varied to see how changing the level of migration affects the behaviour of the system. Simulations were also run allowing parasitoids to migrate according to a giving up time which was calculated based on the time that had passed since last oviposition. Giving up time was varied and the resulting system dynamics were assessed.

## VII. Objectives

In order to understand the dynamics of the system and what processes cause the dynamics that arise from this system, the model was analysed in parts and key parameters were varied. Initially, a model representing a population of aphids was studied. Following this, an aphid-parasitoid system was simulated to which a second parasitoid species was added later. The original 1-host-1-parasitoid model was then simulated again, although on multiple patches. For each of these sub-models/models, parameters were varied that include some or all of the following: aphid fecundity, adult aphid

lifespan, aphid juvenile mortality, grid capacity of aphid juveniles, aphid diffusion, juvenile aphid predation, parasitoid's handling time, parasitoid diffusion, probability of a parasitoid finding an aphid, parasitoid's success of parasitism, giving up time, parasitoid lifespan, proportion of high and low quality habitat and proportion of adult aphid or parasitoid population migrating from one grid to another grid. The following table shows the standard values of parameters that were varied. These values are based on data from the literature and correspondence with Dr. A. Karley and Professor S. Hubbard. Note, not all parameters are shown in the table; only those that are permanent model parameters.

**Table 4.1:** *Baseline parameter values*

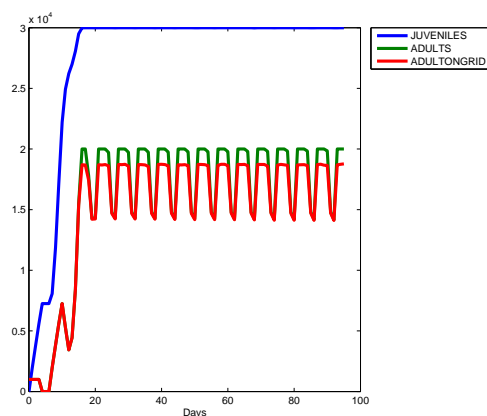
<b>Parameter</b>	<b>Standard value</b>
aphid fecundity (day <sup>-1</sup> )	2
adult aphid lifespan (days)	4 (8 in real time)
aphid diffusion coefficient	1
success of parasitism	1
parasitoid's probability of discovering an aphid in a time-step	$\frac{1}{\text{number of time-steps per day}}$
parasitoid diffusion coefficient	10
parasitoid lifespan (days)	5 (10 in real time)

The individual results plots in the following section and in subsequent chapters show the output of a single simulation run which is a representation of the dynamics commonly observed in the system (with a few exceptions which are noted in the text) given the initial conditions and parameter values used. Other simulation runs with the same conditions, for the most part, gave rise to very similar dynamics both qualitatively and quantitatively.

### 4.3 Aphid Dynamics

In the following simulations the dynamics of an aphid population are analysed by varying parameters that include fecundity, juvenile mortality, random diffusion and adult lifespan. The initial population is comprised of 1000 adult aphids.

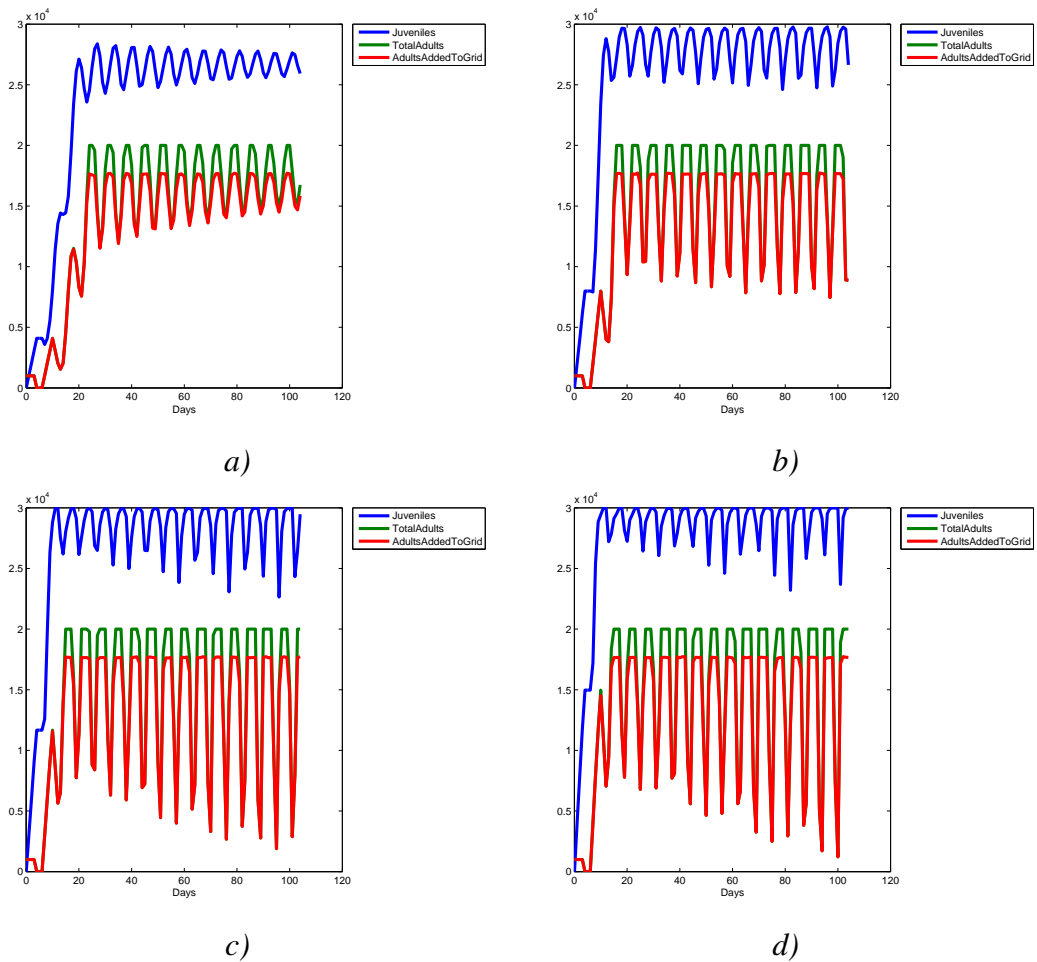
Figure 4.6 shows the system under standard parameter value conditions. Under average conditions, because of density-dependent regulation, the aphid population would be expected to tend towards its carrying capacity  $K_{tot} = K_j + K_a$  over time which is the case here where the total aphid population tends to 50,000.



**Figure 4.6:** Plot illustrating the populations of juveniles and adults over time for the baseline parameter set.

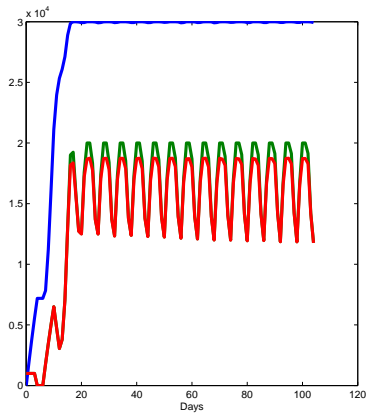
As aphid fecundity is varied there are slight changes in the dynamics. Figure 4.7 shows the dynamics of the system when aphid fecundity was varied and modelled as a continuous process. When aphid fecundity is  $1\text{day}^{-1}$ , the juvenile population tends to a limit slightly below its carrying capacity  $K_j$  and the adult population on the domain tends to a limit slightly below its carrying capacity  $K_a$  (figure 4.7). As aphid fecundity is increased, the juvenile population approaches  $K_j$  and the adult population approaches its limit, though at a faster rate. Also the cycles around the steady-state become more

unstable, increasing in amplitude (particularly in the adult population) as fecundity is increased. Despite changing the way aphid fecundity was modelled from a discrete process (see figure 4.6) to a continuous process (see figure 4.7 b), there is not much change in the behaviour of the system. In both cases the aphid population tends to carrying capacity. One apparent difference when fecundity is modelled as a continuous rather than discrete process is that the juvenile population exhibits small amplitude oscillations with a period of about 1 aphid generation.

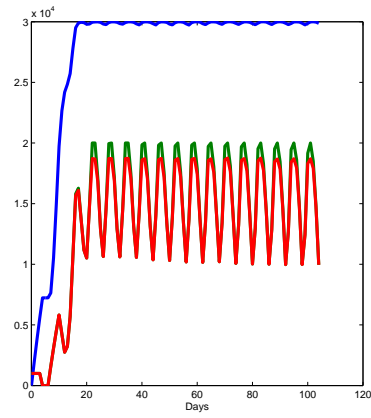


**Figure 4.7:** Plots illustrating the populations of juveniles and adults over time as aphid fecundity is varied. (a), (b), (c), (d) have fecundity of 1, 2, 3, 4 offspring per day, respectively.

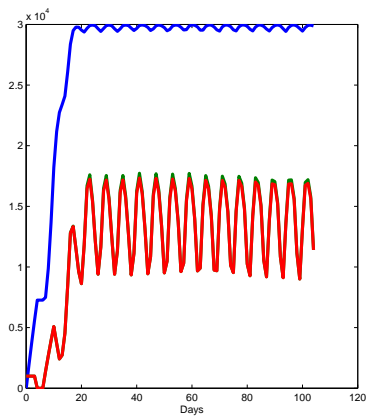
Effects of varying juvenile mortality were also studied. Each day, a fraction of unparasitised aphid nymphs that were about to become adults were killed off and this fraction was varied. Figure 4.8 shows that, in general, as juvenile mortality is increased, the number of adults and the number of juveniles decreases over time. There is no significant change from average conditions until juvenile mortality equals 0.3 which is when the number of adult aphids is reduced. Interestingly, there is little change in the juvenile population until juvenile mortality is 0.5 which is when the juvenile numbers begin to reduce. The adult population is more sensitive to changes in juvenile mortality because juveniles are killed just before they reach adulthood, therefore, the adult population is immediately affected. Meanwhile, new juveniles are being born each day and because aphids have overlapping generations, the cumulative effect is a build-up in the number of juveniles. Only when the stress on the system is increased is there an effect on the juvenile population. When juvenile mortality is 0.9, there is a drastic change where the aphid population verges upon extinction.



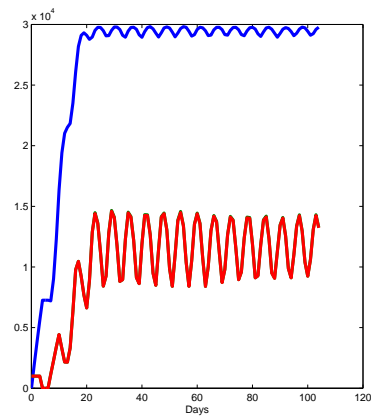
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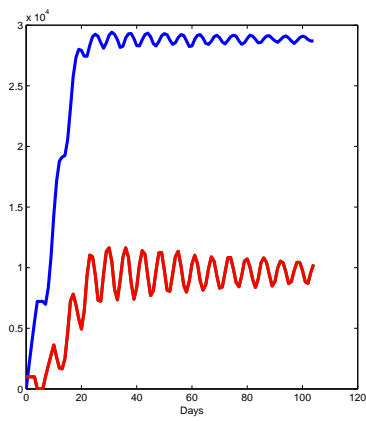
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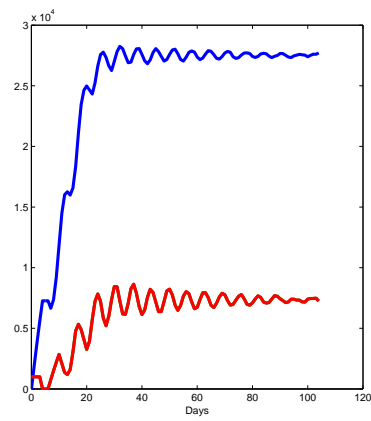
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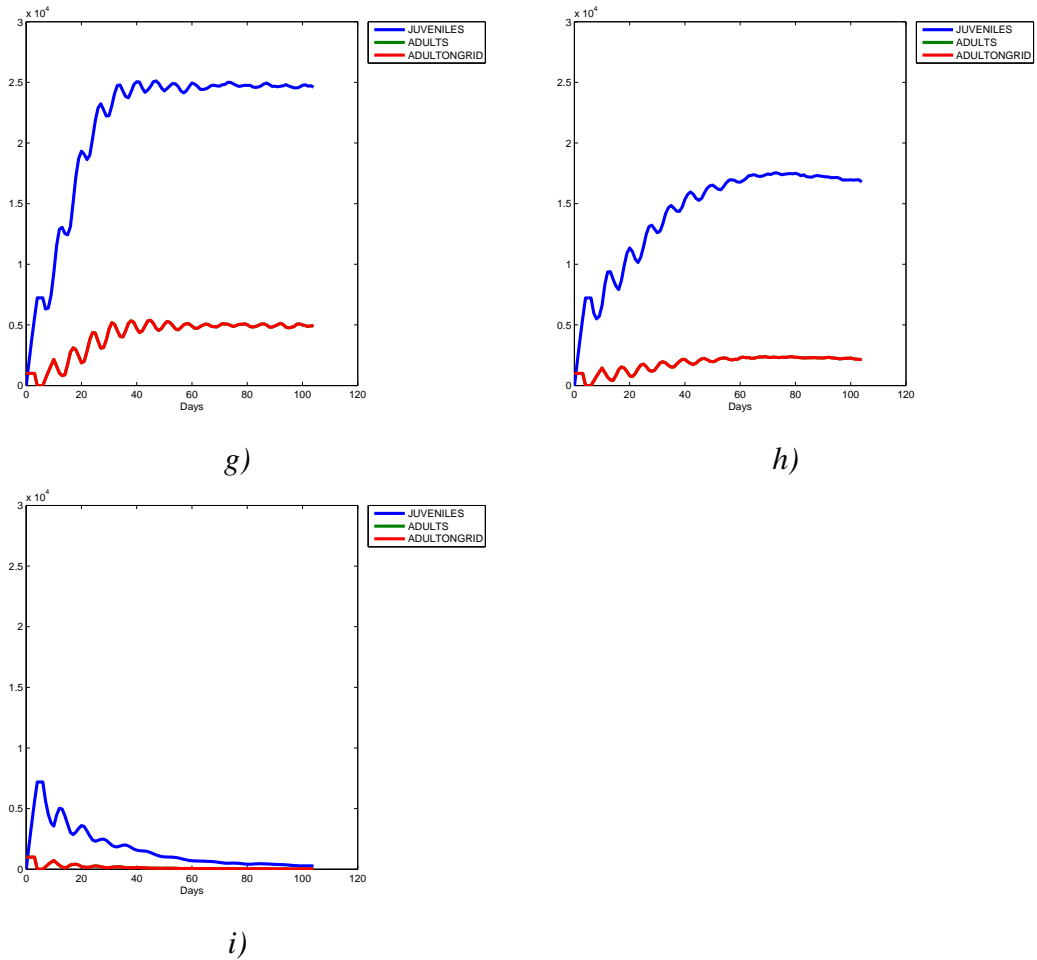
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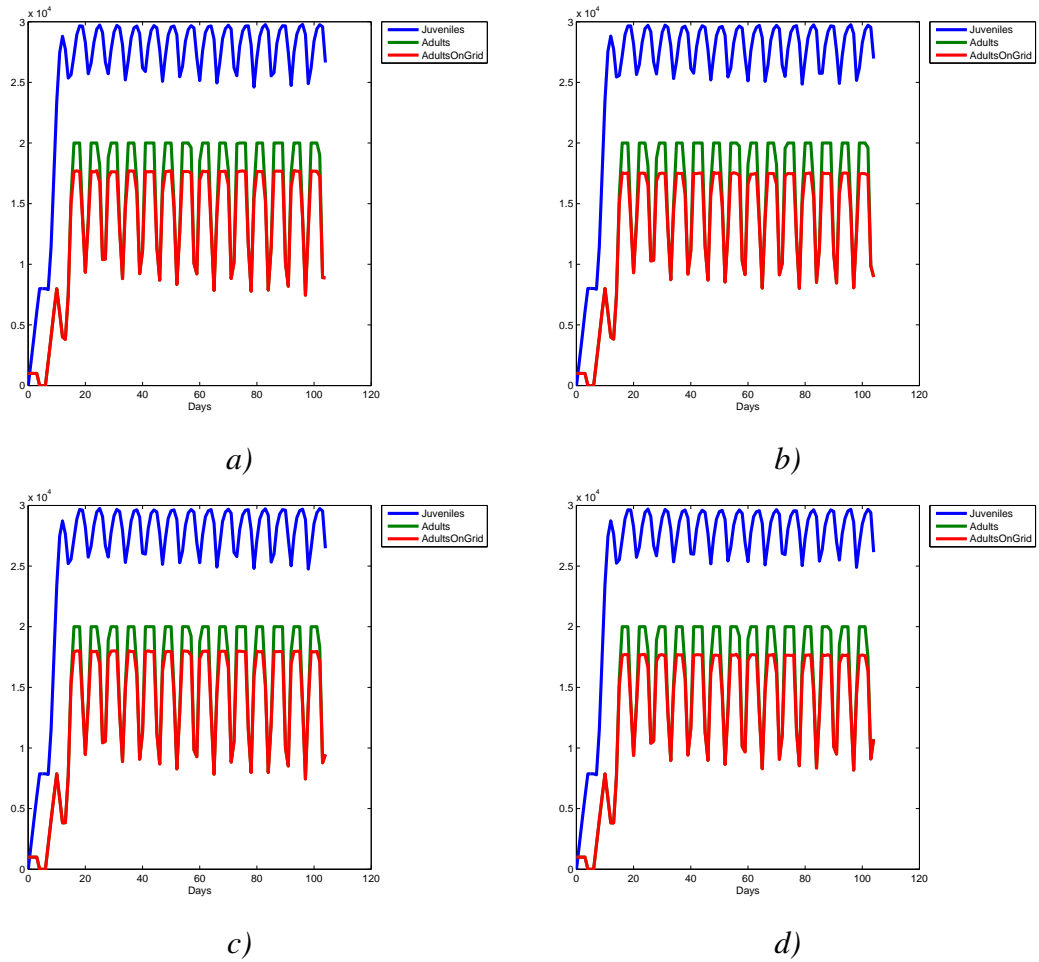
f)



**Figure 4.8:** Plots illustrating the populations of juveniles and adults over time as the fraction of maturing nymphs dying daily is varied. In (a), (b), (c), (d), (e), (f), (g), (h), (i) this fraction is 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, respectively.

Aphid diffusion was also varied. Fecundity was modelled as a continuous process. Figure 4.9 shows the results from varying diffusion. The aphid model does not appear to be very sensitive to changes in the aphid diffusion coefficient. As before when aphid fecundity was increased, when the aphid diffusion coefficient is increased, the juvenile population tends to  $K_j$  and the adult population tends to a limit slightly below  $K_a$ . This is what is to be expected given that the aphid population exhibits density-dependent growth. Juvenile and adult groups also cycle with a periodicity of about 1 aphid generation.

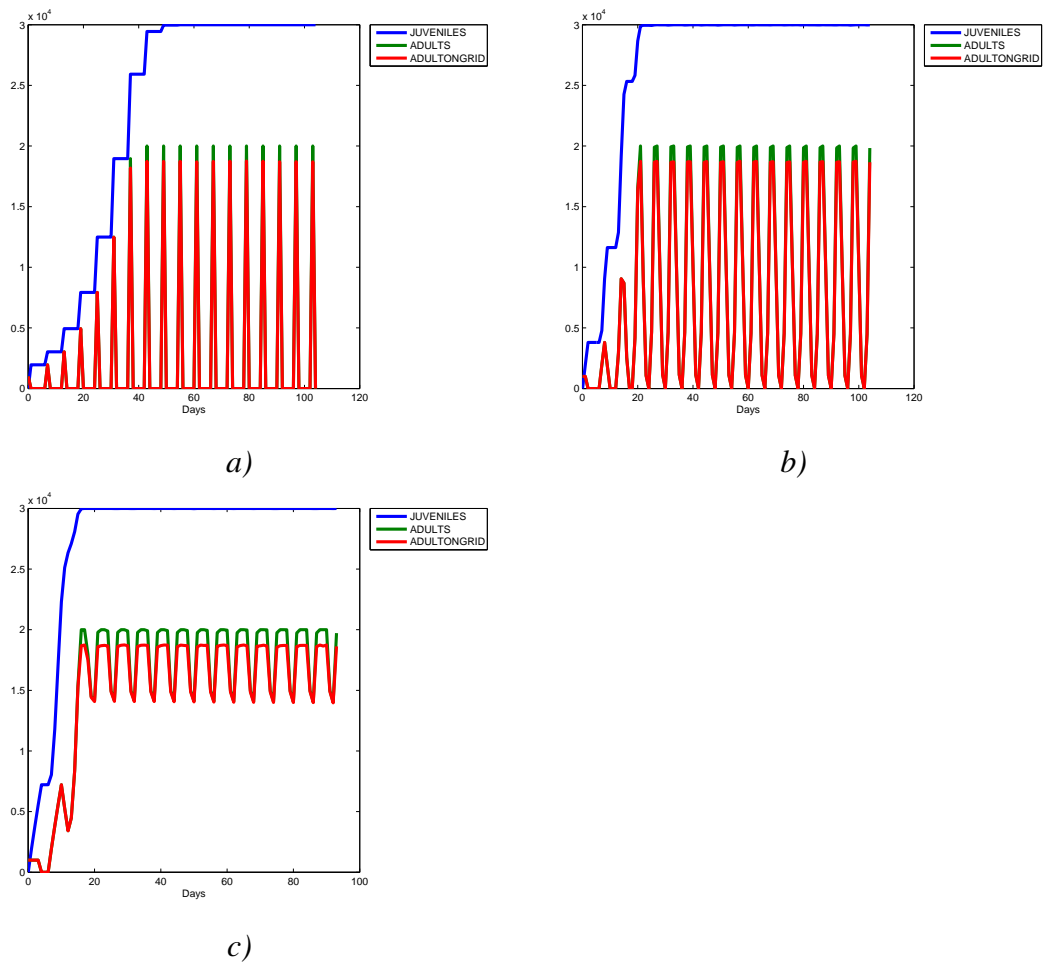




**Figure 4.9:** Plots illustrating the populations of juveniles and adults over time as aphid diffusion is varied. (a), (b), (c), (d) have diffusion of 1, 2, 5, 10, respectively.

In addition to juvenile aphids succumbing to early mortality, adult aphids also may experience early mortality as a result of, for example, changes to the environment. Mortality was implemented and varied in the adult aphid population, but rather than kill a percentage of aphids as I did when juvenile mortality was implemented, I implemented adult mortality by reducing the average adult lifespan of all aphids. The reason for doing it this way was because it was more efficient computationally and therefore gave us an idea of whether the system was sensitive to changes in adult aphid mortality more quickly. Figure 4.10 shows that as adult aphid mortality is reduced (or adult aphid lifespan is increased), the total population seems to increase and tend to

equilibrium more rapidly. The juvenile count rises more steeply as adult lifespan is increased because adults with a longer lifespan have a greater reproductive output by virtue of having more days to reproduce and therefore the rate of increase in juvenile numbers is steeper. The adult count also increases more rapidly as adult aphid lifespan increases because adults are on the grid for a longer period of time, so there will be cumulative increase in the number of adults in the aphid population. In addition to this, because adults with a longer lifespan have a greater reproductive output overall, more juveniles will also be becoming adults which also contributes to the steeper increase in adult numbers. Notice, however, that despite doubling the adult lifespan and therefore the reproductive capacity of adult aphids each time in figure 4.10 a, b and c, the equilibrium level of juveniles does not increase and this is most likely because a carrying capacity ( $K_j = 30,000$ ) is artificially imposed on the number of juveniles that can inhabit the domain. So though aphids with double the adult lifespan have double the reproductive capacity, this is probably not reflected in figure 4.10 because the domain doesn't have the carrying capacity to support such a high production of juveniles.



**Figure 4.10:** Plots illustrating the populations of juveniles and adults over time as adult lifespan is varied. (a), (b), (c) have adult lifespan of 1, 2, 4 days, respectively.

In summary the aphid model, for the most part, did not exhibit a wide array of behaviour as different parameters were varied. In most instances, the aphid population tended to carrying capacity. An exception was when juvenile mortality was increased to high levels causing a dramatic change in behaviour from relatively stable dynamics to near extinction. There was some more subtle variation in dynamics when fecundity and adult lifespan were increased. As fecundity was increased, the amplitude of the cycles around the underlying steady state in the adult population increased suggesting that the system is becoming less stable. In contrast when adult lifespan was increased, the amplitude of the oscillations in the adult population decreased suggesting that the system is becoming more stable.

In most of the results from the aphid model, the adult population and sometimes the juvenile population exhibited cycles around a steady state that have a period of about 1 aphid generation. Generation cycles have been observed in experimental studies of age-structured insect populations with some theoretical studies citing uniform larval competition or cannibalism as possible causes (Sait et al., 1994; Chapman, 1928; Gurney et al., 1983; Gurney and Nisbet, 1985; Briggs et al., 2000). However, it is not clear in this model what mechanism drives the generation cycles and whether they are driven by something completely different from the above-mentioned causal factors. In order to answer this, further exploration of the model is required.

## Chapter 5

# Modelling the Dynamics of the Aphid-Parasitoid System

Many aphid populations peak during the summer season and soon afterwards go through a rapid decline. One of the main factors thought to contribute to the aphid population crash is pressure from natural enemies. As mentioned previously, natural enemies have been used as biocontrol agents. In particular, parasitoid wasps are thought to be effective biocontrol agents because they are highly host specific, have a generation time comparable to that of their host and generate offspring rapidly. Here I have modelled an aphid-parasitoid system that develops the aphid model in chapter 4 and varied parameters in order to gain an understanding of the potential range of dynamics that can emerge from this system and to better understand the underlying biological processes involved in the population dynamics of aphids during ‘peak season.’ By varying the model parameters, information can also be obtained on what biological parameters need to be manipulated in order to limit aphid populations which could in turn inform strategies on how to implement more effective biological control. The model here is used to study a system consisting of the aphid host *Macrosiphum euphorbiae* and the

parasitoid wasp *Aphidius ervi*, but it can be applied to other aphid-parasitoid systems as well. The model was also used to study a system consisting of *M. euphorbiae* parasitised by two species or conspecifics of parasitoids. This chapter is organised into sections beginning with assumptions used in the model followed by results from parameter variation conducted on the aphid-parasitoid system.

## 5.1 Model Assumptions

For the subsequent results, unless otherwise stated, the following assumptions were made:

- 1) In nature, though parasitoids can attack adult aphids, they are not the preferred host. Therefore, for simplicity I assumed that parasitoids only attack juvenile aphids.
- 2) Although it has been shown in lab experiments done on pea aphids that 3rd and 4th instars parasitised by *A. ervi* do develop into adults and can reproduce, their contribution to the overall reproductive output of aphids is not very significant (He, 2008) and ultimately parasitised aphids are eliminated from the population sooner than their non-parasitised counterparts, therefore their influence on the dynamics of the system is not as great. So to simplify the model, I made the assumption that parasitised juveniles do not become adults.
- 3) Juvenile mortality is applied only to aphids that have not already been parasitised which is representative of what occurs in nature as well.
- 4) In simulations where parasitoid interference is implemented, parasitoids foraging on a grid point where there is already another parasitoid have a 30% reduced success of parasitism.

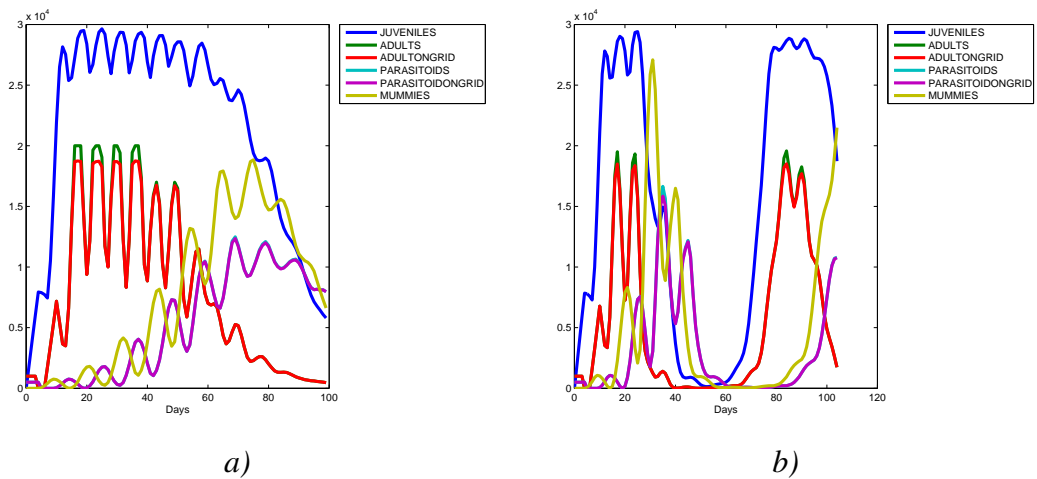
## 5.2 Aphid-Parasitoid Dynamics

Effects of varying key parameters on the dynamics of the model were studied by comparing to a baseline case. Two different foraging behaviours were considered where parasitoids can handle only one aphid per time-step or can handle more than one aphid per time-step analogous to a longer and shorter handling time, respectively. Both strategies will be examined as aphid and parasitoid parameters are varied. Aphid parameters varied include juvenile mortality and adult mortality and parasitoid parameters varied include handling time, the probability that a parasitoid discovers an aphid, length of parasitoid lifespan and the probability of successfully parasitising an aphid. The initial aphid and parasitoid populations are comprised of 1000 adults and 500 parasitoids, respectively.

### 5.2.1 Varying parasitoid foraging behaviour

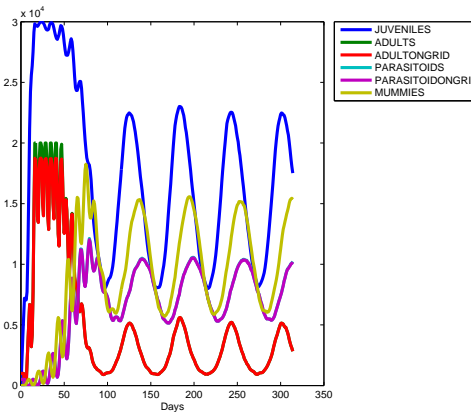
Figure 5.1 compares the dynamics of the system when the two different foraging behaviours are modelled. In both cases, the aphid population peaks at a level approaching carrying capacity and all species populations tend to peak and crash. However, changing the foraging behaviour of parasitoids from allowing them to handle one aphid per time-step to allowing them to handle more than one aphid per time-step creates, at least initially, ‘faster’ dynamics. When parasitoids can handle only one aphid in a given time-step, the population of each species increases and then crashes. In contrast when parasitoids can handle more than one aphid per time-step, there appears to be the beginning of oscillations (two almost complete cycles) reminiscent of Nicholson and Bailey ‘boom and bust’ dynamics. Although, figure 5.2 shows that when the simulation in figure 5.1 a is run for an extended period of time, there are more cycles of

populations increasing and decreasing. Increasing the handling time lengthens the period of the oscillations (at least initially) and that is why cycles are not immediately apparent in figure 5.1 a. The dynamics in figure 5.1 b are ‘faster’ because parasitoids have a shorter handling time, thus making them more efficient. Due to this increased efficiency, parasitoids drive the aphid population to crash more quickly each time after it peaks, driving the oscillations faster. Also the more defined first peak of the mummy trajectory and its higher amplitude in figure 5.1 b suggest a more immediate impact of the parasitoids compared to the scenario in figure 5.1 a where the mummy count takes longer to peak and its amplitude is much lower.



**Figure 5.1:** Plots illustrating aphid and parasitoid populations over time as parasitoid foraging behaviour is varied. Aphid fecundity is modelled as a continuous process. In (a), (b) parasitoids can handle one aphid per time-step and parasitoids can handle more than 1 aphid in a single time-step if the host that they found previously is unsuitable, respectively. Note: Juveniles plotted here and in the figures to follow includes both parasitised and non-parasitised juveniles.



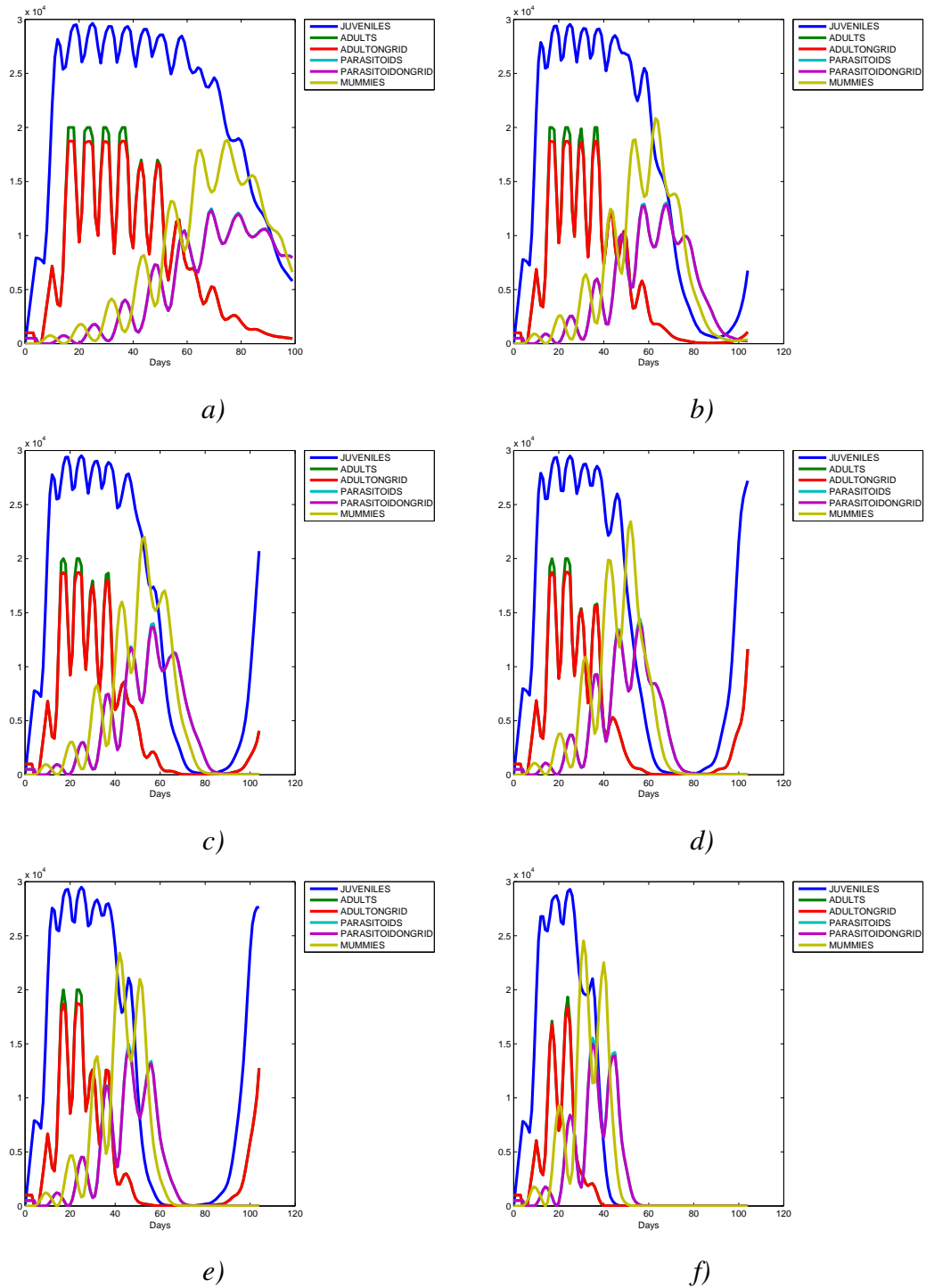


**Figure 5.2:** Plot illustrating aphid and parasitoid populations in figure 5.1 a for an extended period of time.

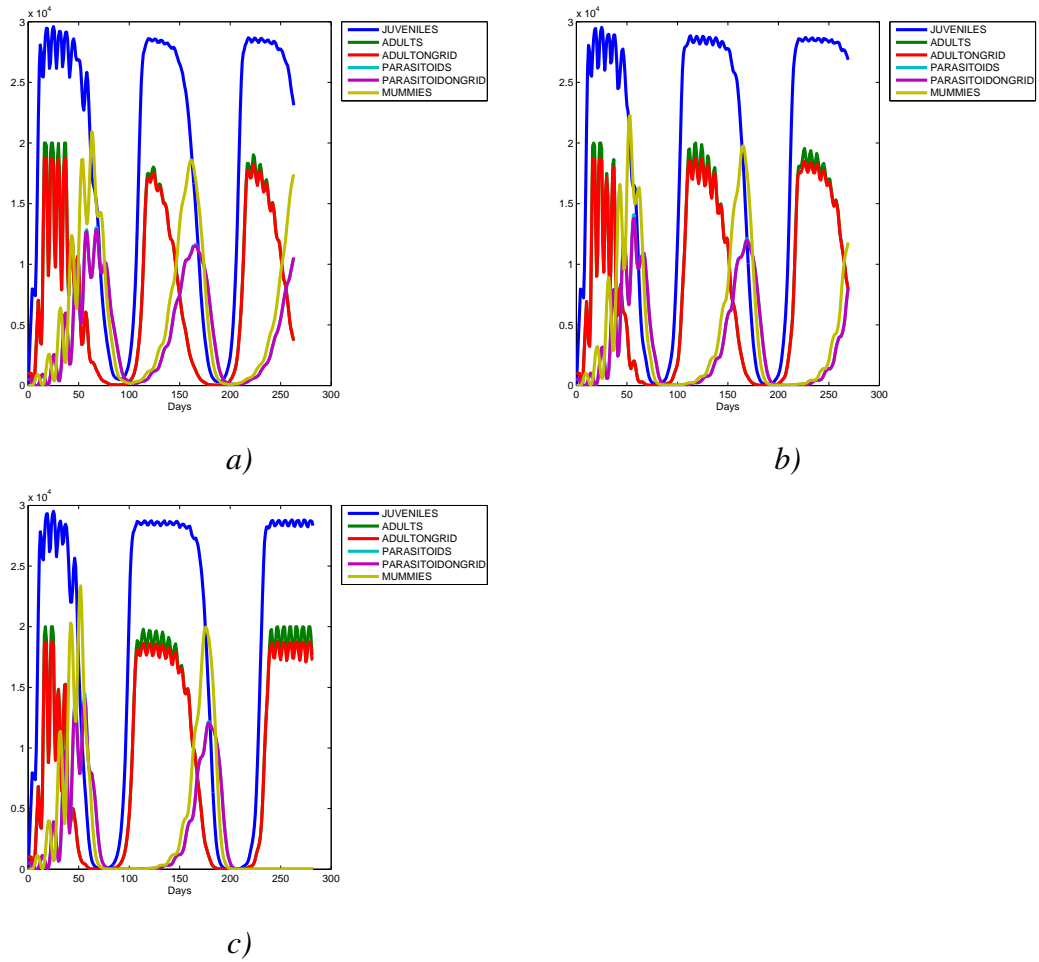
## 5.2.2 Varying the parasitoid probability of discovering a host

In addition to varying the handling time of parasitoids, parasitoids can be made more or less efficient by increasing or decreasing the probability that they discover an aphid, respectively. Figures 5.3, 5.4, 5.5 show the results from varying the probability of discovering an aphid for parasitoids with a long handling time and a short handling time when fecundity is modelled as a continuous process. When parasitoids have a longer handling time, as this probability is increased, the dynamics become more unstable going from what appears to be the beginning of oscillatory dynamics and coexistence to extinction of both species (figure 5.3). Figure 5.4) shows the dynamics in figure 5.3 b, c and d simulated for longer, confirming the presence of oscillations. These oscillations grow in amplitude as the probability of discovery increases. When the probability of discovery is 0.000009, the trough of the oscillations in the aphid population becomes so low that the host population can no longer support parasitoids, leading to the removal of parasitoids from the system. At a probability of discovery of 0.000015, the parasitoids are too efficient and parasitise all the aphids before the population can recover leading to the extinction of both the aphid and parasitoid populations (figure 5.3 f).

Also, noteworthy of comment are the initial transient dynamics in figure 5.4. These are reminiscent of the dynamics observed in the model of Preedy et al. (2007).



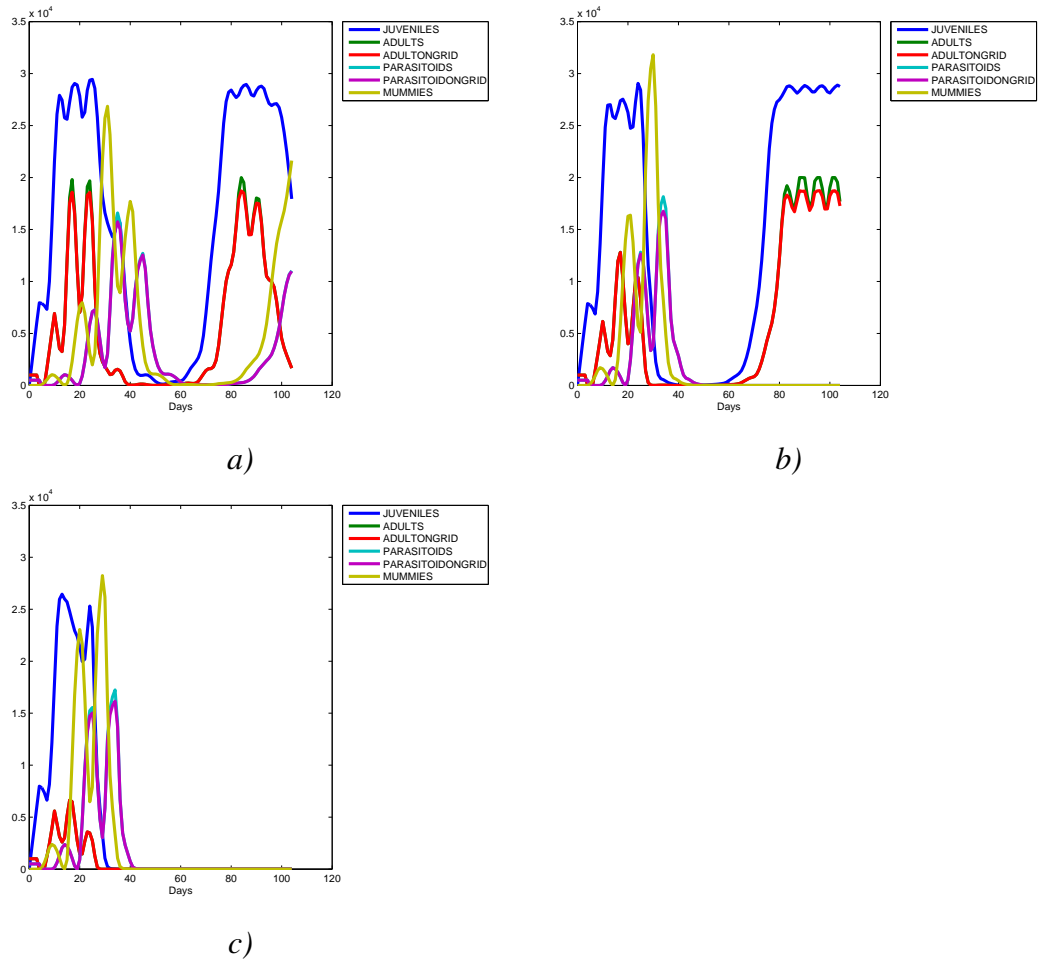
**Figure 5.3:** Plots illustrating aphid and parasitoid populations over time as the probability that a parasitoid discovers an aphid is varied. Parasitoids can handle one aphid per time-step. Aphid fecundity is modelled as a continuous process. Probability of a parasitoid discovering an aphid in (a), (b), (c), (d), (e), (f) is 0.000006, 0.000007, 0.000008, 0.000009, 0.00001, 0.000015, respectively.



**Figure 5.4:** Plots illustrating aphid and parasitoid populations over time as the probability that a parasitoid discovers an aphid is varied. Parasitoids can handle one aphid per time-step. Aphid fecundity is modelled as a continuous process. Probability of a parasitoid discovering an aphid in (a), (b), (c) is 0.000007, 0.000008, 0.000009, respectively.

Figure 5.5 shows that for parasitoids with a shorter handling time, when the probability of a parasitoid discovering an aphid is varied, the pattern of dynamics is similar to that seen when the same probability was varied for parasitoids with a longer handling time. In both instances, as the probability of discovery was increased, the dynamics became more unstable and when this parameter was 0.00001 and 0.000015, the system consistently showed no coexistence and no persistence, respectively. The dynamics differ though in the frequency of the cycles initially. Just as when the different foraging

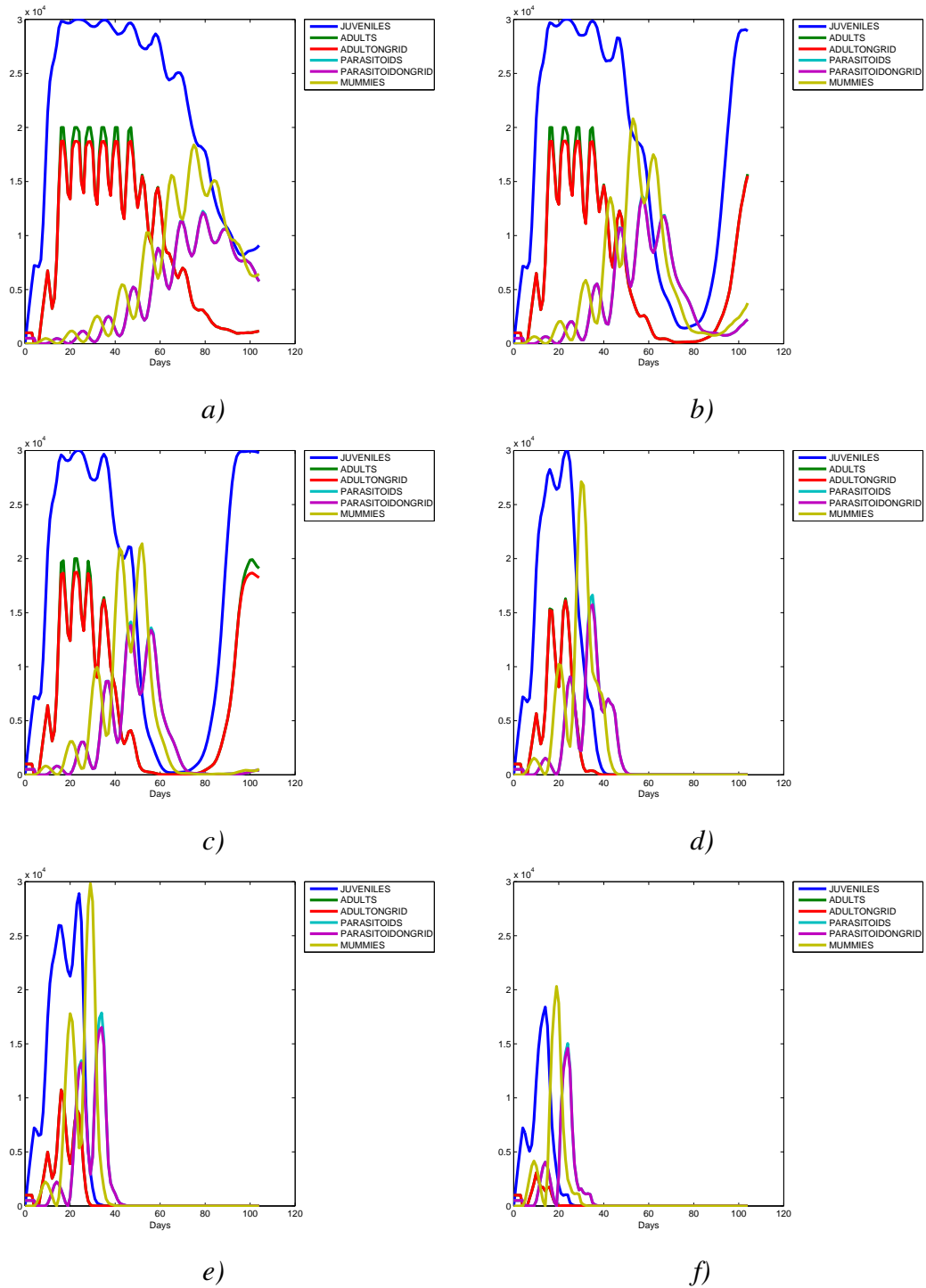
strategies were being compared (see figure 5.1), the dynamics are still ‘faster’ when handling time is shorter and probability of discovery is varied because the parasitoids are more efficient at finding hosts.



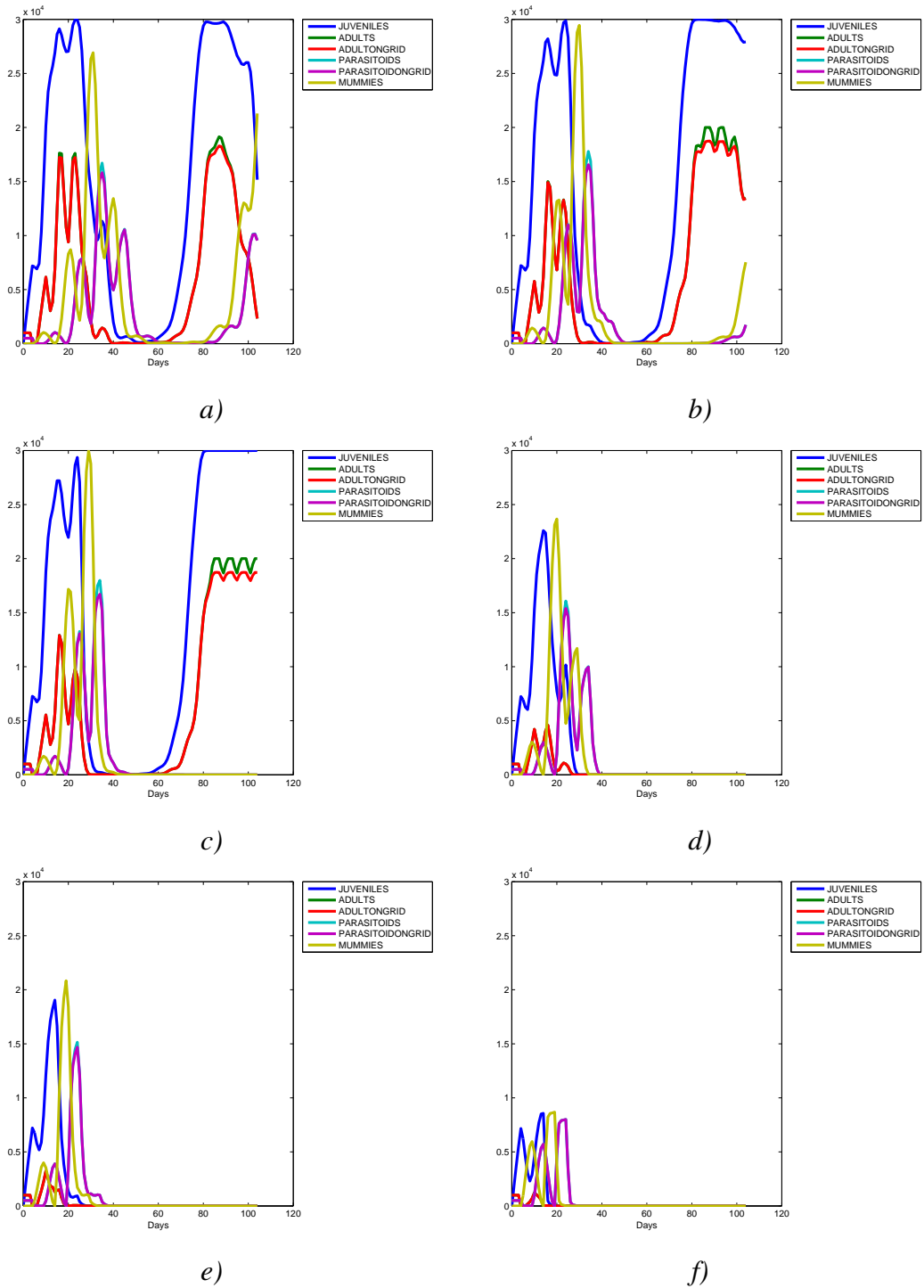
**Figure 5.5:** Plots illustrating aphid and parasitoid populations over time as the probability that a parasitoid discovers an aphid is varied. Parasitoids can handle more than one aphid per time-step. Aphid fecundity is modelled as a continuous process. Probability of a parasitoid discovering an aphid in (a), (b), (c) is 0.000006, 0.00001, 0.000015, respectively.

The simulation varying the probability of a parasitoid discovering an aphid was rerun, but this time with aphid fecundity occurring at the beginning of each day, though the rate of aphid fecundity of 2 aphids/day remains unchanged. Figures 5.6 and 5.7 show

that when parasitoids have a longer and shorter handling time, respectively, as the probability of a parasitoid discovering an aphid is increased the system becomes unstable and tends towards extinction. When the discovery rate is increased, parasitoids find aphids more rapidly, and given that the probability of successfully parasitising an aphid is 1, the parasitoids also parasitise aphids at a faster rate. The rate of parasitism becomes so rapid, in fact, that the parasitoids extinguish the aphid population before it has time to recover. The aphid population crash in turn causes the parasitoid population to crash. Similarly to before, when parasitoids have a shorter handling time the dynamics are faster compared to when parasitoids have a longer handling time. Comparing the dynamics of the system where aphid fecundity is modelled as a continuous process in figures 5.3,5.5 to the dynamics of the corresponding system where aphid fecundity is modelled as a discrete process in figures 5.6,5.7 indicates that the qualitative behaviour of both systems is very similar. Other results (not shown here) also indicated that changing the way aphid fecundity is modelled does not significantly change the dynamics of the system.



**Figure 5.6:** Plots illustrating aphid and parasitoid populations over time as probability of a parasitoid discovering an aphid is varied. Parasitoids can handle 1 aphid per time-step. Probability of a parasitoid discovering an aphid in (a), (b), (c), (d), (e), (f) is 0.000006, 0.000008, 0.00001, 0.00002, 0.00003, 0.00007, respectively.



**Figure 5.7:** Plots illustrating aphid and parasitoid populations over time as the probability of a parasitoid discovering an aphid is varied. Parasitoids can handle more than 1 aphid per time-step. Probability of a parasitoid discovering an aphid in (a), (b), (c), (d), (e), (f) is 0.000006, 0.000008, 0.00001, 0.00002, 0.00003, 0.00007, respectively.

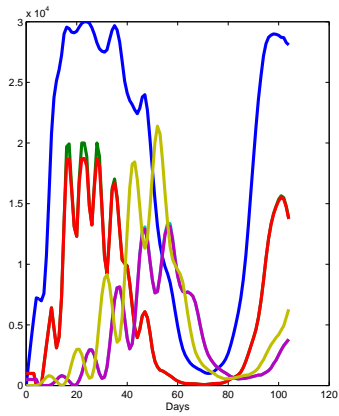


In the model, parasitoid attack rate is determined by the probability of a parasitoid discovering an aphid and the probability of successful parasitism. However, if the probability of success is set to one, varying the probability of discovery would be equivalent to varying the attack rate. Thus far, the baseline value used for parasitoid attack rate has been  $1 \text{ day}^{-1}$  for those parasitoids with a longer handling time, which is unrealistically low. In the field, an attack rate of 1-4 aphids per hour is more typical (correspondence with Professor S. Hubbard). Therefore, attack rate was varied using a more realistic range of parameter values. Also, unlike the previous simulations there is parasitoid interference whereby those parasitoids on a grid point where there is another parasitoid will experience a 30% reduced success of parasitism.

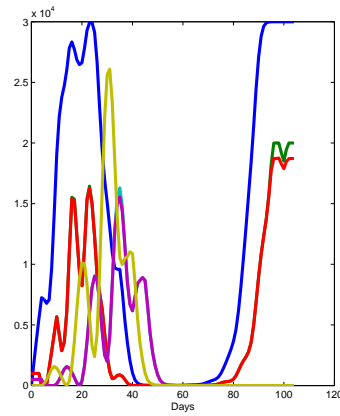
Figure 5.8 shows when parasitoids have a longer handling time and attack rate is varied from 1-4 aphids per hour parasitoids always drive aphids to extinction which is also a plausible scenario in the field. If probability of discovery is decreased to 0.00002 (an attack rate less than 1 aphid per hour), aphids survive and parasitoids become extinct, but if it is decreased to 0.00001, this leads to coexistence. The dynamics in figure 5.8 imply that parasitoids are too efficient suggesting that there may be other aspects of parasitoid biology which moderate parasitoid efficiency that are not being captured in the model. These might include a longer handling time, superparasitism (eggs laid on hosts already parasitised will probably not give rise to new parasitoids as only one larvae emerges as a parasitoid from each host) or predation of mummies.

Comparing the results here with those in figure 5.3 where the probability of a parasitoid discovering an aphid was varied without parasitoid interference suggests that the system without parasitoid interference is more sensitive to changes in the parasitoid's probability of aphid discovery, becoming extinct at a probability of discovery of 0.000015 compared to 0.00003 in the system with parasitoid interference. This suggests that parasitoid interference may stabilise the system. Although in figure 5.3 fecundity is modelled as a process occurring throughout the day whereas in figure 5.8

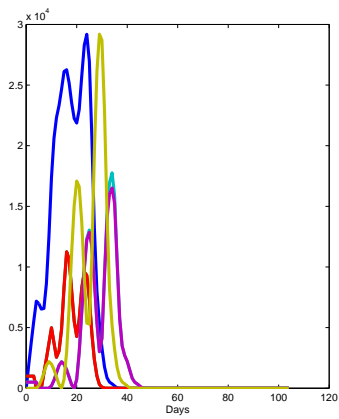
fecundity is modelled as a process that occurs at the beginning of each day (though at the same rate), it is still acceptable to compare the dynamics in these figures because as noted previously, changing the way aphid fecundity is modelled should not significantly alter the dynamics of the system. Therefore, from these results it can be inferred that parasitoid interference does affect the dynamics of the system and is stabilising which is in accordance with other studies (Hassell and May, 1973; Hassell and Varley, 1969).



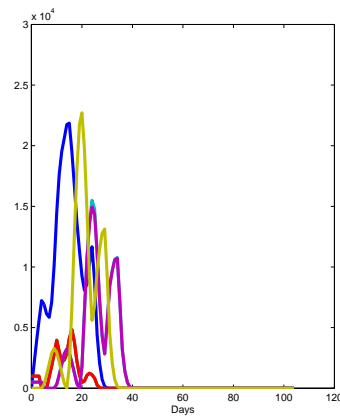
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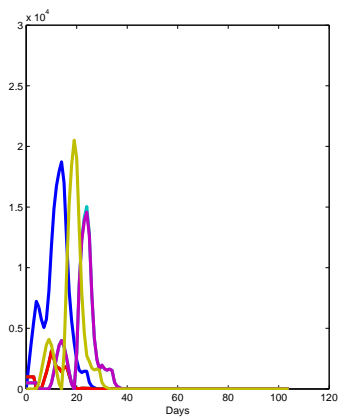
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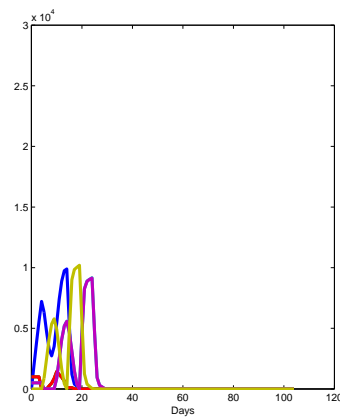
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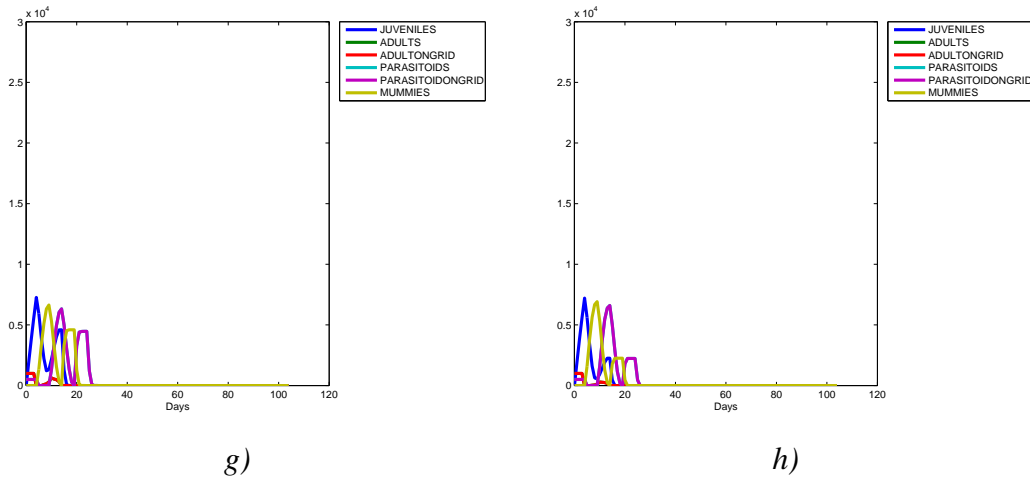
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**Figure 5.8:** Plots illustrating aphid and parasitoid populations over time as probability of a parasitoid discovering an aphid is varied when there is parasitoid interference. Parasitoids can handle 1 aphid per time-step. Probability of a parasitoid discovering an aphid in (a), (b), (c), (d), (e), (f), (g), (h) is 0.00001, 0.00002, 0.00003, 0.00005, 0.00007 (attack rate  $\approx 1$  aphid/hr), 0.00014 (attack rate  $\approx 2$  aphid/hr), 0.00022 (attack rate  $\approx 3$  aphid/hr), 0.00029 (attack rate  $\approx 4$  aphid/hr), respectively.

### 5.2.3 Varying the probability of successful parasitism

Figure 5.9 shows that when probability of successful parasitism is varied for parasitoids with a longer handling time, at low values of this parameter ( $< 0.6$ ), the initial parasitoid population has almost negligible effect on the aphid population and the aphid population tends to a stable equilibrium. The parasitoid population either becomes extinct for very low values of parasitoid success or is very small for slightly higher values of parasitoid success. As the probability of successful parasitism is increased to values of 0.6 and higher, the parasitoid population has a greater impact on the aphid population, although it seems that populations still tend to a stable equilibrium unless the system is really stressed, i.e. when success of parasitism is 0.9 and 1. In figure 5.9 i and j when success of parasitism is 0.9 and 1, there appears to be the beginning of oscillations. Figure 5.10, which shows the simulations in figure 5.9 f, g, h, i and j run for a longer period of time, confirms that the populations in figure 5.9 f, g and h tended to a stable equilibrium and that this was also the case for populations in figure 5.9 i.

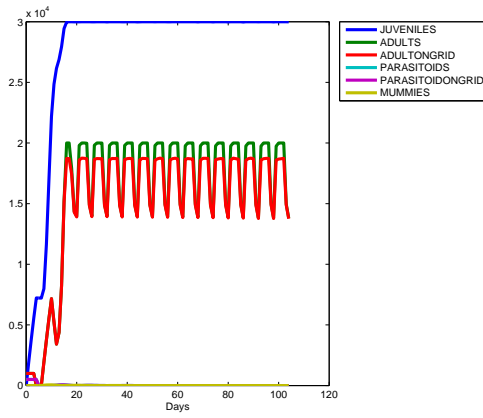
Oscillations only persisted when success of parasitism equaled 1 (figure 5.10 e). These oscillations are parasitoid driven as indicated by the high degree of parasitoid pressure (represented here as successful parasitism) required for oscillatory dynamics to emerge. Figure 5.10 also shows that over time as success of parasitism is increased, the number of aphids decrease while the number of parasitoids increase which is a consequence of increasing parasitism pressure.

Spatial results were obtained for all populations as success of parasitism was varied from 0.6 to 1 on day 124 (in the model) because this was when the aphid population's cycles peaked after the initial transient dynamics in figure 5.10 e, and thus was thought to be an interesting point in time to take a snapshot of the spatial dynamics. By day 124, as the probability of successful parasitism is varied, the system in most cases has not reached equilibrium. Nevertheless, the spatial output in figures 5.11 and 5.12 show that as the probability of successful parasitism is increased, the number of adult and juvenile aphids decreases, except when probability of successful parasitism equals 1. This is because the populations are oscillating and the aphids are at or approaching their peak. Figure 5.13 shows that for parasitoids, on the other hand, first their numbers increase as probability of successful parasitism varies from 0.6 to 0.8, but when this probability is 0.9 and 1.0, parasitoid numbers decreases because populations are not at their equilibrium level here and parasitoids are exhibiting damped oscillations and oscillations, so they could be anywhere between the peak and trough of the oscillation. It may not be appropriate to compare the results here because the system had not quite reached equilibrium at day 124.

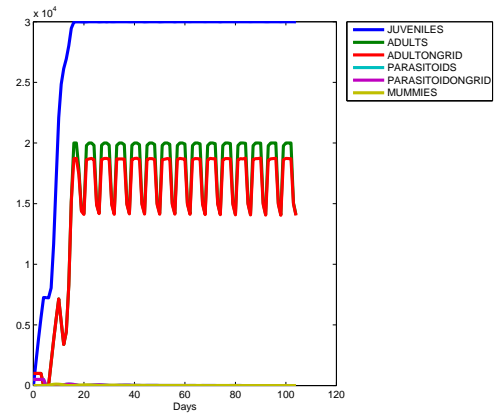
Figure 5.14 shows the results from varying the probability of successful parasitism, but this time with parasitoid interference. As before when success of parasitism was varied, parasitoids have hardly any effect on the aphid population until the probability of success is increased to a value of 0.6. However, this time the system seems to be stable despite increasing the probability of successful parasitism even to 1. Figure 5.15,

which shows the simulations in figure 5.14 f, g, h, i and j run for an extended period of time, indicates that the system tended to a stable equilibrium each time, confirming this analysis. These results also suggest that parasitoid interference is stabilising in agreement with other studies (Hassell and May, 1973; Hassell and Varley, 1969). The addition of parasitoid interference to the system also gives rise to slightly slower dynamics initially, particularly when the probability of successful parasitism is high (see figures 5.9, 5.14 i and j). This is most likely because, as a result of interference, parasitoids are less efficient at attacking aphids and because they are not as efficient, it takes them longer to drive the aphid population to a minimum. Similarly to before, when there was no parasitoid interference, as parasitoid pressure is increased, the number of aphids decreases and the number of parasitoids increases over time).

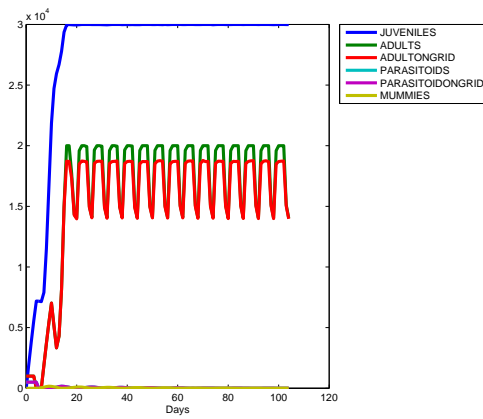
As before, spatial output was obtained on day 124 for the simulations in figure 5.15. Mostly the system seems to have already reached equilibrium by day 124 except for when the probability of successful parasitism is 0.6 and 0.7 (see figure 5.15). Figures 5.16 and 5.17 show that as the probability of successful parasitism is increased, when the system is in equilibrium (for most cases), the number of juvenile and adult aphids decreases and the domain is less densely filled. This makes sense because as the probability of successful parasitism is increased, more juveniles are being killed off which leads to fewer juveniles becoming adults. Figure 5.18 shows that parasitoids, in contrast, seem to increase and the domain becomes more densely filled as the probability of successful parasitism is increased from 0.6 to 0.7. As the probability of successful parasitism is increased further, however, there is not much change in the spatial dynamics.



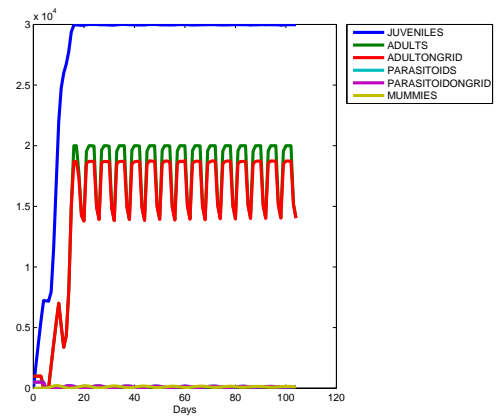
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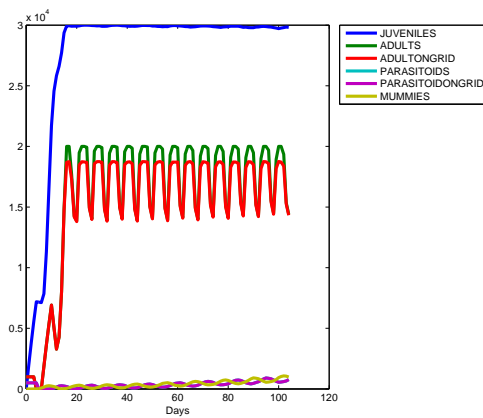
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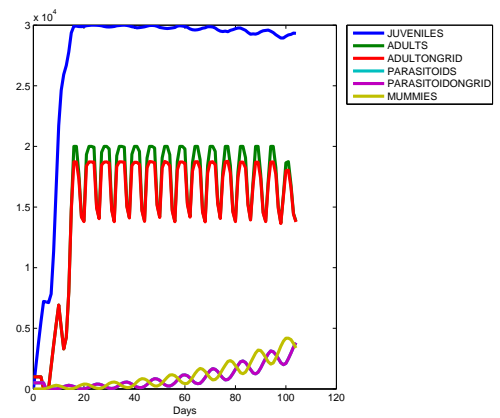
c)



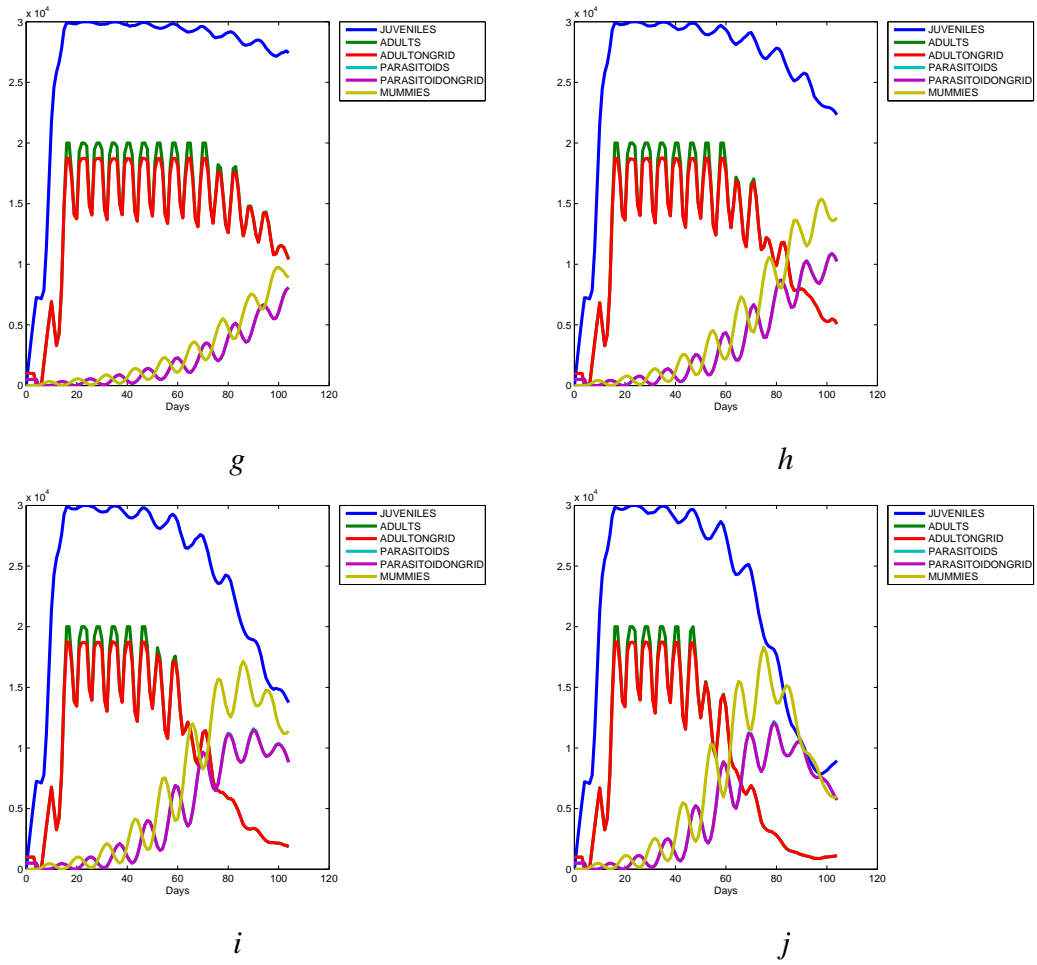
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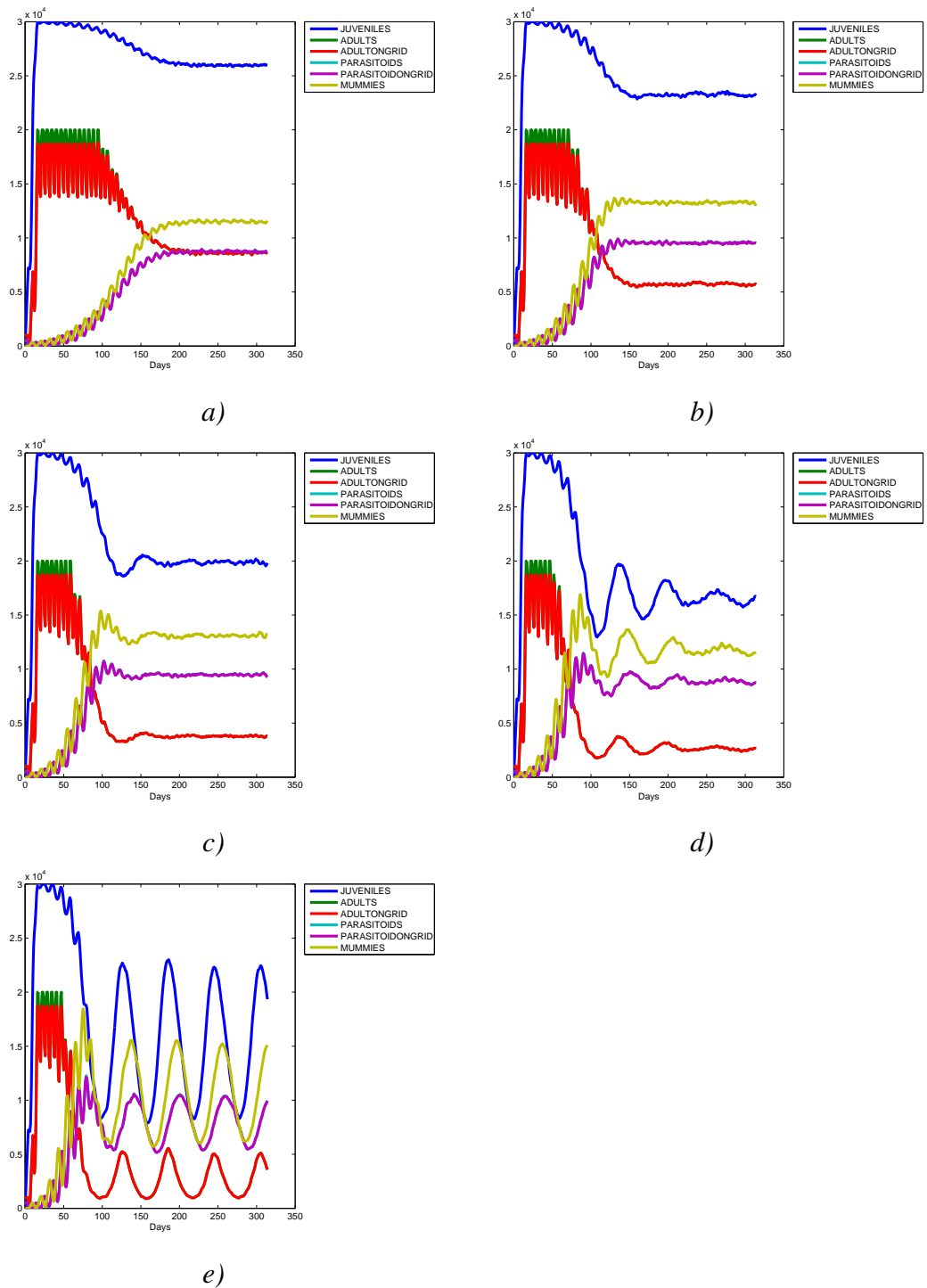


f)

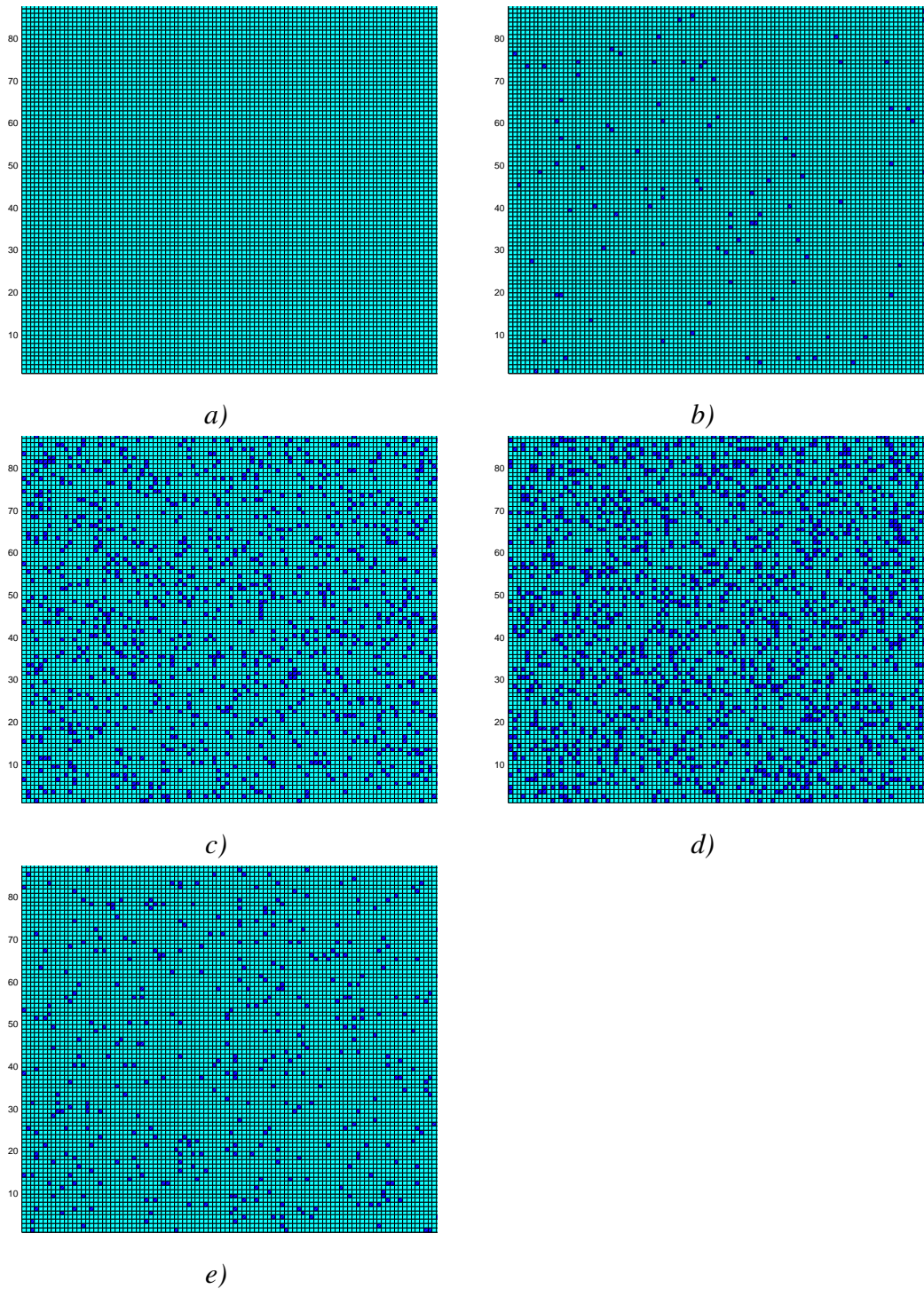


**Figure 5.9:** Plots illustrating aphid and parasitoid populations over time as success of parasitism is varied. Parasitoids can handle 1 aphid per time-step. Success of parasitism in (a), (b), (c), (d), (e), (f), (g), (h), (i), (j) is 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1, respectively.

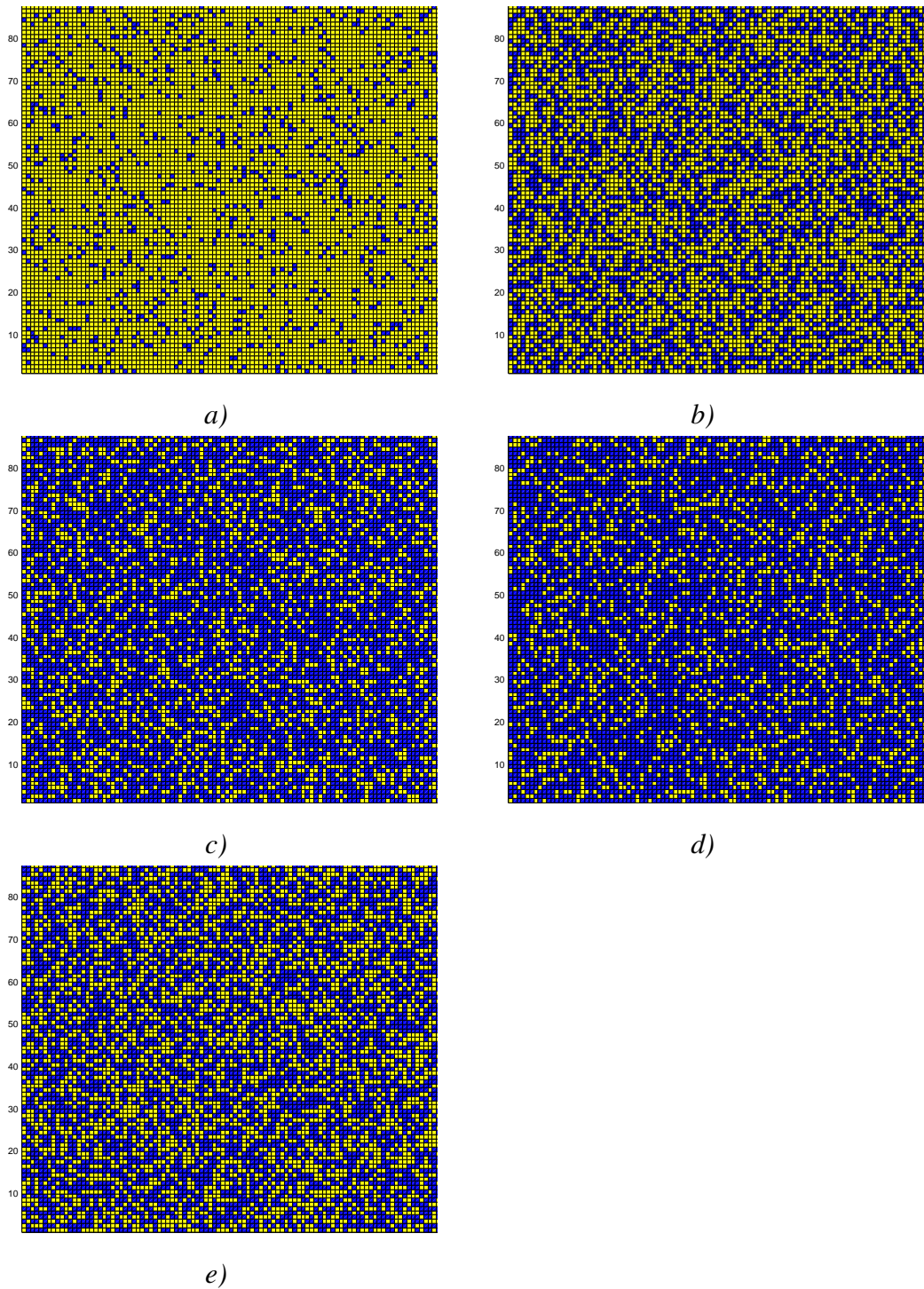




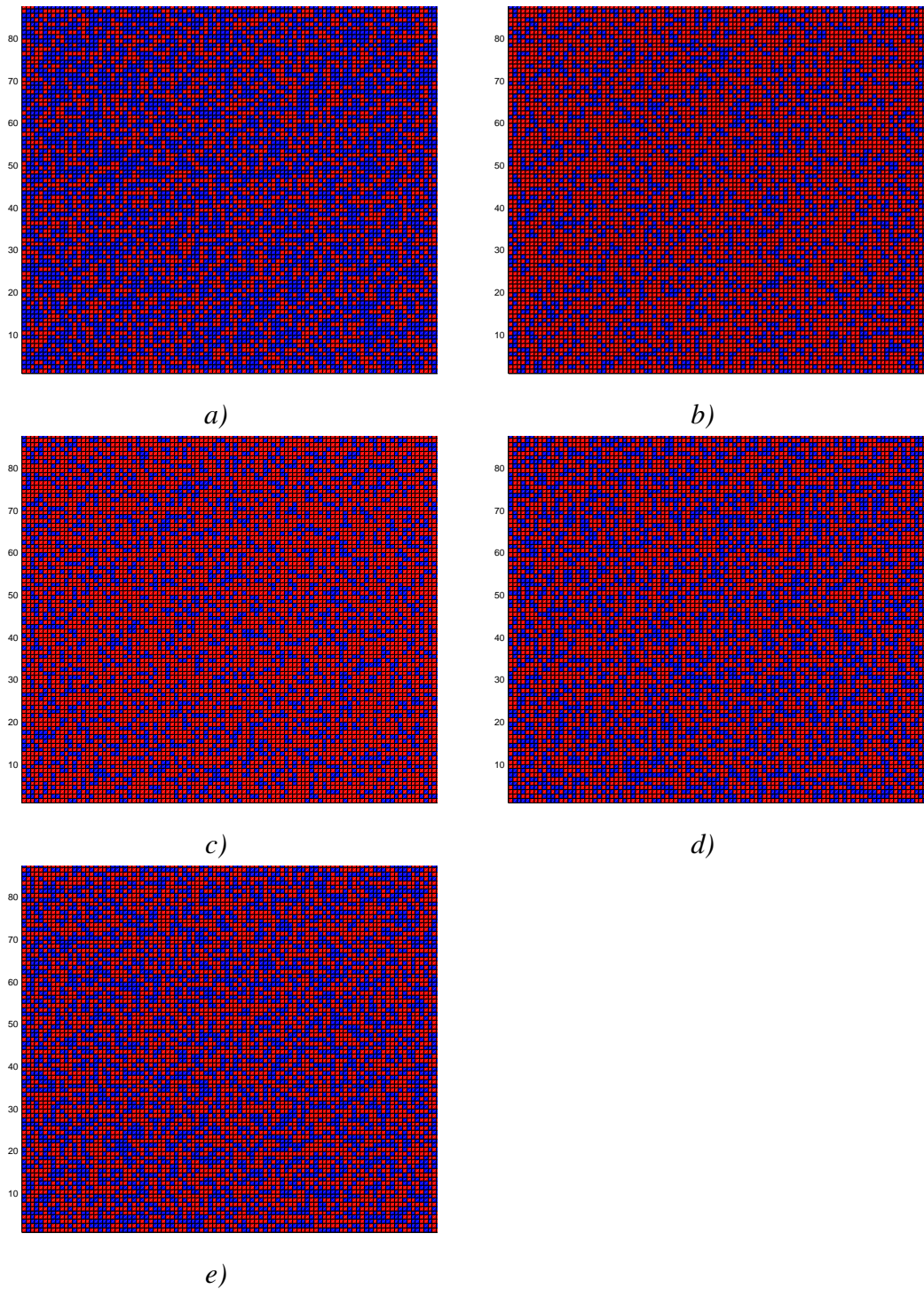
**Figure 5.10:** Plots illustrating aphid and parasitoid populations over time as success of parasitism is varied. Parasitoids can handle 1 aphid per time-step. Success of parasitism in (a), (b), (c), (d), (e) is 0.6, 0.7, 0.8, 0.9, 1, respectively.



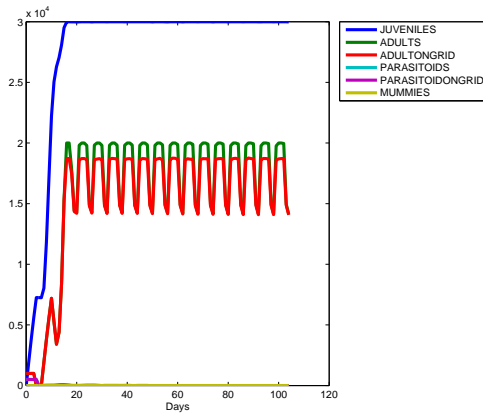
**Figure 5.11:** *Plots illustrating the spatial dynamics of juvenile aphids on day 124 in figure 5.10. The light blue pixels represent juvenile aphids and the dark blue pixels represent empty space. (a), (b), (c), (d), (e) correspond to a success of parasitism of 0.6, 0.7, 0.8, 0.9, 1, respectively.*



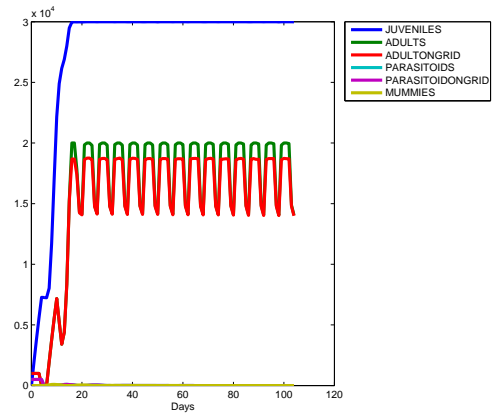
**Figure 5.12:** Plots illustrating the spatial dynamics of adult aphids on day 124 in figure 5.10. The yellow pixels represent adult aphids and the dark blue pixels represent empty space. (a), (b), (c), (d), (e) correspond to a success of parasitism of 0.6, 0.7, 0.8, 0.9, 1, respectively.



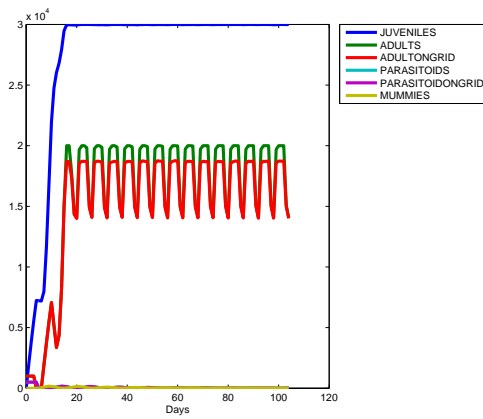
**Figure 5.13:** *Plots illustrating the spatial dynamics of parasitoids on day 124 in figure 5.10. The red pixels represent parasitoids and the dark blue pixels represent empty space. (a), (b), (c), (d), (e) correspond to a success of parasitism of 0.6, 0.7, 0.8, 0.9, 1, respectively.*



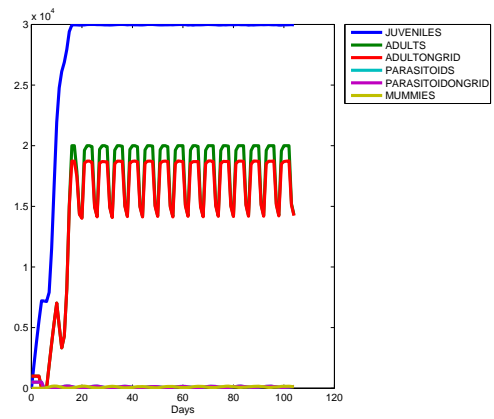
a)



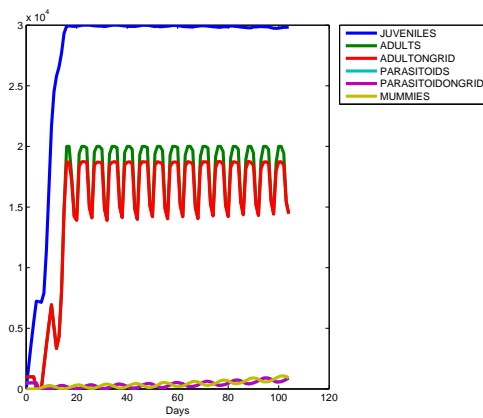
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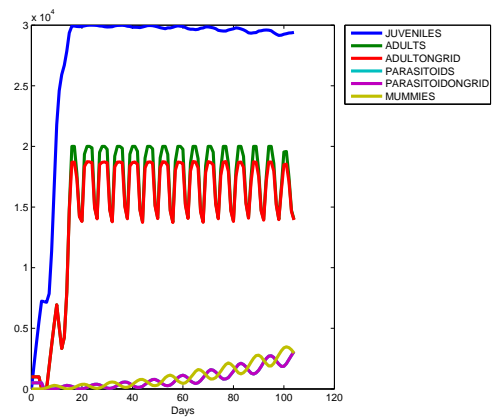
c)



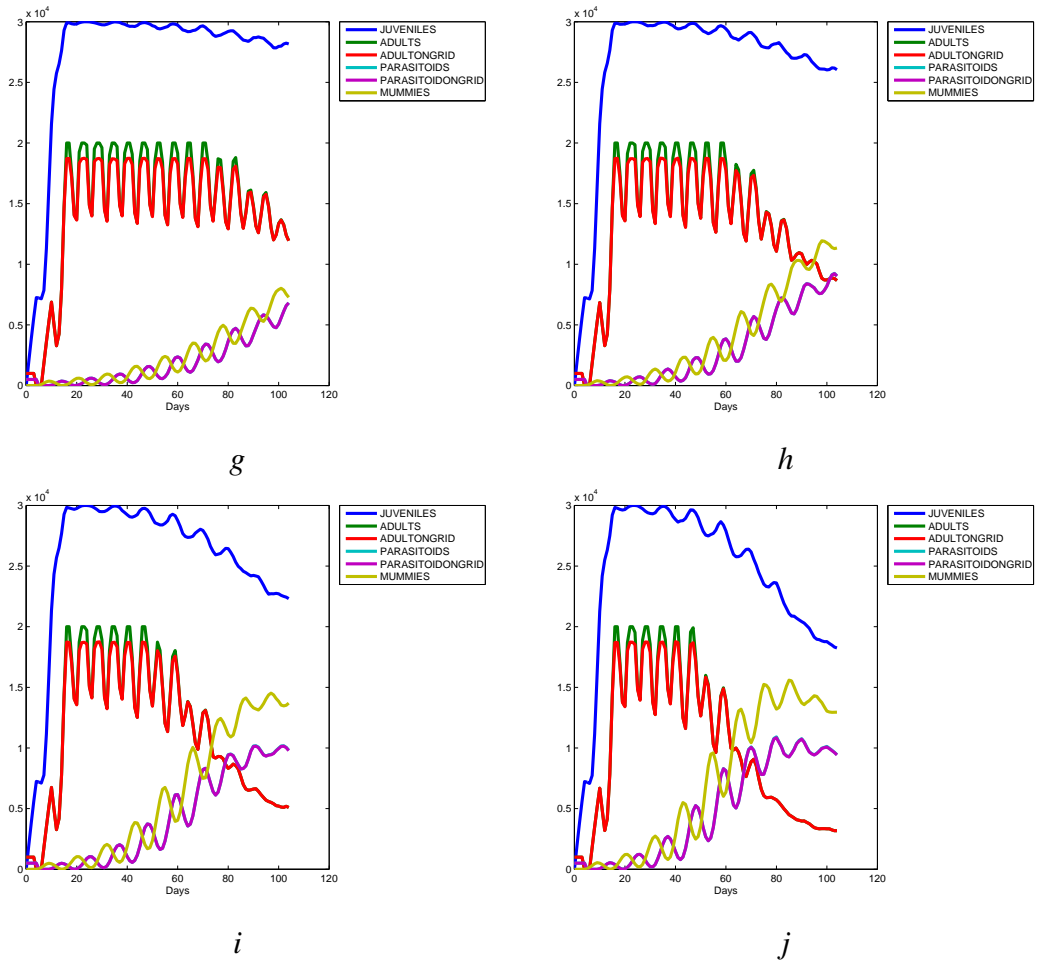
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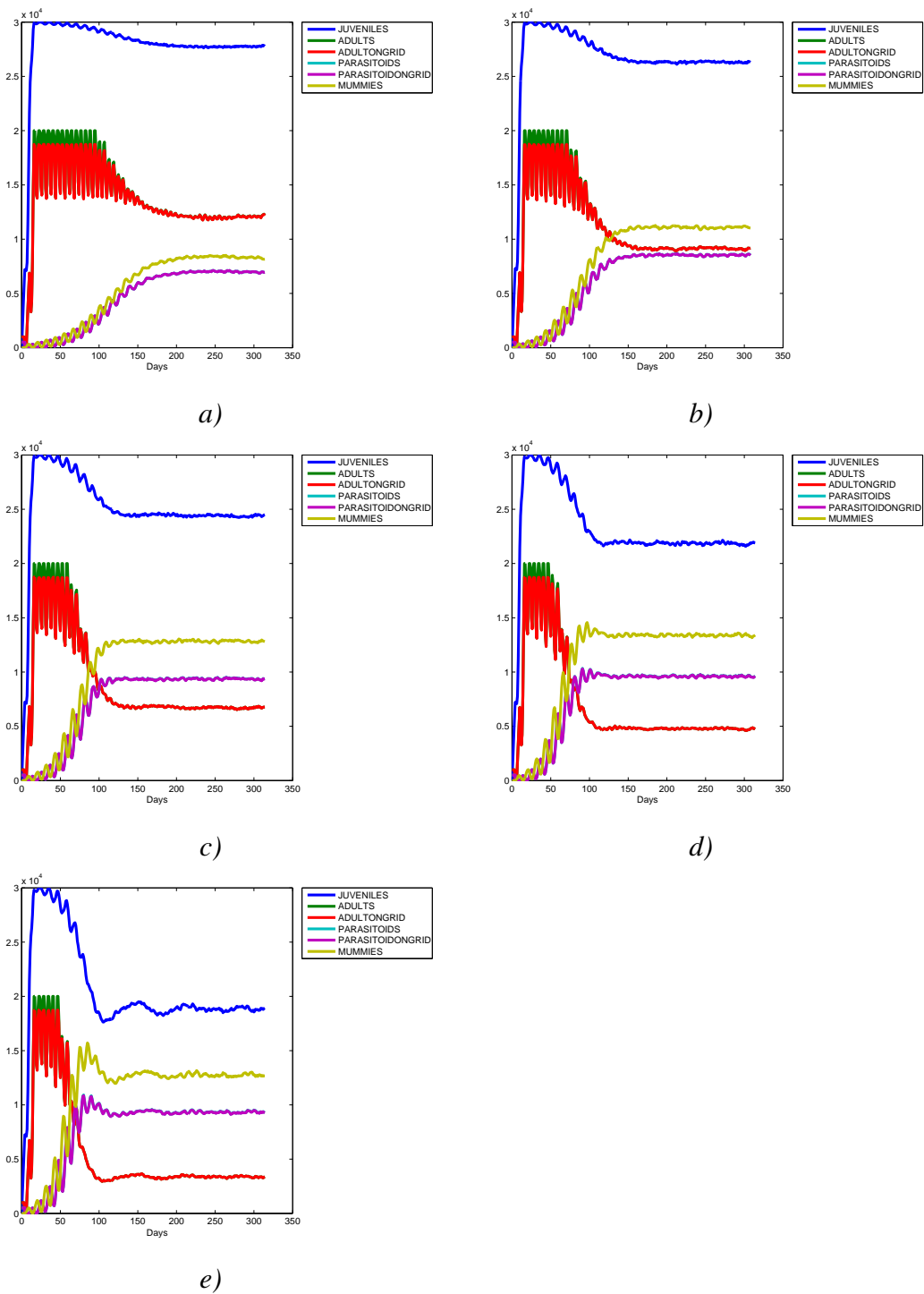
e)



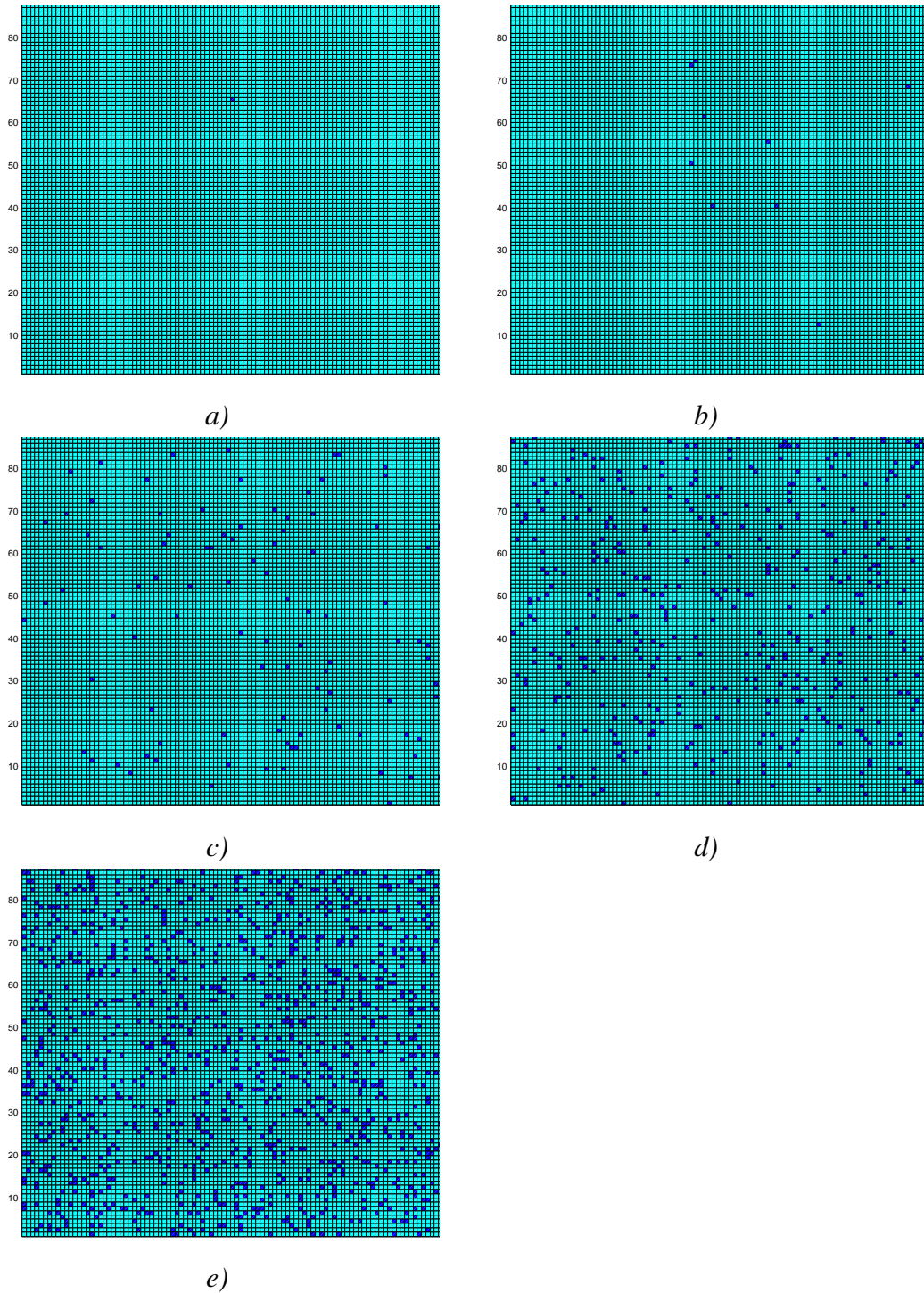
f)



**Figure 5.14:** Plots illustrating aphid and parasitoid populations over time as success of parasitism is varied when parasitoid interference is implemented. Parasitoids can handle 1 aphid per time-step. Success of parasitism in (a), (b), (c), (d), (e), (f), (g), (h), (i), (j) is 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1, respectively.

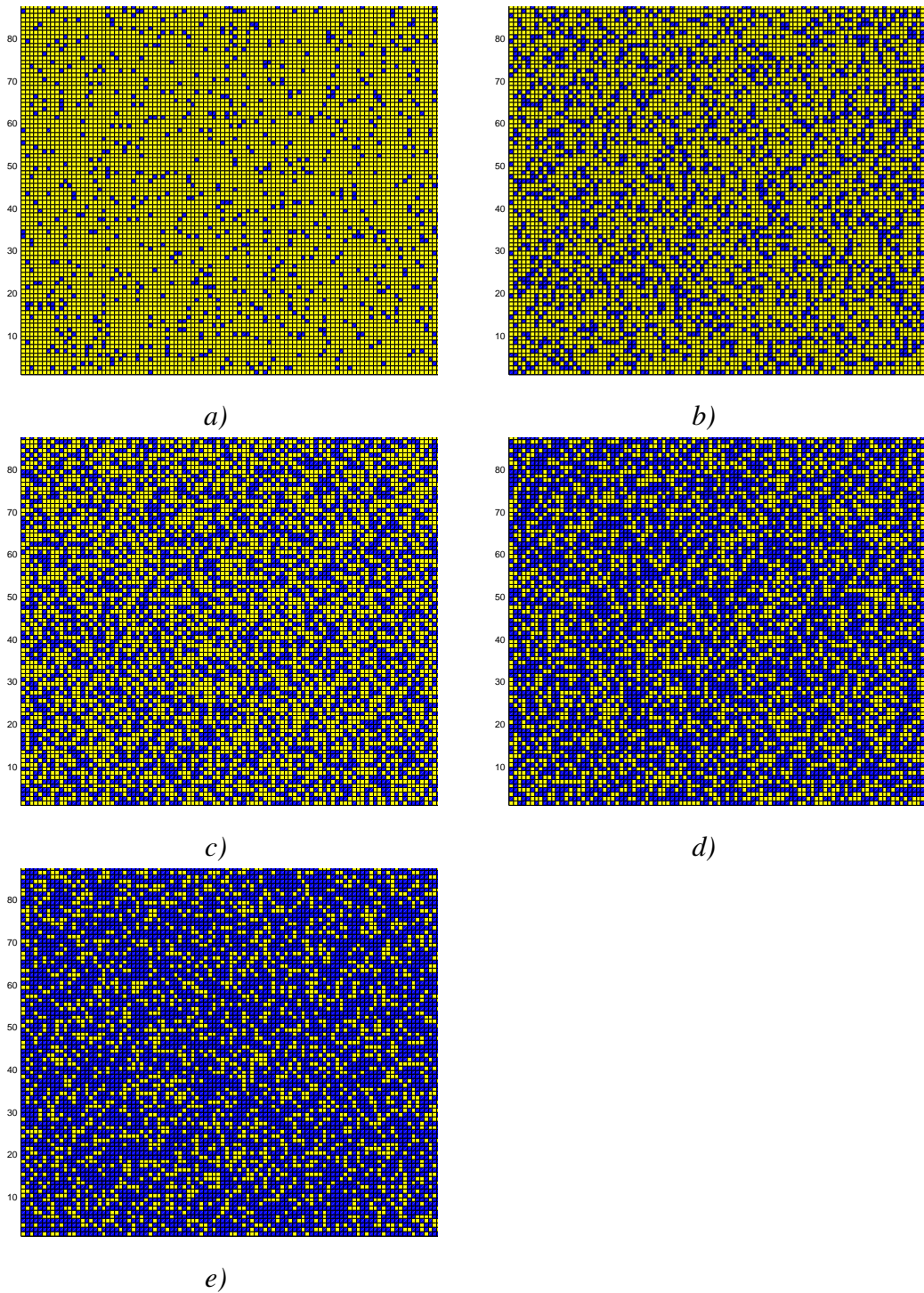


**Figure 5.15:** Plots illustrating aphid and parasitoid populations over time as success of parasitism is varied when there is parasitoid interference. Parasitoids can handle 1 aphid per time-step. Success of parasitism in (a), (b), (c), (d), (e) is 0.6, 0.7, 0.8, 0.9, 1, respectively.

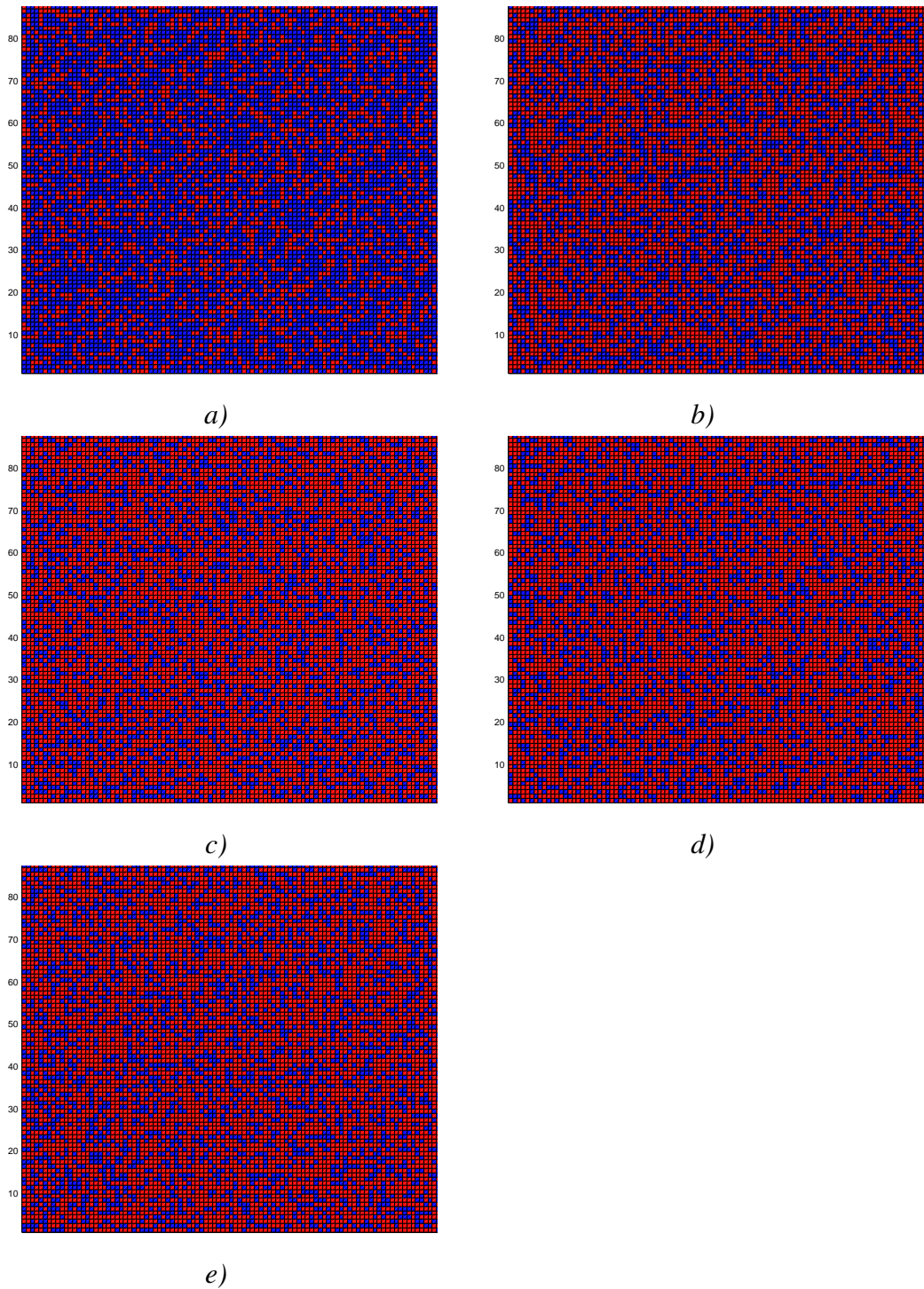


**Figure 5.16:** Plots illustrating the spatial dynamics of juvenile aphids on day 124 in figure 5.15. The light blue pixels represent juvenile aphids and the dark blue pixels represent empty space. (a), (b), (c), (d), (e) correspond to a success of parasitism of 0.6, 0.7, 0.8, 0.9, 1, respectively.





**Figure 5.17:** Plots illustrating the spatial dynamics of adult aphids on day 124 in figure 5.15. The yellow pixels represent adult aphids and the dark blue pixels represent empty space. (a), (b), (c), (d), (e) correspond to a success of parasitism of 0.6, 0.7, 0.8, 0.9, 1, respectively.



**Figure 5.18:** *Plots illustrating the spatial dynamics of parasitoids on day 124 in figure 5.15. The red pixels represent parasitoids and the dark blue pixels represent empty space. (a), (b), (c), (d), (e) correspond to a success of parasitism of 0.6, 0.7, 0.8, 0.9, 1, respectively.*

## 5.2.4 Varying adult mortality

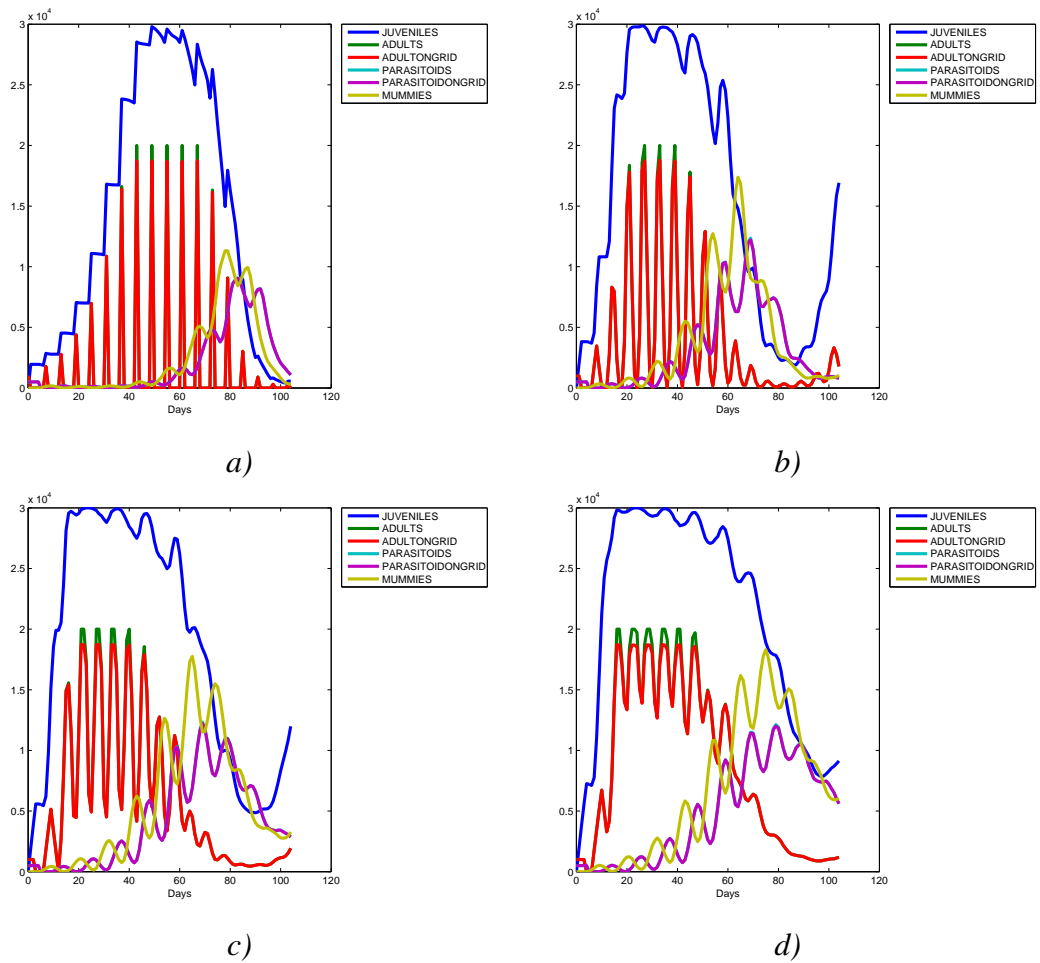
Since aphid populations are slightly sensitive to changes in adult mortality (see results from chapter 3), adult aphid mortality was also varied in the aphid-parasitoid model by similarly reducing average adult aphid lifespan. Figure 5.19 shows that when parasitoids have a longer handling time, increasing adult mortality (or reducing adult lifespan from 4 to 2 days) seems to contribute to faster and more unstable dynamics (indicated by the increase in amplitude of the initial oscillation). The faster dynamics as adult mortality is increased likely occurs because increasing adult mortality leads to reduced production of juveniles, and thus because there are fewer juveniles to parasitise, the parasitoid population drives the aphid population to a trough more rapidly, thereby perpetuating the cycles at a faster rate. When adult aphid lifespan is 1 day, it is not clear whether the populations are about to crash because all populations in the last time-step shown are positive (figure 5.19 a). However, the fact that the low point of each population is verging closer to 0 suggests that the system is more unstable than in figure 5.19 b. An interesting observation about the dynamics is that the juvenile production does not seem to change despite increasing adult aphid lifespan and therefore reproductive capacity. However, as mentioned before in chapter 3, because of the carrying capacity imposed on juvenile aphids, there is not enough resources to support more than 30,000 juveniles. Therefore, although aphids with a longer lifespan are producing more offspring per individual, it is likely that many of the offspring do not survive due to limited resources.

Figure 5.20 shows that when parasitoids have a shorter handling time, similarly to the system with parasitoids with a longer handling time, increasing adult aphid mortality destabilises the system which goes from coexistence in figure 5.20 a to coexistence, but with really low parasitoid numbers in figure 5.20 c to extinction of parasitoids in figure 5.20 d. Parasitoid numbers become dangerously low or extinct as adult aphid

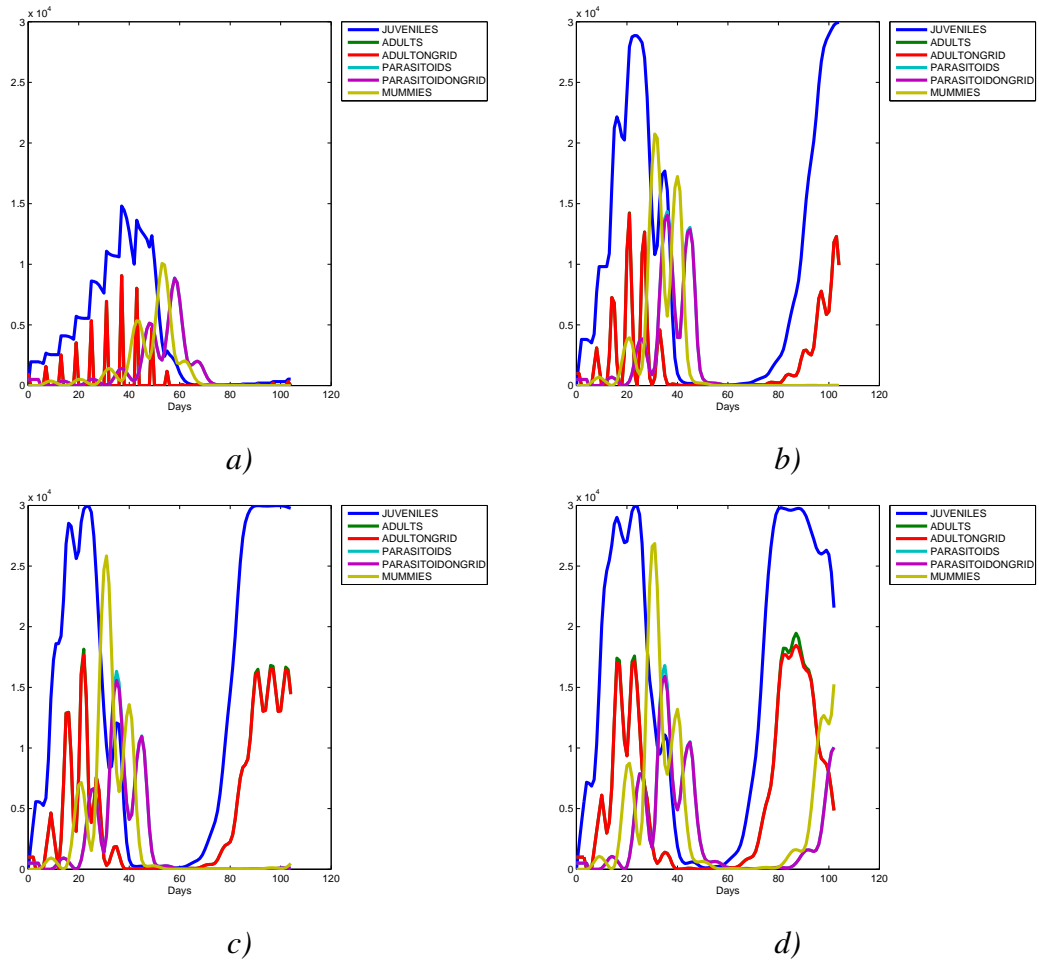
mortality increases (or adult aphid lifespan decreases) because days allocated for aphid reproduction become fewer thereby reducing juvenile production and consequently the number of hosts for parasitoids. In contrast to when parasitoids have a longer handling time, overall the dynamics are faster because parasitoids are more efficient. The greater efficiency of parasitoids with shorter handling time is also reflected in higher peak counts for mummies and parasitoids in figure 5.20 a, b and c in comparison to the corresponding subfigures in figure 5.19. Looking at figures 5.19 and 5.20 more closely, when parasitoids have a shorter handling time, as adult mortality increases the number of adult aphids seems to decrease, whereas when parasitoids have a longer handling time, the adult population appears to consistently tend towards its carrying capacity of 20,000 aphids. This is in part because the parasitoids with a shorter handling time reduce the number of juveniles that become adults more so than those parasitoids with a longer handling time. This compounded with the effect of reducing juvenile production from decreasing adult aphid lifespan leads to far fewer juveniles becoming adult as adult aphid mortality is increased. The effect is especially dramatic when adult aphid lifespan is reduced to 1 day where there is also a staggering reduction (by half) in juvenile production.

Interestingly, in figure 5.20 there is a trend seen in prior results, that despite doubling adult aphid lifespan and therefore reproductive capacity, this is not always reflected in the juvenile population (figure 5.20 a and c). So I tested the previous hypothesis that because of the way density dependence was modelled in the system, the reproductive output was being underestimated. I did this by plotting the number of newborn juveniles that were killed instantly after birth (i.e. new juveniles not added to the grid) because the domain was already at carrying capacity. Figure 5.21 shows that as adult lifespan is increased, so is the number of newborn juveniles not added to the grid (the black trajectory) as well as cumulative production of juveniles (those not added and added to the grid). Therefore, as adult lifespan is doubled, aphids are in fact producing

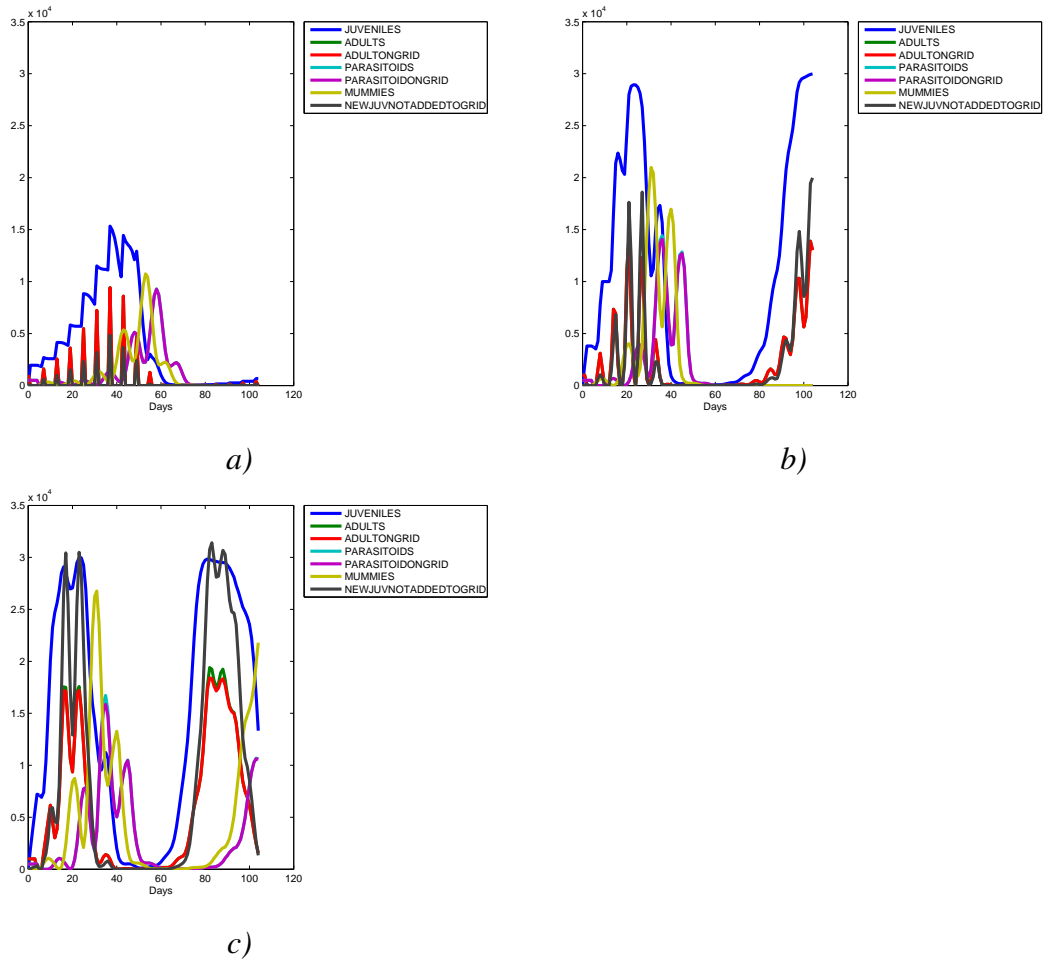
significantly more offspring, however, because of the carrying capacity imposed on juvenile aphids, some of these offspring do not survive. This result confirms the previous hypothesis and also provides an explanation for the lack of variation in juvenile production as adult aphid lifespan was varied in figures 4.10 and 5.19.



**Figure 5.19:** Plots illustrating aphid and parasitoid populations over time as adult aphid lifespan is varied. Parasitoids can handle 1 aphid per time-step. Adult lifespan in (a), (b), (c), (d) is 1, 2, 3, 4 days, respectively.



**Figure 5.20:** Plots illustrating aphid and parasitoid populations over time as adult lifespan is varied. Parasitoids can handle more than 1 aphid per time-step. Adult lifespan in (a), (b), (c), (d) is 1, 2, 3, 4 days, respectively.



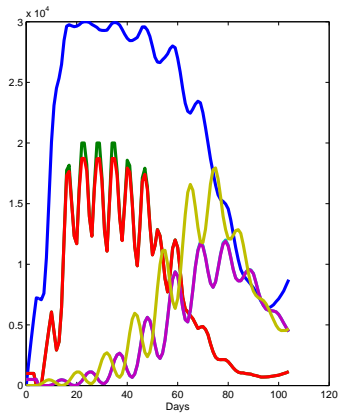
**Figure 5.21:** Plots illustrating aphid and parasitoid populations over time as adult lifespan is varied. Parasitoids can handle more than 1 aphid per time-step. Adult lifespan in (a), (b), (c) is 1, 2, 4 days, respectively.

### 5.2.5 Varying juvenile mortality

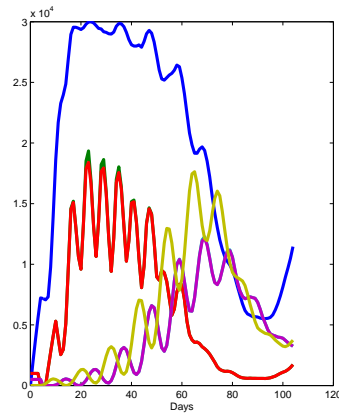
The previous chapter showed that the dynamics of the aphid population were sensitive to changes in juvenile mortality, particularly the adult population, and when the system was really stressed, the aphid population verged upon extinction. Figures 5.22 and 5.24 show that varying juvenile mortality in the aphid-parasitoid system has a similar effect. Addition of parasitoids to the system, however, reduces aphid numbers and does not

lead to a stable equilibrium in the aphid population when juvenile mortality is 0.1-0.7 in comparison to the aphid-only system. When parasitoids have a longer handling time, as juvenile mortality is increased, population numbers of all species decrease and the dynamics change from what appears to be the beginning of oscillations to populations verging on extinction (the parasitoid population becomes extinct, but the aphid population is still greater than zero) (figure 5.22). Figure 5.23, which shows the cases in figure 5.22 h and i for an extended period of time, confirms the existence of persistent oscillations and extinction of species as the system became more stressed. It is thought that a bifurcation probably occurs when juvenile mortality is varied from 0.8 to 0.9 because of the qualitative change in dynamics. When handling time is shorter a similar pattern of behaviour emerges to when handling time is longer, although again it seems that the dynamics are 'faster' (figure 5.24).

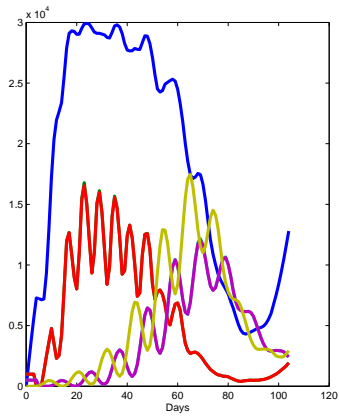




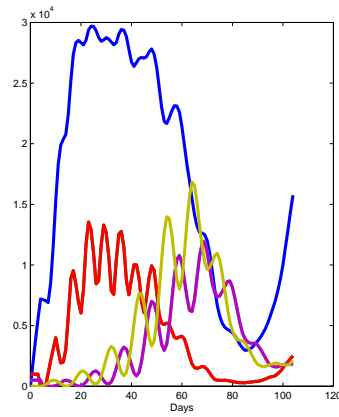
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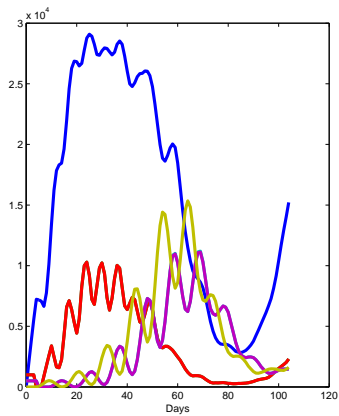
b)



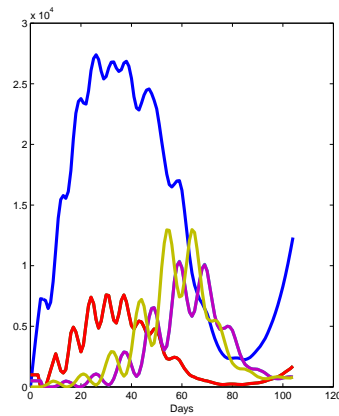
c)



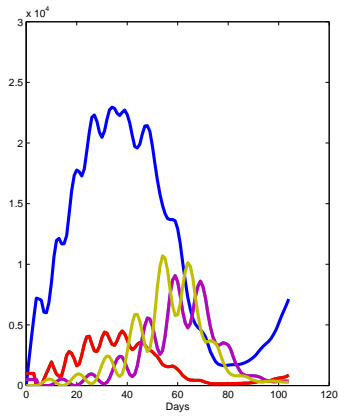
d)



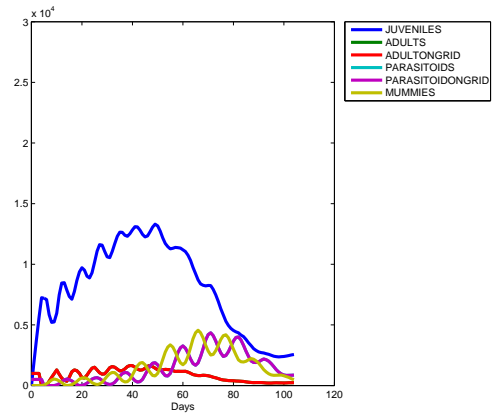
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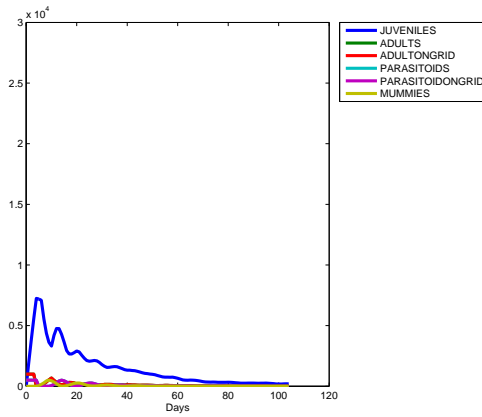
f)



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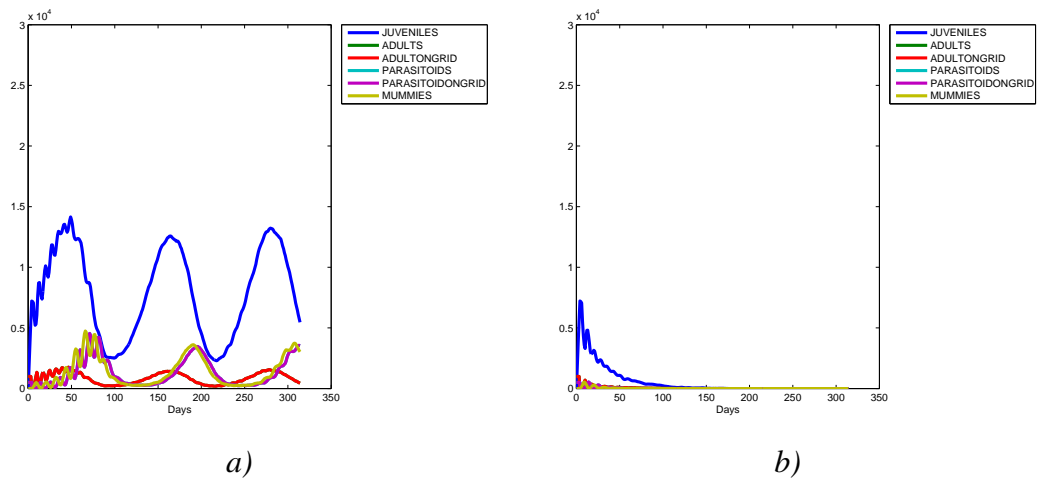


h)

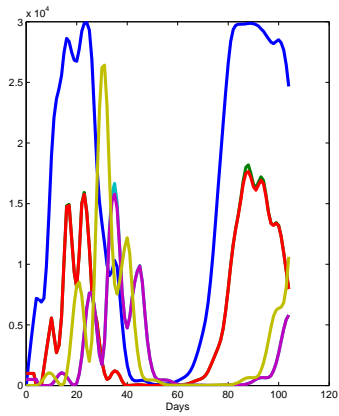


i)

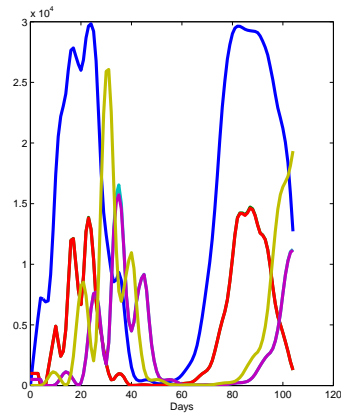
**Figure 5.22:** Plots illustrating aphid and parasitoid populations over time as juvenile mortality is varied. Parasitoids can handle 1 aphid per time-step. Juvenile mortality in (a), (b), (c), (d), (e), (f), (g), (h), (i) is 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, respectively.



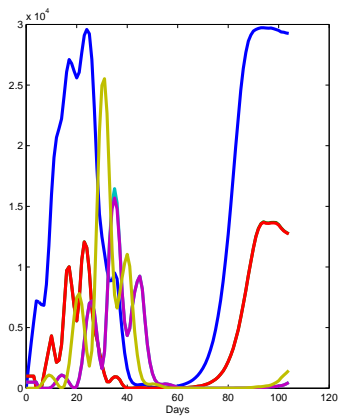
**Figure 5.23:** Plots illustrating aphid and parasitoid populations in figure 5.22 h and i for an extended period of time. Parasitoids can handle 1 aphid per time-step. Juvenile mortality in (a), (b) is 0.8 and 0.9, respectively.



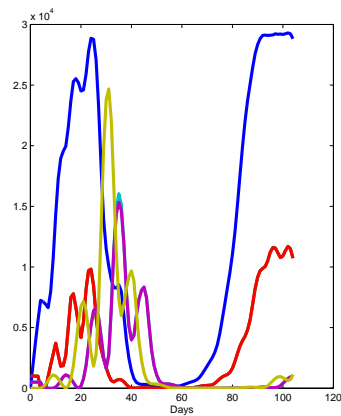
a)



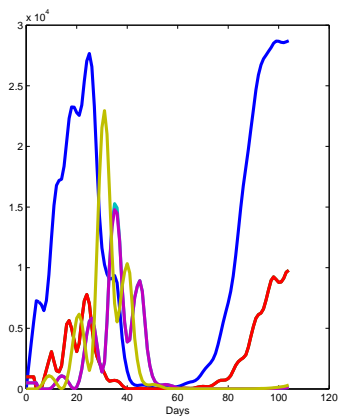
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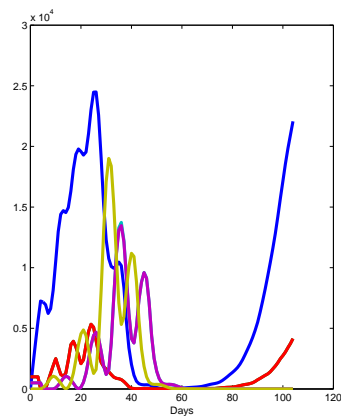
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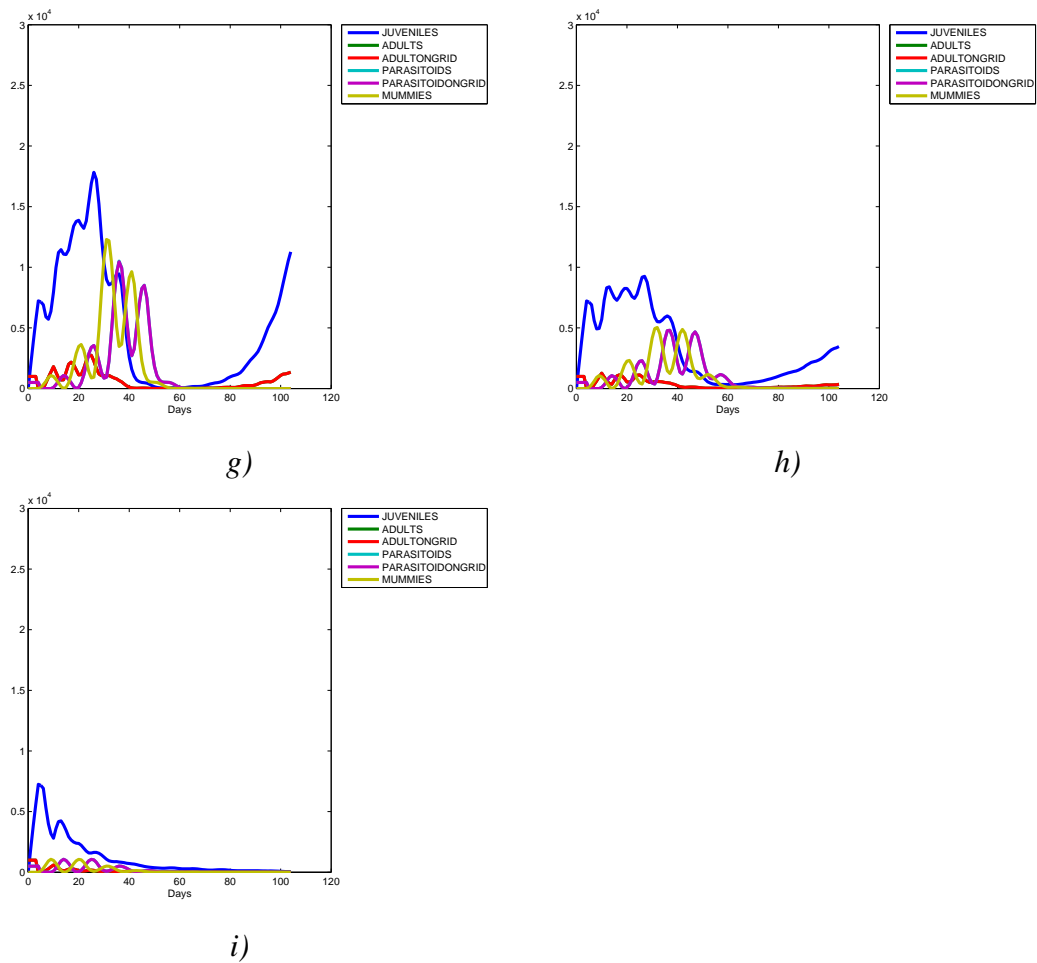
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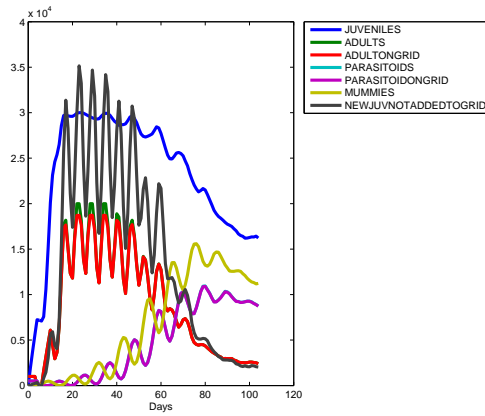


**Figure 5.24:** Plots illustrating aphid and parasitoid populations over time as juvenile mortality is varied. Parasitoids can handle more than 1 aphid per time-step. Juvenile mortality in (a), (b), (c), (d), (e), (f), (g), (h), (i) is 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, respectively.

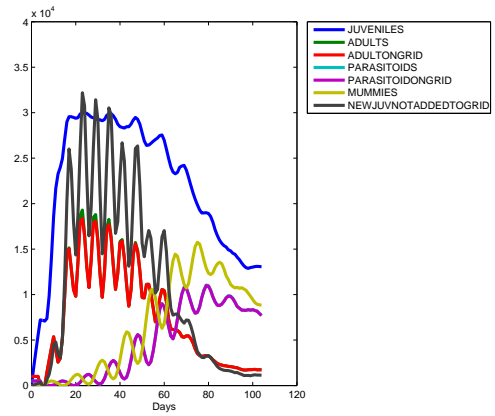
Aphid juvenile mortality was varied again to see whether increasing this parameter could account for the number of newborn juveniles not being added to the population because of the way density dependence is imposed in the system (see section 4.2). Unlike the previous time when juvenile mortality was varied (see figures 5.22,5.24), for the system with parasitoids with a longer handling time, there is also the additional effect of parasitoid interference. Note: in the system with parasitoids with a shorter handling time, there is no parasitoid interference. For both systems with the different types of parasitoid foragers, I have also kept track of the number of aphid newborns

not added to the population over time unlike before when juvenile mortality was varied. Figure 5.25 shows that when parasitoids have a longer handling time, as before, it seems that increasing juvenile mortality has more of an effect on the adult aphid population, although in general all populations decrease as this parameter is increased. Also, there is a dramatic shift in dynamics from what appears to be the beginning of oscillations to populations on the brink of extinction as juvenile mortality is increased from 0.8 to 0.9 as before. The addition of parasitoid interference seems to 'slow' the pace of the dynamics. This is most likely because the parasitoids are less efficient than before and it therefore takes them a longer period of time to drive the aphid population to a trough. Figure 5.26 shows that the pattern of dynamics when parasitoid handling time is shorter is very similar to the dynamics when parasitoid handling time is longer, although the dynamics are faster.

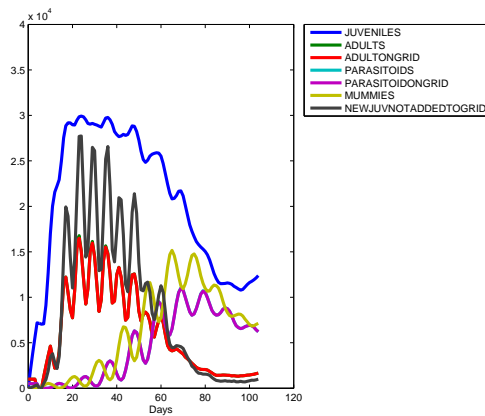
Figures 5.25 and 5.26 show that as juvenile mortality is increased (for both systems with different types of parasitoid foragers), the number of newborn aphids not added to the grid decreases. Realistically not all juvenile aphids survive to adulthood in the field, and to capture this reality, juvenile mortality ought to be made a permanent parameter in the model. As well, figures 5.25,5.26 show that the number of juveniles not added to the grid significantly declines when juvenile mortality is  $\geq 0.6$ . Therefore, making juvenile mortality a permanent parameter in the model could potentially account for many of the juvenile aphids not being added to the grid because of the density dependence that has been artificially imposed on the system.



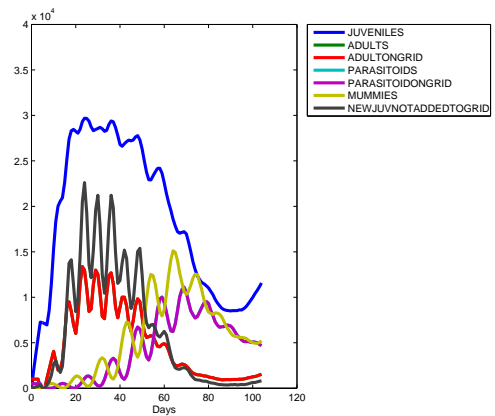
a)



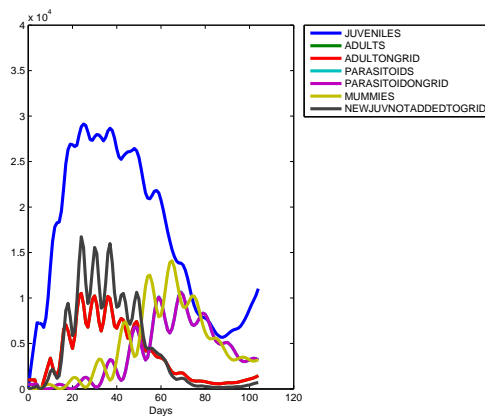
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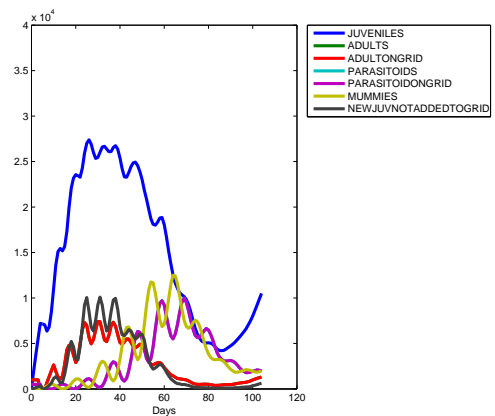
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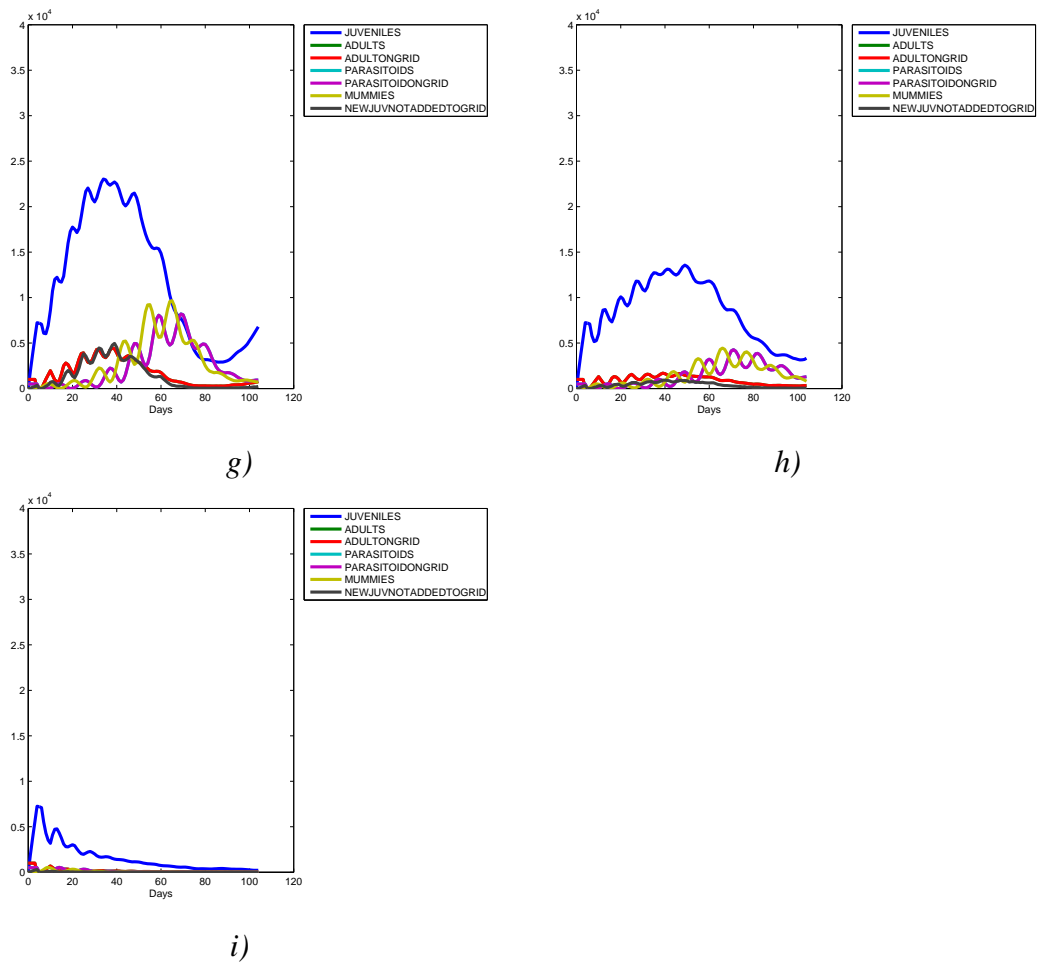
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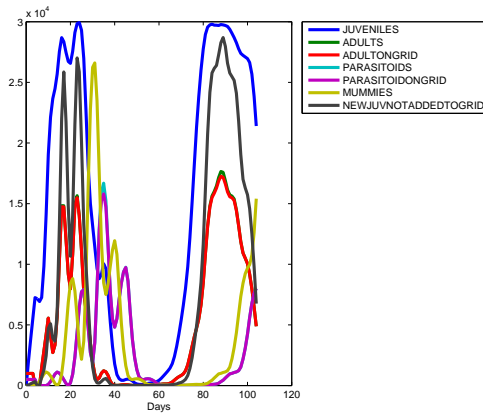


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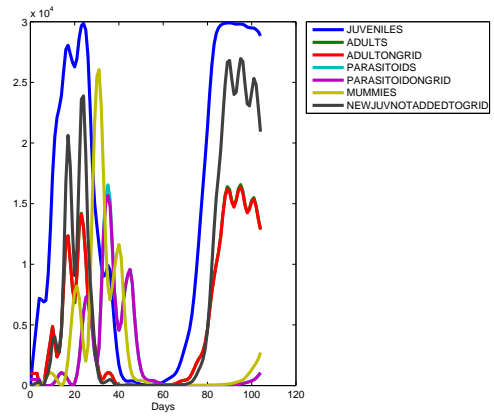


**Figure 5.25:** Plots illustrating aphid and parasitoid populations over time as aphid juvenile mortality is varied. Parasitoids can handle 1 aphid per time-step and there is parasitoid interference. Juvenile mortality in (a), (b), (c), (d), (e), (f), (g), (h), (i) is 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, respectively.

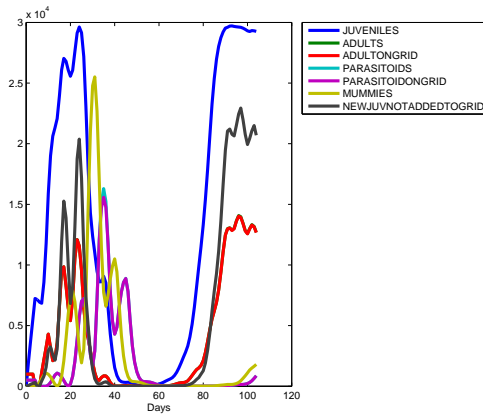




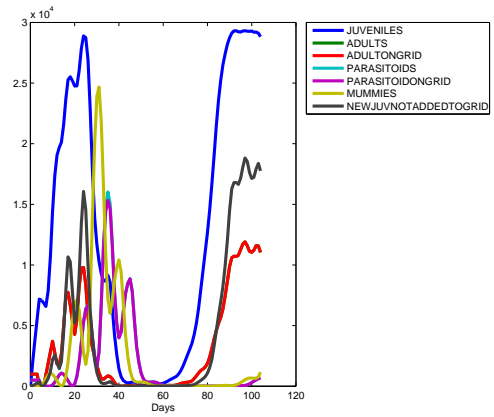
a)



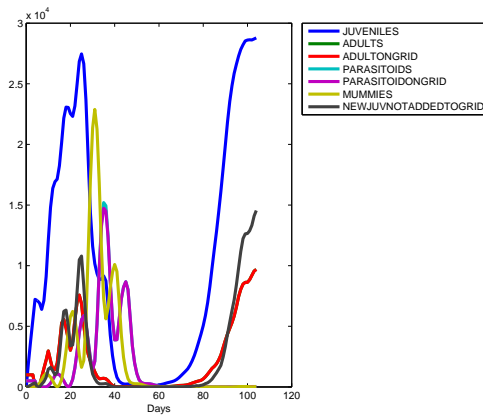
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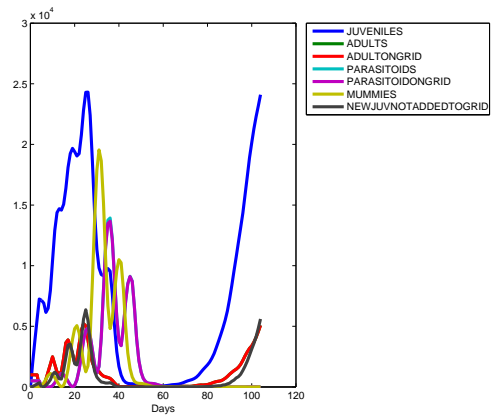
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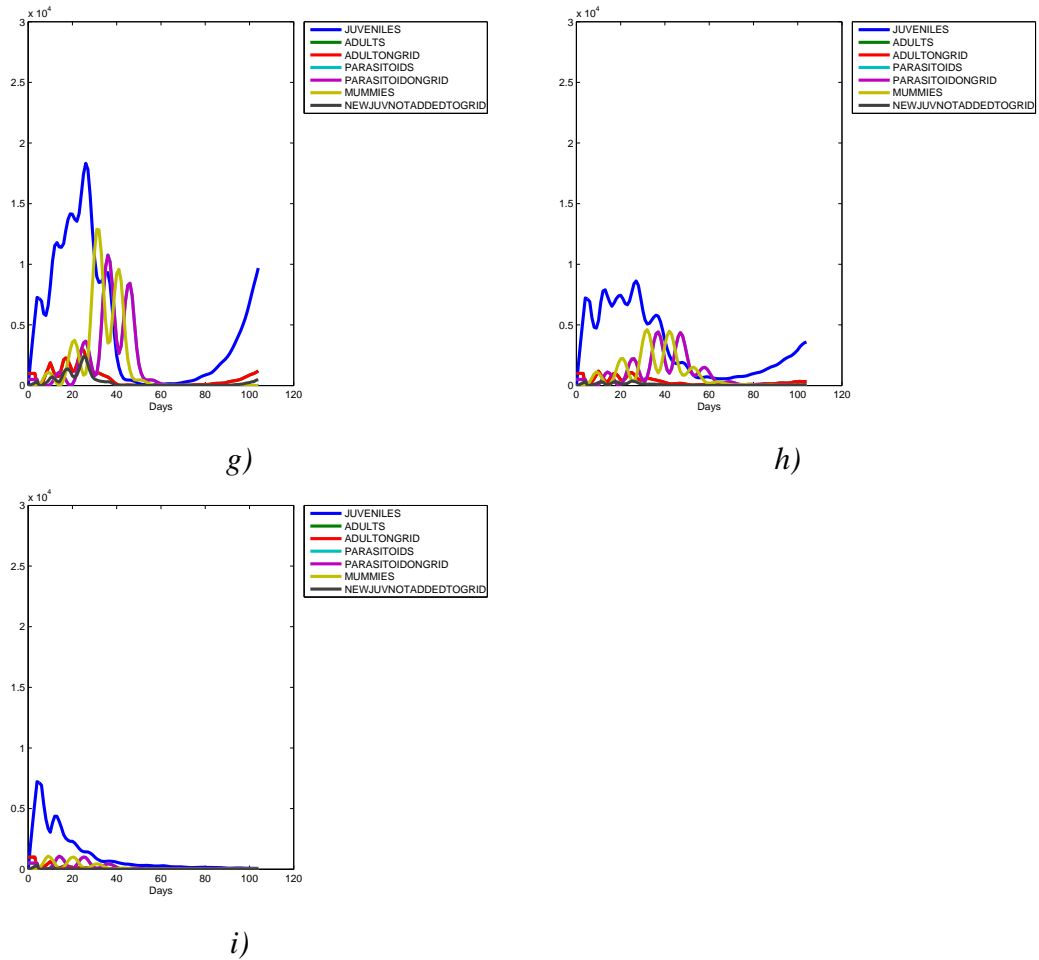
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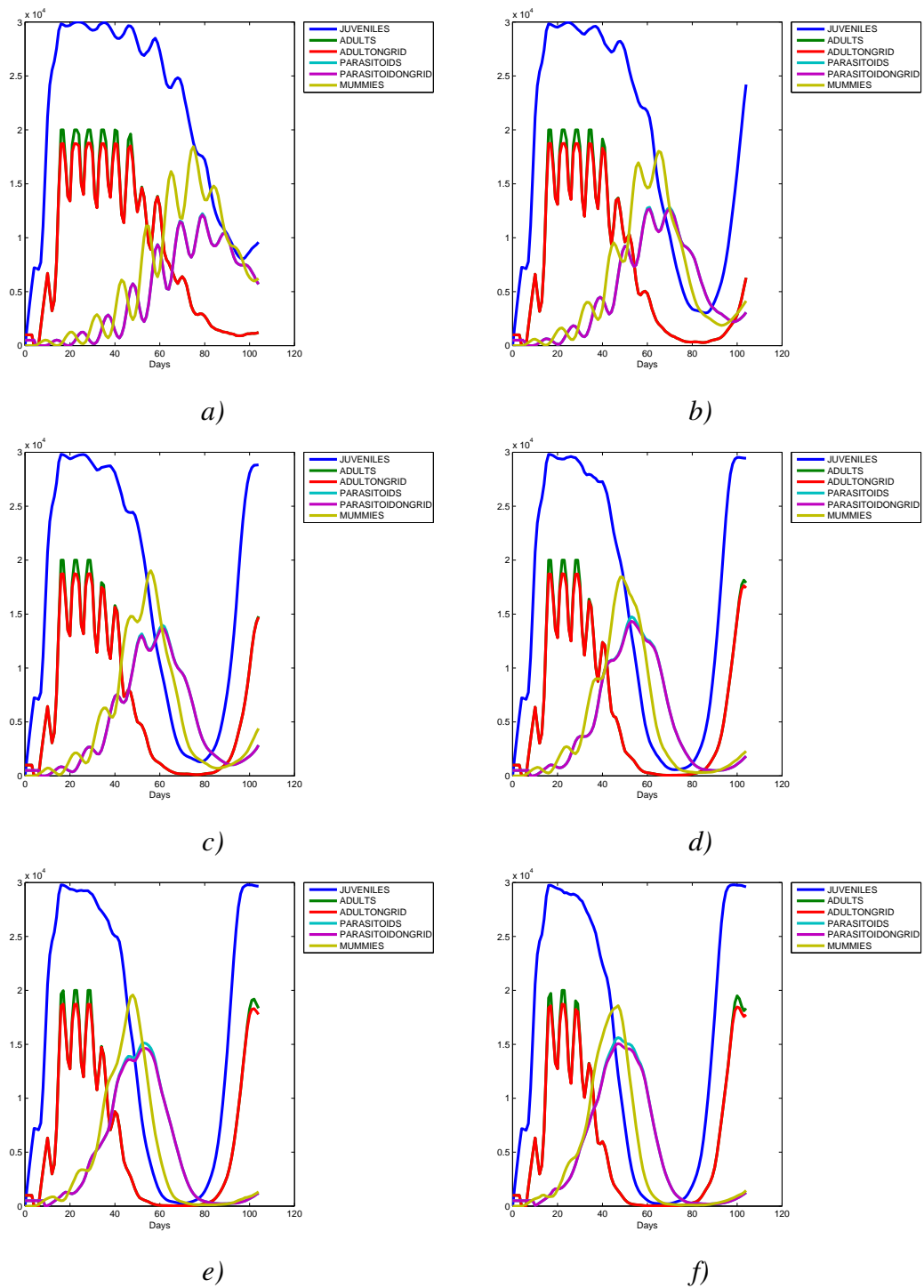
**Figure 5.26:** Plots illustrating aphid and parasitoid populations over time as aphid juvenile mortality is varied. Parasitoids can handle more than 1 aphid per time-step. Juvenile mortality in (a), (b), (c), (d), (e), (f), (g), (h), (i) is 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, respectively.

### 5.2.6 Varying length of parasitoid lifespan

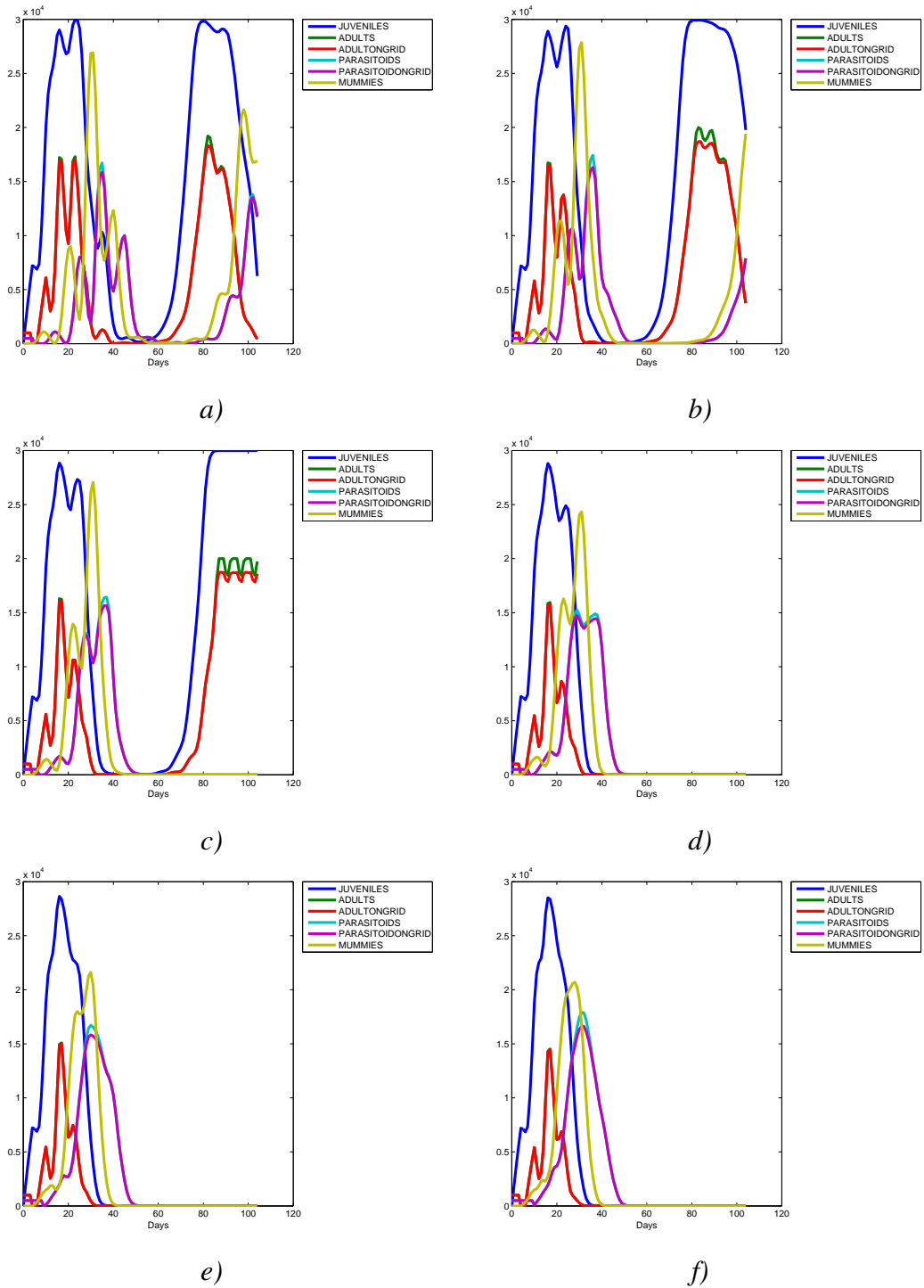
In the field parasitoids survive anywhere from 10-20 days, with very few actually surviving to 20 days (correspondence with Professor S. Hubbard). Length of parasitoid lifespan was varied using this as the parameter range, but as 12 hour days are used in the model, this would be equivalent to a parasitoid lifespan ranging from 5-10 days. Figure 5.27 shows that when parasitoids have a longer handling time as the parasitoid's

lifespan is increased, the dynamics become faster (at least initially). This is a result of increasing parasitoid pressure due to increasing parasitoid lifespan. Increasing parasitoid lifespan allows parasitoids to remain on the grid for a longer period of time and increases the parasitism pressure. This increase in pressure drives aphids to crash more rapidly, driving the pulse of oscillations faster. The increase in parasitoid pressure also results in oscillations of increasing amplitude, suggesting that the system is becoming more unstable.

Figure 5.28 shows the results of varying parasitoid lifespan when parasitoids have a shorter handling time. As parasitoid lifespan is increased from 5 to 7 days, parasitoids become extinct and increasing parasitoid lifespan further leads to both species becoming extinct. The dynamics here tend towards extinction quite rapidly unlike the system where parasitoids have a longer handling time because parasitoids are more efficient due to their shorter handling time and this combined with increasing parasitoid lifespan exerts more pressure on the aphid population.



**Figure 5.27:** Plots illustrating aphid and parasitoid populations over time as parasitoid lifespan is varied. Aphid lifespan remains constant and is 10d. Parasitoids can handle no more than 1 aphid per time-step. Parasitoid lifespan in (a), (b), (c), (d), (e), (f) is 5, 6, 7, 8, 9, 10 days, respectively.



**Figure 5.28:** Plots illustrating aphid and parasitoid populations over time as parasitoid lifespan is varied. Aphid lifespan remains constant and is 10d. Parasitoids can handle more than 1 aphid per time-step. Parasitoid lifespan in (a), (b), (c), (d), (e), (f) is 5, 6, 7, 8, 9, 10 days, respectively.

In short, the addition of parasitoids to the aphid model gave rise to more varied dynamics compared to those generated from the aphid model alone. Variation in key parameters produced stable dynamics, oscillations, no coexistence or extinction. In most of the simulation results from the aphid-host parasitoid model there was also an initial period of transient dynamics.

Two different foraging behaviours were examined for the majority of the simulations conducted here, one in which parasitoids have a long handling time and another in which they have a short handling time. Lengthening handling time gave rise to slower dynamics (at least for the timescale observed here). In some instances, individual parameters were also varied with and without implementation of parasitoid interference in the system. Results from these simulations indicated that parasitoid interference had a stabilising impact on the system in accordance with other host-parasitoid studies (for eg. Hassell and May (1973); Hassell and Varley (1969)).

It seemed as though increasing the values of parameters that enhanced parasitoid foraging efficiency or parasitoid pressure on aphids such as probability of discovering an aphid, probability of successful parasitism and parasitoid lifespan made the system less stable whereas diminishing their efficiency by implementing parasitoid interference in the model made the system more stable. Interestingly, when probability of successful parasitism was varied and parasitoid interference was also modelled (see figure 5.15), the destabilising effect of increasing the success of parasitism (as illustrated in figure 5.10) was subdued, so much so, that there was almost no change in the qualitative behaviour of the system. This suggests that the effect of parasitoid interference, as it is modelled here, may be stronger than the effect of increasing the parasitoid's probability of successful parasitism.

In regards to the behaviour of the system when aphid parameters were varied, increasing adult aphid lifespan had a stabilising effect whereas increasing juvenile mortality had a destabilising effect on the system which is in agreement with the results from the aphid model.

The results from the aphid-host parasitoid model can be compared to those of other aphid-host/host parasitoid models. Lopes et al. (2007) showed that aphid population growth rate and parasitoid generation time had a significant effect on the dynamics of an aphid-host parasitoid system using a flux-based model (see section 2.2 for a description of the model). In particular, they found that reducing aphid population growth rate and enhancing the efficiency of parasitoids by decreasing parasitoid generation time reduced aphid numbers. Other studies have also indicated that decreasing parasitoid generation time can limit the abundance of pests (Briggs and Godfray, 1996; Rochat, 1997). In the simulations of the aphid-host parasitoid model developed here, aphid growth rate and parasitoid development time were not varied. Although, aphid fecundity was varied in the simulations of the aphid model (see section 4.3), the decrease of which had a slightly destabilising effect on the dynamics. That said, the aphid-host parasitoid model developed here did show that probability of a parasitoid discovering an aphid, handling time, probability of successful parasitism and parasitoid interference, i.e. parameters that affect foraging efficiency, do have a notable impact on the dynamics of the aphid-host parasitoid system both quantitatively and qualitatively. Nevertheless, it may be worthwhile to study the implications of varying aphid growth rate and parasitoid generation time in the aphid-host parasitoid model here as they have been considered important parameters in other studies and see how the results compare.

## **Chapter 6**

# **Modelling Additional Complexity in the Aphid-Parasitoid System**

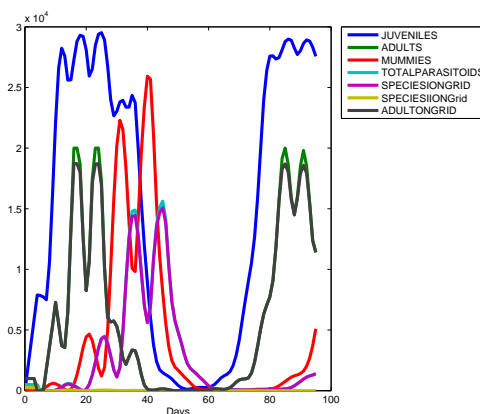
The aphid-parasitoid model described in chapter 5 was developed by considering multispecies host-parasitoid interactions, spatial heterogeneity and multiple non-adjointing patches separately in the model and the dynamics of the modified system were studied by changing key parameters. Among the parameters varied were parasitoid's probability of discovering an aphid, patch area, predation on juvenile aphids, grid capacity of juveniles, parasitoid diffusion, juvenile aphid mortality, fraction of individuals migrating and giving up time. The assumptions of the aphid-parasitoid model described in chapter 5 apply to the simulations described in this chapter as well unless otherwise noted.



## 6.1 Aphid-Two-Parasitoid-Species Dynamics

In nature it is not uncommon for multiple parasitoid species to parasitise the same host species (Hackett-Jones et al., 2008). Previous models have tried to capture the dynamics of multispecies host-parasitoid systems (see section 3.1). I attempted to do the same by modelling the dynamics of a system consisting of an aphid parasitised by two different species of parasitoids (labelled I and II respectively). Both parasitoid species had the same set of initial conditions and parameters bar one.

Species I has a probability of discovering an aphid that is ten times greater than species II. Figure 6.1, which illustrates the dynamics of the system, shows that species I outcompetes species II and species II becomes extinct because it is far less efficient at locating hosts. The dynamics here are similar to those of an aphid-single-parasitoid-species system with a parasitoid's probability of discovering an aphid equal to 0.000006 (see figure 5.1 b). In both instances the beginning of oscillatory dynamics is apparent and the aphid population tends to carrying capacity.



**Figure 6.1:** Plot illustrating dynamics of a host parasitised by two competing parasitoids, species I with a probability of discovering an aphid=0.000006 and species II with a probability of discovering an aphid=0.0000006. Parasitoids can handle more than one aphid per time-step. Aphid fecundity is modelled as a continuous process. Initial populations consist of 1000 adult aphids and 500 parasitoids, about half of which are species I and half of which are species II.

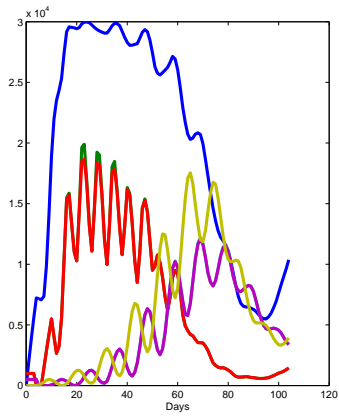
## 6.2 Aphid-Parasitoid Dynamics on Two Patches

Quality of resources for aphids tends to be heterogeneous in space both on the individual host plant and at greater spatial scales (Dixon, 1998) and this has a direct impact on aphid fecundity, survival, morphology and distribution. It is therefore important to consider the effect of spatial heterogeneity on aphid populations. Here an aphid-parasitoid system is modelled on a grid comprised of two patches, one of good quality and the other of poor quality, while varying the area of each patch. On the good quality patch juvenile aphid mortality is 0.1 and on the bad quality patch juvenile aphid mortality is 0.9. Adult aphids and parasitoids can move between patches.

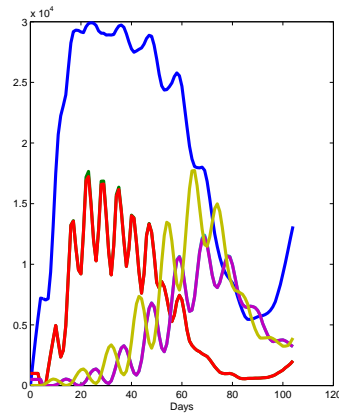
Figure 6.2 shows when juvenile mortality is varied between patches and parasitoids have a longer handling time, increasing the area of the poor quality patch has hardly any effect on the qualitative dynamics. In all cases, there is the appearance of the beginning of oscillations. There is a decrease in population numbers as the area of the bad patch is increased. This effect is more pronounced in the adult aphid population though because juvenile mortality is applied just before juveniles become adults and therefore the impact is more immediately felt by the adult population. Figure 6.3 shows when parasitoids have a shorter handling time, the system is more sensitive to changes in the fraction of the domain that is of poor quality. At first glance, increasing the area of the bad patch reduces the population numbers and also decreases the momentum of the second host-parasitoid cycle. Similarly to when parasitoids had a longer handling time, increasing the area of the bad patch also seems to have a greater effect on the adult aphid population. However, the overall effect on the system is more dramatic compared to the system with parasitoids with a longer handling time particularly in figure 6.3 g, h and i where there is a significant decline in the number of juveniles. This is because of the combined effect of the average increase in juvenile mortality over the domain and the greater efficiency of parasitoids as a result of having a shorter

handling time. The increase in juvenile mortality produces fewer adults which in turn leads to a lower production of new juveniles, and therefore the rate of increase of the juvenile population is lower. This compounded with the greater efficiency of the parasitoids causes the drastic decline in aphid numbers in figure 6.3 g, h and i. As well as being more sensitive to changes in patch area, the system where parasitoids have a shorter handling time exhibits faster dynamics compared to when parasitoids have a longer handling time.

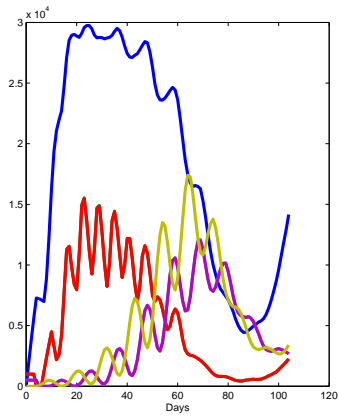
By calculating the average mortality across both patches, the dynamics of the two-patch system can be compared to those of the corresponding system without patches. This was done for both cases of fast and slow parasitism. Overall, the dynamics of the non-patchy and corresponding patchy system are very similar (see figures 5.22,6.2 and figures 5.24,6.3). However, when juvenile mortality is 0.8 in the non-patchy system and is 0.82 in the corresponding patchy system (i.e. the bad patch is 90% of the grid) it would seem that for both fast and slow parasitism, the aphid population is higher in the patchy system than in the non-patchy system despite the former having a higher juvenile mortality rate. The patchiness of the system may be stabilising when juvenile mortality is especially high and this may account for the non-intuitive dynamics.



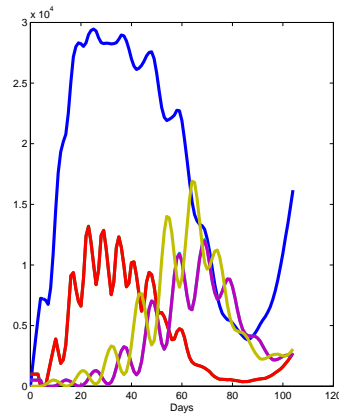
a)



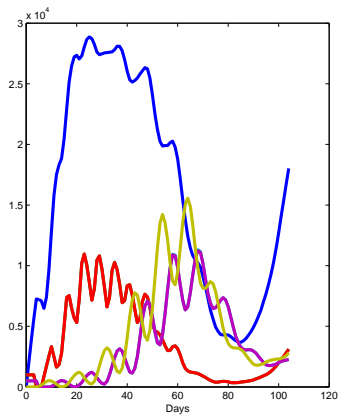
b)



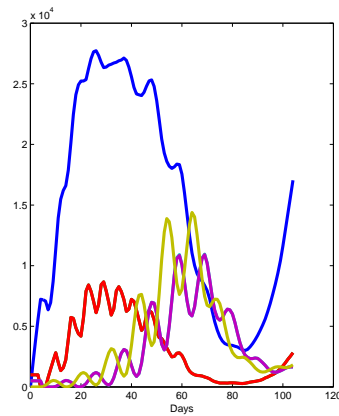
c)



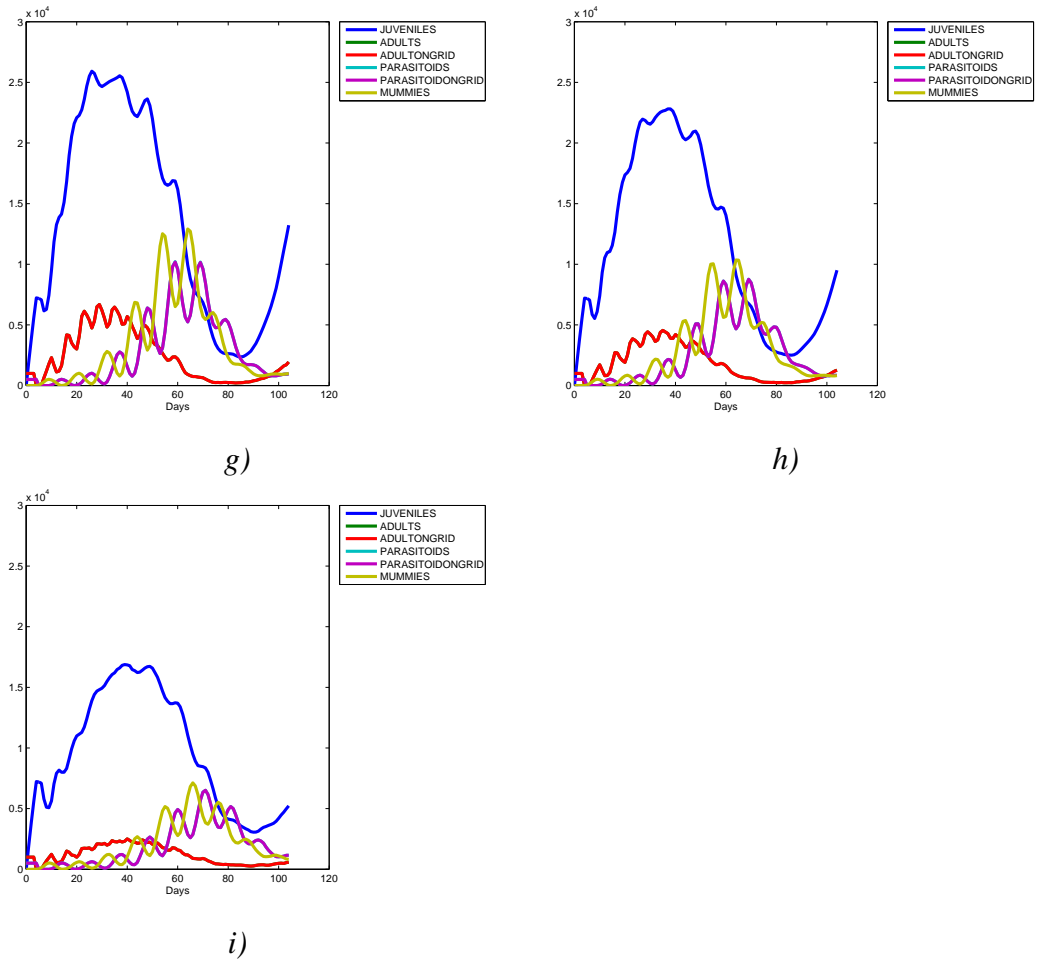
d)



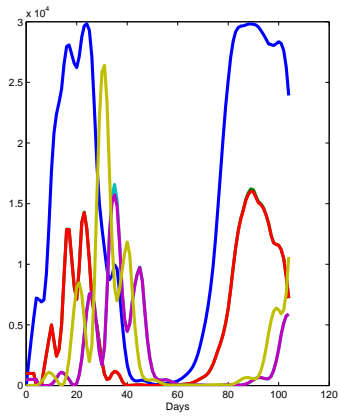
e)



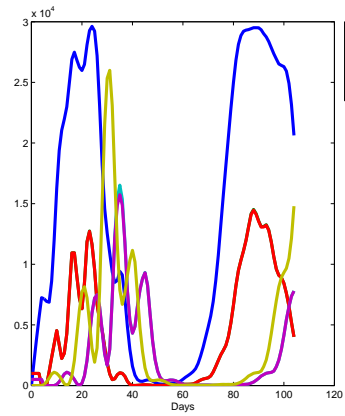
f)



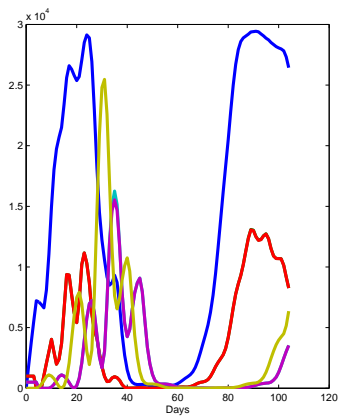
**Figure 6.2:** Plots illustrating aphid and parasitoid populations over time on a grid consisting of two patches, one of good quality and the other of low-quality, as the area of each patch is varied. Parasitoids can handle 1 aphid per time-step. Initial populations consist of 1000 adult aphids and 500 parasitoids distributed randomly over the entire grid. The fraction of the grid comprising the bad patch in (a), (b), (c), (d), (e), (f), (g), (h), (i) is 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90%, respectively. The rest of the grid consists of the good patch in plots a-i.



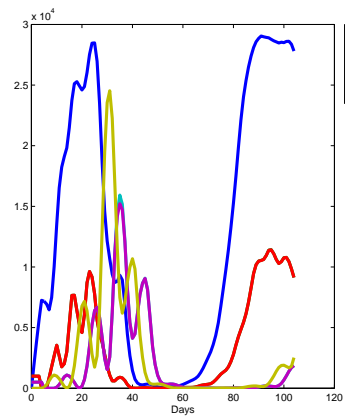
a)



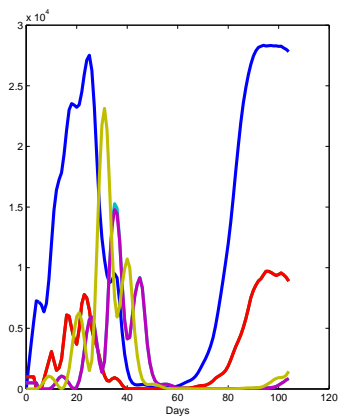
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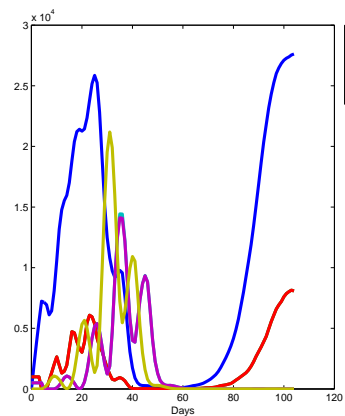
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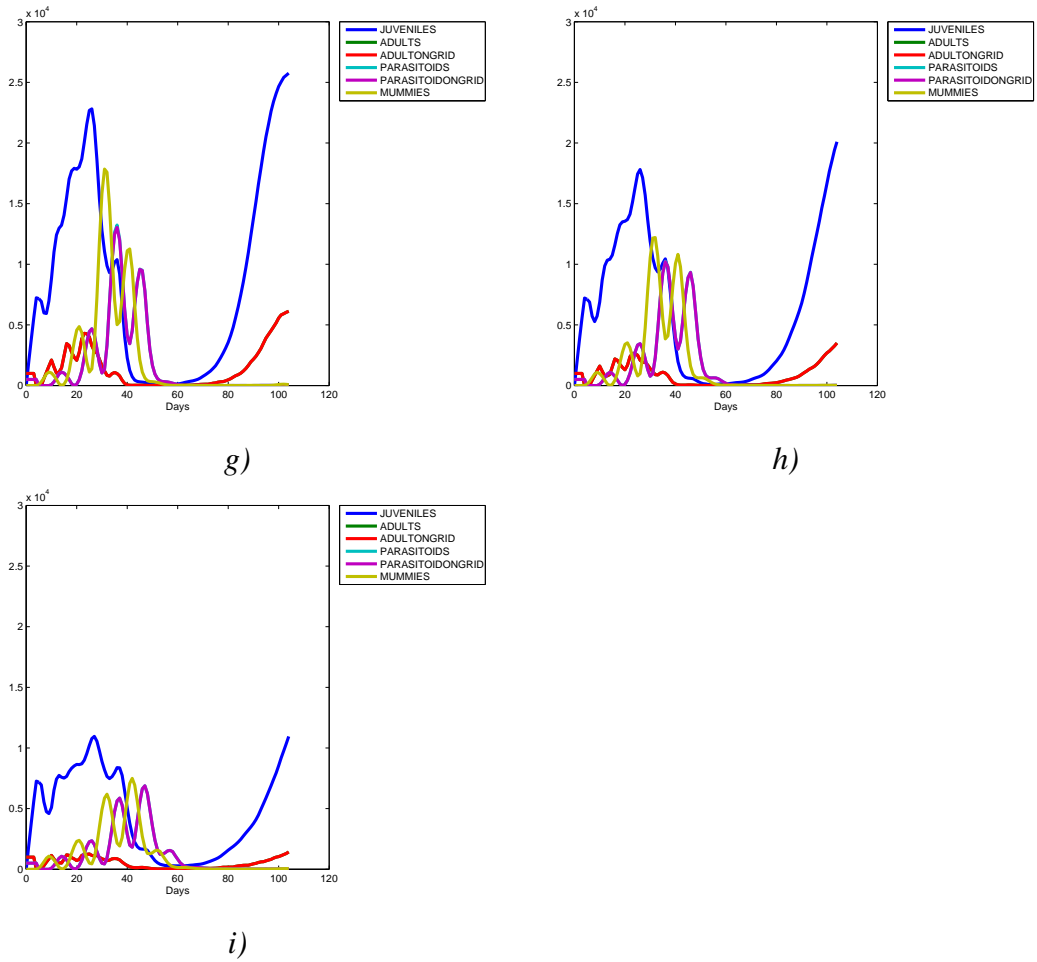
d)



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**Figure 6.3:** Plots illustrating aphid and parasitoid populations over time on a grid consisting of two patches, one of good quality and the other of low-quality, as the area of each patch is varied. Parasitoids can handle more than 1 aphid per time-step. Initial populations consist of 1000 adult aphids and 500 parasitoids distributed randomly over the entire grid. The fraction of the grid comprising the bad patch in (a), (b), (c), (d), (e), (f), (g), (h), (i) is 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90%, respectively. The rest of the grid consists of the good patch in plots a-i.

## **6.3 Aphid-parasitoid dynamics with long-distance within-patch movement in aphids only**

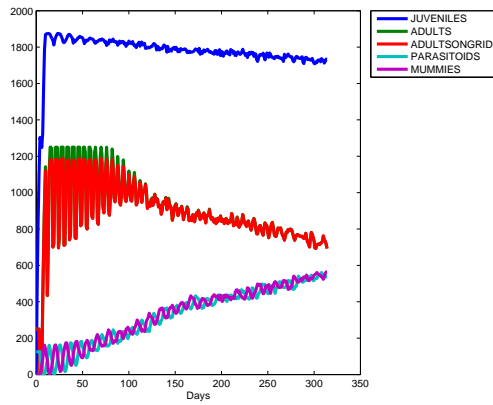
The simulations so far have included ‘flyers’ which are individuals that have not found a space on the grid to inhabit due to local overcrowding and are therefore temporarily taken off the grid. This is both a computational device and also reflective of aphid biology where adult individuals take flight/walk in search of a new location when there is local overcrowding. In the following model simulations there are no parasitoid ‘flyers’ and as such parasitoids only move by diffusion within patches. There is also no cap on the number of parasitoids per grid point and parasitoids are assumed to have a long-handling time and experience parasitoid interference. In order to increase computational efficiency, a domain size of  $25 \times 25$  was used (i.e.  $\Delta x = 0.04$ ) and  $\Delta t$  was recalculated as 0.00001 which satisfies the stability condition in equation 4.7. For the modified grid size total juvenile and adult aphid carrying capacities are 1875 and 1250, respectively for one grid. In this section the dynamics of the aphid-parasitoid system on a single grid and multiple grids are analysed.

### **6.3.1 Single grid dynamics**

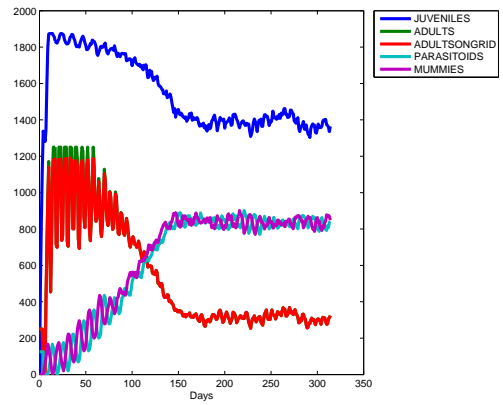
Parameters varied for the aphid-parasitoid system posed on the single grid included parasitoid’s probability of discovering an aphid, juvenile predation, grid capacity of juveniles and parasitoid diffusion. Figures 6.4 and 6.5 show that when the probability of a parasitoid discovering an aphid is varied a range of dynamics emerge. At low values of this parameter the system is stable. A bifurcation occurs between parameter values of 0.000035 and 0.00004 giving rise to oscillations that increase in amplitude upon further increase of this parameter. Perturbing the system even more leads to extinction of both aphids and parasitoids. The increasing instability of the system as



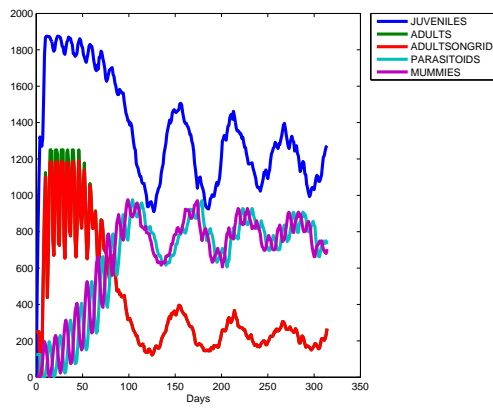
the probability of discovery is increased was also observed in the system with ‘flyers’ and is driven by the same mechanism (see section 5.2.2). The similar behaviour of the systems with and without parasitoid ‘flyers’ suggests that the presence of ‘flyers’ in the system has little impact on the dynamics. This is probably because individuals that become ‘flyers’ are only taken off the grid temporarily and therefore the total number of parasitoids in the system remains unchanged.



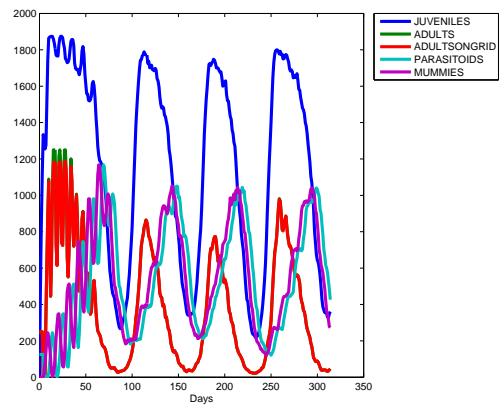
a)



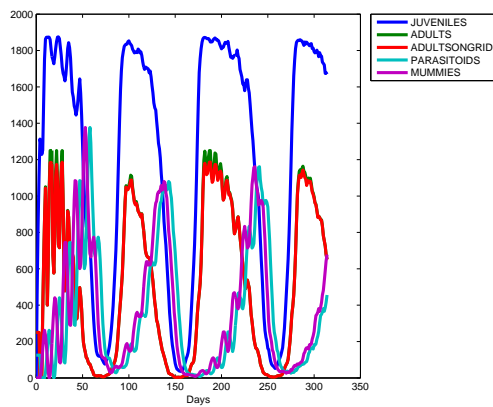
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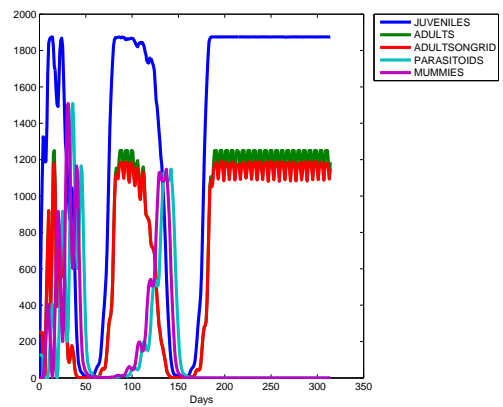
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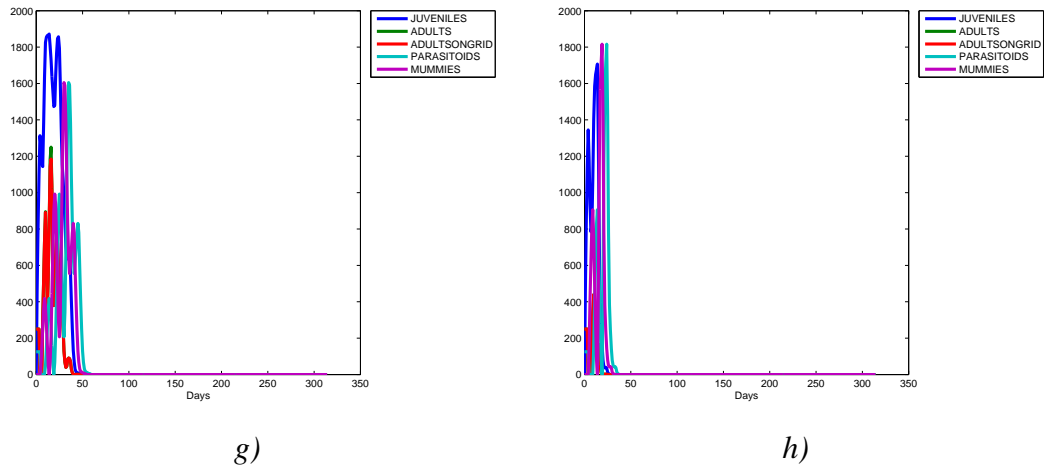
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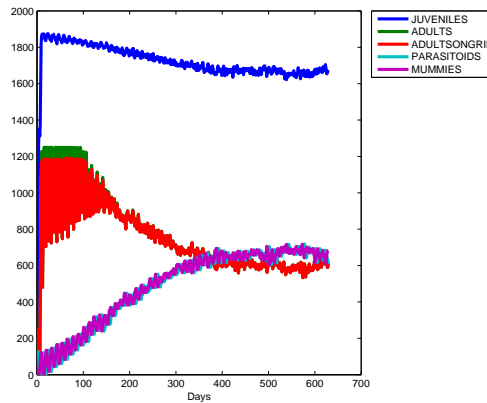
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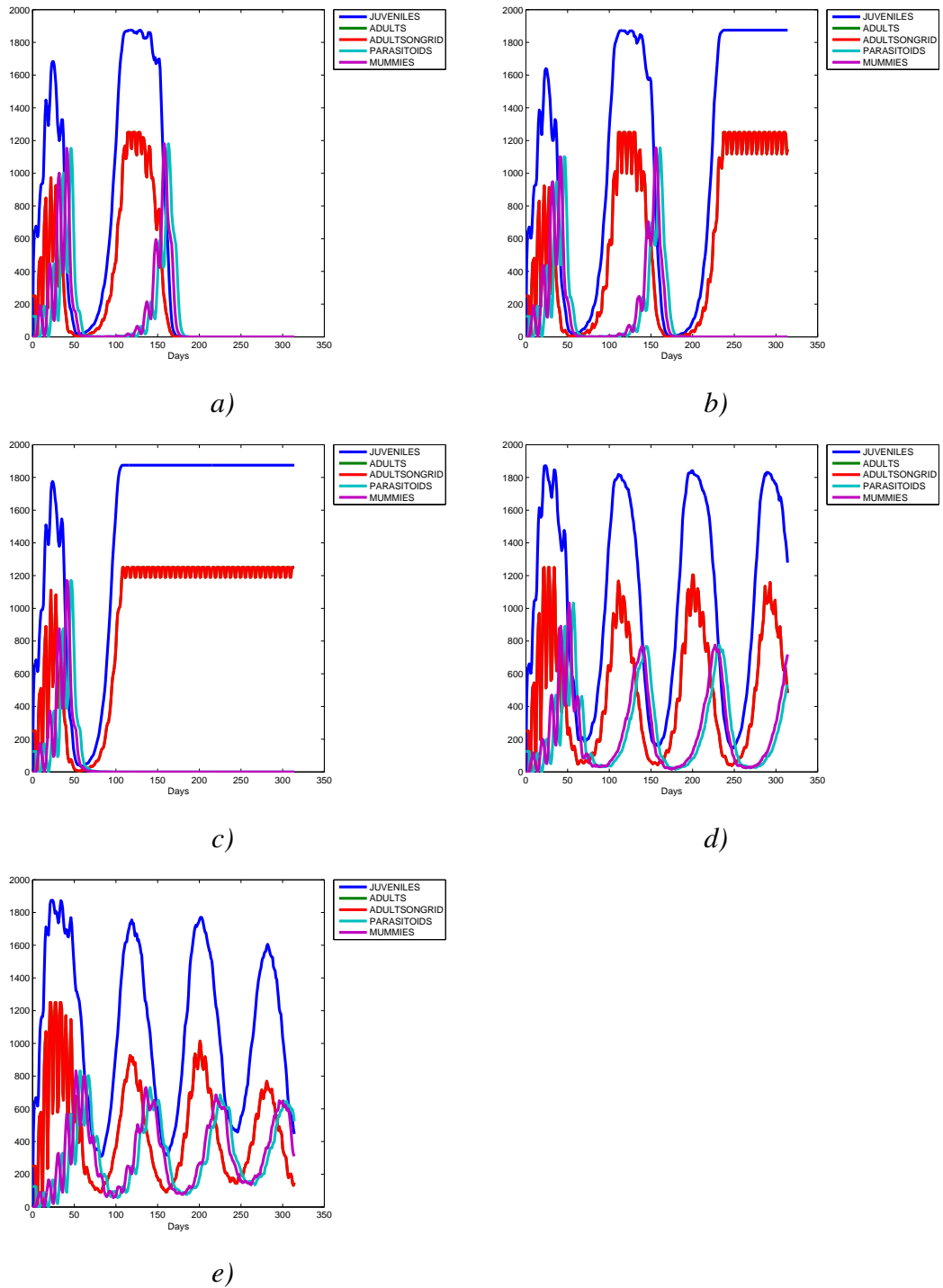
**Figure 6.4:** Plots illustrating aphid and parasitoid populations over time as the probability of a parasitoid discovering an aphid is varied. Initial populations consist of 250 adult aphids and 125 parasitoids. Probability of a parasitoid discovering an aphid in (a), (b), (c), (d), (e), (f), (g), (h) is 0.00003, 0.000035, 0.00004, 0.00005, 0.00006, 0.00009, 0.0001, 0.0003, respectively.



**Figure 6.5:** Plot illustrating the dynamics of figure 6.4 a run for an extended period of time.

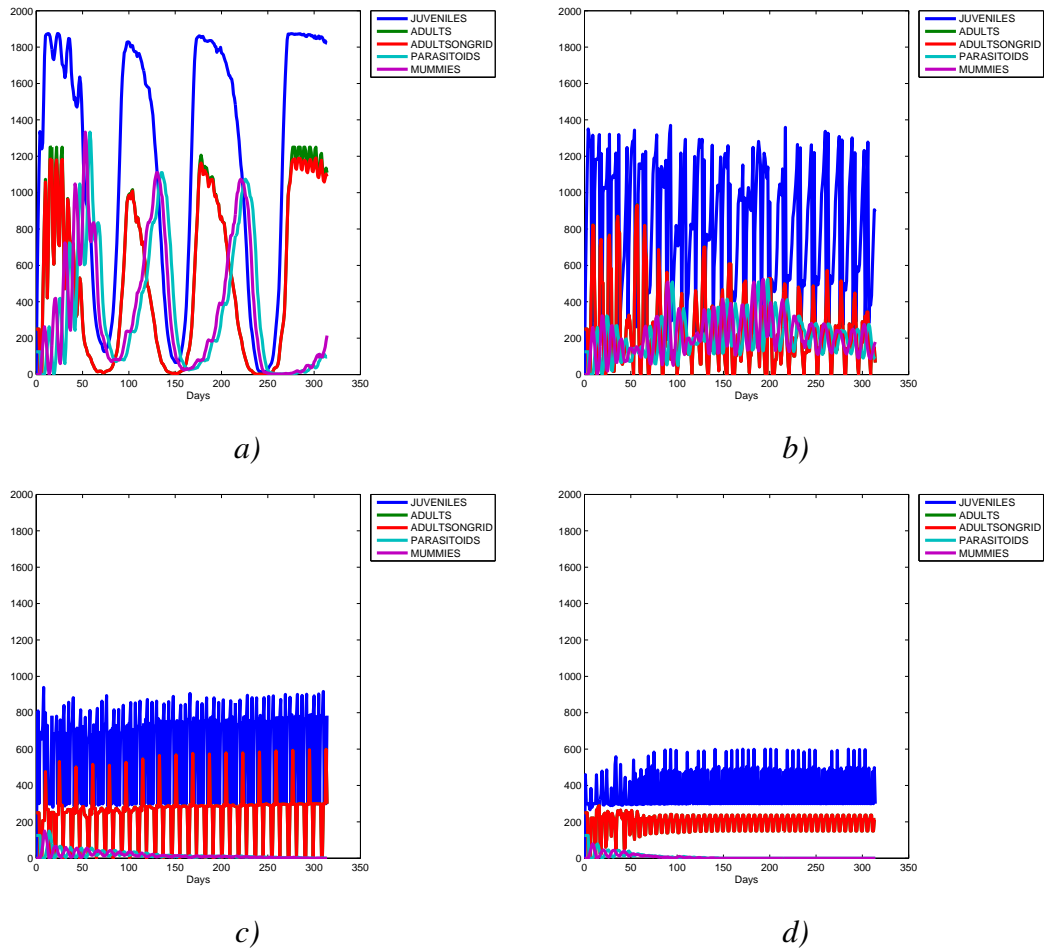
The efficiency of parasitoids is not only determined by their probability of discovering an aphid, but also by their diffusion rate. Parasitoids with a faster diffusion rate will locate aphid hosts more quickly and thus will be more effective at controlling the aphid population than parasitoids with a slower diffusion rate. This was also observed when

parasitoid diffusion was varied in the model. Figure 6.6 shows that at higher values of parasitoid diffusion, the aphid-parasitoid system becomes extinct because parasitoids are very efficient and drive the host population to crash. Reducing parasitoid diffusion, however, allows aphids to persist long-term although parasitoids die out because, whilst they have not driven the aphid population to crash, they drive them to extremely low levels that are unable to support a viable parasitoid population (figure 6.6 b and c). In figure 6.6 c because of the parasitoids' lower efficiency, the system would be expected to be more stable than in figure 6.6 b, but this somewhat illogical result is probably due to stochasticity in the model. Reducing parasitoid diffusion further allows for coexistence of aphids and parasitoids and gives rise to oscillations of decreasing amplitude (figure 6.6 d and e). As parasitoid diffusion is reduced, there is also a decrease in peak parasitoid numbers particularly in figure 6.6 d and e which is reflective of the reduced efficiency of parasitoids. Overall, reducing parasitoid efficiency has a stabilising effect on the system which was exemplified by varying parasitoid diffusion and the probability that a parasitoid discovers an aphid.



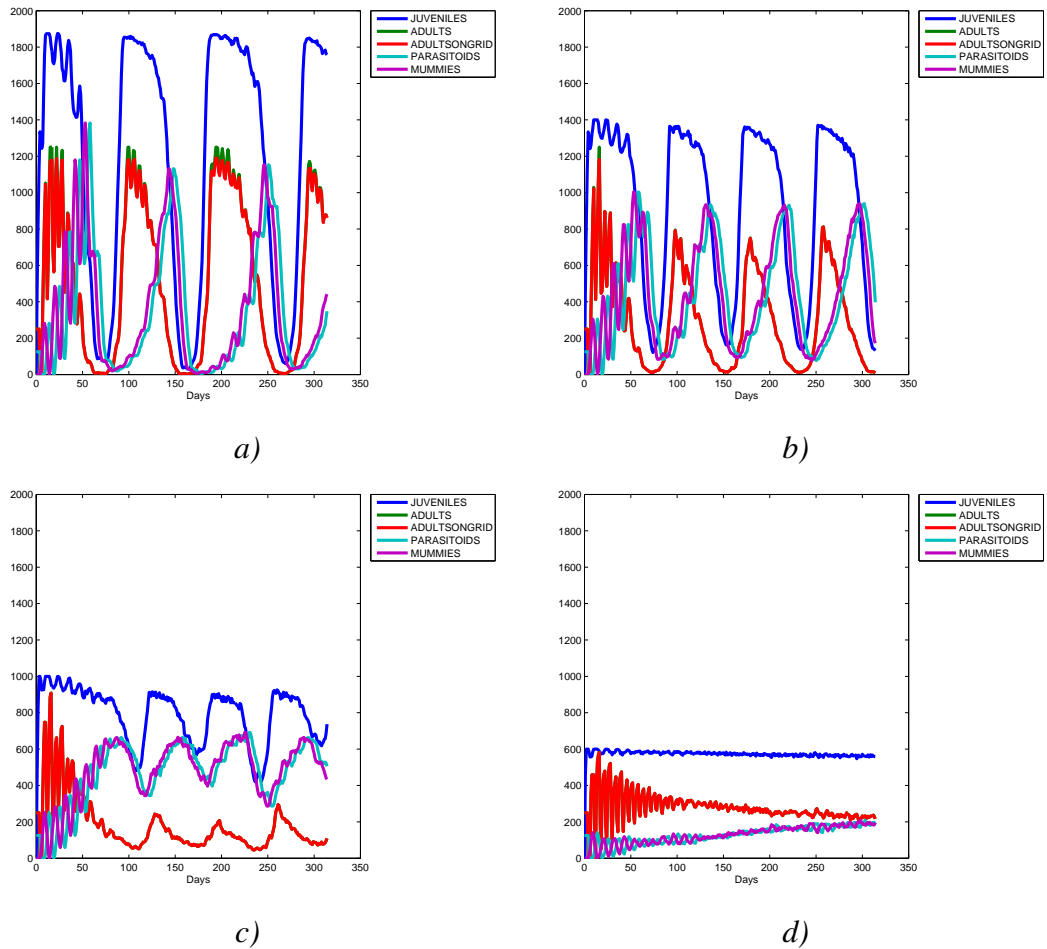
**Figure 6.6:** Plots illustrating aphid and parasitoid populations over time as parasitoid diffusion is varied. Initial populations consist of 250 adult aphids and 125 parasitoids. The probability of a parasitoid discovering an aphid is 0.0001. Parasitoid diffusion in (a), (b), (c), (d), (e) is 1, 0.1, 0.01, 0.001, 0.0001, respectively. Aphid diffusion remains constant and is 0.0001.

In another scenario the juvenile aphid population was given a threshold beyond which juveniles (unparasitised and parasitised alike) were killed so that only 300 remained. This scenario could be analogous to a situation where, in addition to parasitoids, there are predators that consume both parasitised and unparasitised juveniles and have a discovery minimum of 300 juvenile aphids. Figure 6.7 shows the results of varying the threshold. Figure 6.7 a is the control without any threshold and shows predator-prey oscillations. Applying a juvenile population threshold in figure 6.7 b generates quasi-periodic dynamics. However, decreasing this threshold number leads to the disappearance of parasitoids because the combined effect of the lower juvenile population size threshold as well as predation does not allow the juvenile population to sustain a viable parasitoid population (figure 6.7 c and d). Also, increasing the threshold appears to decrease the frequency of oscillations since predation is not as regular an occurrence when the threshold is higher.



**Figure 6.7:** Plots illustrating aphid and parasitoid populations over time as juvenile predation is varied. Initial populations consist of 250 adult aphids and 125 parasitoids. In (a) there is no change to the system. In (b), (c), (d) when there are more than 1400, 1000 and 600 juveniles, respectively juveniles are killed off until 300 remain.

In addition to a cap of 3 juveniles per grid point, a carrying capacity was applied to juveniles across the entire domain so that excess juveniles in the population beyond grid capacity were killed off. Figure 6.8 shows the outcome of varying the grid capacity of juveniles. It appears that reducing this variable stabilises the system which transitions from oscillations of decreasing amplitude to stable coexistence. By reducing juvenile grid capacity, the overall number of juveniles becomes reduced making it harder for parasitoids to find hosts and thereby stabilising the system.



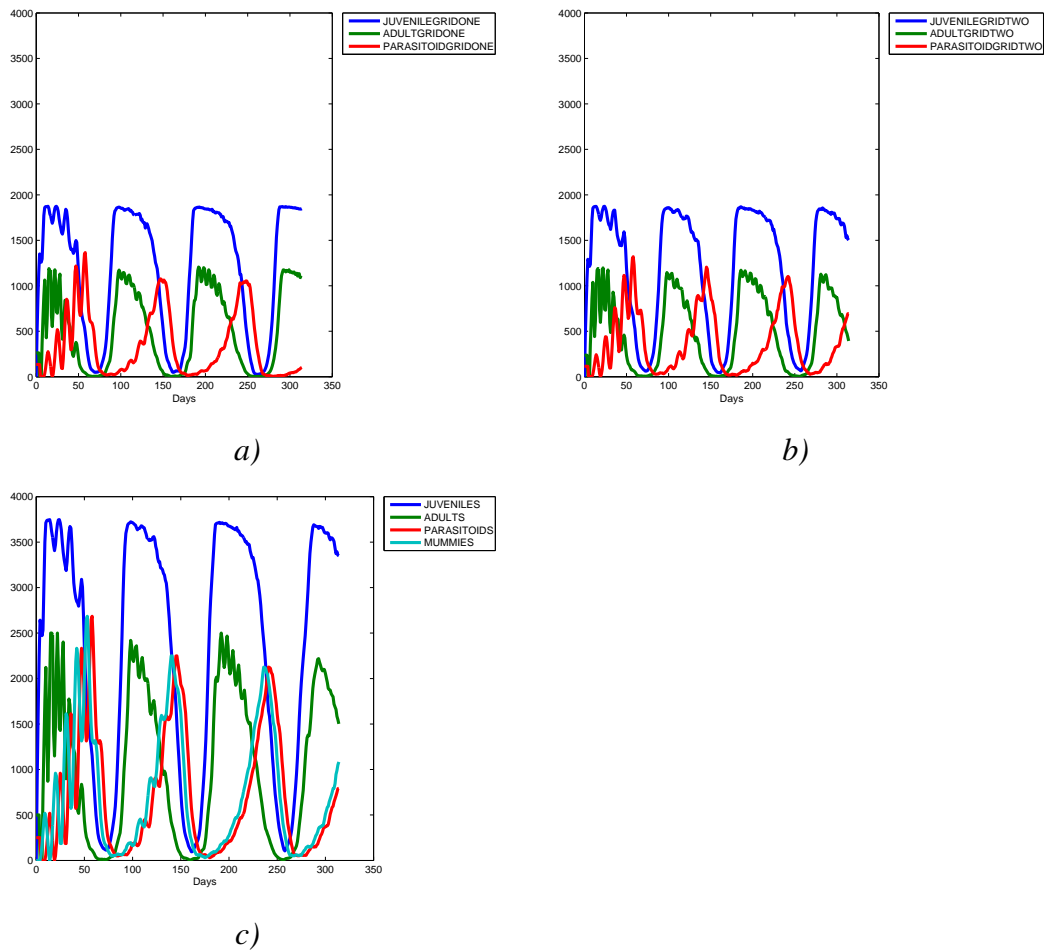
**Figure 6.8:** Plots illustrating aphid and parasitoid populations over time as the grid capacity of juveniles is varied. Initial populations consist of 250 adult aphids and 125 parasitoids. In (a) there is no additional juvenile grid capacity. In (b), (c), (d) excess juveniles over 1400, 1000 and 600 juvenile aphids, respectively are killed off.

### 6.3.2 Multiple grid dynamics

An aphid-host parasitoid system was modelled on two grids/patches separated by a distance  $x$ , where  $x$  is very small. The initial populations of parasitoids and aphids on both patches are approximately equal and all other initial conditions for both patches are the same. The assumptions for the single grid model in the previous section apply here as well except there are now two  $25 \times 25$  grids rather than one. A simulation was



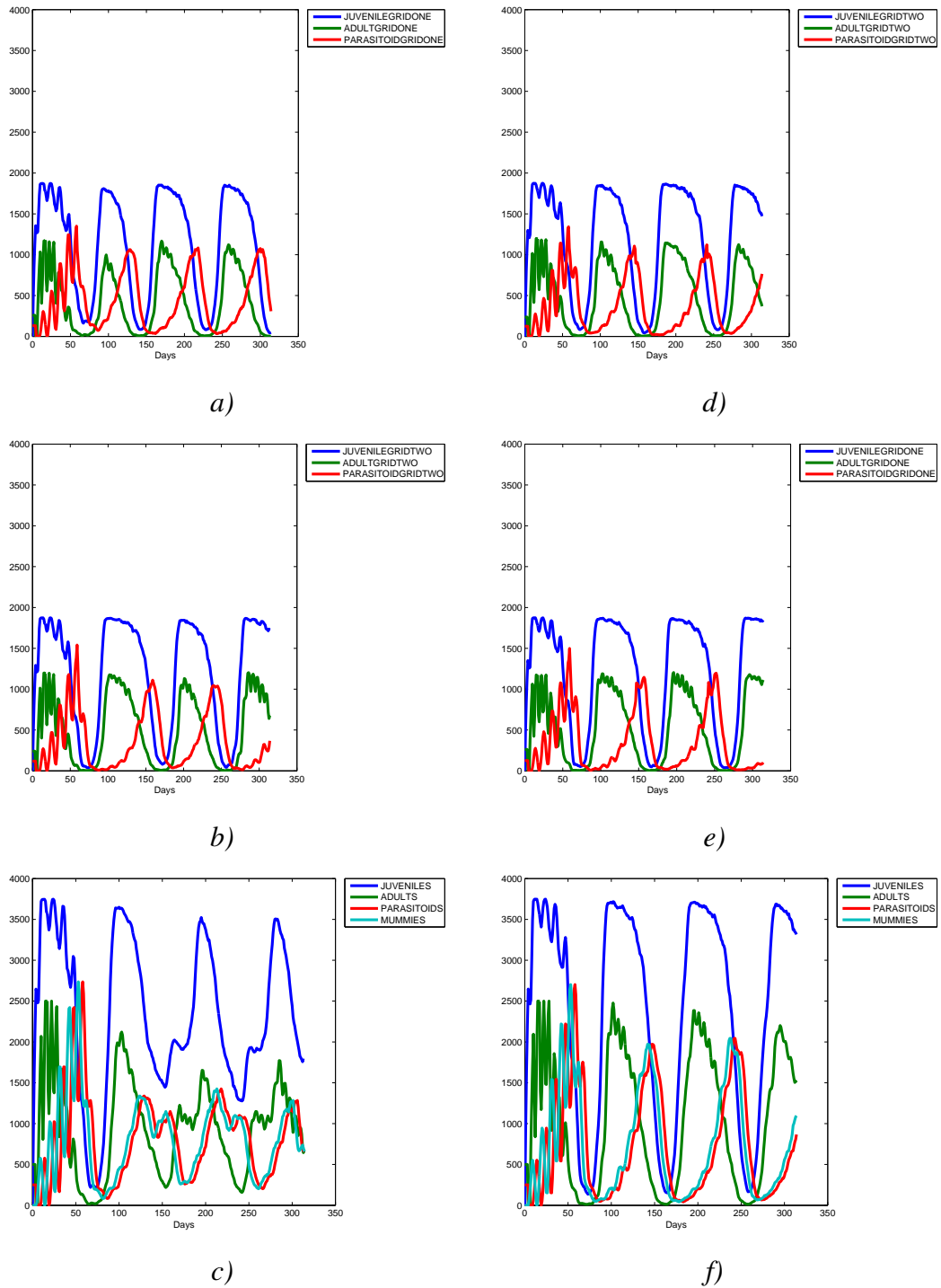
run first with the populations on each patch not interacting and when the populations on both patches exhibit cycles (see figure 6.9). Finding a set of parameters when the two patch system cycles was key because the next objective was to model migration between patches, and migration seems to have a greater impact on the dynamics when the underlying system cycles.



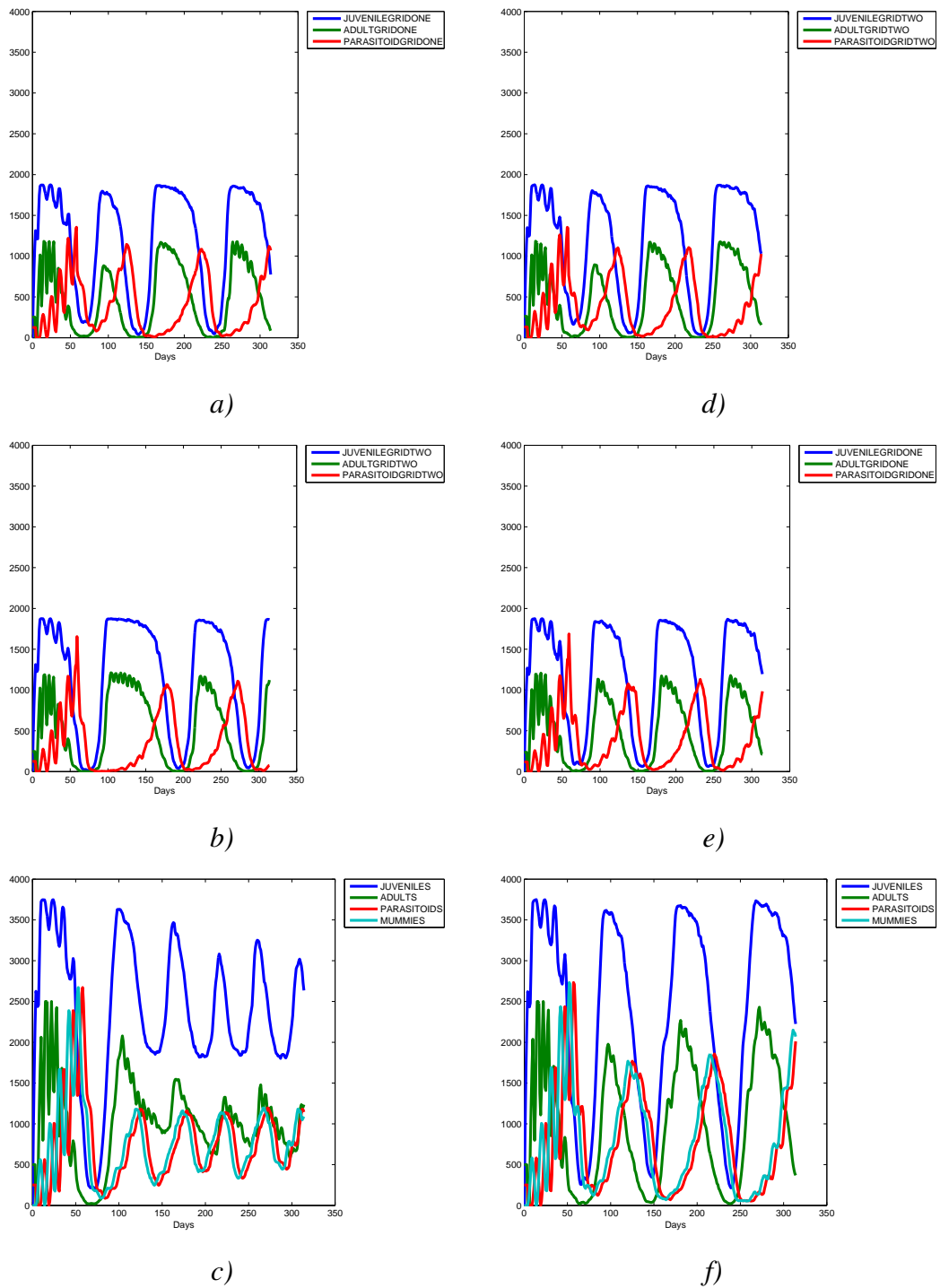
**Figure 6.9:** Plots illustrating the dynamics of aphid and parasitoid populations on two non-interacting grids. Initial populations consist of 500 adult aphids and 250 parasitoids total for both grids. (a), (b), (c) show populations on grid 1, populations on grid 2 and the combined populations on grids 1 and 2 (with the adults trajectory representing the combined adult aphid populations on grids 1 and 2 and adult aphid ‘flyers’ hovering over grids 1 and 2), respectively.

Parasitoids were allowed to migrate between patches which is analogous to flight, and since the distance between patches is very small flight time was considered to be negligible. Parasitoid migration was modelled in one direction, i.e. from patch 1 to patch 2 or from patch 2 to patch 1 and parasitoids were removed from the donor patch and transplanted immediately to the recipient patch approximately when the number of parasitoids in the non-interacting system in figure 6.9 c peaked. This model of parasitoid migration may not be representative of field populations, but was done mainly to see how the system behaves when multiple interacting patches are modelled. The fraction of the parasitoid population on the patch that migrates to the other patch was varied from 20-90%. Figures 6.10,6.11,6.12,6.13,6.14 show the results from simulating migration from grid 1 to 2 and grid 2 to 1.

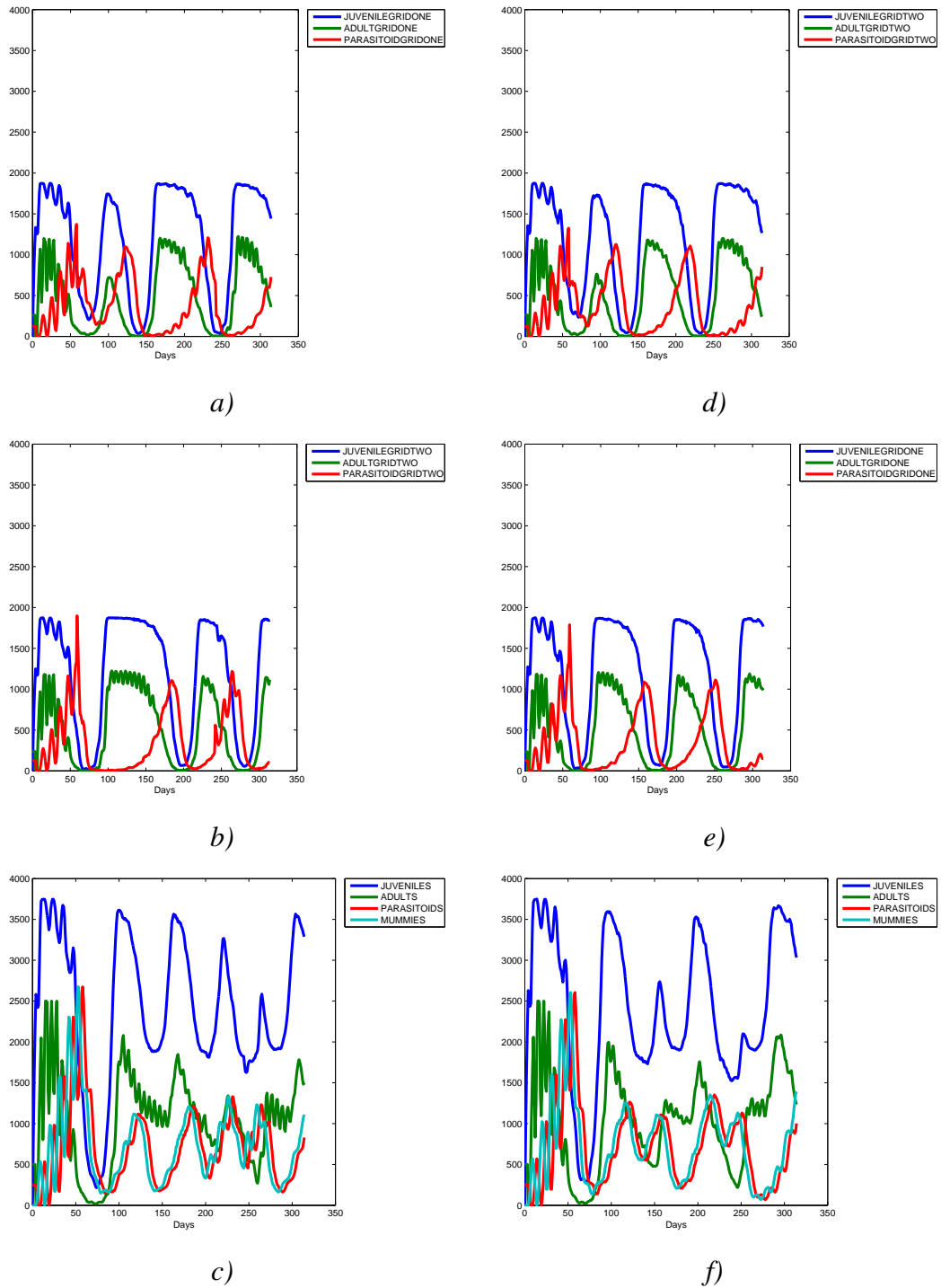
The results show that all populations on the recipient and donor grids exhibit oscillatory dynamics as migration levels are varied. As migration levels are varied and the population cycles on the donor and recipient patches become out of phase, the dynamics of the combined output for the two patches becomes quasi-periodic. These dynamics are very different to the dynamics generated when parasitoid migration is simulated at 10 day intervals.



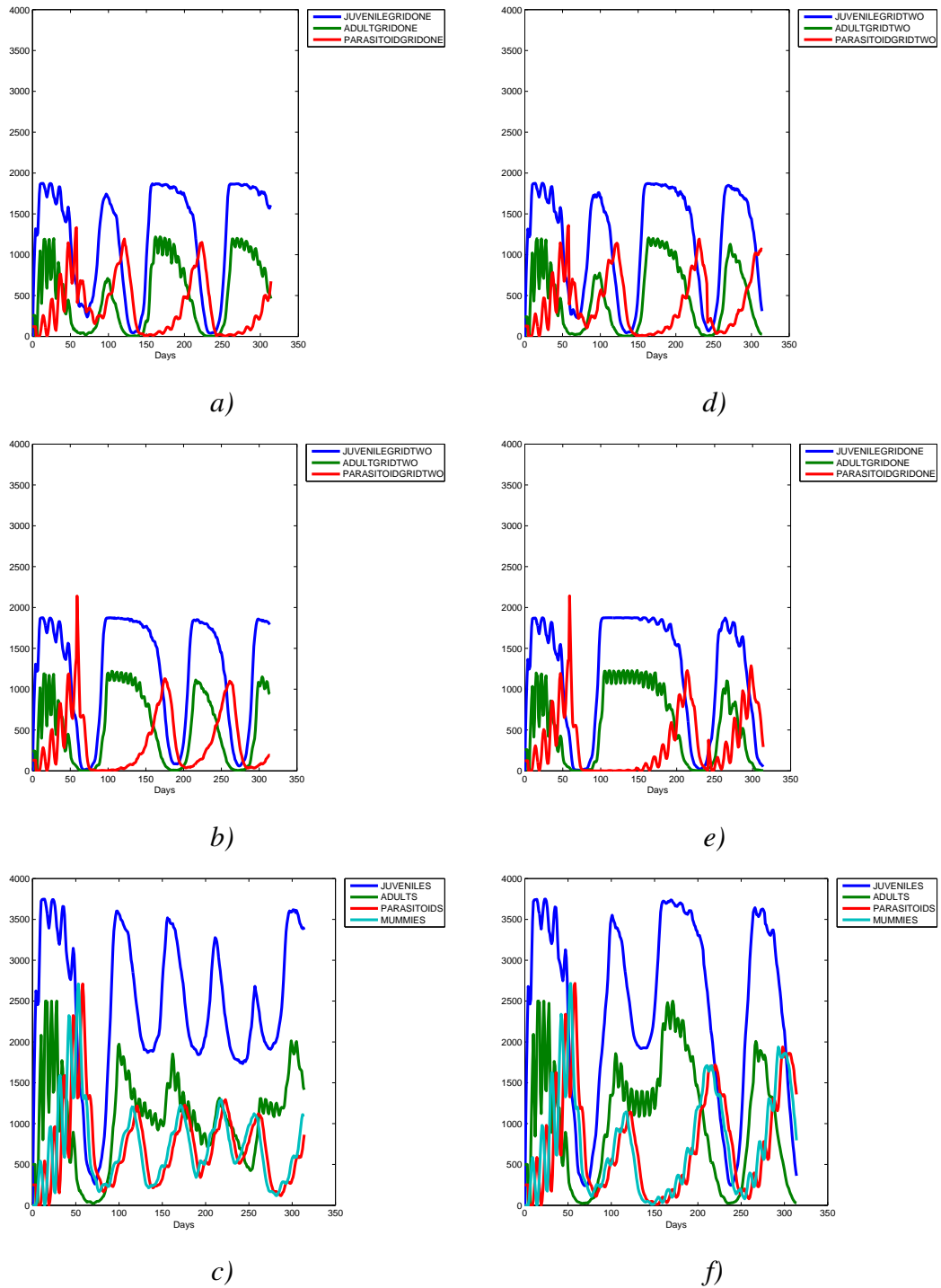
**Figure 6.10:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 20% of parasitoids on the donor grid move to the recipient grid when parasitoid numbers in the non-interacting 2-patch system peak in figure 6.9 c. Initial populations consist of 500 adult aphids and 250 parasitoids total for both grids. Plots in column 1 describe movement from grid 1 to grid 2 and plots in column 2 describe the reverse. (a), (d) show the donor grid populations; (b), (e) show the recipient grid populations; (c), (f) show the combined populations (with the adults trajectory representing the combined adult aphid populations on grids 1 and 2 and adult aphid ‘flyers’ hovering over grids 1 and 2).



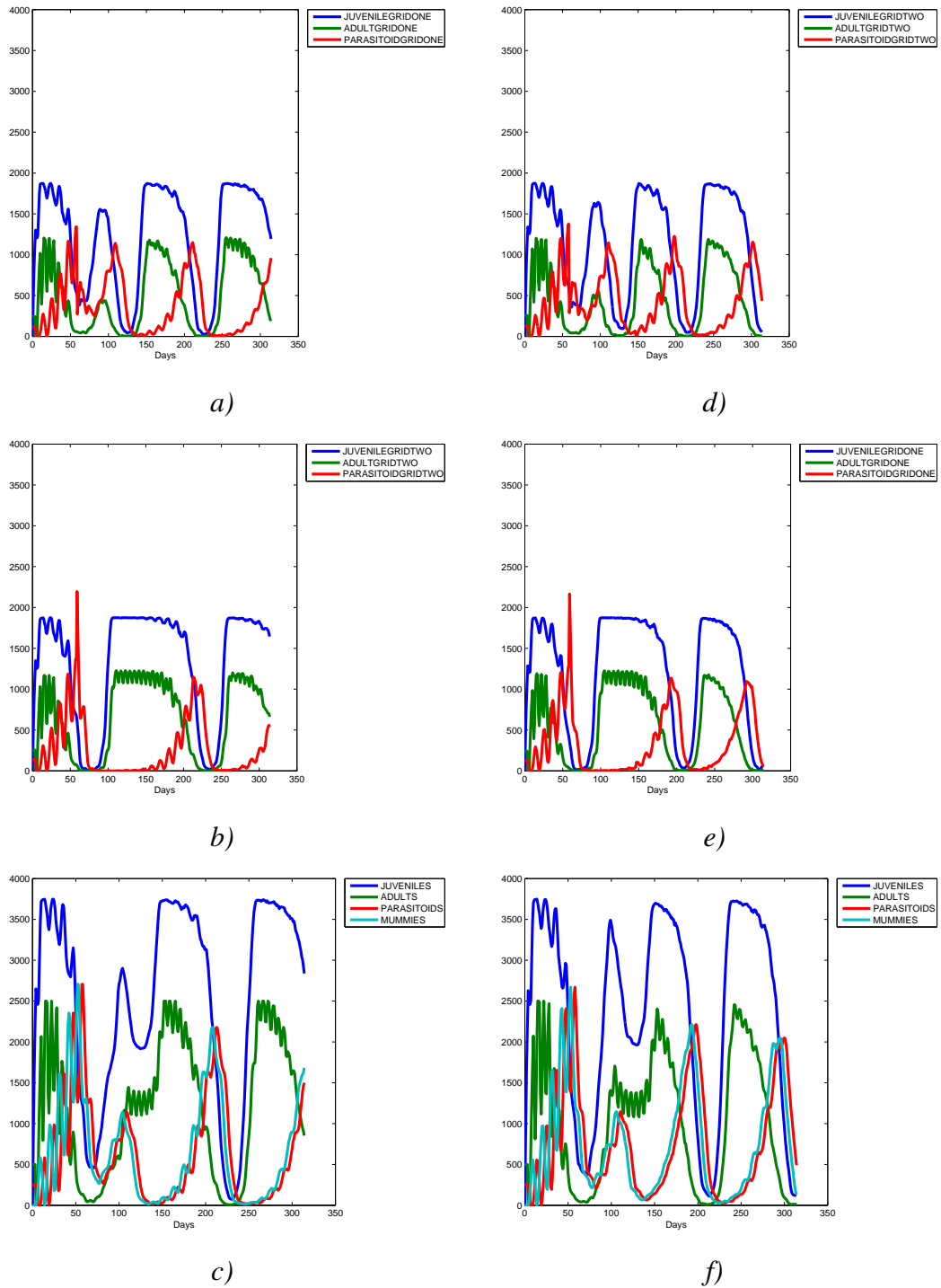
**Figure 6.11:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 40% of parasitoids on the donor grid move to the recipient grid when the non-interacting 2-patch system peaks in figure 6.9. See figure 6.10 for simulation conditions and a description of the individual plots.



**Figure 6.12:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 60% of parasitoids on the donor grid move to the recipient grid when the non-interacting 2-patch system peaks in figure 6.9. See figure 6.10 for simulation conditions and a description of the individual plots.



**Figure 6.13:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 80% of parasitoids on the donor grid move to the recipient grid when the non-interacting 2-patch system peaks in figure 6.9. See figure 6.10 for simulation conditions and a description of the individual plots.



**Figure 6.14:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 90% of parasitoids on the donor grid move to the recipient grid when the non-interacting 2-patch system peaks in figure 6.9. See figure 6.10 for simulation conditions and a description of the individual plots.

Migration of parasitoids was modelled again under the same conditions as before except parasitoids were removed from the donor grid every 10 days (20 days in real time) including day 0 rather than at peak levels in the non-interacting system. Again, this was done mainly to see how the system behaves when multiple interacting patches are modelled rather than to capture the biological realism of the system. Figures 6.15,6.16,6.17, 6.18,6.19 show the results from simulating migration from grid 1 to grid 2 when the fraction of parasitoids removed from the donor grid is varied from 20-90%. Other results (not shown here) indicated that transferring parasitoids from grid 2 to grid 1 generated similar dynamics to transferring parasitoids from grid 1 to grid 2. This is what would be expected since other than the direction of migration conditions remained the same.

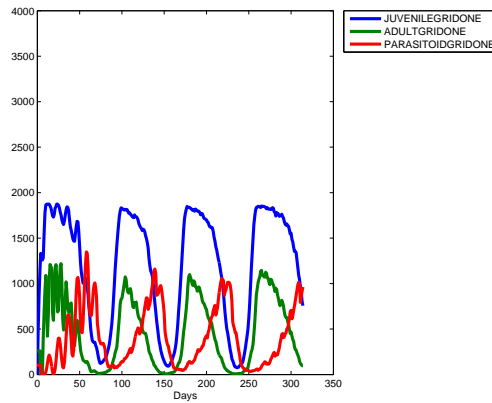
As the fraction of parasitoids migrating was increased the dynamics, characterised by predator-prey oscillations, became more erratic. This was observed both in the dynamics of the individual patches and the combined behaviour of the two patches. In terms of the individual grids, as the level of migration is increased the amplitude of the parasitoid population's cycles on the recipient grid increases, although perhaps not linearly. This result is logical as transferring more parasitoids to the recipient grid will mean greater numbers of parasitoids and therefore the parasitoid population would be expected to peak to higher numbers. Increasing migration levels appears to have the opposite effect on the juvenile population on the donor grid where the juvenile population's cycles decrease in amplitude. This may be because the transfer of parasitoids from the donor grid alleviates parasitoid pressure on the juvenile population on the donor grid and therefore, as levels of migration are increased, the parasitoid population is less likely to drive the juvenile population to very low levels. For all levels of migration, the parasitoid population trajectory has cycles within cycles with a period of about 10 days. These cycles within cycles, which grow in amplitude as the level



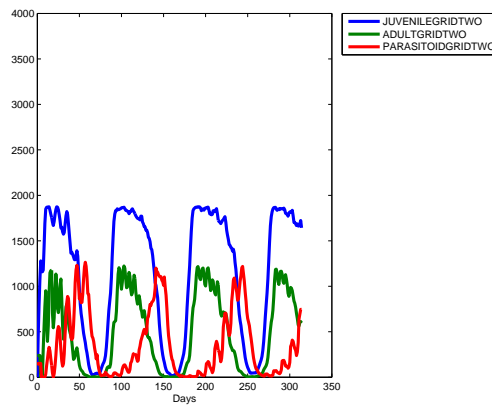
of migration is increased, most likely represent the reduction in parasitoids when migration occurs followed by parasitoid growth, followed by yet another migration event when the parasitoid population dips down again. The recipient parasitoid population also has cycles within cycles (though not always with a periodicity of 10 at levels of migration from 20-70%) which increase in amplitude as migration levels increase. At migration levels  $\geq 80\%$ , the parasitoid population's cycles within cycles are of period 10. While the period of cycles within cycles is not consistently 10 for all levels of migration, these cycles also are most likely perpetuated due to parasitoid migration. Note when 50% of the parasitoid population on one grid is transferred to the other grid in figure 6.16, the recipient grid does not show sustained oscillations for all populations. However, in the output from simulating migration from grid 2 to grid 1, all populations on the recipient grid exhibit sustained oscillations. This difference in behaviour is likely due to the stochasticity of the model.

In terms of the dynamics of the recipient grid in relation to its respective donor grid, the oscillations of the populations on the recipient grid after the initial transient dynamics tend to be of greater amplitude, noticeably for juveniles and parasitoids because there is less parasitoid pressure from parasitoids and fewer parasitoids on the donor grid relative to the recipient grid as a result of migration. Also, the parasitoid population peaks at higher numbers on the recipient grid compared to the donor grid most of the time as migration levels are varied. This also is a result of the greater number of parasitoids on the recipient grid. The oscillations of the populations on the recipient grid also have lower trough counts relative to the populations on the donor grid which is likely due to the greater parasitoid pressure exerted as a result of migration. Also, as levels of migration are increased the oscillations of the corresponding populations on the donor and recipient grids become more out of sync, particularly at levels of migration  $\geq 70\%$  where the dynamics are noticeably 'faster' on the recipient grid in comparison to the donor grid.

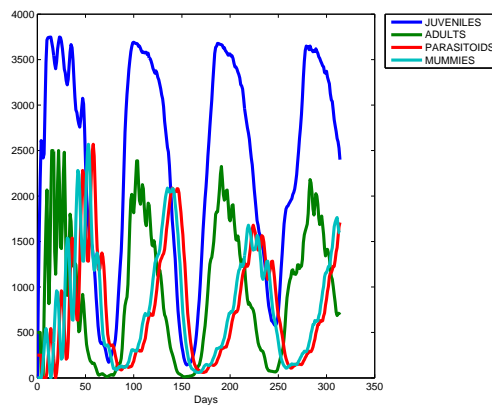
The combined dynamics of the 2-patch system suggests that increasing levels of migration generates faster dynamics. According to figure 6.17 a bifurcation appears to occur when the fraction of the parasitoid population migrating is increased to 60%, where there is a notable decrease in the amplitude of oscillations for each species after the initial transient dynamics and parasitoid dynamics characterised by cycles within cycles, though not always of period 10. At even higher levels of migration, the aphid population also appears to exhibit dynamics characterised by cycles within cycles.



a)

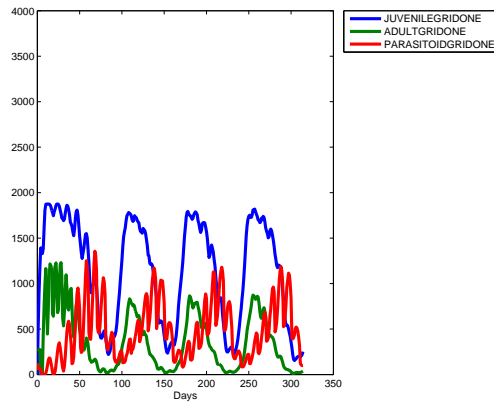


b)

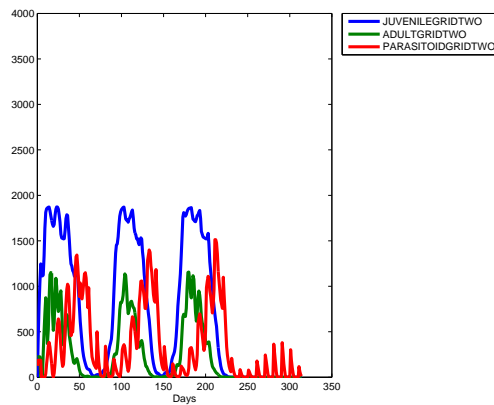


c)

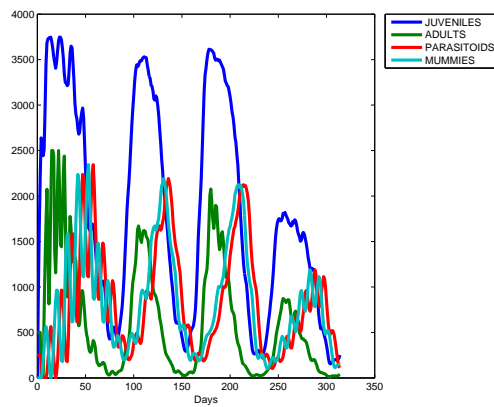
**Figure 6.15:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 20% of parasitoids on grid 1 move to grid 2 every 10 days. Initial populations consist of 500 adult aphids and 250 parasitoids total for both grids. (a), (b), (c) show populations on grid 1, populations on grid 2, combined populations on grids 1 and 2 (with the adults trajectory representing the combined adult aphid populations on grids 1 and 2 and adult aphid ‘flyers’ hovering over grids 1 and 2), respectively.



a)

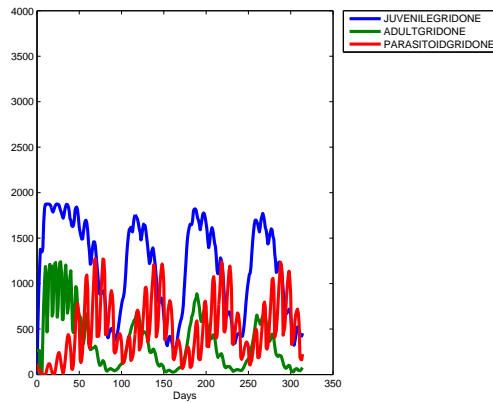


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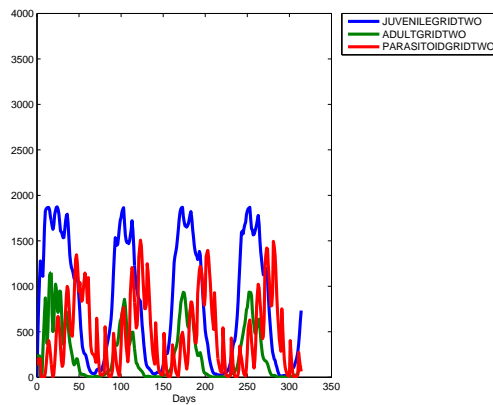


c)

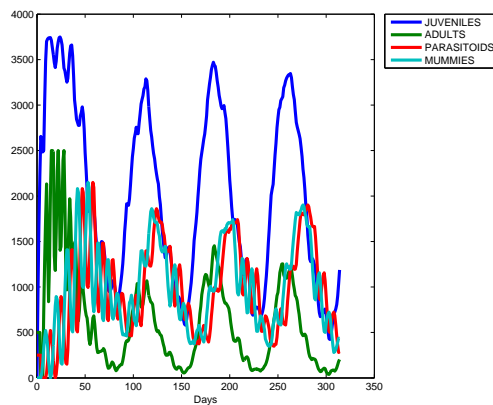
**Figure 6.16:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 50% of parasitoids on the donor grid move to the recipient grid every 10 days. See figure 6.15 for simulation conditions and a description of the individual plots.



a)

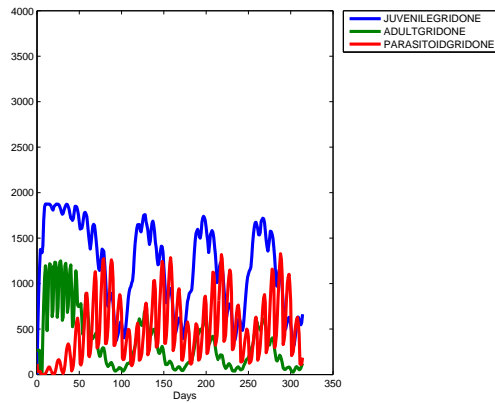


b)

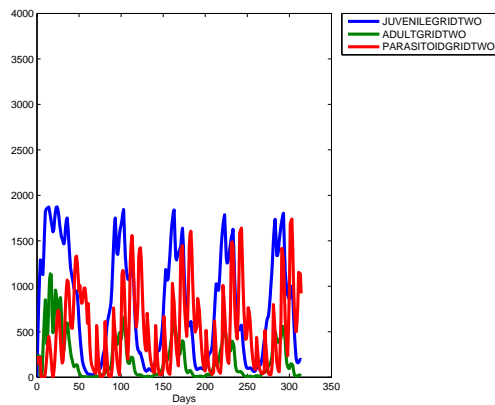


c)

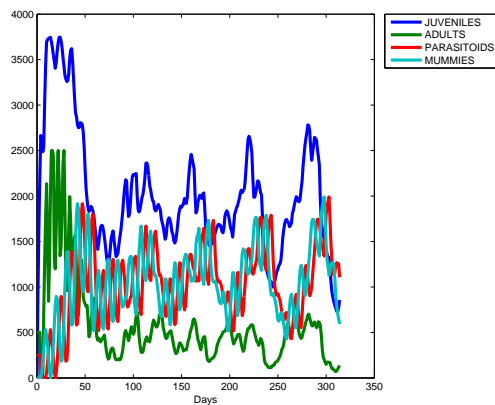
**Figure 6.17:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 60% of parasitoids on the donor grid move to the recipient grid every 10 days. See figure 6.15 for simulation conditions and a description of the individual plots.



a)

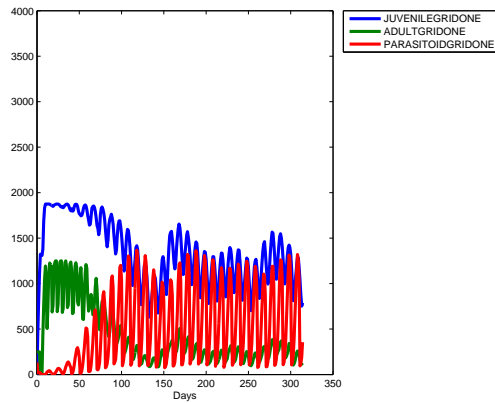


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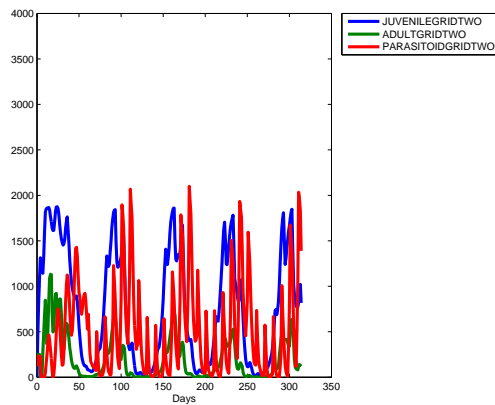


c)

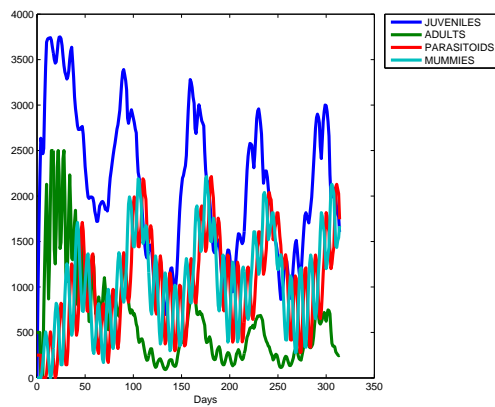
**Figure 6.18:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 70% of parasitoids on the donor grid move to the recipient grid every 10 days. See figure 6.15 for simulation conditions and a description of the individual plots.



a)



b)



c)

**Figure 6.19:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 90% of parasitoids on the donor grid move to the recipient grid every 10 days. See figure 6.15 for simulation conditions and a description of the individual plots.

## **6.4 Aphid-parasitoid dynamics with diffusive within-patch movement**

Continuing in the same vein as the previous simulations, the following results describe the dynamics of an aphid-parasitoid system without parasitoid *and* aphid ‘flyers.’ As there are no ‘flyers,’ aphids and parasitoids move solely by diffusion within a patch. The assumptions made here are the same as those made in section 6.3 except there are no adult aphid ‘flyers’ and there is no cap of 2 adult aphids per grid point. Density dependence is only applied directly to juvenile aphids with a cap of 3 juveniles per grid point, although this density-dependent control indirectly affects adults through its effect on juveniles. As before, single grid and multiple grid dynamics of the system were analysed.

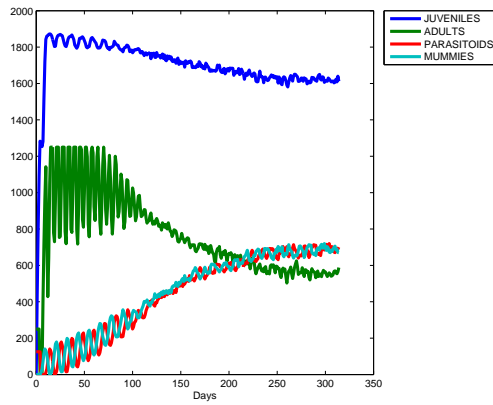
### **6.4.1 Single grid dynamics**

For the single grid system the following parameters were varied: the parasitoid’s probability of discovering an aphid, juvenile aphid mortality and parasitoid diffusion. Simulation results where the aforementioned parameters were varied for both the system described previously and a system where the adult aphid population has a carrying capacity of 1250 for the entire grid suggest that removing a cap on the number of adult aphids does not appear to have a significant effect on the temporal dynamics of the system. In the later system adult aphids were assigned a grid carrying capacity rather than a carrying capacity of 2 adults per grid point because there were no aphid ‘flyers’ to alleviate the effects of local overcrowding. Figures 6.20 and 6.21 show the similar behaviour of the systems when the probability of a parasitoid discovering an aphid was varied. This behaviour and the fact that adults are still experiencing density-dependent control indirectly through juveniles in the system without a cap on the number of adults

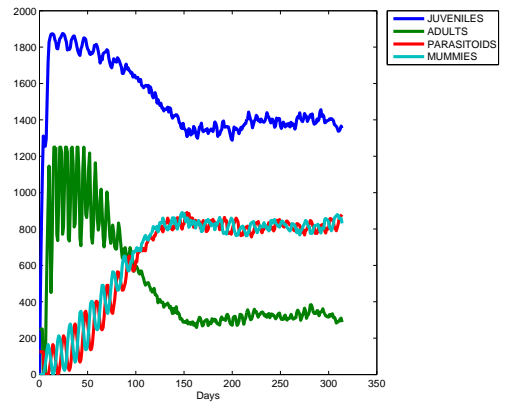


suggest that eliminating the assumption of direct density-dependent control for adults will not significantly change the behaviour of the model.

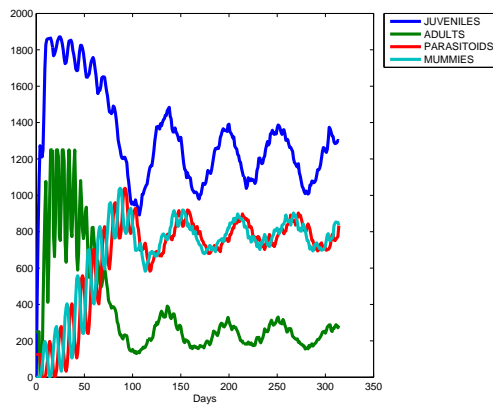
The aphid-parasitoid system without aphid and parasitoid 'flyers,' (i.e. the system without direct density dependence applied to adults) exhibited similar increasingly unstable dynamics and appeared to have similar bifurcation values to the aphid-parasitoid system without parasitoid 'flyers' when the parasitoid's probability of discovering an aphid was increased (see figure 6.4 for comparison). It is interesting that despite changing certain assumptions of the model, very similar behaviour is observed when this parameter is varied in both the system without parasitoid and the system without parasitoid and aphid 'flyers.' This is not quite the case, however, when parasitoid diffusion was varied.



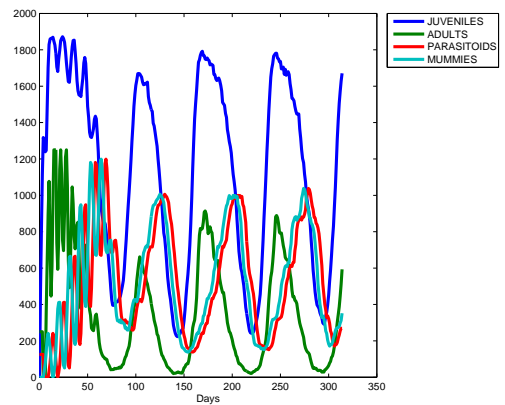
a)



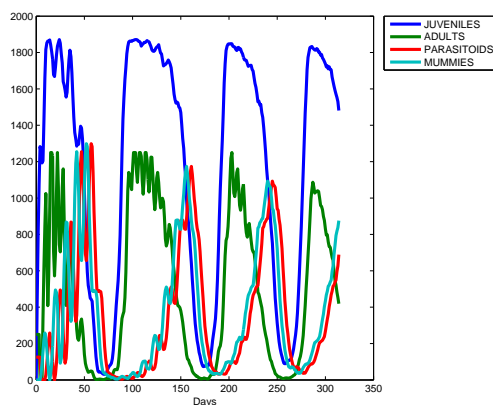
b)



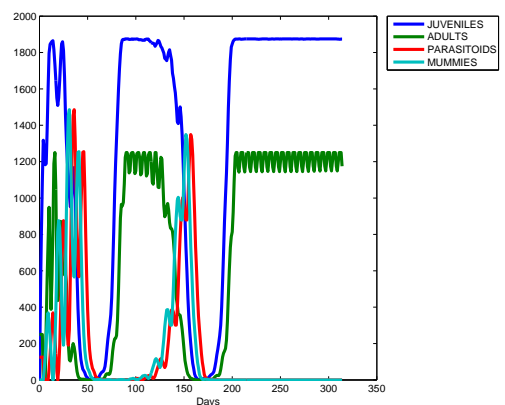
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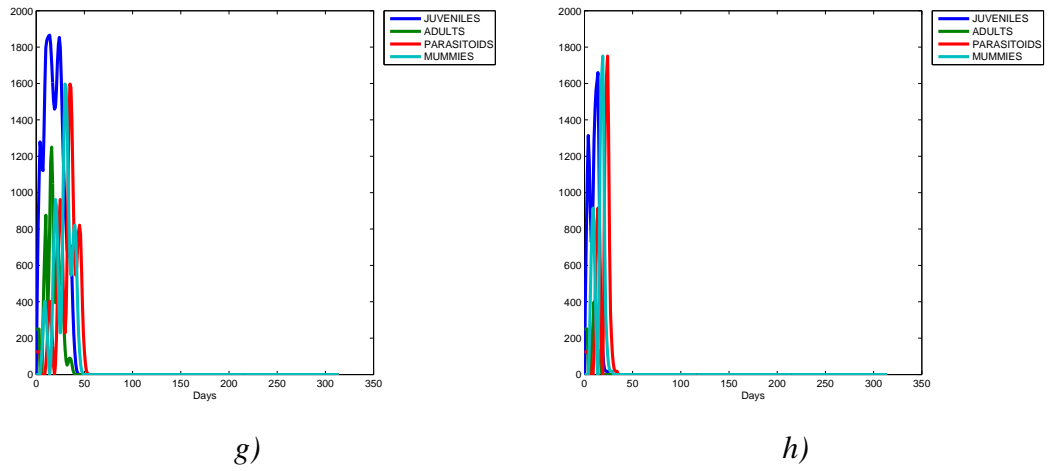
d)



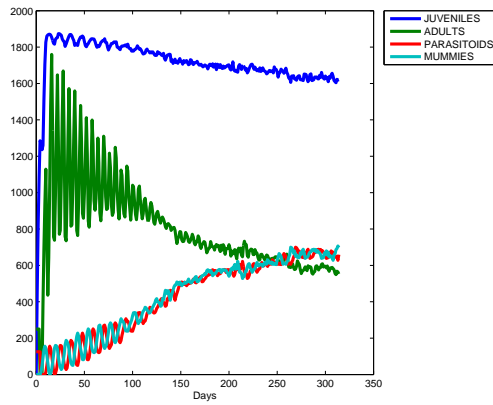
e)



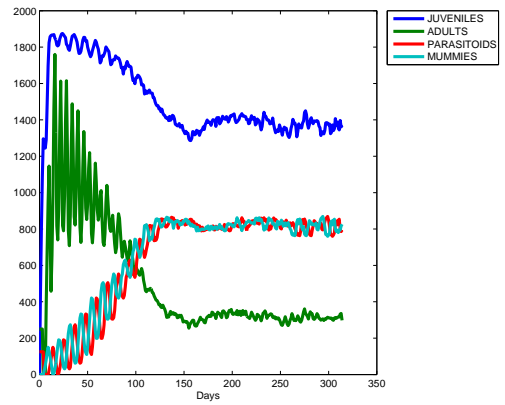
f)



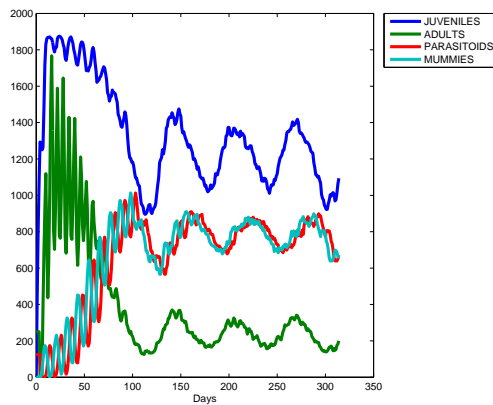
**Figure 6.20:** *Plots illustrating aphid and parasitoid populations over time while the probability of a parasitoid discovering an aphid is varied. There is a grid carrying capacity of 1250 for adult aphids in addition to the cap of 3 juveniles per grid point that is already implemented in the model. Initial populations consist of 250 adult aphids and 125 parasitoids. Probability of a parasitoid discovering an aphid in (a), (b), (c), (d), (e), (f), (g), (h) is 0.00003, 0.000035, 0.00004, 0.00005, 0.00006, 0.00009, 0.0001, 0.0003, respectively.*



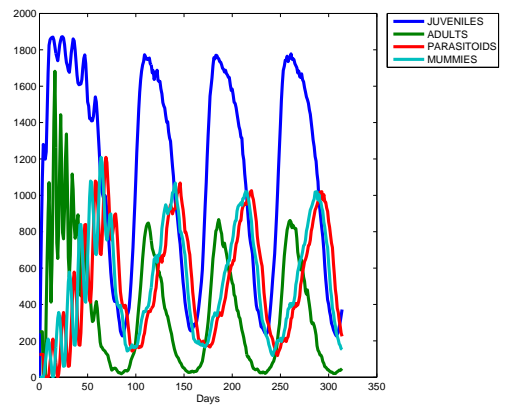
a)



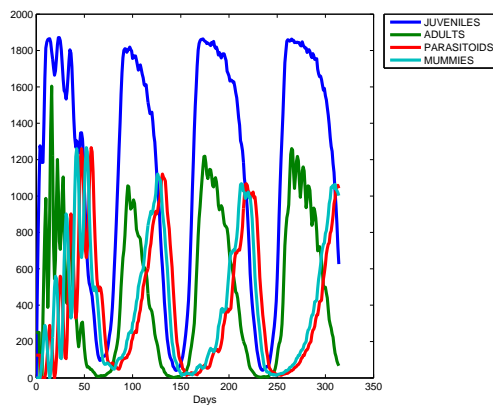
b)



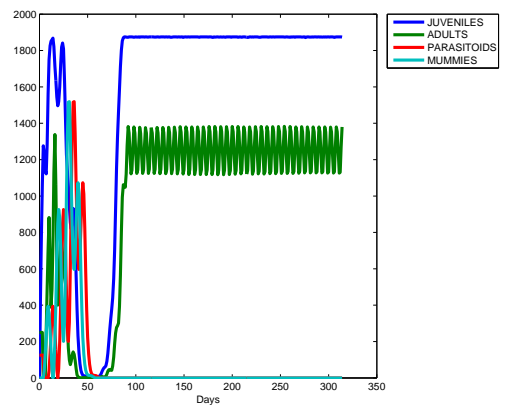
c)



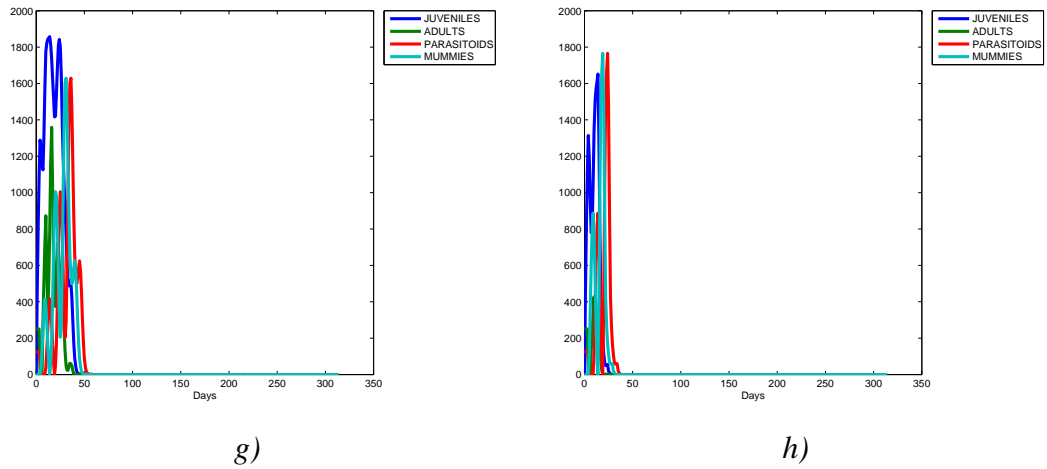
d)



e)



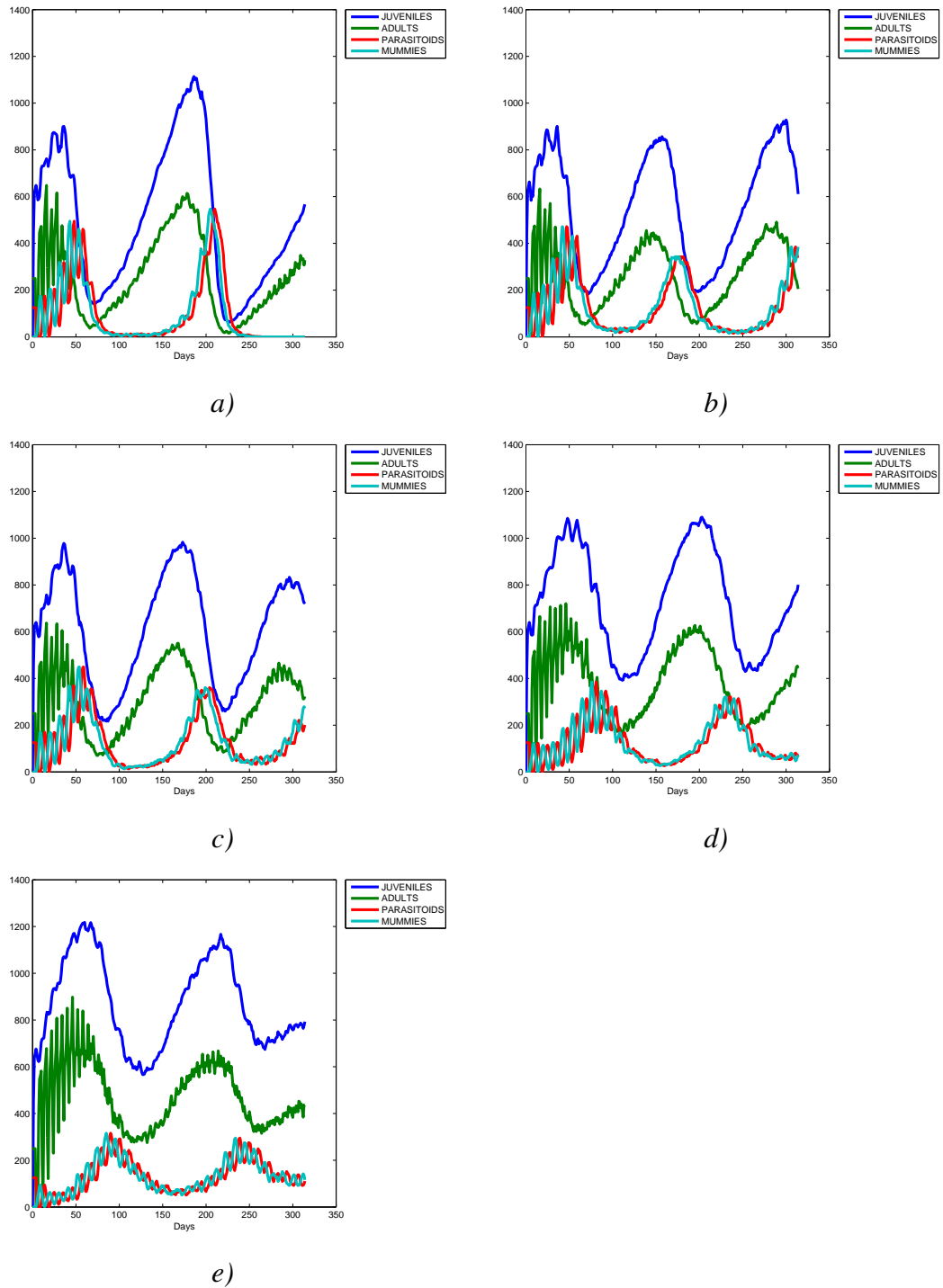
f)



**Figure 6.21:** Plots illustrating aphid and parasitoid populations over time while the probability of a parasitoid discovering an aphid is varied. Unlike figure 6.20 there is no density dependence applied directly to adult aphids. Initial populations consist of 250 adult aphids and 125 parasitoids. Probability of a parasitoid discovering an aphid in (a), (b), (c), (d), (e), (f), (g), (h) is 0.00003, 0.000035, 0.00004, 0.00005, 0.00006, 0.00009, 0.0001, 0.0003, respectively.

Figure 6.22 shows that the system without aphid and parasitoid ‘flyers’ similarly to the system without parasitoid ‘flyers’ (see figure 6.6 for comparison) exhibits dynamics that transition from no coexistence, to oscillations and what appears to be damped oscillations as parasitoid diffusion is decreased. The underlying mechanism for the increasing stability as parasitoid diffusion is decreased is the same for both systems, that is as parasitoids move slower or become less efficient at finding hosts, the aphids and parasitoids are more likely to coexist and the system is more likely to be stable. While decreasing parasitoid diffusion has a stabilising effect in both systems, the system without parasitoid and aphid ‘flyers’ appears to exhibit coexistence for a greater range of parasitoid diffusion parameter values. Also, when parasitoid diffusion is 1 in the system without parasitoid ‘flyers’ the entire system becomes extinct, whereas, in the system here only parasitoids are extinguished. This would suggest that the system here is not as sensitive to changes in parasitoid diffusion. Perhaps this is because in the system without parasitoid ‘flyers,’ there are still aphid ‘flyers’ being randomly

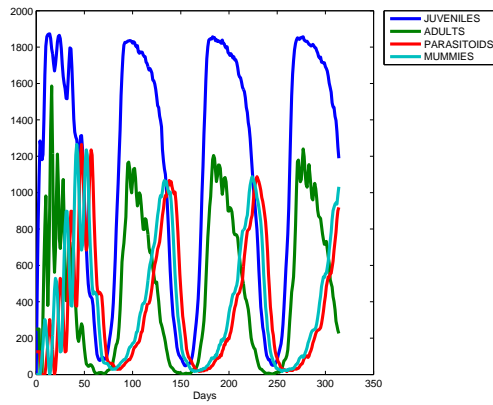
distributed anywhere on the grid if they are unable to find a place to settle due to local overcrowding and thus if parasitoids have a faster diffusion rate, this would be of greater advantage in a system where aphids are more evenly distributed across the grid. In contrast, in the system here aphids can only move via random diffusion and there is no limitation on the number of adults on a given grid point, so adults will more likely lay juveniles or potential hosts less evenly across the grid. Therefore having a faster diffusion rate may not be as advantageous to the parasitoid in the system modelled here.



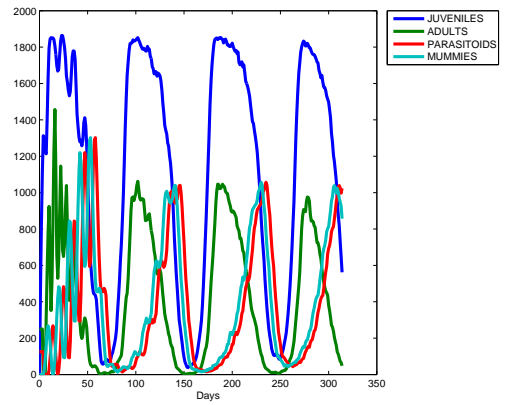
**Figure 6.22:** Plots illustrating aphid and parasitoid populations over time while varying parasitoid diffusion. Initial populations consist of 250 adult aphids and 125 parasitoids. The probability of a parasitoid discovering an aphid is 0.0001. Parasitoid diffusion in (a), (b), (c), (d), (e) is 1, 0.1, 0.01, 0.001, 0.0001, respectively. Aphid diffusion remains constant and is 0.0001.

Juvenile mortality was also varied in the system without aphid and parasitoid ‘flyers.’ Figure 6.23 shows that the resulting behaviour of the system was similar to that of the system with parasitoid and aphid ‘flyers’ when juvenile mortality was varied (see figure 5.25). As in the system with ‘flyers,’ varying juvenile mortality has a more pronounced effect on the adult aphid population which is logical since juveniles experience mortality right before entering adulthood in the model. However, when the system is sufficiently stressed, i.e juvenile mortality is at least 60%, there is a noticeable reduction in all populations. Similarly to the system with ‘flyers,’ there is no qualitative change in dynamics until juvenile mortality is increased to 90% where the entire system collapses (or is near collapse). Prior to that, the aphid and parasitoid populations appear to coexist as oscillating populations which also seems to be the case for the system with ‘flyers’ where the beginning of oscillatory dynamics are apparent. Again, it is interesting how the system without ‘flyers’ emulates the dynamics of the system with ‘flyers’ quite closely as the system is being perturbed.

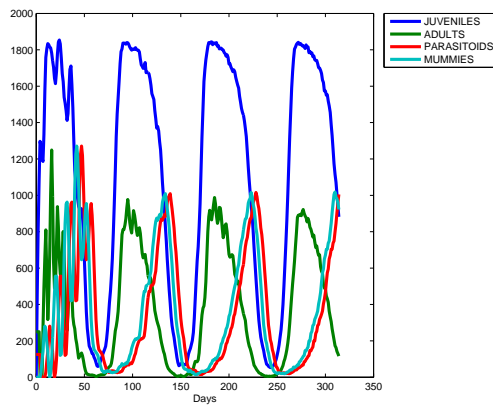




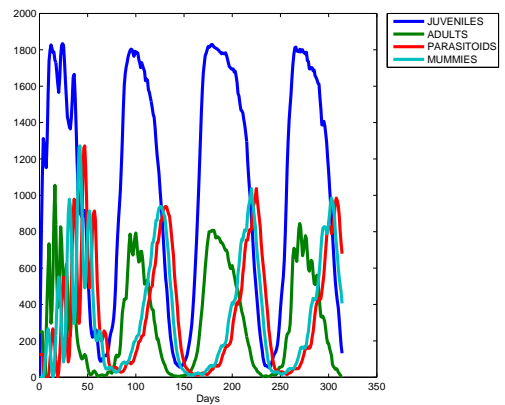
a)



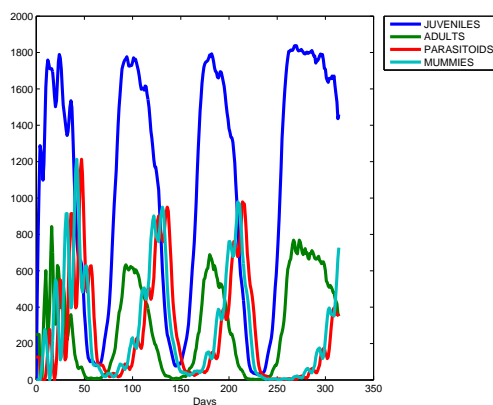
b)



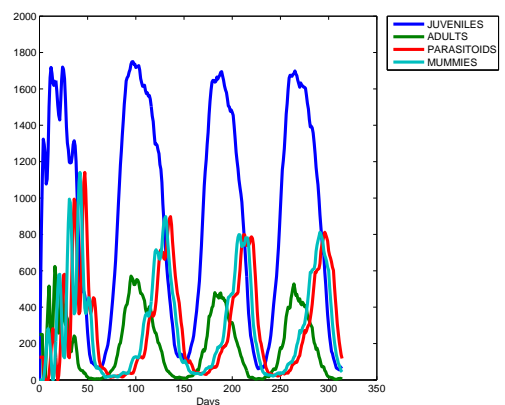
c)



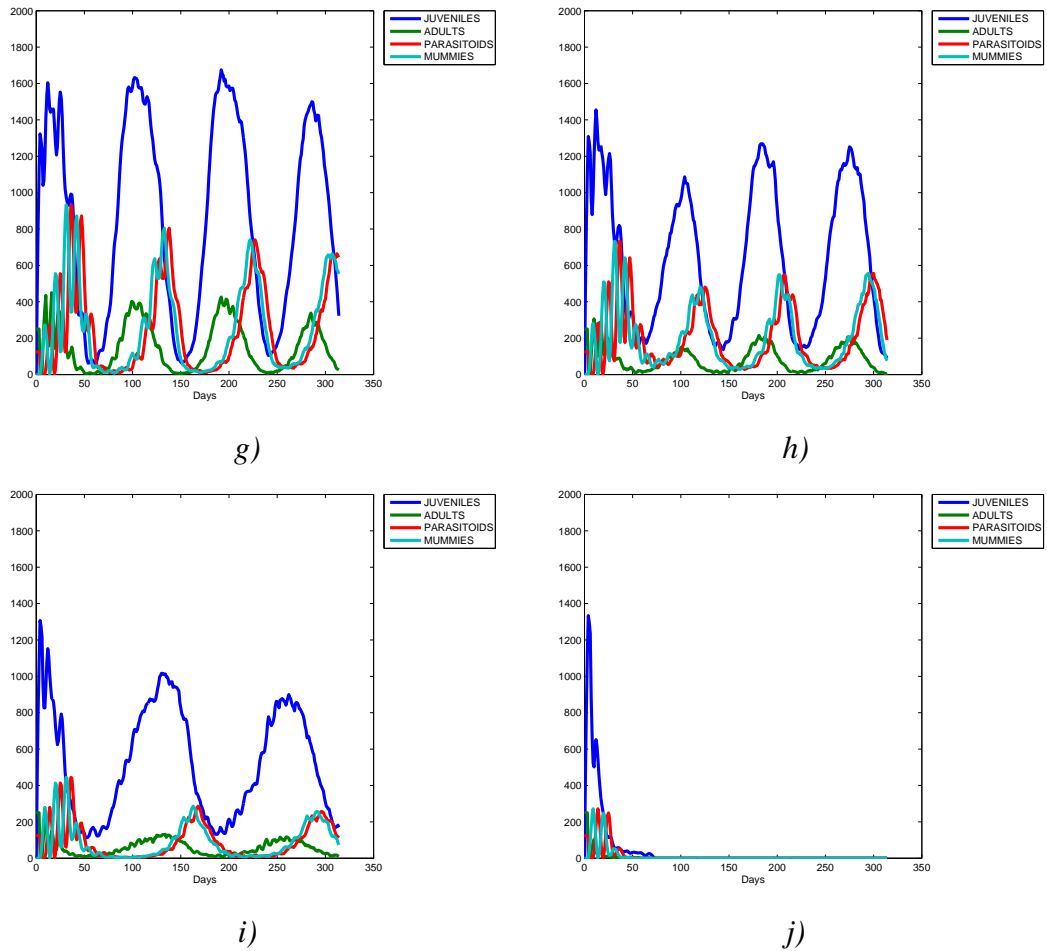
d)



e)



f)



**Figure 6.23:** Plots illustrating aphid and parasitoid populations over time while juvenile mortality is varied. Initial populations consist of 250 adult aphids and 125 parasitoids. Juvenile mortality in (a), (b), (c), (d), (e), (f), (g), (h), (i), (j) is 0%, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90%, respectively.

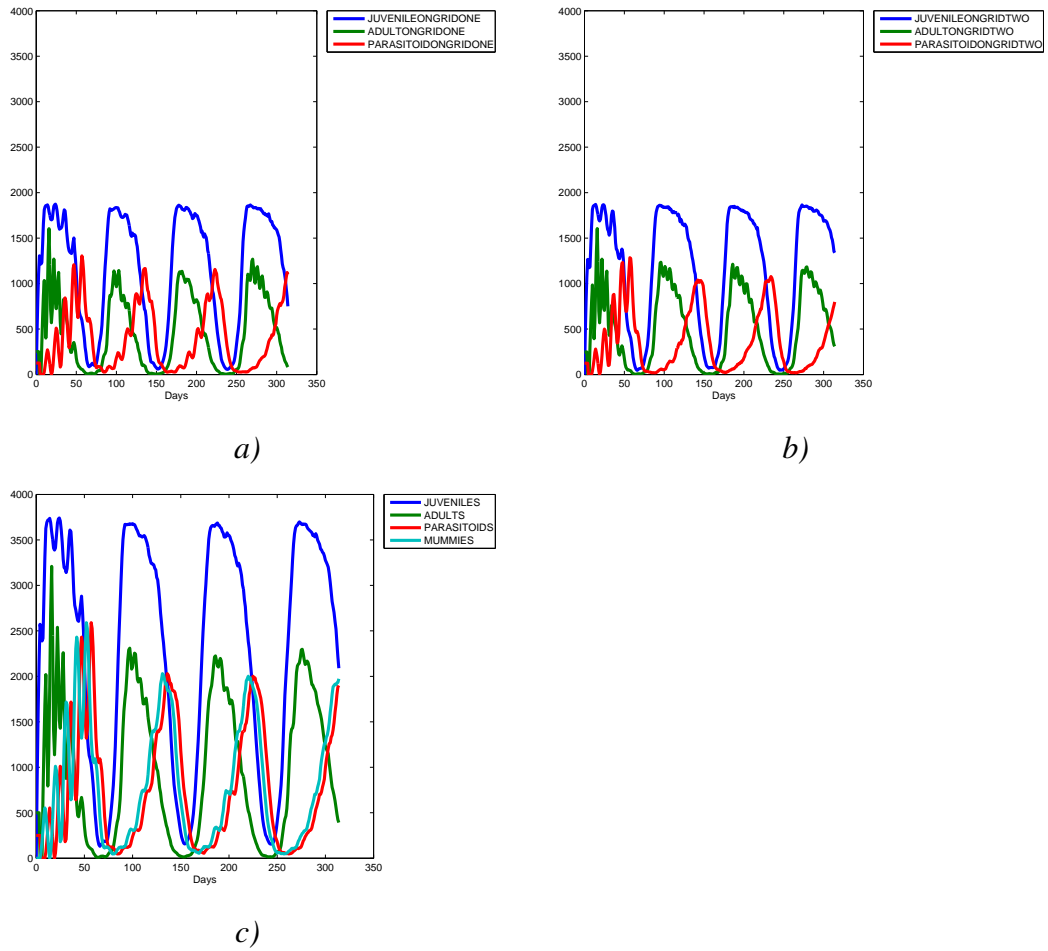
## 6.4.2 Multiple grid dynamics

Aphids and parasitoids were modelled on a two-patch system as described previously in section 6.3.2 with migration of adult aphids from grid one to two or grid two to one (results only shown for migration in one direction here), a scenario similar to aphid flight. Adult aphids were removed from the donor grid at the approximate time when the number of adult aphids in the non-interacting two-patch system peaked in

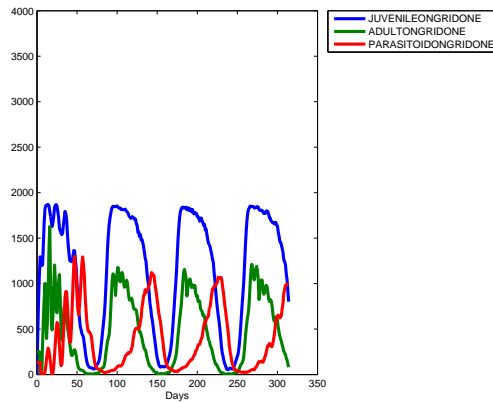
figure 6.24 c and were transplanted to the other grid immediately. This scenario could be representative of aphid populations in the field where adult aphids respond to overcrowding by producing alate offspring or flying away from densely populated areas. The fraction of the adult aphid population that was removed from the donor grid was varied from 20-90%.

Figures 6.24,6.25,6.26,6.27,6.28 show qualitatively there is not much difference in the behaviour of the system with and without aphid migration and as the level of aphid migration is varied. The dynamics of the combined 2-patch system and the individual patches are characterised by similar cyclical behaviour despite varying levels of aphid migration. The only noticeable change is in the periodic behaviour of the adult aphid population. As the levels of aphid migration are increased, the adult peak counts on the recipient grid increases which makes sense because increasing numbers of aphids are being transferred over to the recipient grid approximately when the non-interacting two patch system peaks. The adult aphid population and the juvenile population on the donor grid have a sharp dip when the recipient grid has a sharp peak which is obvious at 50% adult aphid population transfer and becomes more prominent as migration levels increase. These sharp needlelike peaks and dips in the recipient and donor adult aphid populations most likely depict the gain and loss of adult aphids due to migration and the dips in the juvenile population on the donor grid most likely represent the reduced offspring production resulting from the loss of adults. The sharp dips in the juvenile population can also be seen in the output of the combined two-patch system at aphid population transfers  $\geq 70\%$ . Also, note at 20% adult aphid transfer, the population cycles on the recipient grid and the combined two-patch output are slightly irregular which is most likely a result of the stochasticity of the model.

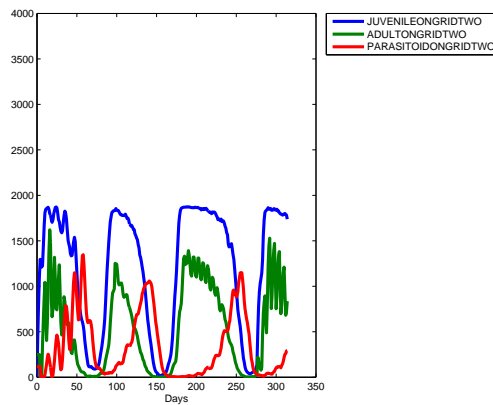
Varying the level of aphid migration has little effect on the qualitative dynamics of the system and does not seem to affect the dynamics of the parasitoid and juvenile host populations significantly. Taking away adult aphids when the non-interacting system peaks does not have a long-term effect on the juvenile population (or the adult population for that matter) on the donor grid because despite reducing the number of adults on the donor grid and consequently causing a slight dip in the juvenile population at significant levels of migration, the juvenile population bounces back because of the high fecundity of aphids and because the aphid population is at a relative peak. Transferring aphids to the recipient grid also does not have a long-term impact on the juvenile population because the juvenile population cannot exceed 1875 aphids due to resource limitation and though adults are being added to the recipient grid and potentially should increase the reproductive output on the recipient grid, this is when the recipient patch is at a relative peak, so the potential increase in juveniles is actually being impeded by the juvenile carrying capacity. As the juvenile population, which are the only hosts for parasitoids, are not significantly affected by aphid migration, the parasitoid populations on the recipient and donor grid are not affected much either by aphid migration.



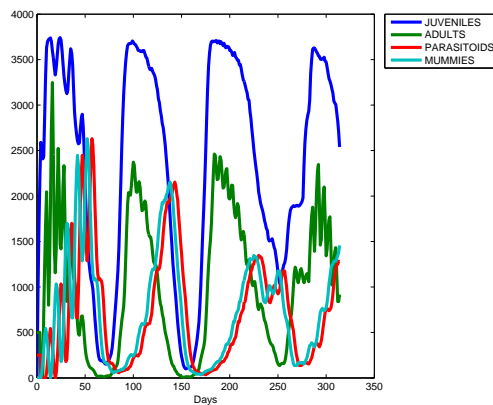
**Figure 6.24:** Plots illustrating the dynamics of aphid and parasitoid populations on two non-interacting grids. Initial populations consist of 500 adult aphids and 250 parasitoids total for both grids. (a), (b), (c) show populations on grid 1, populations on grid 2 and the combined populations on grids 1 and 2, respectively.



a)

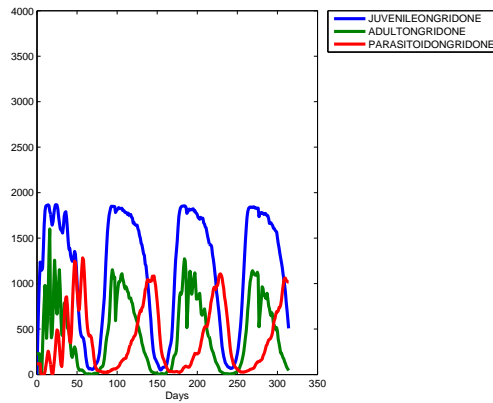


b)

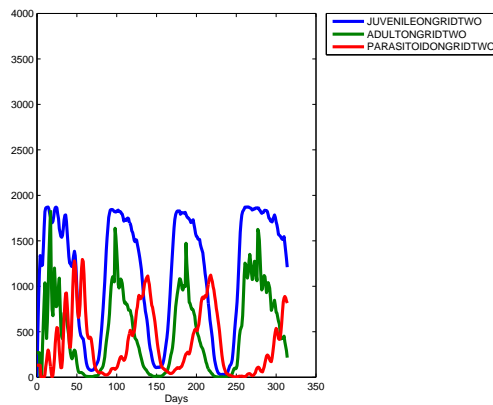


c)

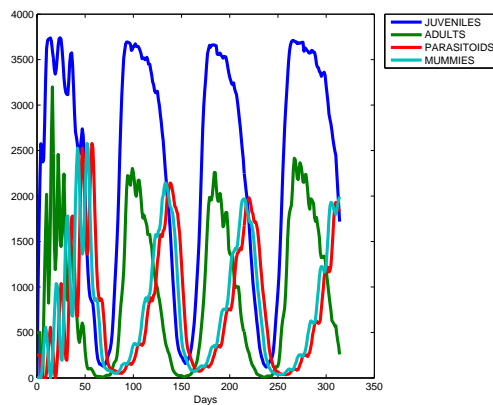
**Figure 6.25:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 20% of adult aphids on grid 1 move to grid 2 when adult numbers peak in the non-interacting 2-patch system in figure 6.24 c. Initial populations consist of 500 adult aphids and 250 parasitoids total for both grids. (a), (b), (c) show populations on grid 1, populations on grid 2, combined populations on grids 1 and 2, respectively.



a)

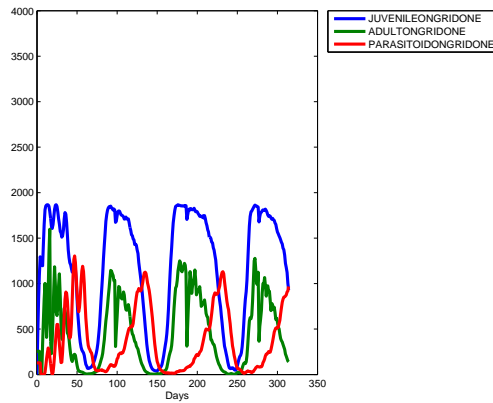


b)

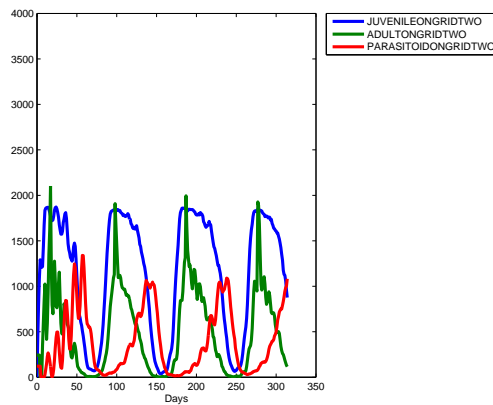


c)

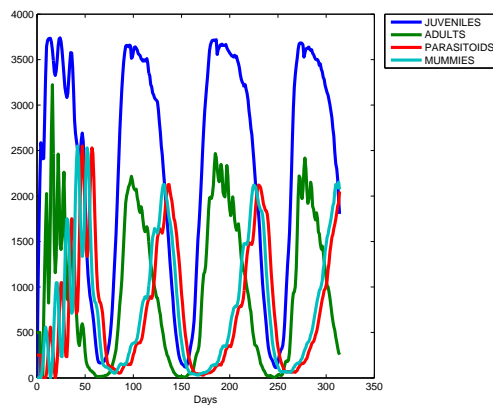
**Figure 6.26:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 50% of adult aphids on the donor grid move to the recipient grid when the two non-interacting grids peak in figure 6.24. See figure 6.25 for simulation conditions and a description of the individual plots.



a)



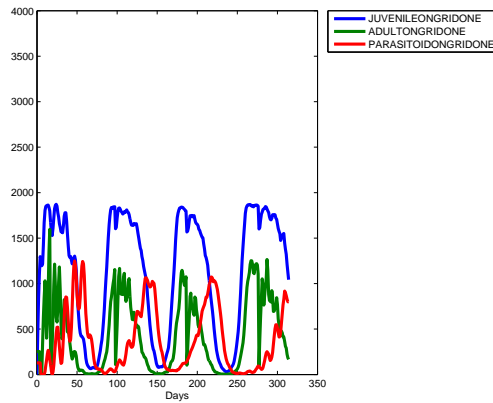
b)



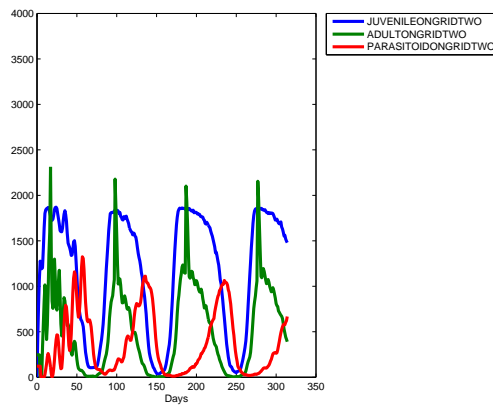
c)

**Figure 6.27:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 70% of adult aphids on the donor grid move to the recipient grid when the two non-interacting grids peak in figure 6.24. See figure 6.25 for simulation conditions and a description of the individual plots.

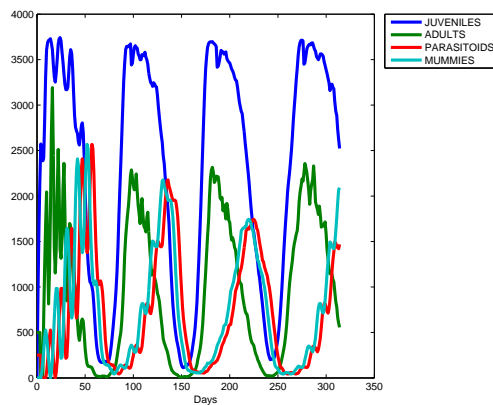




a)



b)

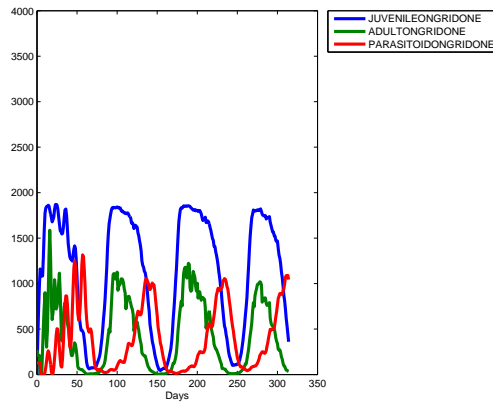


c)

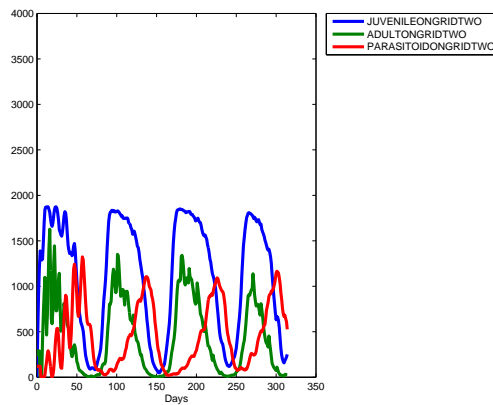
**Figure 6.28:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 90% of adult aphids on the donor grid move to the recipient grid when the two non-interacting grids peak in figure 6.24. See figure 6.25 for simulation conditions and a description of the individual plots.

Aphid migration was modelled again under the same conditions as the previous set of simulations except rather than removing adult aphids when the non-interacting system peaked, adult aphids were removed every 10 days (20 days in real time) including day 0. While migration of aphids every 10 days may not be representative of nature, this was done to obtain a better idea of how the system responds to aphid migration. Figures 6.29,6.30,6.31,6.32,6.33 show the results. Again, varying the level of aphid migration does not appear to have a large impact on the dynamics for the same reasons as mentioned above. At all levels of migration, the populations cycle both on the individual patches and in the combined output for the system. As migration levels are increased, the dynamics become noisier on the individual patches. On the recipient patches, the adult aphid population has cycles that spike in value and these spikes grow in magnitude as the level of aphid migration is increased. These spikes occur about every 10 days and thus represent the incoming migrants added to the adult population. The slightly irregular dynamics of the recipient patch and in the graph of the combined output at 60% aphid transfer are likely due to the stochasticity of the model.

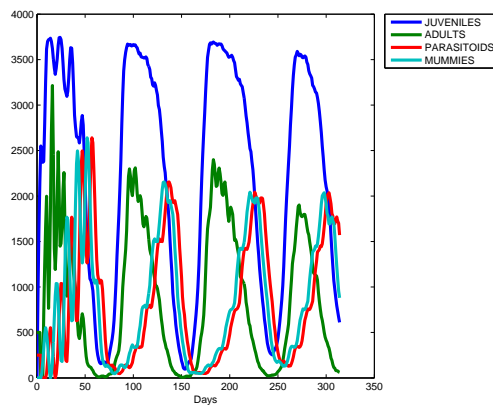
The donor adult population meanwhile exhibits cycles which have sharp dips that increase in magnitude as the level of migration is increased. These dips in adult numbers occur about every 10 days, representing the removal of migrants. These dips of increasing magnitude about every 10 days are also obvious in the juvenile population on the donor grid at levels of migration  $\geq 50\%$  (note the output for migrating 50% of adults from one patch is not shown here). These features in the juvenile population most likely represent the reduced reproductive output of adults on the donor grid due to adults emigrating.



a)

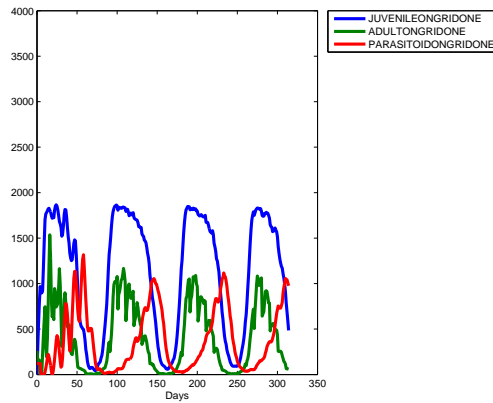


b)

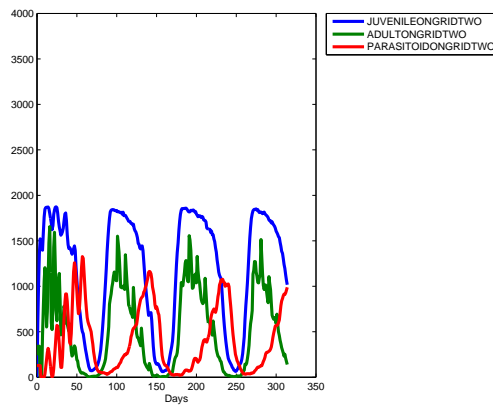


c)

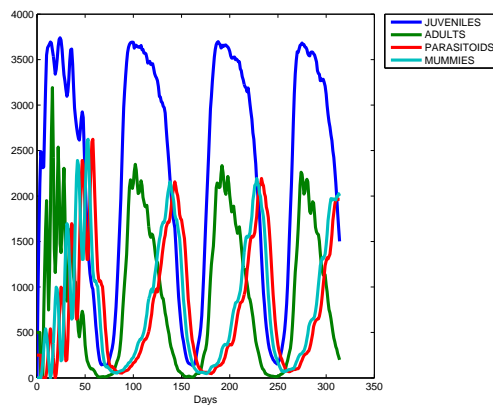
**Figure 6.29:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 20% of adult aphids move from grid 1 to grid 2 every 10 days. Initial populations consist of 500 adult aphids and 250 parasitoids total for both grids. (a), (b), (c) show populations on grid 1, populations on grid 2, combined populations on grids 1 and 2, respectively.



a)

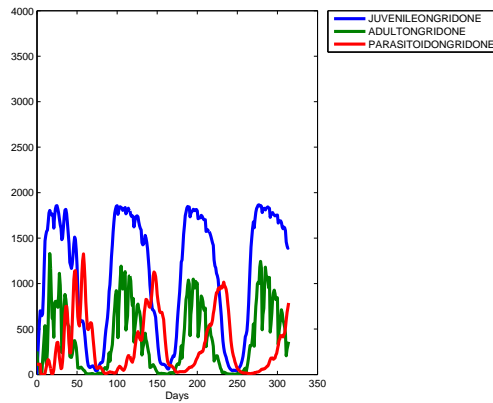


b)

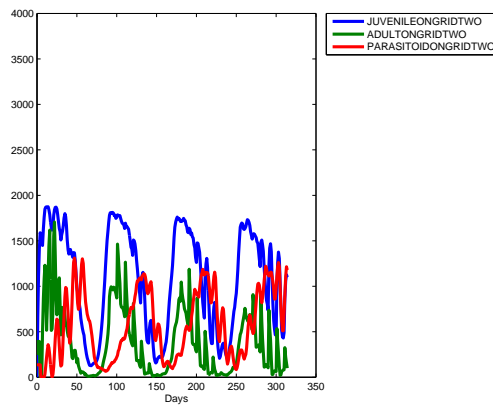


c)

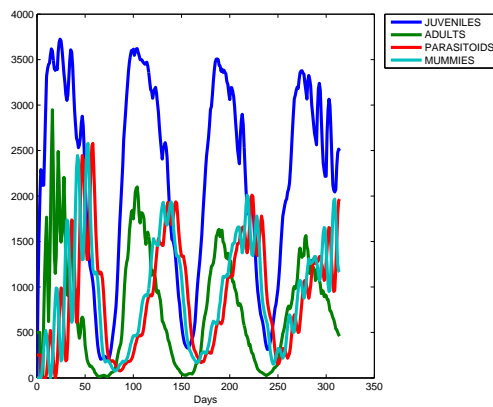
**Figure 6.30:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 40% of adult aphids on the donor grid move to the recipient grid every 10 days. See figure 6.29 for simulation conditions and a description of the individual plots.



a)

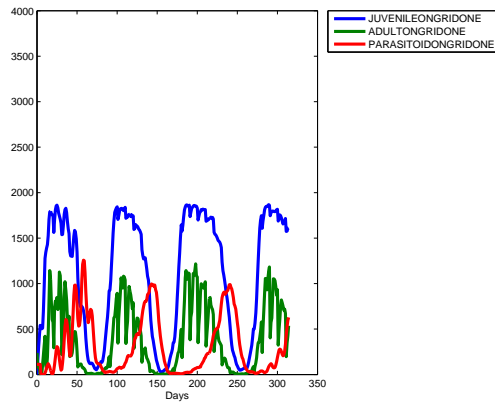


b)

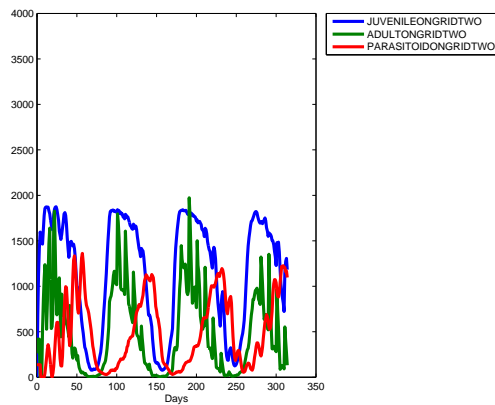


c)

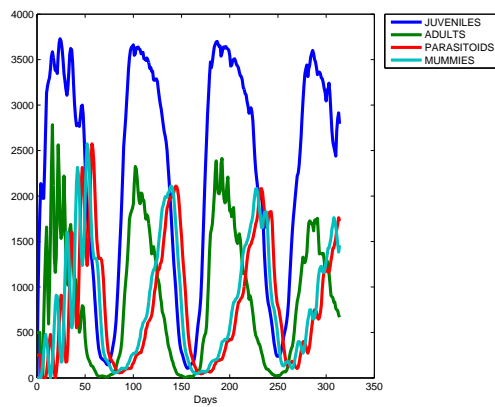
**Figure 6.31:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 60% of adult aphids on the donor grid move to the recipient grid every 10 days. See figure 6.29 for simulation conditions and a description of the individual plots.



a)

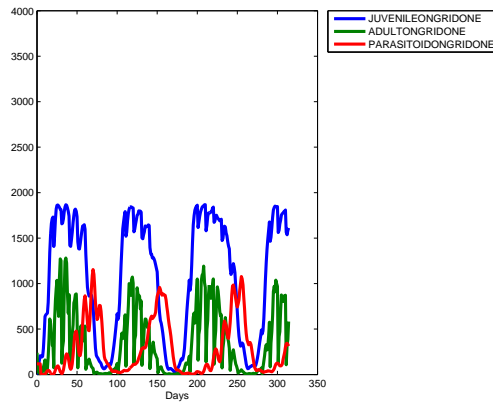


b)

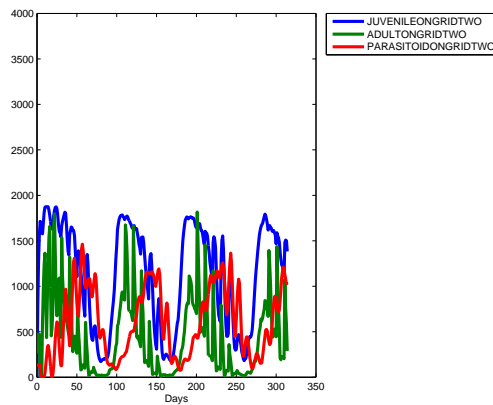


c)

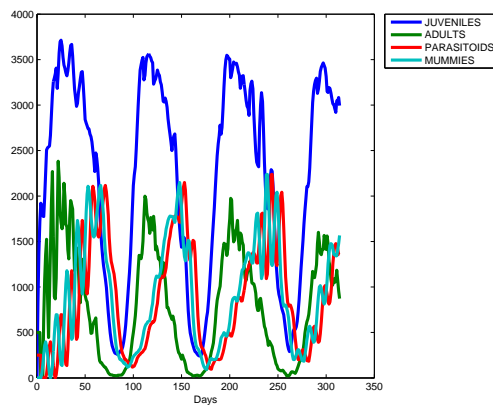
**Figure 6.32:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 70% of adult aphids on the donor grid move to the recipient grid every 10 days. See figure 6.29 for simulation conditions and a description of the individual plots.



a)



b)



c)

**Figure 6.33:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when 90% of adult aphids on the donor grid move to the recipient grid every 10 days. See figure 6.29 for simulation conditions and a description of the individual plots.

Since varying the level of adult aphid migration did not seem to have a large impact on host-parasitoid dynamics, the effect of parasitoid migration on the system was explored further by modelling continuous migration of parasitoids. This was achieved by implementing a giving up time for parasitoids, whereby if the time since last oviposition is equal to the giving up time, then parasitoids immediately migrate to the other patch. The continuous model of parasitoid behaviour is more representative of field populations than allowing parasitoids to migrate every 10 days or when the parasitoid population peaks in the non-interacting two patch system. Migration was modelled in one direction, i.e. from patch 1 to 2 or patch 2 to 1 while varying giving up time. Increasing giving up time is similar to decreasing the rate of migration.

Figures 6.34,6.35,6.36,6.37,6.38,6.39,6.40,6.41 show that, with a few exceptions, increasing giving up time has a destabilising effect on the combined two-patch system when giving up time is less than 22000 time-steps. In figure 6.42 when giving up time is 22000 time-steps, the behaviour of the combined two-patch system seems to become more stable. The combined system's pattern of behaviour as giving up time is varied can be understood in terms of the dynamics of the individual patches and their behaviour in relation to one another.

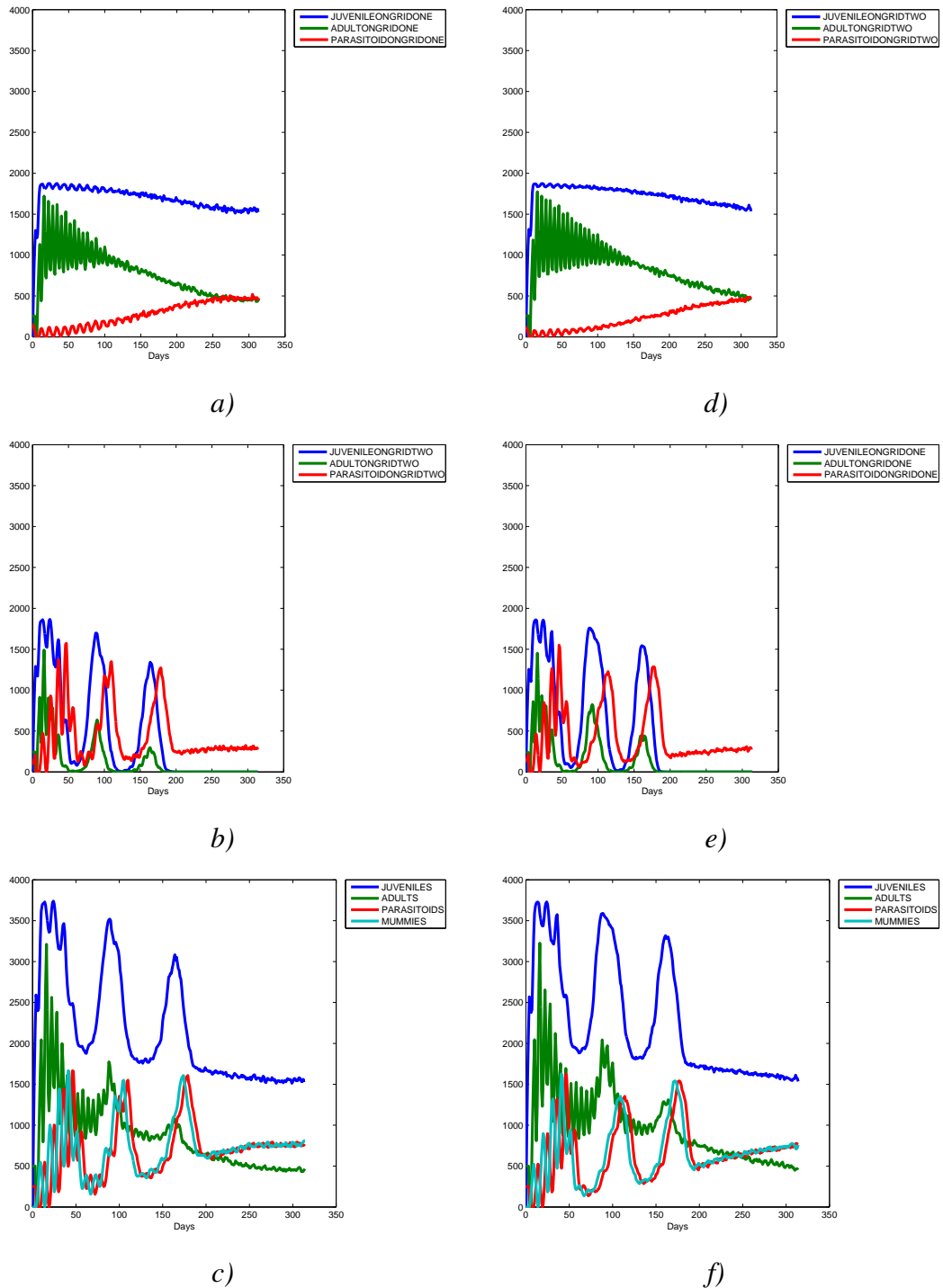
As giving up time is increased, the system on the donor patch becomes more unstable, transitioning from stable equilibrium (figures 6.34,6.35) to damped oscillations (figures 6.36,6.37) and to cycles of increasing amplitude (figures 6.38,6.39,6.40,6.41,6.42). A shorter giving up time means that it is more probable that a parasitoid will leave the donor patch when compared to a longer giving up time. Therefore at lower values of giving up time (i.e. 6000-12000 time-steps), more parasitoids will be emigrating from the donor grid, reducing the size of the donor parasitoid population more so than when parasitoids have a longer giving up time. The smaller size of the parasitoid population exerts less pressure on the aphid population leading to stable kinetics on the donor grid. At larger values of giving up time (i.e. 15000-22000 time-steps), however, there



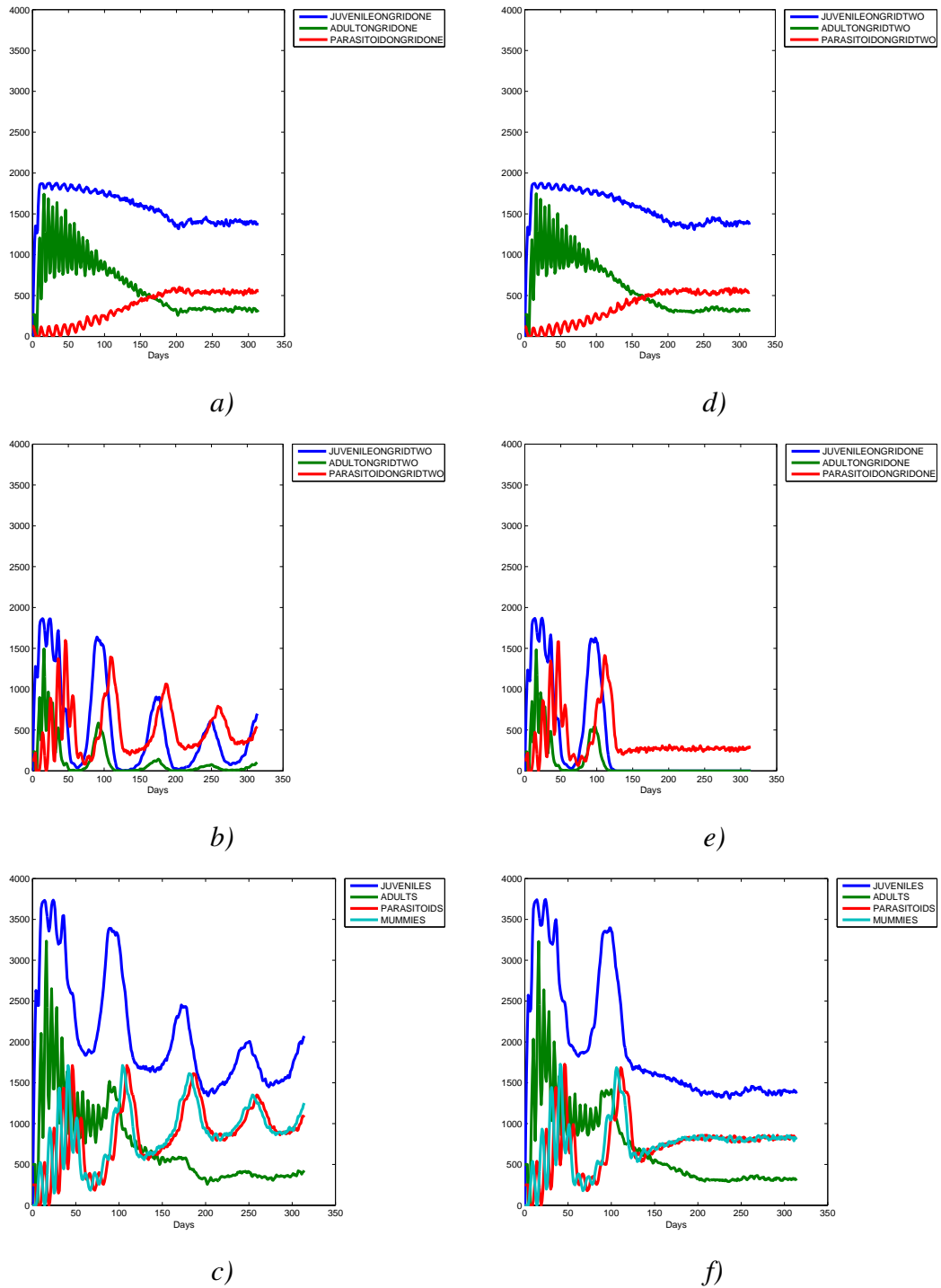
is less of a tendency for parasitoids to leave the donor grid and therefore the parasitoid population grows to large enough numbers to exert sufficient pressure on the aphids to drive predator-prey cycles.

The system on the recipient patch (with a few exceptions) transitions from no coexistence to coexistence of aphid and parasitoid populations that cycle (though the cycles are not always uniform) as giving up time is increased. At values of giving up time between 6000-15000 time-steps (see figures 6.34,6.35,6.36,6.37), the system on the recipient patch exhibits the beginning of predator-prey oscillations that later die out. There is no coexistence and only a parasitoid population remains on the patch that is maintained by continuous migration. The aphid population becomes nonexistent probably because of the increased parasitisation pressure due to immigration at a relatively fast rate. Figure 6.35b does not seem to follow this behaviour. The aphid population quickly declines and tends to 0, but oscillations persist. This irregular behaviour is due to the stochastic individual-based nature of the model. As giving up time is increased to values of 17000 time-steps and greater (figures 6.39,6.40,6.41,6.42), most of the time hosts and parasitoids coexist because the longer giving up time means parasitoids will not as readily leave the donor patch, thereby reducing the number of incoming migrants to the recipient patch and reducing parasitoid pressure on aphids in this patch. In some instances, however, this is not necessarily the case. For example in figure 6.39 e it appears that the aphid population is heading towards extinction (the aphid population still persists within the time frame shown, but at very low numbers) and in figure 6.41 e the aphid population becomes extinct while the parasitoid population is maintained by migration. These dynamics are a consequence of the individual-based stochastic nature of the model and the very low numbers of aphid individuals observed at these parameter values which suggests that there will be instances where the aphid population does actually become extinct.

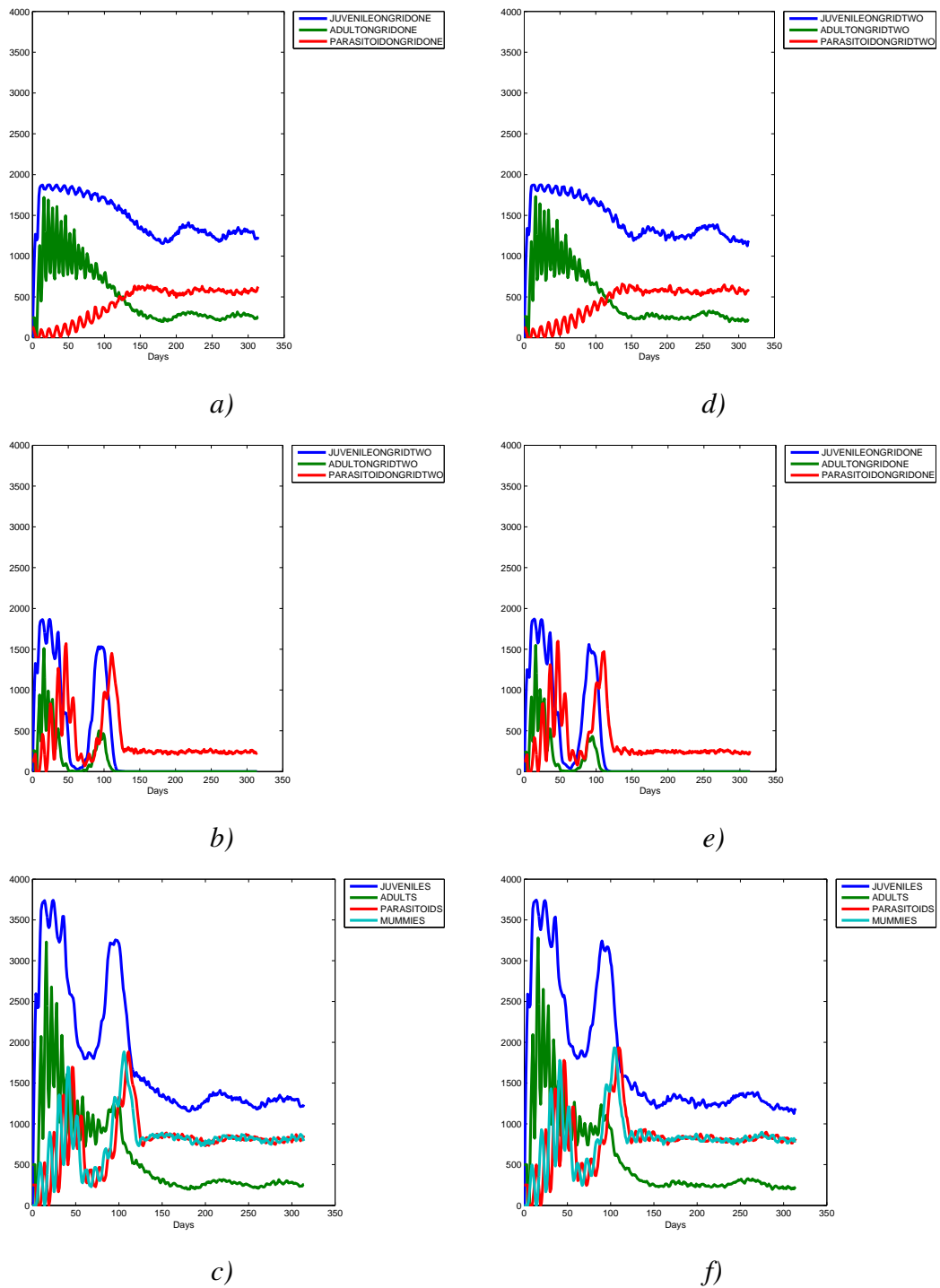
At relatively low values of giving up time (6000-12000 time-steps), the combined two-patch system exhibits damped oscillations, a product of the short-lived predator-prey oscillations on the recipient patch (with the exception of figure 6.35b where the oscillations persist) and the stable kinetics on the donor patch. Increasing giving up time further gives rise to cyclical behaviour, although the cycles are not regular (figure 6.38 c and f). At higher values of giving up time (17000-20000 time-steps), the cycles on the recipient grid tend to be of higher frequency than those on the donor grid. These out of phase cycles generate heterogeneous dynamics in the dynamics of the combined two-patch system. An exception is figure 6.40c where the dynamics are oscillatory. The higher frequency of cycles on the recipient grid is likely a result of the influx of parasitoid migrants which increase parasitoid pressure on aphids, thereby perpetuating predator-prey cycles faster. When giving up time is increased to 22000 time-steps, the combined two-patch system exhibits oscillatory dynamics (figure 6.42).



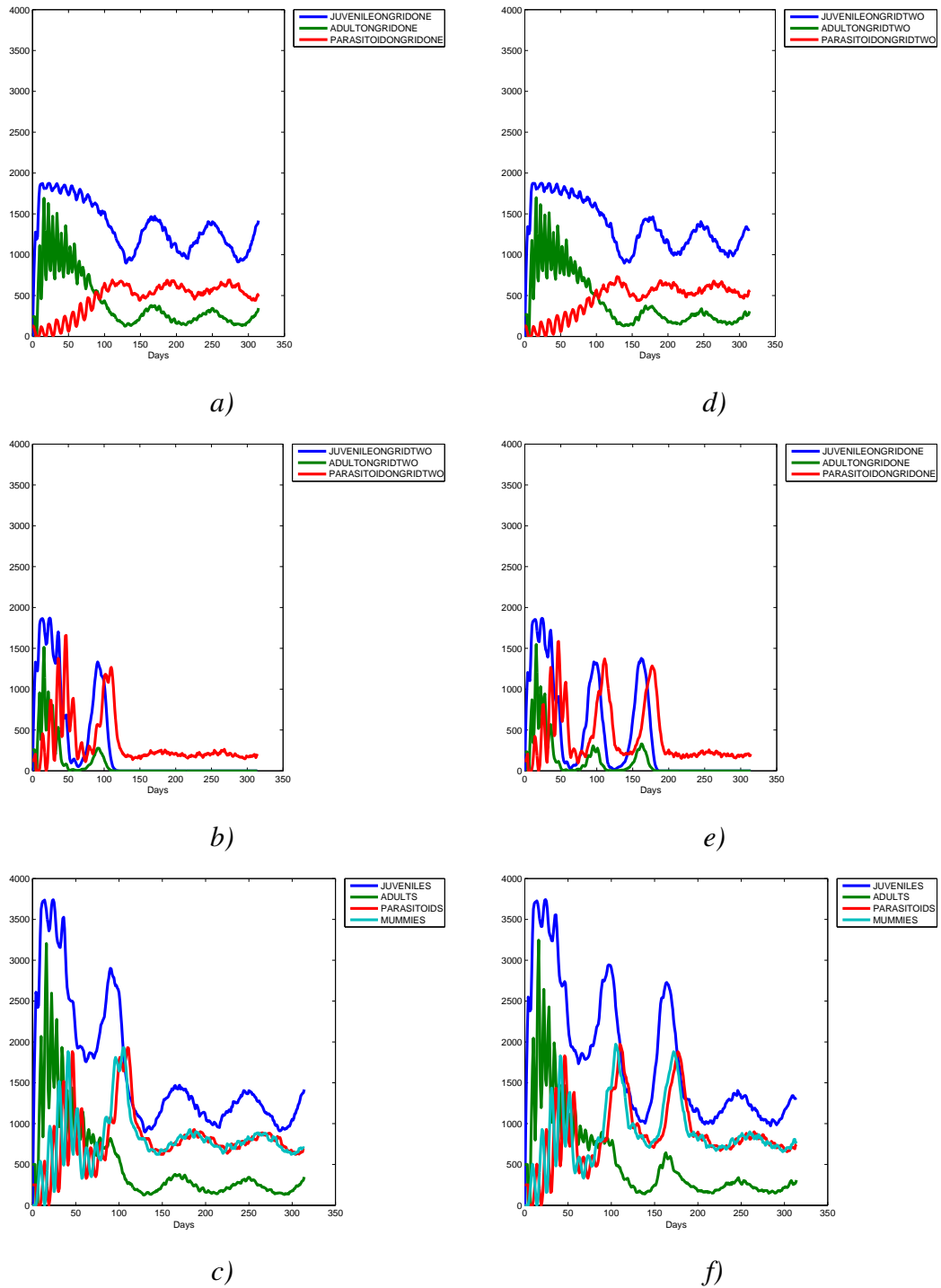
**Figure 6.34:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when parasitoids on the donor grid move to the recipient grid according to a giving up time. Initial populations consist of 500 adult aphids and 250 parasitoids total for both grids. Figures in column 1 describe movement from grid 1 to grid 2 and figures in column 2 describe movement from grid 2 to 1. (a), (d) show populations on the grid that is the source of the migrants; (b),(e) show populations on the grid that receives the migrants; (c), (f) depict the combined populations. Giving up time is 6000 time-steps.



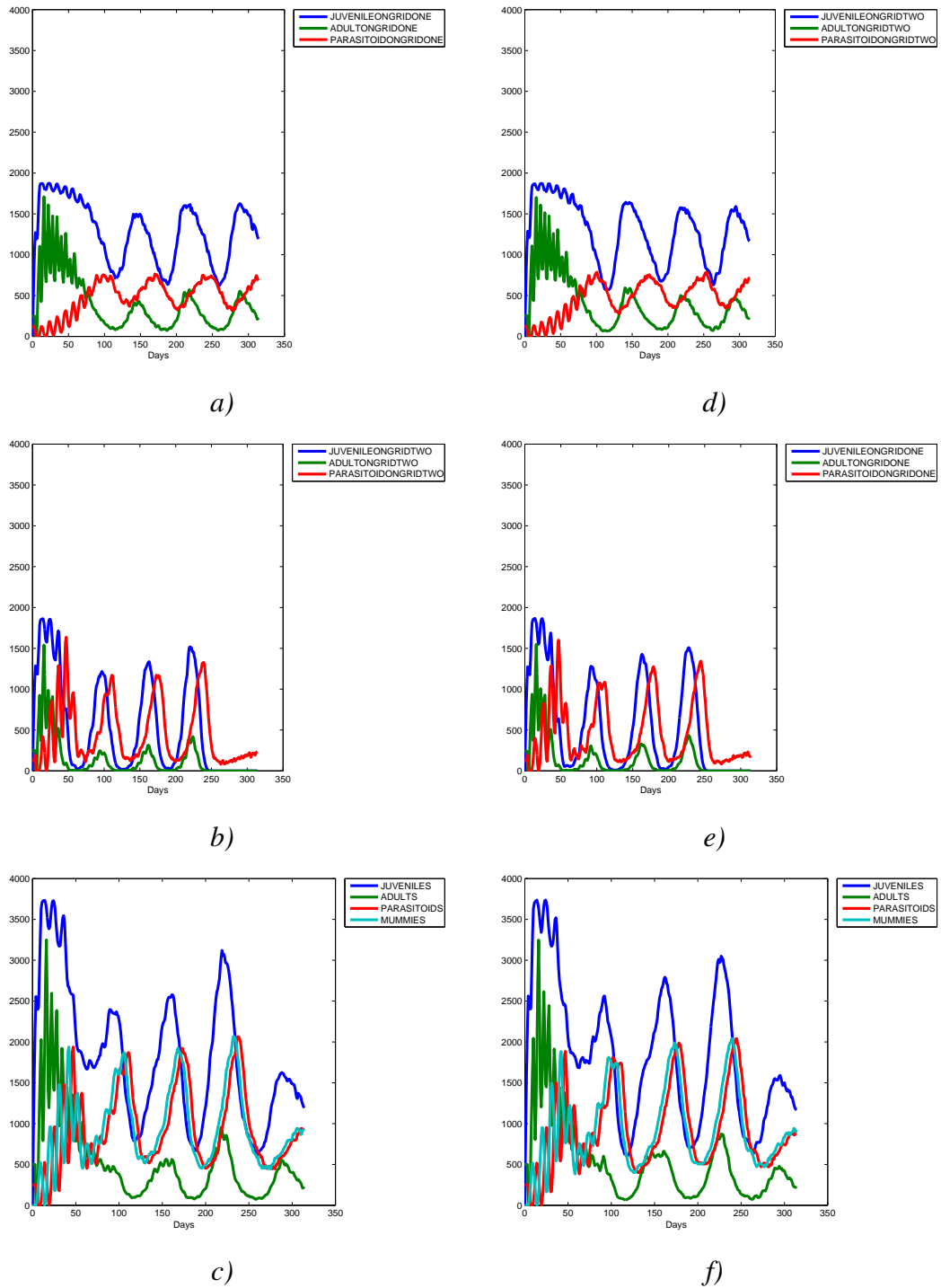
**Figure 6.35:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when parasitoids on the donor grid move to the recipient grid according to a giving up time. Giving up time is 8000 time-steps. See figure 6.34 for simulation conditions and a description of the individual plots.



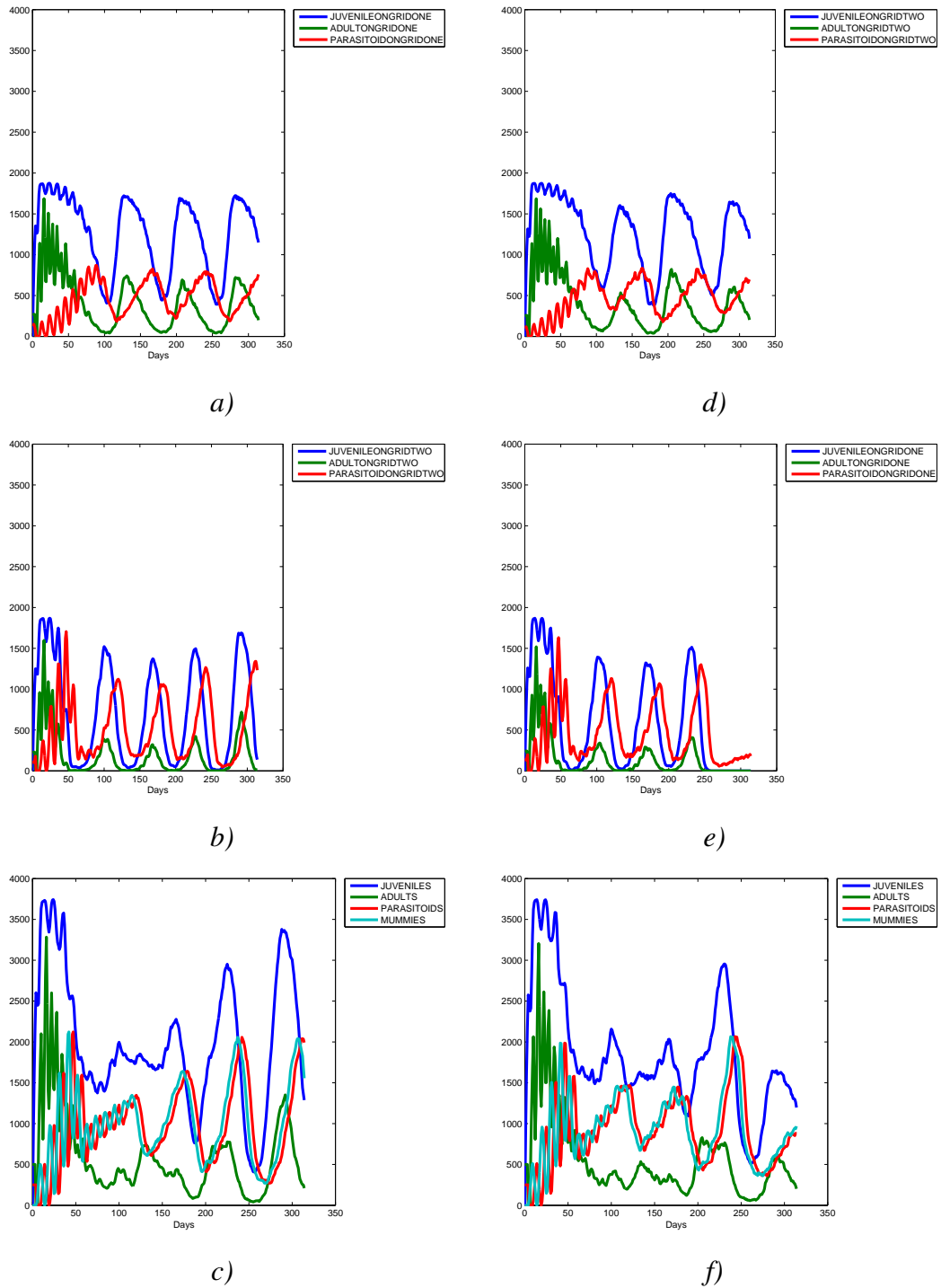
**Figure 6.36:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when parasitoids on the donor grid move to the recipient grid according to a giving up time. Giving up time is 10000 time-steps. See figure 6.34 for simulation conditions and a description of the individual plots.



**Figure 6.37:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when parasitoids on the donor grid move to the recipient grid according to a giving up time. Giving up time is 12000 time-steps. See figure 6.34 for simulation conditions and a description of the individual plots.

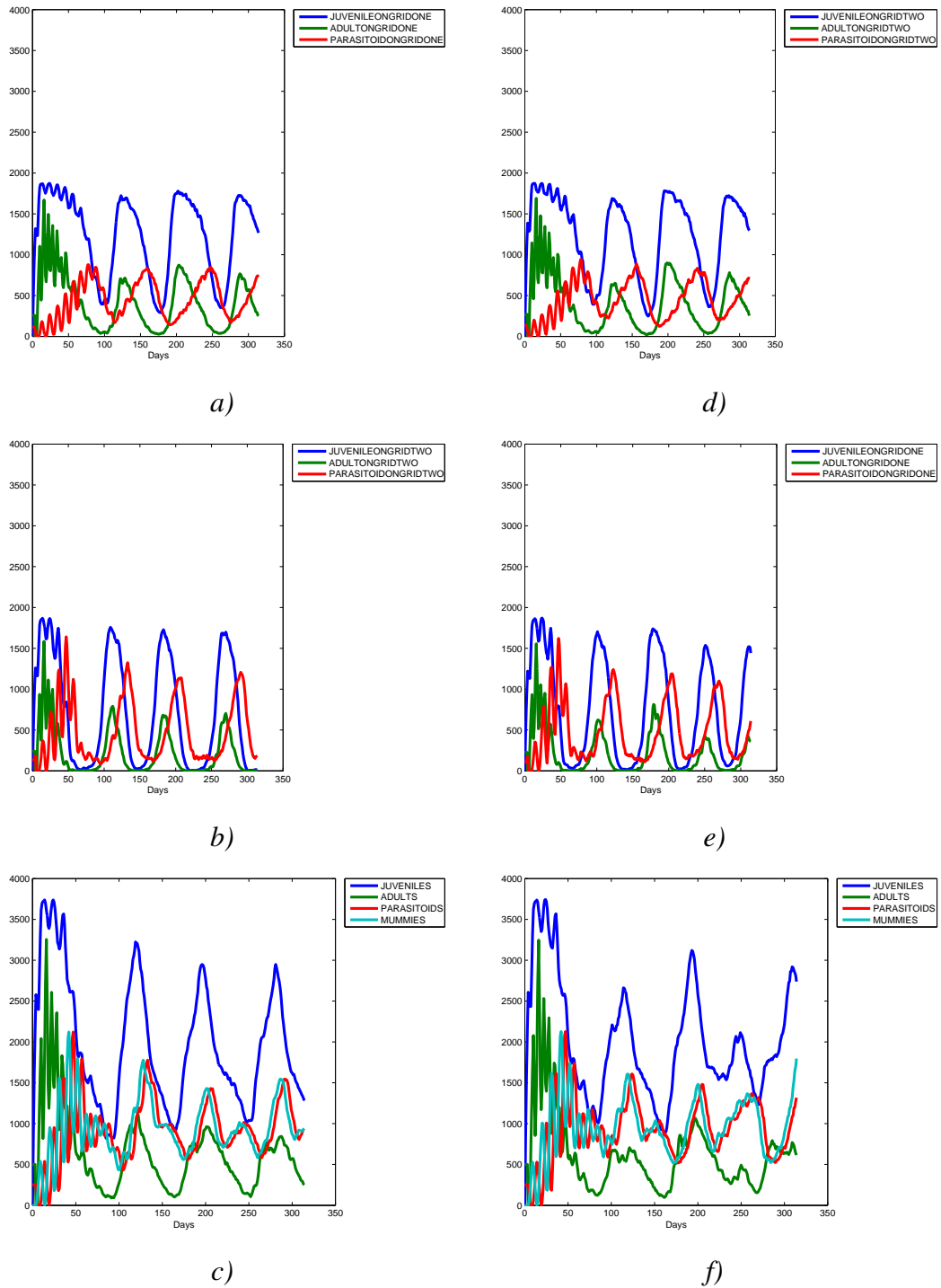


**Figure 6.38:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when parasitoids on the donor grid move to the recipient grid according to a giving up time. Giving up time is 15000 time-steps. See figure 6.34 for simulation conditions and a description of the individual plots.

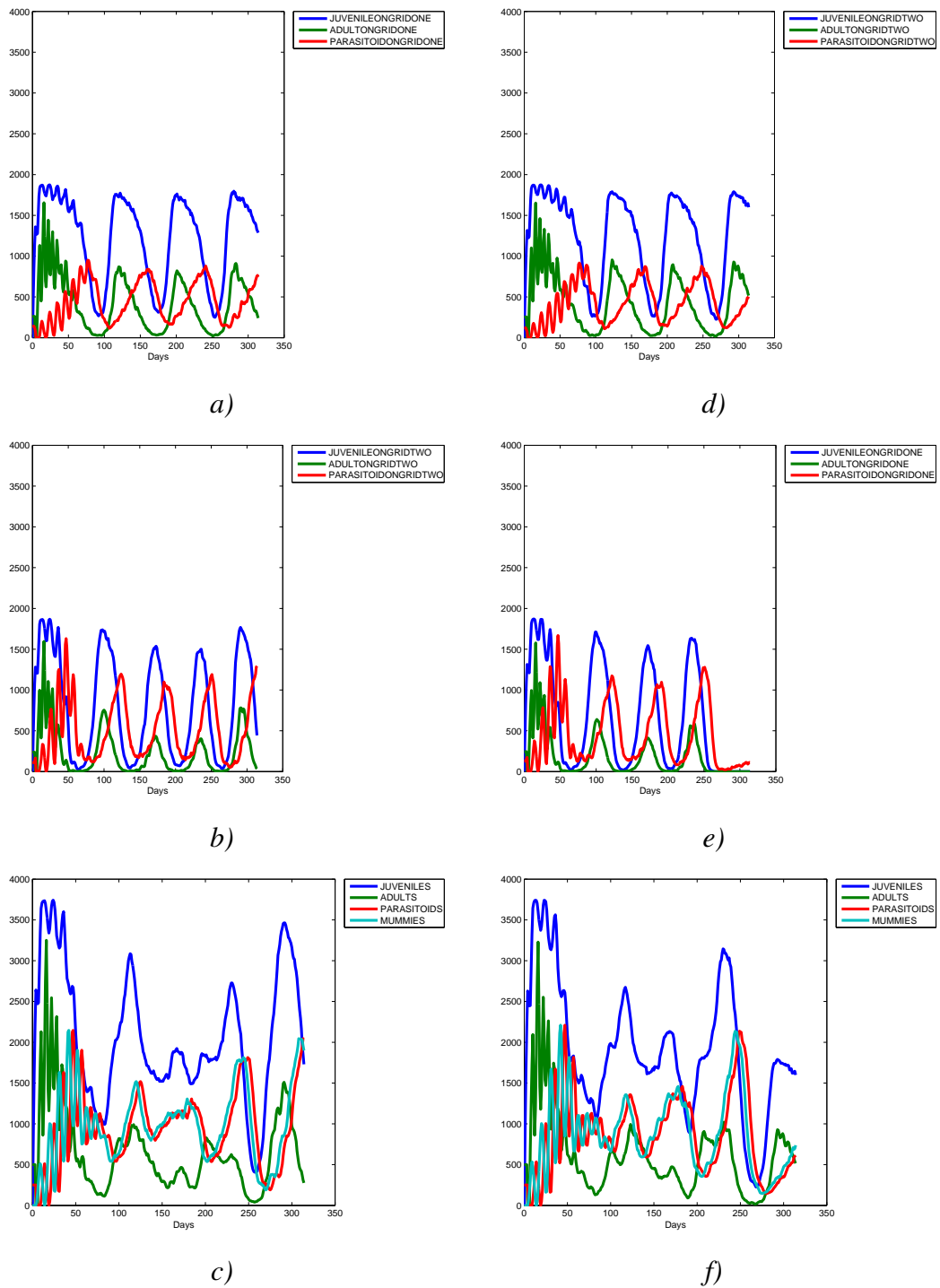


**Figure 6.39:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when parasitoids on the donor grid move to the recipient grid according to a giving up time. Giving up time is 17000 time-steps. See figure 6.34 for simulation conditions and a description of the individual plots.

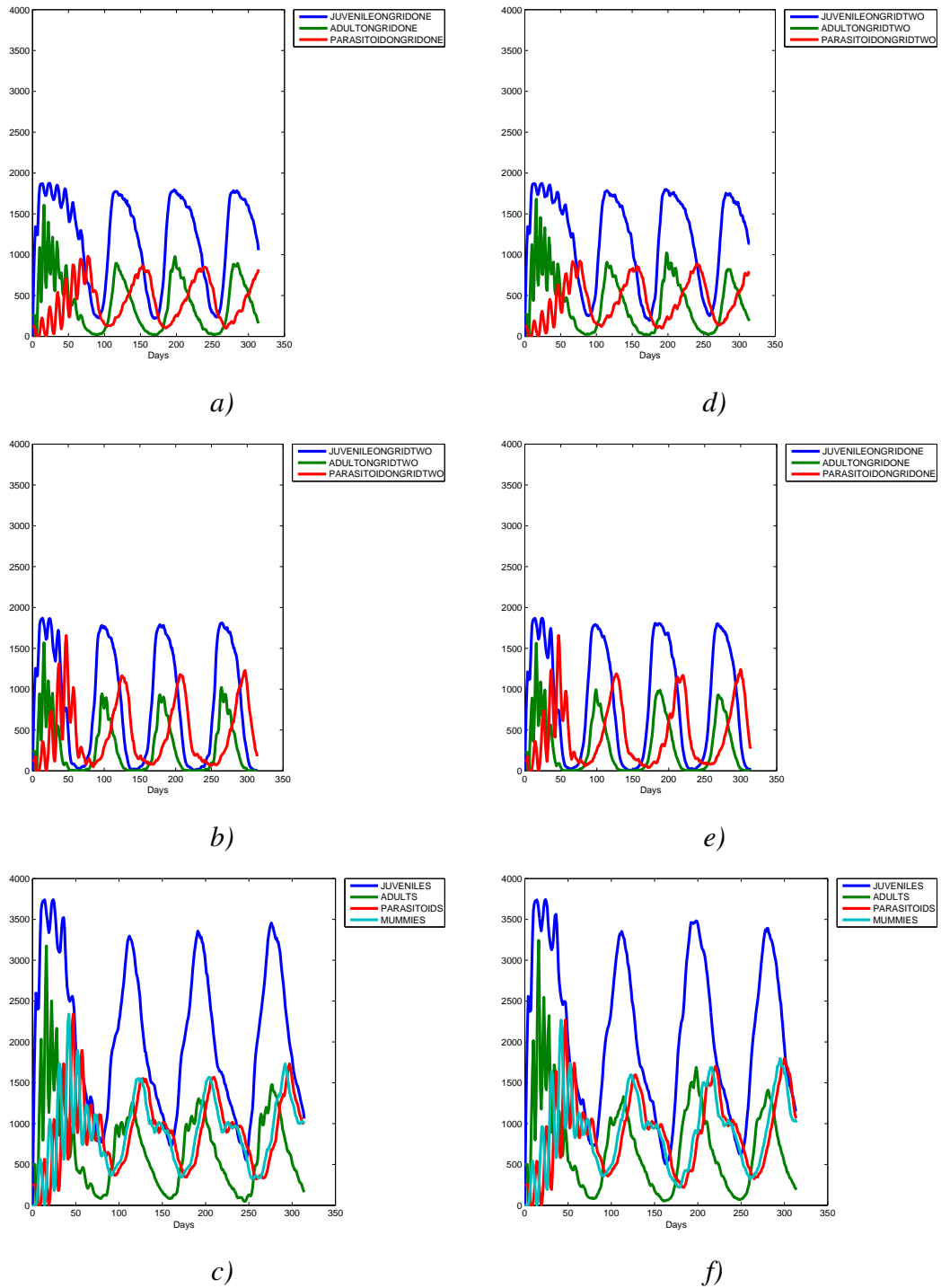




**Figure 6.40:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when parasitoids on the donor grid move to the recipient grid according to a giving up time. Giving up time is 18800 time-steps. See figure 6.34 for simulation conditions and a description of the individual plots.



**Figure 6.41:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when parasitoids on the donor grid move to the recipient grid according to a giving up time. Giving up time is 20000 time-steps. See figure 6.34 for simulation conditions and a description of the individual plots.



**Figure 6.42:** Plots illustrating the dynamics of aphid and parasitoid populations on two grids when parasitoids on the donor grid move to the recipient grid according to a giving up time. Giving up time is 22000 time-steps. See figure 6.34 for simulation conditions and a description of the individual plots.

A couple of interesting observations made in this chapter were 1) varying the same parameters in the aphid-parasitoid model with or without parasitoid and/or aphid ‘flyers’ generates similar dynamics qualitatively and 2) varying levels of juvenile predation or parasitoid migration between patches in one direction can give rise to irregular dynamics.

The first observation relates to when juvenile mortality, parasitoid diffusion and the probability of a parasitoid discovering an aphid were varied in the models with or without ‘flyers’ or without parasitoid ‘flyers.’ These models not only differed in the presence or absence of ‘flyers,’ but also in their assumptions regarding density dependence. Regardless, when the same parameter was varied, the general pattern of the system’s behaviour was very similar. This suggests that taking a reduced approach to modelling the aphid-host parasitoid system by taking away some of the model assumptions may be adequate for capturing the dynamics of the system. Furthermore, this approach would be more computationally efficient and therefore would give an idea of the behaviour of the system in response to changes in parameter values more quickly.

The second observation refers to the quasi-periodic dynamics generated when juvenile predation was modelled and when the level of directional migration in the parasitoid population was varied. The single grid aphid-host parasitoid model, with the exception of modelling juvenile predation, did not give rise to irregular dynamics. However, when multiple interacting patches were modelled and the levels of parasitoid migration were varied, irregular dynamics were more common.

In the model here migration between patches is asymmetric. This is in contrast to the majority of metapopulation models which represent migration between patches as symmetric Vuilleumier and Possingham (2006) (for eg. the work of Hastings (1993)

and Jansen (1995) which showed that dispersal between patches can have a stabilising influence on the system). The work of Goldwyn and Hastings (2009), however, does consider the impact of asymmetric dispersal on the dynamics of a two patch predator-prey system similarly to the work done here. Using a phase model, Goldwyn and Hastings (2009) examined the effect of low levels of asymmetric dispersal in the prey or predator on the phase dynamics of two coupled predator-prey oscillators (where migration in one direction is considered as strongly asymmetric). When the intrinsic dynamics of the patches are the same and there is significant asymmetrical coupling, there is a stable equilibrium where the dynamics of both patches are almost synchronous. In the case of one-directional migration, these dynamics are a result of the donor patch essentially forcing the recipient patch into phase with itself. Synchronous dynamics are associated with reduced system persistence in metapopulations (Goldwyn and Hastings, 2009, and references within) which suggests that strong asymmetric coupling may be destabilising. In comparison to the work here, Goldwyn and Hastings (2009) do not examine as high levels of migration. That said, it may be worthwhile to explore whether the synchronous dynamics observed here, particularly when there is aphid migration, are a result of asymmetric dispersal.

## Chapter 7

### Discussion and future work

Peak season for *M. euphorbiae* lasts for approximately 100 days (Karley et al., 2003). However, the model developed here was run beyond the duration of the peak season because the dynamics are of mathematical as well as biological interest. Though the model captures the dynamics of *M. euphorbiae* and *A. ervi*, it can also be applied more generally to other aphid-parasitoid systems and host-parasitoid systems that have overlapping generations.

The results as they are presented, i.e. for the extended duration, show that the aphid population in the absence of natural enemies grows logistically. The aphid population appears not to be that sensitive to changes in parameters (with the exception of juvenile mortality), tending to its carrying capacity for most of the parameter values explored here. Analysing aphid population dynamics in relation to the peak season (i.e. first 50 days in the model) reveals that the aphid population does not crash during this time-frame. This result may be plausible since the aphid model does not incorporate any decreasing intrinsic growth rate as a result of plant maturation or natural enemy component, factors that may be instrumental in the onset of the mid-summer population crash (Karley et al., 2004).

The addition of parasitoids to the system gives rise to a more diverse range of dynamics. Dynamics of models with and without ‘flyers’<sup>1</sup> and with only parasitoid ‘flyers’ were analysed. Like other host-parasitoid systems, predator-prey oscillations are characteristic of the different models. Other behaviour that emerges include stable dynamics, no coexistence and extinction. For the most part, the single patch/grid dynamics of the models developed here do not include more complex behaviour with the exception of when juveniles are killed off when their population surpasses a threshold so that only 300 juveniles remain. Introducing multiple patches and migration of individuals between patches does, however, generate more complex dynamics which in effect are a combination of the chaotic dynamics observed in Preedy et al. (2007) and the regular oscillations observed in Preedy (2006). In nearly all the results from the various aphid-parasitoid(s) models developed here there is also an initial period of transient dynamics which was also noted in the dynamics of the host-2-parasitoid-pathogen system modelled by Preedy et al. (2007).

Parasitoids in the model with ‘flyers’ were modelled with both a short and a long handling time. Shorter handling time resulted in ‘faster’ dynamics (at least initially) when compared to a longer handling time because parasitoids with a shorter handling time are more efficient and thus perpetuate the predator-prey oscillations faster. When parasitoid interference was implemented, the system with ‘flyers’ became more stabilised. In contrast to the model simulations with ‘flyers,’ in the aphid-parasitoid model simulations without parasitoid ‘flyers’ and without either aphid or parasitoid ‘flyers,’ the efficiency of parasitoids was always limited by a longer handling time and parasitoid interference.

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<sup>1</sup> Individuals taken off the grid temporarily to relieve local overcrowding.

Parameter variation conducted for the different aphid-parasitoid models (i.e. those with ‘flyers’ of both hosts and parasitoids and those without ‘flyers’ of either one or both hosts and parasitoids) indicated that the probability that a parasitoid discovers an aphid, adult mortality (particularly when parasitoids have a shorter handling time), juvenile mortality, length of parasitoid lifespan, probability of successful parasitism, patch area, juvenile predation, grid capacity of juveniles, parasitoid diffusion, level of parasitoid migration and giving up time are all sensitive parameters. Despite changing some of the assumptions in the aphid-parasitoid model with ‘flyers’ (and parasitoids characterised by a longer handling time) to generate the aphid-parasitoid model with only aphid ‘flyers’ and relaxing some of the assumptions in this model to generate the aphid-parasitoid model with no ‘flyers,’ each model generated similar temporal dynamics when the same parameter was varied. In particular, the probability of a parasitoid discovering an aphid in all three models which when increased generates more instability, parasitoid diffusion in the models without parasitoid and aphid and parasitoid ‘flyers’ and juvenile mortality in the models with ‘flyers’ and without aphid and parasitoid ‘flyers.’



The following table summarises the results and shows the behaviour that emerges from the model(s) when key parameters are varied.

**Table 7.1:** *Summary of results*

<b>Parameter</b>	<b>Effect of its increase</b>
juvenile mortality	stable/oscillatory dynamics that become more unstable
handling time	dynamics become 'slower'
juvenile predation	quasi-periodic dynamics that become oscillatory around an underlying steady state
success of parasitism	stable dynamics that become oscillatory
probability of aphid discovery	stable dynamics that become oscillatory and more unstable
parasitoid diffusion	oscillatory dynamics that become more unstable
parasitoid lifespan	'faster' dynamics/oscillatory dynamics that become more unstable
juvenile grid capacity	stable dynamics that become oscillatory
parasitoid migration	quasi-periodic behaviour, oscillations that become cycles within cycles
giving up time	stable dynamics that become oscillatory, quasi-periodic and oscillatory again
adult aphid lifespan	dynamics become more stable

Analysing the population dynamics of the aphid-parasitoid(s) system during the peak season reveals that similarly to other aphid/aphid-natural enemy models that describe pest species (for eg. Matis et al. (2008a, 2007); Karley et al. (2003)), initially the aphid population grows almost exponentially due to the aphids' high fecundity. Although, contrary to the predictions and observations from other theoretical and field studies (see chapter 2), this peak is not always followed by a complete crash during the peak

season period in the models developed here. For example, when parasitoids have a longer handling time, i.e. are less efficient, the aphid population does not crash during this timeframe for most parameter values explored here except when the system is stressed by increasing the probability of discovering an aphid in all the various aphid-parasitoid models and by increasing parasitoid diffusion in the aphid-parasitoid model without parasitoid ‘flyers.’ By contrast, for parasitoids with a shorter handling time, the aphid population does crash during the peak season period for most of the parameter values used here. This is most likely because the parasitoids with a shorter handling time are more efficient and therefore can drive the aphid population to a trough quicker than parasitoids with a longer handling time. The aphid population crashes with parasitoids with a longer handling time when the probability of discovering an aphid is increased and when parasitoid diffusion is increased (in the system without parasitoid ‘flyers’) because the parasitoids become more efficient at finding aphids. In the system without parasitoid and aphid ‘flyers,’ increasing parasitoid diffusion does not induce a crash during peak season probably because there are no aphid ‘flyers’ and aphids are therefore less evenly distributed across the grid making speed less of an advantage to the forager. This result highlights the importance of spatial considerations when trying to understand and capture the dynamics of host-parasitoid systems and demonstrates how modelling space explicitly can affect the temporal dynamics of the system.

The period of time between the aphid population peak and aphid population crash for most of the results where the aphid population does crash within 100 days was 52 or 54 days. This is far greater than what has been observed in the field, i.e.  $\leq 10$  days (Karley et al., 2003) which may be plausible since parasitoids have not been shown to be the only cause of the mid-summer crash and other factors such as predation, disease and changes in plant quality may also be contributing factors (correspondence with Dr. A. Karley). However, increasing the probability of a parasitoid discovering an aphid can reduce the duration of this period by about half, and when the system is really

stressed and parasitoids have a shorter handling time to 14 days. In the results where the aphid population does crash within 100 days, varying the probability of discovering an aphid parameter also leads to greater deviation from baseline values of the duration of the period between the population peak and crash. The duration of the period from the aphid population peak to its crash differs significantly from baseline values when parasitoid discovery is changed probably because natural enemy pressure is one of the main factors that induces the population crash and therefore varying the degree of parasitoid pressure on aphids by varying the probability of discovery should change how quickly the aphid population declines.

There is a lot of scope for developing the model described here, both mathematically and biologically. To extend the work here mathematically, this system could be modelled using an alternative spatially explicit approach such as integrodifference equations and the spatio-temporal dynamics of both approaches could be compared. The framework for the alternative model would comprise a system of integrodifference equations for a host-parasitoid interaction posed on a 2-D domain, similar to that shown in the equations given by 7.1 where  $M_{t+1}(x, y)$  and  $Q_{t+1}(x, y)$  represent the density of hosts and parasitoids, respectively at point  $(x, y)$  at time  $t + 1$ .

$$M_{t+1}(x, y) = \frac{c^2}{2\pi} \int_{\Omega} \int_{\Omega} e^{-c((x-u)^2+(y-v)^2)} M_t(u, v) \exp\left(r \left(1 - \frac{M_t(u, v)}{K}\right) - \alpha Q_t(u, v)\right) dudv \quad (7.1)$$

$$Q_{t+1}(x, y) = \frac{c^2}{2\pi} \int_{\Omega} \int_{\Omega} e^{-c((x-u)^2+(y-v)^2)} \cdot e M_t(u, v) (1 - \exp(-\alpha Q_t(u, v))) dudv$$

with spatial domain  $\Omega_2 = (-L, L) \times (-L, L)$ .

In the system of equations in 7.1,  $c$  represents the dispersal constant of the host and parasitoid,  $r$  represents the growth rate of the host,  $K$  is the carrying capacity of the host,  $\alpha$  is the rate at which hosts are parasitised,  $a$  is the parasitoid's searching efficiency,  $e$  is the conversion efficiency of hosts to parasitoids and  $(u, v)$  represents a point on the domain. As the host in the individual-based model has overlapping generations, the model given by the equations in 7.1 would need to be modified as the integrodifference approach describes a system with non-overlapping generations. Future work would include exploring ways to modify this approach to capture overlapping generations.

Another possibility of expanding the work done here would be to model an aphid-parasitoid system with both aphid and parasitoid migration between two non-adjacent patches. Although the results here indicated that aphid migration between patches has little effect on the qualitative behaviour of the system, it may be interesting to explore the combined effect of aphid and parasitoid migration on the population dynamics. Also, in the simulations conducted here, migration was only modelled in one direction. It may be interesting to explore migration between patches in both directions and additionally make one patch a source and the other a sink.

Spatio-temporal heterogeneity has been observed in other host-parasitoid models (Preedy et al., 2007; Pearce et al., 2006; Schofield et al., 2005a). However, the spatial dynamics of the system described here were not fully explored and future work will include exploring the spatial aspect of the model more and possibly conditions in the model that do generate spatio-temporal heterogeneity.

In terms of developing the model biologically, a time-dependent fecundity parameter could be incorporated into the model to represent changes in aphid performance as plants mature over the peak season. Currently the model does not represent the effect

of changes in plant quality on aphid population dynamics, a factor which has been implicated in the aphid population crash. Karley et al. (2003) mentions that though aphid populations can crash without experiencing any changes in fecundity, under these circumstances the aphid population would crash much later than field populations. This may account for why the aphid population in this model takes much longer to crash than what has been observed in the field. Costamagna et al. (2007) also demonstrates the important role that changing plant quality has in triggering a decline in aphid numbers by successfully fitting an exponential model with decreasing intrinsic growth rate to soybean aphid data using degree days. The model does not account for natural enemy pressure, but does suggest that temperature and changes in plant quality can cause a decline in aphid populations. However, it is not clear from the model whether the soybean aphid populations can crash in the absence of natural enemies because the data fitted, while demonstrating an increase followed by a decrease in aphid numbers, does not indicate a complete population crash. The information above suggests that more than one factor may be involved in triggering the mid-summer population crash and this is worth exploring in future work.

Another possibility for extending the model described here is by introducing aphid morphology, i.e. flyers and nonflyers into the model in order to evaluate the importance of each type of dispersal and to see how varying the percentage of the population that are flyers and do fly affects the dynamics, particularly the spatial dynamics of the system. As the model stands now, the foraging behaviour of parasitoids is quite simple, although it might be interesting to make their foraging behaviour more complex by introducing a type II functional response or chemotaxis.

In the model with 'flyers' newly emerged parasitoids are given a random location to settle (analogous to flight) and if the grid point that they are assigned is full, then they are immediately killed. This is not how older parasitoids are treated when the grid point that they move to by random diffusion is full. These parasitoids are given two

more opportunities to locate a grid point that is not at capacity anywhere on the grid, and if unsuccessful, are taken off the grid and given two more opportunities in each subsequent time-step until they succeed. This inconsistent treatment of newly emerged and older parasitoids is not biologically justified, however, it probably will not result in significantly different dynamics from a model that does treat newly emerged and older parasitoids that happen upon a grid point at capacity similarly. As part of extending the work done here, the model with ‘flyers’ could be rerun with newly emerged and older parasitoids having more consistent habitat location rules to verify what is already suspected about the behaviour of the model.

The results from the models suggest parasitoids are not the sole cause of the mid-summer population crash in agreement with Karley et al. (2004) who suggest that more likely a combination of factors are involved in the population crash. Nevertheless the output from the model shows that pressure from natural enemies such as parasitoids can significantly depreciate aphid numbers and can lead the aphid population to crash, although this tends to take much longer than what has been observed in the field. This suggests that the models developed here are able to capture some of the processes and dynamic changes that occur during peak season. Looking beyond the dynamics of peak season, the models here gave rise to a range of dynamics and modelling juvenile aphid predation and multiple patches connected by parasitoid migration gave rise to more complex dynamics. There has been little theoretical study of the mid-summer population crash and spatial dynamics of aphid/aphid-natural enemy systems and much of this work fails to take into account spatial heterogeneity. The work produced here does touch on these areas, but further exploration is required to broaden our understanding of the mechanisms involved in the onset of the mid-season crash and the spatial dynamics of these types of systems. This work also develops upon previous host-parasitoid models, marrying the approaches of Pearce et al. (2006) and Schofield et al. (2002) by taking a continuous approach similar to Pearce et al. (2006)

where the host has overlapping generations and combining this with the approach of discretising PDES to derive movement probabilities for individuals used by Schofield et al. (2002), the product of which is a continuous time individual-based model. This is a novel approach to modelling host-parasitoid systems and the work here illustrates the type of dynamics that can emerge from this type of system.

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# Glossary

**alate** winged.

**apterous** wingless.

**biological control** a method of pest control that uses natural enemies of pest species to limit their population growth.

**generation cycles** cycles with periodicity of one generation.

**generation time** period of time that lapses in an individual's lifetime before it starts producing offspring.

**giving up time** an arbitrary period of time that governs when a parasitoid wasp moves to another patch based on its time since last oviposition.

**handling time** time required for a parasitoid/predator to handle a host/prey individual.

**instar** refers to the different stages of juvenile development (aphids have four in total).

**larvae** used to describe the offspring of parasitoids.

**mummy** the carcass of the parasitised aphid in which the parasitoid larva pupates before becoming an adult.

**nymphs** juvenile aphids.

**oviposition** the process of egg-laying in parasitoid wasps whereby the parasitoid uses its ovipositor, a structure on the lower part of its abdomen, to sting the host and transport eggs into the host.

**parasitoid interference** competition between parasitoids that impairs their foraging success.

**parthenogenesis** a form of asexual reproduction.

**peak season** is primarily comprised of the summer months when parthenogenetic females are at high densities on secondary host plants.