

Coccinellid Predation on *Aphis helianthi*:
Diffusive Instability and Pattern Formation In Predator-Prey Systems

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On my honor, I have neither given nor received unauthorized aid on this thesis.

Table of Contents

Acknowledgments	v
Abstract	1
Introduction	2
Space in Ecology	2
Effects of Spatial Processes	5
Pattern Formation by Diffusion-driven Instabilities	6
Two Attractor Systems and Bimodality	12
Natural History of the System	14
Methods	19
Model Development	19
Model Structure	23
Parametrization	31
Results	36
Model Outputs	36
Statistical Signatures	38
Discussion	42
Space in our System	43
Ladybug Distribution and Diffusive Instability	45
Development of two attractors, one repellor, and bimodality	47
Bidirectionally causality and Implications for Equilibria	49

Conclusions	53
Continuing Work	53
Addendum	55
Figure Legends	57
Works Cited	62
Tables	65
Table 1: Parameter ID and values	65
Table 2: regression statistics for figures	66
Figures	68
Figure 1.1	68
Figure 1.2	68
Figure 1.3	69
Figure 2.1	69
Figure 2.2	69
Figure 3	70
Figure 4	70
Figure 5	71
Figure 6	71
Figure 7	72
Figure 8	72
Figure 9.1	73
Figure 9.2	73

Figure 9.3	74
Figure 10	74
Figure 11	75
Figure 12	75
Figure 13.1	76
Figure 13.2	76
Figure 14	77
Figure 15	77
Figure 16	78
Figure 17	78
Figure 18	79
Figure 19	79
Figure 20	80

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Abstract

*Spatial context in predator-prey systems has proven to have important dynamical consequences. Instabilities and spatial pattern formation driven by diffusion (Turing pattern formation) have been extensively observed and theorized on, but empirical examples of Turing pattern formation in ecological systems are few. In this study we construct and analyze a reaction-diffusion equation model of the aphid species *Aphis helianthi* under predation by two species of ladybugs: *Coccinella septempunctata* and *Hippodamia convergens*. The structure and parametrization of the model is entirely field derived and in analysis of model output it is compared extensively to field observations.*

This system fits the well known framework for diffusive instability and pattern formation: an activator-inhibitor system in which the inhibitor (predator) diffuses substantially faster than the activator (prey). Theory predicts that under these conditions the inhibitor will fail to strike a normal equilibrium with the activator; rather diffusing away from activator outbreaks too quickly to contain them, subsequently over-inhibiting the surrounding lower densities of activator (undermatching). This usually results in a patchy, bimodal distribution of prey resulting from cubic density dependence driven by undermatching.

Aphid population distribution in the field is clearly bimodal and patchy. We looked for several indications of diffusive instability in field data; bimodality, cubic density dependence, and undermatching were all found. The focus of this paper is on a mathematical model we developed from field data to gain insight into the workings of the system. I found the model matched field data very well and corroborated the hypothesized functioning of a diffusive instability.

I explored the role of self attraction (aggregation) among ladybugs. Aggregation is not considered a hallmark of diffusive instability but in this case it created some preytaxis in ladybugs (allowing aphids to act as an activator). Preataxis by aggregation is slow though, which allowed some aphid populations to avoid detection long enough to reach the high attractor of cubic density dependence.

Finally I considered the nature of space in our system. Although our model is constructed in Euclidean space it demonstrates some features of a network. Network structured systems manifest Turing patterns primarily as bimodal distributions. They also facilitate understanding of ladybug behavior and may increase efficiency of computer model execution.

Introduction

Space in Ecology

For at least 60 years there has been discussion of the implications of spatial distribution of species within their habitats. Accompanying this discussion there have been both theoretical and empirical mathematical analyses of these distributions and the factors creating them (see Skellam, 1951 for discussion of theoretical population dispersal by random-walk). Indeed, over a century ago Clement Reid (1899) observed the post-ice age dispersal of oaks in England and considered methods of accelerated diffusion (compared with the slow dispersal one might expect for oaks without outside interference). Although Skellam did make the mathematical simplification of reducing space to one dimension (to ease the analysis of random-walk dispersal) these early considerations of space remained largely within the conceptual realm of space as a

continuous medium. While continuous space makes sense conceptually (it is the way we experience it daily) it is certainly not the only, nor always the most useful way to conceptualize space mathematically.

As spatial considerations made inroads to more strictly ecological considerations, new conceptions of space were introduced. One such consideration was interspecific competition and coexistence, which Levins & Culver (1971) found to be explicable using a metapopulation model. Considering space as islands, or patches, of similar habitat, without considering continuous space or specific coordinates, simply the discrete nature of patches, and thus the ability to describe individual species in terms of multiple populations, allowed the prediction of coexistence. This explanation was useful where non-spatial explanations failed to explain coexistence, rather predicting competitive exclusion due to excessive niche overlap. This approach is easily applicable to any parasitic species, in which case the 'islands' represent hosts. Instead of considering density or specific movements of individuals, these models tend to consider local extinction and colonization rates (i.e. for each patch) by different species. See also Horn & MacArthur (1972) and Cohen (1970) for further examples of coexistence in island/patchy habitats.

In his 1990 review Kareiva outlines three characterizations of space used in ecological models: continuous, island (as described above) and what he calls "stepping-stone" models in reference to the presence of patches which populations explicitly 'step' between. These models have patches with explicit spatial locations in some coordinate system, between which at least some of the species being modeled are able to redistribute. In some ways this method combines the characteristics of an island model

and a continuous space model, creating discrete populations within a metapopulation while re-introducing explicit distances and redistribution. Fujita (1983) describes how a plant-prey-predator system, which would be unstable as one patch, may persist in a stepping-stone model, allowing a relatively weak but fast prey with an unstable food source to survive by continuously colonizing new patches, eventually returning to patches where they had previously been driven extinct (allowing host plant recovery and abandonment by predators). Simply put, while individual populations may be driven extinct, the metapopulation survives.

Another conception of space, perhaps more common in infrastructure design but also emerging in ecology, is network space. In continuous and stepping-stone space, explicit spatial dimensions implicitly emphasize the importance of proximity; we call this laterally connected space. Due to the tendency of many effects (i.e. diffusion, attraction) to decay or dissipate with distance, we would expect locations/patches that are closer together to have more influence on each other than a pair that are further apart. Often this is the case; if your neighbor sprays pesticide on his yard on a windy day it is much more likely to affect your yard than if a yard five miles away is sprayed with pesticide. There are exceptions however; delayed flights from the Chicago airport are much more likely to affect travelers in New York City than commuters coming in on trains from the suburbs of Chicago. In network space the level of connection between locations (or 'nodes') depends more on the number and strength of the pathways between them than on physical distance. Strong connections between nodes outweigh the effects of proximity (in euclidean space) of a weakly connected node. Little ecological analysis has been

performed from the perspective of network space, with the notable exception of studies of ants (i.e. Millonas, 1992).

Effects of Spatial Processes

It has long been recognized that a heterogeneous habitat, with a diversity of niche spaces, will lead to greater species diversity than a homogeneous habitat (easily explained by non-spatial population ecology theory). However, most metapopulation models consider patches of *similar* habitat and predict higher species richness than would be expected in a single patch of that habitat type (Levins & Culver 1971, Cohen 1970). Such findings suggest that spatial processes allow for more diversity in an *homogeneous* environment than conventional ecological theory would suggest. Levin (1974) observes that a patchy, and thus more species-rich, distribution may develop on a single “initially homogeneous environment due to what may be random initial events (e.g., colonization patterns)” (pp. 223) that cause the environment to become heterogeneous.

While non-spatial models can easily be used to describe reproduction and predation among populations, the simple element of dispersal, which sparked Reid’s (1899) interest, is clearly spatial. Any decent spatial model should consider both dispersal and reproduction and/or predation. Reaction-diffusion equations are powerful tools that allow the inclusion of all of these elements; see Murray (2003) for an in-depth explanation of reaction-diffusion theory. Here ‘reaction’ may refer to interspecies interactions (i.e. predator-prey) (Turchin, et. al., 1998) and/or to local population growth (Kareiva, 1990), while ‘diffusion’ refers to dispersal of one or more of the involved species.

The potential for reaction-diffusion equations to create patterns has long been recognized in biology (see Meinhardt & Klingler, 1987, for a reaction-diffusion explanation of pattern formation on mollusk shells). As reaction-diffusion equations saw increasing use in theoretical ecology, it became evident that there too they created patterns, in this case in the distribution of populations on *homogeneous* environments (Holmes, et. al., 1994). Contrary to conventional wisdom, when local interactions (i.e. reproduction, predation) were considered in space with diffusion, it appeared that *diffusion* drove instabilities that created spatial patterns (see Levin & Segel, 1976, for an early example in theoretical ecology). These diffusion-driven instabilities were first described by Turing (1952) in an explanation of morphogenesis and are thus called Turing instabilities, and the resulting patterns ‘Turing patterns.’ Normally we would expect diffusion to be a homogenizing influence, rather than a destabilizing one, which is why these results are so remarkable, again pointing to the significance of spatial processes.

Pattern Formation by Diffusion-driven Instabilities

Diffusion Driven Instabilities

The processes by which diffusion creates these counter-intuitive instabilities and spatial patterns have been well studied and condensed into a set of conditions for pattern formation in a number of reviews (Holmes, et. al., 1994; Turchin, et. al., 1998; Kareiva, 1990). A predator-prey system should fit an activator-inhibitor framework, as most do. Prey tend to activate, or promote the growth rate of both prey (through reproduction) and predators (predators require prey to survive and reproduce). In non-spatial classical (i.e.

Lotka-Volterra) predator-prey models, the predators and prey should come to a stable equilibrium where an increase in prey will be reduced by a parallel increase in predators, and an increase in predators will be reduced by self limitation. If the same local interactions are placed in a spatial setting and predators diffuse sufficiently faster than prey, predators will tend to diffuse away from where they 'should' be (i.e. local peaks in prey density). Diffusion limits the ability of predators to create the equilibrium which would be expected in the absence of diffusion. This allows local peaks in prey density to actually increase further in density, while surrounding lower-density areas are subjected to a disproportionately large predation pressure (as predators diffuse into these areas from nearby peaks), further suppressing prey density.

Ideal Free Distribution

To clarify the process, diffusion-driven instability can be contrasted with the condition that non-spatial models implicitly assume: ideal free distribution (IFD). IFD was described formally by Fretwell & Lucas (1970) in regards to birds self-distributing among patches of habitat, but the principle is equally well applied to predators distributing among patches of prey. Essentially a set of habitat patches are assumed to have different levels of suitability to a species; it is assumed that increasing density of that species within a patch always *decreases* its suitability due to competition (ignoring the Allee effect, that at very low population densities increasing density increases likelihood of reproductive success). It is further assumed that: a) all individuals do (and are free to) settle in the habitat most suitable to them and b) all individuals within one habitat experience the same suitability (defined as expected success rate). Given these

assumptions individuals should self-distribute in a manner such that they all experience the same suitability of habitat. If any individual experiences less 'suitability' than it would elsewhere, it will move elsewhere (under these assumptions); this will simultaneously increase average suitability of the patch it left (due to decreased density) and decrease the average suitability of the patch it arrives in (due to increased density). This process will continue until an equilibrium is reached in which the average suitability of every patch is equal (as balanced by its intrinsic suitability against density of individuals). In the case of a predator distributing among patches of prey, without considering its reproduction (as the model described in this paper is constructed to do), suitability is defined as marginal rate of prey intake by each predator. So an ideally free distributed predator population would self-distribute solely based on individual decision-making in such a way that each individual experiences the same marginal rate of prey intake (I will call this patch 'payoff').

In this situation a predator would be distributed with an equal ratio of predator to prey in all patches, assuming a flat functional response (intake prey at the same rate regardless of prey density). However, very few predators have a flat functional response; most increase intake rate with increasing prey density, so one would expect an even higher ratio of predators to prey in areas of high prey density and a lower ratio in areas of low prey density (thus competition in the prey-rich areas would decrease intake rate to a level equal to that obtained by predators in prey-poor patches; the assumptions of IFD dictate that self-distributing predators would find the distribution at which these intake rates are equal). Here another implicit assumption of IFD, proven necessary to achieve

IFD by Cressman & Krivan (2006), is that individuals never move to a patch with lower payoff (given that individuals *always* choose the patch with the highest payoff).

Even on relatively small spatial scales, there are obvious problems with the assumptions of IFD. For individuals to be ‘ideal’ (i.e. choose the most suitable patch of habitat) they must have perfect knowledge of the available patches of habitat at all times. To distribute freely, movement between and entrance into patches of habitat must be ‘free’ (come at no cost to the individual). Due to social or physical limitations, entrance to a patch already dense with predators may not be ‘free’ to an individual, and movement between patches requires an amount of energy which increases with distance. Finally, to meet the condition set forth by Cressman & Krivan (2006), all movements would have to be based on informed decisions by the individual, and never on simple diffusion. A diffusing predator could nonetheless closely approximate IFD if its preytaxis (or tendency of predators to move towards areas of higher prey density) was sufficiently large to counteract diffusive movement.

Preytaxis is the reason the predator must diffuse “sufficiently” faster than the prey diffuse for pattern formation to take place. Mathematically this may be defined: if D_{inh} and D_{act} are the diffusion constants of the inhibitor (predator) and activator (prey) respectively, then diffusive instabilities will appear when D_{inh}/D_{act} exceeds a threshold (Nakao & Mikhailov, 2010). The threshold depends, in part, on the level of preytaxis demonstrated by the predator. The overall rate of diffusion by predators must exceed that of the prey *and* at least counteract the effect of preytaxis. Meeting these conditions, a predator will diffuse away from local peaks in activator (prey) density into surrounding areas of relatively low activator density. In this circumstance diffusion reduces per capita

predation pressure in areas of high prey density and increases it in areas of low prey density. The resulting distribution is called undermatching of resources (Jackson, et. al., 2004; Krivan, 2008) because high payoff patches are underutilized.

Undermatching is the link between diffusion and instability; it results from diffusion and creates instabilities. In summary, under IFD predators should distribute so as to obtain equal payoff in all patches, but due to random movements of individuals they tend to diffuse away from patches of high payoff and end up in surrounding patches of lower payoff. This leads to an inverse proportion between predator-to-prey ratio and prey abundance; increasing prey abundance decreases predation risk. In other words prey experience safety in numbers, consistent with Turchin & Kareiva (1989) who found that aphids aggregate to reduce risk of predation. This introduces instability because rather than reach one stable equilibrium per Lotka-Volterra dynamics, patches of high prey density are subject to lower than IFD predation pressure and will grow, while low prey density patches experience higher than IFD predation pressure and will be reduced (high prey populations grow and low prey populations are reduced!) (Turchin, et. al., 1998).

Additional Conditions and Considerations

Although as mentioned above preytaxis tends to inhibit diffusive instabilities, it is important to note that it also plays a role in creating them. In systems where predator reproduction is slow relative to that of prey (such as the aphid-ladybug system I will consider in this paper) individual movements are the primary influence on predator distribution; in this case preytaxis is the primary way in which the activator (prey) can activate the inhibitor (predator), one of the necessary conditions for diffusive instabilities.

Kareiva & Odell (1987) describe at length a similar aphid-ladybug system in which they find ladybugs demonstrate preytaxis by using area-restricted search, essentially slowing down when they encounter prey but moving further/more frequently when not encountering prey.

Although the condition usually stated for diffusive instability is the *minimum* diffusion rate of the inhibitor, as might be expected for dynamics in any model, there is a range of parameter values for which the dynamic holds true. That is to say, there is an upper bound to diffusion as well. Turchin (1989) conducted an analysis on aggregating populations in which he found that varying the diffusion rate yielded a range of values that yield two stable equilibrium densities, while above or below that range of values only one stable equilibrium was obtained.

Types of Patterns

The resulting spatial patterns in continuous space tend to be either regular ridges and troughs of prey and predator density or a checkerboard of peaks and (round) valleys (Holmes, et. al., 1994). Most theoretical and empirical studies of diffusive instability look at either continuous space or regularly structured patches in euclidean space (Mimura & Murray, 1978; Comins & Hassel, 1996; Maron & Harrison, 1997) and look for characteristic activator-rich patches with sharp boundaries (Turchin, et. al., 1998). Othmer & Scriven (1971) showed that Turing instability and pattern formation should be applicable to network-organized systems. Since then a small body of work has been produced on Turing instabilities in network space, but mostly in small, regularly structured networks in chemical or cellular systems (Othmer & Scriven, 1974;

Horsthemke, et. al., 2004). Despite the obvious applicability of network space to many ecological settings (see Hanski, 1998, for a metapopulation example), little work has been done with Turing instabilities in ecological networks. Recently Nakao & Mikhailov (2010) studied Turing pattern formation in large random networks, including an adaptation of a predator-prey model with diffusion-driven instabilities from Mimura & Murray (1978). In a non-euclidean network space the idea of a regularly shaped pattern loses meaning, but in their study Nakao & Mikhailov (2010) observed that Turing instabilities in networks lead to “spontaneous differentiation of the network nodes into activator-rich and activator-low groups” (p. 1).

Two Attractor Systems and Bimodality

While most analyses of Turing patterns in euclidean space focus on the spatial structure of the pattern, the structure they describe and the nature of diffusive instability imply the same phenomenon observed in network-organized systems by Nakao & Mikhailov (2010): a bi-modal distribution of patch/node population sizes. Turchin, et. al. (1998) observe that activator-rich patches should grow to the carrying capacity of the prey (due to ineffective predation levels), while activator-poor patches should be driven to a “very low level” (due to higher than IFD predation).

While diffusive instability removes the conventional Lotka-Volterra equilibrium from a model, it certainly does not do away with equilibria altogether. If that were the case, and large populations continued to grow while small populations continued to be reduced, the implications would be unrealistic; small populations would disappear and large ones would grow to infinity. While it is possible for small populations to disappear,

it is unlikely in a system of many patches/nodes with some level of prey diffusion (i.e. colonization). Indefinite growth of the high populations is obviously impossible. Rather than this unlikely scenario, the system will usually bifurcate into a two-attractor, repellor structure. Fig 1.1 shows a very simple linear density dependence¹ such as might be expected for a population with no predation and a carrying capacity. Fig 1.2 shows a likely cubic density dependence resulting from a diffusive instability; a low attractor (the low prey populations with excessive predation), a high attractor (high prey populations with minimal predation reaching carrying capacity), and a repellor in the middle (below which we expect populations to be driven down to the low attractor, and above which we expect populations to “escape” to the high attractor). Figure 1.3 shows how cubic density dependence is derived from the factors operating in the field. The red line is a linear density dependence (i.e. density dependence without predation). The blue line shows per capita predation rate on prey for an undermatching predator with a type II functional response. The green line is the difference between these two curves; predation rate is subtracted from growth rate to give a net growth rate, the result is cubic. We would expect this structure to lead to a bimodal population distribution with a distribution of populations around each attractor. In the absence of distinct environmental heterogeneity, we would expect most populations to be normally distributed, so in homogeneous environments, bimodal distributions are a strong sign that a diffusive instability is operating.

Such a population distribution is observed in the annual outbreaks of *Aphis helianthi* on *Yucca glauca* in the high plains of Colorado. Several hallmarks of Turing

¹ If the reader is not familiar with density dependence graphs please see addendum A1.

pattern formation are present in the this example. The predators of *A. helianthi*, two species of ladybugs (*Coccinella septempunctata* and *Hippodamia convergens*), are much more mobile than the aphids (i.e. have a higher diffusion rate), while rapid population growth of aphids combined with relatively random colonization of plants readily creates the random initial perturbations needed to activate the mechanisms of diffusive instability. The resulting distribution of aphid populations within a yucca field under ladybug predation is far from normal. Natural ecological systems rarely exhibit theoretically predicted characteristics with great accuracy, in part because of the array of factors operating that cannot all be considered simultaneously in theory, and in part due to the limited number of observations resources for field work usually allow. Nonetheless, Kummel observed a significantly bimodal distribution of aphid populations in a 2007 time series study of a yucca field in 8 out of 30 days, and most of the remaining days the distribution was strongly skewed (Kummel et. al., in press). The evidence for Turing pattern formation is strong and gave impetus to the study described here.

Natural History of the System

The *Yucca glauca*, also known as plains yucca, thrives in arid and semi-arid climates, particularly in sandy soils and disturbed areas. Its distribution stretches from Canada to Texas through the western Great Plains (Tyrl, et. al., 2002), including the high plains of eastern Colorado where our study sites were located. The durability of the yucca leaves makes insect damage and wildlife browsing minimal. However, during inflorescence, the emerging raceme (flowering stalk), is more delicate, succulent, and

susceptible to insect damage (personal observation) (wildlife browsing of raceme is also much more likely than browsing on other plant parts).

The primary insect herbivore of the *Y. glauca* in our study area is the aphid species *Aphis helianthi* (Palmer, 1952). These aphids have a number of reproductive adaptations, allowing specialization throughout the season and under changing seasonal conditions. The feeding season of the aphids on yucca is limited to the bud and flower stages of the inflorescence, little more than 30 days. During this stage reproduction is almost entirely asexual as females give birth to live female nymphs that mature in the course of a few days; several nymphs are often born daily to a single female. We found these normal females to be essentially bound to the plant they are born on; small amounts of wandering behavior by foot was observed; however, small size and lack of long-range sensory organs make traversing inter-plant distances nearly impossible for an aphid on foot. However, as a plant becomes crowded, or the food quality it provides deteriorates, production of winged aphids is triggered. Wing morphs readily emigrate in search of new plants. Although they also seem to lack targeting abilities, they find new plants by diffusion of large numbers of winged morphs. Successfully landed wing morphs colonize the new plant, giving birth to normal, non-winged aphids.

Death of aphids is primarily through coccinellid predation (discussed below). Other factors which may influence death rate include a lack of 'cleaning services' by ants (discussed below), extreme weather (heavy rain, high winds), and disturbance by animals or humans.

At the end of the yucca feeding season aphid populations migrate to their overwintering host *Cornus* (dogwood) (Robinson & Chen, 1969). Later in the season day

length and temperature triggers the production of sexual females and males. These mate and produce eggs which overwinter on *Cornus*, hatching into wing morphs in the spring to restart the colonization process. Previously these aphids were thought to be a separate species (*Aphis yuccae*), but Palmer (1952) found them to be identical to the sunflower aphid (*Aphis helianthi*). Given Palmer's finding it was realized that during other parts of the season these aphids are able to exploit a wide range of resources, including the entire *Asteraceae* (sunflower) family.

In our study area the primary predators of *A. helianthi* are two species of ladybugs (or 'coccinellids'), seven spotted and convergent (*Coccinella septempunctata* and *Hippodamia convergens*). Our data indicate that *A. helianthi* are the primary prey of these coccinellids, making these an ideal system for study of predator-prey dynamics. The coccinellids have a much longer lifespan than aphids; they overwinter on mountaintops where relatively constant temperatures allow them to remain in stable diapause (personal communication, Kummel). In the spring they descend in search of prey; although they are generalist predators, many individuals preferentially specialize on certain prey species as a result of developing 'tastes' early in the life cycle, possibly even during the larval stage (personal communication, Kummel). Presumably many of the coccinellids we studied preferred *A. helianthi*. The time series data set previously collected by Kummel (2007) showed that total ladybug number in a field of yucca closely tracked total aphid number, with a slight time lag-- classic predator-prey dynamics. Distinct from purely classical predator-prey dynamics, however, is the fact that ladybug number is controlled by ladybug *behavior*, not population dynamics (whereas aphid numbers are controlled by population dynamics). While coccinellid birth and death do take place within the system,

they are both relatively minimal compared with coccinellid immigration and emigration. Aphid number, on the other hand, is controlled primarily by reproduction and death (the latter being controlled primarily by predation).

Although our studies suggest that coccinellids lack sensory capabilities to directly detect aphids from any significant distance, they do demonstrate some preytaxis. We believe this targeting is driven by a combination of attraction to conspecifics (*not* directly to prey) affecting flight destination choices and the effect of aphid number on decision-making of ladybugs on plants. Over a relatively short range (up to about two meters), coccinellids display significant preference for plants with more conspecifics (in-flight decision making). On plants with many aphids, coccinellids are less likely to leave; they are retained by higher aphid number (on-plant decision making). Essentially coccinellids demonstrate area restricted search (as in Kareiva & Odell 1987) and a preference for higher conspecifics density.

When aphid availability is high, coccinellids can consume them in large numbers, up to about 65 per day per coccinellid by our calculations. Even more voracious are the larvae that hatch from eggs laid on the plants by mating coccinellids. These larvae, lacking wings, are more or less bound to their 'parent' plant until they develop wings; in the growth process they eat aphids very rapidly (as well as each other and other coccinellid eggs).

Coccinellids are predated upon by the checkered fly beetle (*Trichodes alvearius*), which has a similar appearance (at least in terms of coloring) to the coccinellid, but is much larger. *T. alvearius* are also winged and a significant threat to coccinellids, grasping them with large mandibles and tearing them apart. We did not study extensively the

behavior of *T. alvearius*, but anecdotally they seemed to arrive at plants with high coccinellid number. Coccinellids are sensitive to their presence and quickly leave the plant following their arrival.

Another critical aspect of this system is the aphid mutualism with ants. Many species of ants will 'farm' aphids, collecting excess sap and defending them from lady bugs. Because the phloem sap that aphids eat enters them at pressure (from the plant), they consume more than they can digest so some of it is shunted past their digestive tracts and excreted directly. If left unchecked, these sugary excretions dry on the aphid, debilitating and eventually killing it. Most aphid colonies are tended at least occasionally by ants, which carry off the sugary excretions as food for the ant colonies. Ants have also been observed carrying aphids, possibly to disperse and colonize new plants. Ants also release a pheromone that promotes aphid aggregation (reduces diffusion). Many of the species that tend aphids will also defend them fiercely from coccinellid predation. We observed ants attacking and killing several coccinellids, or more commonly, frightening them off.

Given the complexity of the natural system, we can easily see why the theoretical prediction of a bimodal distribution of populations was not clearly met at all times. The fact that the system *did* demonstrate a significant bimodal distribution on 8 out of 30 days and was strongly skewed to the right (towards where the second, smaller mode is observed) the rest of the time is very strong evidence that aphid density dependence is not operating with a single attractor under coccinellid predation. A two-attractor system driven by diffusive instability seems probable.

Methods

Model development

We attempted to describe this system through differential equation models, which we parametrized in the field. Building on previous research by Miro Kummel and Alex Tom, our team was able to quickly begin constructing models. The natural system at play is quite complex, and there would be significant challenges in any attempt to model all the elements described above, so some simplification was in order for the purpose of creating a model that would be intelligible, able to shed some insight on the driving factors at play, and testable without access to super-computing capacity.

We chose to explain the system with a deterministic model using a set of ordinary differential equations. We then considered what aspects of the natural system were essential to describe aphid pattern formation. Aphids clearly had to be included. If we were to describe any pattern formation among distinct aphid populations, then space had to be included in some way; at the very least populations had to be distinct (i.e. separate yucca plants).

Without any other factors aphids would simply approach carrying capacity as the principal factor influencing aphid death is predation by coccinellids. This necessitates the inclusion of predatory coccinellids. These three elements should be sufficient to create pattern formation; the ‘paint’ (aphids) out of which to form a pattern, the ‘canvas’ (some form of space) on which the pattern will appear, and the ‘brush’ (coccinellids) with which to influence the ‘paint’ (aphids) into a pattern.

These three elements can essentially be condensed into two equations, one for aphids and one for both coccinellid species, which, for simplicity’s sake, we treat as one

here. Then these equations are repeated in a matrix for each explicit plant to introduce space. Each equation will determine the population of its respective species on one plant; however all aphid and all coccinellid equations will be identical (respectively) except for plant identifying tags.

The two equations must include interactions with other plants, and this is where space can be made explicit or implicit. A pattern (non-normal distribution of population sizes) could form on an array of plants that are all equally accessible to each other (implicit space), or explicit distance between each pair of plants in the system could be introduced by mapping them on some coordinate system. We chose to work explicitly in two-dimensional space using plant coordinates from the real 2007 field site data for the majority of our model runs.

To construct these two equations we must further consider what factors within natural history of aphids and coccinellids are essential to describe the patterns we observe. These must be parametrized and written into the equations. The interconnected nature of systems means that we cannot include the entire natural history of aphids nor ladybugs, because in a complete picture several elements that we have chosen to leave out are interwoven with those elements we have included. Ants and coccinellid larvae are definitely a part of the natural history of aphids, but here we choose to leave them out for practicality.

The target output from our model is populations over time of aphids and ladybugs, so the important factors are those that affect population size on any plant. The four main factors that affect any population's size are reproduction, immigration, death,

and emigration. We considered each of these factors for both species, including the most relevant ones in their respective equations.

For aphids we considered immigration, reproduction, and death (by predation) to be the primary drivers of population size, while emigration and death by other causes play a much smaller role and were left out. Immigration, while never very large in absolute magnitude, is very important because it allows unpopulated plants to be colonized. Reproduction is obviously important as aphid reproduction is very rapid; in the course of several days a plant colonized by only a few winged aphids can reach population levels in the thousands through reproduction alone. Death by predation is critical as it is the primary reducer of population; small numbers of ladybugs can eat down a population of a thousand aphids in just a couple of days.

We did not include emigration or death by other causes in the aphid equation because these factors were relatively minimal. Emigration does not occur until a plant's population is approaching carrying capacity (when wing morphs start being born), and at that point only the new births (wing morphs) are able to emigrate. Although this may mean a large number of total migrants, it is a small number relative to the plant population, and that is essentially already accounted for in the parametrized carrying capacity. Death by other causes is relatively small (compared with predation) on the relevant time scale (about 30 days); however there are definitely significant numbers of aphids that die from weather, lack of tending by ants, ungulate browsing, and other physical disturbances. Leaving out these factors is justified for two reasons: one, it would over-complicate the model, making it hard to isolate causal factors in outputs, and two,

we are principally interested in the potential influence of ladybug predation on pattern formation.

For the ladybugs we considered immigration and emigration both between plants and into/out of the system; we did not include birth or death. This means that ladybug dynamics are entirely behavioral and have nothing to do with population dynamics. This, again, is an approximation of reality, one which we hope proves complex enough to be useful, but simple enough to allow insight. The importance of immigration and emigration to the dynamics on individual plants is obvious as coccinellids are highly mobile, making tens to hundreds of flights per day, rapidly changing numbers on plants.

The factors we ignore in the ladybug equation take more careful justification, as several of them anecdotally appear to affect local dynamics significantly. Population dynamics factors are ignored (birth and death); these factors are much less significant than movement on the time scale we are looking at. Birth of larvae certainly affects aphids on the plant where they are born, but they do not hatch until the end of the flowering season and the dynamics we see develop before they hatch. Ignoring larvae is essentially an application of Ocam's razor, aiming to make the simplest functional explanation of reality we can. Coccinellid death really is minimal in the relevant time frame; a few are killed by ants and *T. alvearius*, but very few. While these two insects do not greatly affect the death rate of ladybugs, they do affect the emigration rate; coccinellids actively avoid these threats (hence their minimal effect on death rate). If on developing the model it was found to be seriously lacking capacity to explain the natural phenomena observed, we would seriously consider studying ants and the checkered fly beetles further. Once again, we aim to determine whether without these factors we can

explain the system reasonably well, but these are two factors that would be next on the list for addition to the model if a need is demonstrated.

Model Structure

The nuts and bolts of the model take each of the factors described above and turn them into terms within differential equations that describe the rates of change of aphid and ladybug numbers on all plants. The equations are broken down below term by term.² Terms which increase the number of organisms on a plant (reproduction and immigration) are added, while terms that decrease that number (death and emigration) are subtracted. Each term deals explicitly with one of those four processes. Sometimes more than one term is needed for the same process because there are multiple sources or causes of that process (i.e. in the ladybug equation there are three terms describing immigration; one for within-system immigration, or redistribution, one for immigration into the system from outside by attraction, and one for random immigration into the system from outside).

As you refer to the equations you will notice that aphid and ladybug numbers are always referred to as A_i or L_i rather than just A and L . This is because these equations actually describe the aphid and ladybug numbers on *one plant*. 'i' is a placeholder, although in discussion of the equations we often refer to "plant 'i'" there is no such plant; it is just a shorthand way of saying "on any individual plant." For software to actually run this model it must first construct a table of equations in which 'i' in both equations is

² You can recognize a single term in the equations by the subtraction and addition symbols, except for subtraction and addition that is wrapped up inside parentheses or fractions, and the resulting sum or difference is multiplied or divided by something else. Otherwise, a minus or plus sign indicates the end of one term and beginning of another.

replaced, one whole number at a time, with all the numbers from 1 through ‘n’ (the number of plants in that particular model run). The processes are the same for each plant, but the individual plants are distinct. The modeling software creates tables to keep track of the actual numbers of aphids and ladybugs on each plant. As the model runs these tables grow; in the aphid table the number of aphids on each plant is recorded at every time step in a new column (with one plant on each row); the ladybug table does the same thing. Every time you see $L_i(t)$, this refers to number of ladybugs on plant ‘i’ at time ‘t’ (likewise for $A_i(t)$ and aphids); $L_{12}(3.6)$ refers to the number of ladybugs on plant 12 at 3.6 days into the model run. Plant numbers are always whole, because plants are discrete; time does not have to be a whole number because the time steps are much smaller than the unit of time we are using (days).

All the other letters, both Greek and Roman, in the terms are parameters (with the exceptions of M and Q, described under Eq. 2.2), constants which describe aspects of the system (i.e. how many aphids a ladybug can eat in a day). All of these parameters were determined through analysis of data from experiments in the field, which are described below (under “Parametrization”).

The differential equation for aphids is composed of three terms that control aphid population growth and decline on individual plants:

Eq 1

$$\frac{dA_i}{dt} = \alpha + A_i(t) \cdot (\kappa \log_{10}(A_i(t) + 1) + r_0) - \frac{\lambda \cdot L_i(t) \cdot A_i(t)}{h + A_i(t)}$$

Term by term:

(1) Immigration

Eq 1.1 α

Immigration is described very simply as a constant daily flux of aphids (α) onto all plants. Field observations were congruent with this approach; for most of the flowering season large numbers of wing morphs were diffusing from various sources. These morphs showed no ability to select certain yucca over others, or even yucca over other objects, so a constant (though small) flux into all plants in the system seemed reasonable. As described above, emigration is not important, so the source of the wing morphs is not specified (reasonable even when total system population is low, because wing morphs can and do usually have sources outside the study area).

(2) Reproduction

Eq. 1.2 $A_i(t) \cdot (\kappa \log_{10}(A_i(t) + 1) + r_0)$

Reproduction is described as log-linear density dependent growth. r_0 is the vertical intercept, i.e. maximum growth rate. κ is the parametrized coefficient of the \log_{10} of population+1; in other words it is the slope of the density dependence line or the rate that growth rate decreases with increasing aphid population. The carrying capacity can be found from these parameters as such: $10^{(r_0 / \kappa)}$.

(3) Predation

Eq. 1.3
$$\frac{\lambda \cdot L_i(t) \cdot A_i(t)}{h + A_i(t)}$$

Predation is described as a simple type II functional response. We found the maximum feeding rate (λ) of about 65 aphids/day, and the half saturation rate (h) of about 238 aphids (that is, when a plant has 238 aphids, ladybugs will feed at half of their maximum feeding rate).

The differential equation for ladybugs is composed of four terms that control the growth and decline of ladybug numbers on individual plants:

Eq. 2

$$\frac{dL_j}{dt} = -\mu \frac{L_j(t)}{1 + \sigma \cdot A_j(t)} + \omega \frac{L_j(t)}{1 + c \cdot L_j(t)} + \psi$$

$$+ \sum_{j=1}^n \frac{\mu \cdot L_j(t)}{1 + \sigma \cdot A_j(t)} \frac{Q[j, i] \left(1 + \phi \cdot M[j, i] \left(\frac{L_j(t)}{1 + c \cdot L_j(t)}\right)\right)}{\sum_{k=1}^n Q[j, k] \left(1 + \phi \cdot M[j, k] \left(\frac{L_k(t)}{1 + c \cdot L_k(t)}\right)\right)} + g$$

Term by term:

(1) Diffusion removing ladybugs from each plant

$$-\mu \frac{L_j(t)}{1 + \sigma \cdot A_j(t)}$$

Eq 2.1

Diffusion is described as a base diffusion rate mediated by aphid numbers on the plant; ladybugs are less likely to leave a plant that has a large aphid population. The total diffusion rate is described by a base diffusion rate (μ), which decreases as aphid number increases. A retention rate (σ) controls this reduction, the fraction by which the addition

of a single aphid reduces diffusion (a very small number, but with large aphid numbers, total diffusion rate is significantly reduced).

(2) Arrival of ladybugs who left other plants-- Assignment of diffusing ladybugs by attraction to conspecifics

Eq 2.2

$$\sum_{j=1}^n \frac{\mu \cdot L_j(t)}{1 + \sigma \cdot A_j(t)} \frac{Q[j, i] \left(1 + \phi \cdot M[j, i] \left(\frac{L_i(t)}{1 + c \cdot L_i(t)} \right) \right)}{\sum_{k=1}^n Q[j, k] \left(1 + \phi \cdot M[j, k] \left(\frac{L_k(t)}{1 + c \cdot L_k(t)} \right) \right) + g}$$

This rather complicated term describes the redistribution of ladybugs within the system. Part of the complexity arises from the fact that to consider redistribution we are obliged to look at things from multiple perspectives simultaneously; individual ladybug behavior must inform our prediction of where they will decide to go from a plant they leave (many possible destinations), but the model can only consider one plant at a time, so we must find how many ladybugs will arrive at one plant (from many possible sources). The arrivals on any one plant are made up of those ladybugs that have departed from every other plant.

To explain this process first we consider where the ladybugs departing a plant (the red plant in Fig. 2.1 or plant 'j' in Eq. 2.2) will go. We accomplish this by calculating the number of ladybugs leaving the red plant and comparing (as we believe a ladybug would) all the possible destinations. To consider one destination (the green plant in Fig. 2.1 or plant 'i' in Eq. 2.2) we calculate how attractive it is (considering number of conspecifics

on it, and how far away it is), and compare that with how attractive all the other options are (the sum of attractiveness of all other plants plus the attractiveness of leaving the system). The resulting quotient is the *proportion* of ladybugs leaving the red plant that will go to the green plant.³ Then we consider the same green plant, and assign a new plant to be the red plant, repeating the process, until we have considered all the possible sources (Fig 2.2), and sum up how many ladybugs from each source arrive at the green plant, giving the arrivals at plant ‘i’ for that time step. Then that entire process is repeated, assigning a new plant to be the green plant, until all plants have been considered as green plants, completing the redistribution process for one time step.

More specifically, in Eq. 2.2 the goal of this term is to sum all the ladybugs arriving at plant ‘i’ (green) from all possible plants ‘j’ (red); thus the term inside the primary sum ($j=1$) determines how many ladybugs diffusing off plant ‘j’ (red) will arrive on plant ‘i’ (green). To determine the number of ladybugs arriving at ‘i’ from ‘j’ we first calculate the number of ladybugs leaving ‘j’ and multiply it by the relative attractiveness of plant ‘i.’ The number of ladybugs leaving ‘j’ is the familiar diffusion term which has been addressed above. Next we will address how we determine the relative attractiveness of plant ‘i’ as a ratio of the perceived attractiveness of ‘i’ over the total perceived attractiveness off all possible destinations from ‘j.’

³ Note that ladybugs leaving the ‘red’ plant do not simply compare all their options and select the most attractive one; rather proportion of attractiveness coming from each plant indicates the *proportion* of those ladybugs leaving the red plant that will arrive at each plant respectively. This also means that ladybugs are not discrete in our model; rather the outcome represents an average of the distribution of possible outcomes. It is entirely possible for a plant to have a ladybug number of 0.5 at any given time; in real terms this means that the average of the distribution of expected discrete ladybug numbers on that plant at that point in time is 0.5.

The second (largest) quotient in Eq. 2.2 determines this *relative* attractiveness of plant 'i.' First, in the numerator, we determine the attractiveness of 'i.' One can think of the attractiveness of 'i' as the product of ladybug number, scaled for saturation of attractiveness (by the divisor 'c'), and Φ (rate of attractiveness), but this ignores distance. To take distance into consideration we parametrized both the decay of diffusion with distance (likelihood of a flight of a particular length) and the decay of attraction with distance (ability of ladybugs to detect conspecifics). Two matrices (Q and M) represent decay of diffusion and attraction respectively. $Q[i,j]$ references the matrix Q and pulls the diffusion decay constant that exists between 'i' and 'j' calculated based on the distance between the two plants. $M[i,j]$ does the same for the decay of attraction. Thus the entire numerator determines the attractiveness of 'i' from the perspective of 'j.'

To determine the proportion of ladybugs that will fly to 'i' from 'j' we need to consider what their other options are. In the denominator we sum the attractiveness of all plants in the system (labeled 'k') from the perspective of 'j' together with the attractiveness of leaving the system, represented as a constant attractiveness of flying to some non-yucca or out-of-system destination, labeled 'g.' Thus the denominator represents the total attraction a ladybug leaving 'j' will perceive. If 10% of that total attraction comes from 'i' then 10% of ladybugs leaving 'j' will arrive at 'i.'

Having determined the number of ladybugs arriving from 'j' at 'i,' the primary sum then repeats this process for every plant in the system, at which point we have the total number of ladybugs arriving at 'i' from diffusion off all plants within the system. Keep in mind that 'i,' 'j,' and 'k' all are sets that include all plants in the model run, so self-flights are considered. In other words, when considering the arrivals at 'i' one must

consider that ‘i’ could also be a source. When the ‘j’ counter is equal to the ‘i’ counter then the model evaluates the attractiveness of a self-flight against the attractiveness of the rest of the system.

(3) Arrival from outside system by attraction

$$\omega \frac{L_j(t)}{1 + c \cdot L_j(t)}$$

Eq 2.3

This term is similar to the attraction segment of the previous term except that there is no decay with distance because we are considering ladybugs arriving from outside the system, so we don’t know their initial distance. Essentially this term accounts for those ladybugs that are arriving from outside of the system and are more likely to select a plant with more ladybugs than one with fewer as they fly in. As in the previous term, attraction to conspecifics is saturating. The attractiveness of the individual plant is modified by the constant ω which we calculated based on availability of ladybugs outside of the system.

(4) Arrival from outside system by diffusion

$$\psi$$

Eq. 2.4

This term simply applies a constant low rate of immigration (ψ) onto all plants. This is realistic because inevitably a few ladybugs will randomly arrive at any plant flying in from outside the system. Although this number is small, it serves a practical purpose: the only other means of arrival of ladybugs into the system relies on conspecific attraction, so if there are no ladybugs initially, or they all leave, then they would never

come back without this term (this is not just mathematically convenient but realistic; ladybugs do arrive where there were previously none).

Parametrization

The parameters used in the model above all describe real characteristics of insect behavior or natural history. All of them were determined experimentally in the field. Following are descriptions of the methods we used to find them broken down by types of experiments, and then by individual parameter. For reference Table 1 contains all parameters, descriptions, values, and dimensions.

Sticky Aphid Traps

α : Immigration of aphids (3 aphid*day⁻¹)

Initially we were not sure how to describe immigration of wing morphs. To get a spatial sense of the process we placed 22 wooden stakes in concentric circles around an isolated raceme with a high aphid population producing wing morphs. The stakes were approximately the size of a flowering raceme of yucca and coated in Tanglefoot ®, a sticky insect-trapping resin. The stakes were placed on doubling radii in the following distribution: 1 at 25 cm, 3 each at 50cm, 1m, 2m, 4m, 8m, and 6 at 16m. Stakes were evenly distributed around their radii, taking care to offset them from one radii to the next to reduce the potential for any shadow effect. We conducted this experiment several times at the US Air Force Academy (USAFA). We returned to count winged aphids after two days, or one day, and in one case hourly for four hours. As would be expected from a diffusing source, we found logarithmic decay of number of aphids stuck with distance.

We fit the following log decay: $\text{aphids stuck} = a - b \cdot \ln(\text{distance})$ the relationship was statistically significant in five out of eight trials.

Given that isolated high aphid populations are rare, we began to wonder whether these spatial patterns would have dynamic consequences in a normal yucca field, where between-plant distances are typically less than 1m. To assess this, and to see if wing morphs seem to have any decision-making capabilities, we conducted another sticky stake experiment. In this case we found racemes producing wing morphs, and we placed two stakes equidistant from each raceme (taking care not to place either of them closer to any *other* wing morph-producing aphid population), one 20cm from an un-colonized raceme, and one in interstitial space (not near any raceme). We set 14 of these pairs and counted them after one and two days. We found no significant difference between next-to-plant stakes and interstitial stakes, suggesting that wing morphs do not target racemes, but find them by simple diffusion. Combining the interstitial and next-to-plant stakes we analyzed the number of aphids stuck as explained by distance from a potential aphid source (no less than 900 aphids). We found a marginally non-significant logarithmic decay ($R^2=0.129$, $p=0.061$, $n=28$, $\text{aphids trapped} = 2.968 - 0.184 \cdot \ln(\text{dist})$ with distance (distance ranging from 2m to 10m).

Given these findings and typical plant-plant distances in a yucca field, we chose to describe aphid immigration as a simple constant arrival rate. To find this rate we set out a new set of 22 stakes and counted the aphids stuck to them hourly for four hours. We considered the increase in stuck aphids every hour (the new arrivals), to find an hourly arrival rate. We found an average arrival rate of about 0.25 aphid/(stake*hr), giving an arrival rate of about 3 aphids/day (assuming 12 hours of activity) on each yucca.

Predator Exclusion

κ : Slope of log linear density dependence ($-0.2113 \text{ aphid}^{-1} \cdot \text{day}^{-1}$)

r_0 : y-intercept of aphid growth rate (0.8521 day^{-1})

To parametrize the density dependence of aphid reproduction in the absence of predation we constructed eleven wood-framed screen cages to exclude ladybugs from yucca. We caged eleven yucca with a range of initial populations, from four to 270. The cages excluded ladybugs, but ants were able to tend the populations entering through small holes around the base. Removable lids on the cages allowed us to return and count the populations on each plant once a day (at a consistent time) for 19 days. By the end of the experiment several populations were over 5000, giving us a complete picture of density dependence.

To corroborate these data we also collected data from the USAFA site that was in the early stages of colonization and ladybugs had not yet arrived. There we tracked 33 populations for two days.

At both sites we found nearly identical parameters for a log-linear density dependence; growth rate of aphids decreased linearly with the \log_{10} of aphid population. κ , the slope we found to be -0.2113 and r_0 , the y-intercept, $.8521$ ($p < .0005$). This means that free of predation aphid populations would reach one stable equilibrium (carrying capacity).

Observation of Coccinellids

λ : Maximum feeding rate of ladybugs ($65 \text{ aphid} \cdot \text{day}^{-1}$)

h : Half saturation constant for ladybug feeding (238 aphid)

We observed 34 yucca racemes with varying aphid populations (from 0 to 3700 aphids) and ladybug numbers. We counted the aphid populations once and then counted both species of ladybug, noting how many were eating, every ten minutes 15 times to determine what portion of their time they spent eating. In previous experiments Kummel determined the average time it takes a ladybug to eat an aphid, allowing us to project feeding rates based on frequency of feeding.

To find feeding rate of ladybugs we assumed that they ate with the same average frequency for 14 hours of activity daily given that we observed ladybugs do not feed at night but do feed all day. We used the previously found handling time of an aphid: 86.5sec by *H. convergens* and 63.5sec by *C. septempunctata*. We plotted feeding rates against aphid number on plant, and found a type II functional response with a maximum feeding rate of 65 aphids/day, and a half saturation constant of 238 aphids.

μ : Diffusion rate of ladybugs off a plant (40.61 day⁻¹)

σ : Reduction in diffusion rate with additional aphids (4.07*10⁻⁴ aphid⁻¹)

To parametrize the diffusion of ladybugs we simply plotted departures/(ladybug*time) against aphid number from previously collected data. We found a significant decrease in departures with increasing aphid number. This showed that aphid number affects ladybug decision to take flight; racemes with higher aphid numbers retain ladybugs. The base diffusion rate, μ , with no aphids is the y-intercept, which we found to be 40.61 day⁻¹. We found that departure rate was inversely proportional to aphid number with a constant, σ , which with non-linear regression we found to have a value of 4.07*10⁻⁴ aphid⁻¹.

δ : Rate of decay with distance of ladybug diffusion (0.95 m⁻¹)

ϵ : Rate of decay of attraction with distance (1 m^{-1})

Φ : Rate of attractiveness of ladybug ($30.53 \text{ ladybug}^{-1}$)

c : Saturation constant for ladybug attraction (0.5 ladybug^{-1})

g : Attractiveness of non-yucca/leaving system (8.16 unitless)

To analyze ladybug in-flight decisions we carefully observed a relatively isolated patch of yucca consisting of nine racemes. We measured all inter-raceme distances and counted aphids on all racemes once. Inter-raceme distances ranged from 40 to 225 cm and aphid number ranged from 90 to 3400. Then we counted ladybug numbers on each raceme and started tracking the origin and destination of every flight off of any of those racemes for one hour. Every 15 minutes we recounted ladybug numbers on each raceme. We repeated this in the same patch, and then twice again in a different patch with 22 racemes. We tracked a total of 265 flights.

For all the flights we recorded we had the following information: distance, origin aphid number, origin ladybug number, destination aphid number, destination ladybug number, as well all this data for every possibility within the patch that was *not* chosen by the ladybug. Ladybug numbers and flights were actually also divided out by species. We also counted ant numbers and morphotypes on plants, but did not include them in our analysis. We analyzed flights separately by species, but used primarily the results from the *H. convergens* flights because they made up the large majority of ladybugs and flights at all of our field sites.

δ , ϵ , Φ , c , and g were all determined using maximum likelihood analysis in mathematica from the flight data set described above. Essentially we give the computer the data set (including all flights, and the conditions where they came from, where they

did go, and where they didn't go) and a form with which to explain that data (i.e. a model structure) and it calculates the parameters to maximize the likelihood of observing the outcome we observed.

ω : Rate of attraction of ladybugs from outside systems (10 day^{-1})

ψ : Diffusive immigration of ladybugs from outside system ($0.5 \text{ ladybug} \cdot \text{day}^{-1}$)

These two parameters were calculated from 2007 time series data describing arrivals on plants *not* described by activity on the nearest neighbor plant. Arrivals were plotted against ladybugs on the plant. ψ is simply the y-intercept (the number of ladybugs which arrive on plants with no ladybugs on them), and ω is the slope.

Results

Note that statistics and co-efficient values for all regressions shown in figures can be found in Table 2.

Model Outputs

As described above, the modeling software stores tables of aphid and ladybug numbers for every plant for every time step as it runs. These tables would not be a very practical way to look at the output of the model though; they have as many rows as plants in the model run (107 in our complete model, and 40 in most of our trials) and tens or hundreds of thousands of columns, depending on how long the model is run and the time step it chooses. Instead we turn the tables into plots of aphid and ladybug numbers over time. This is the first output we usually look at, and it contains a lot of information;

although our eyes are not adept at ‘seeing’ the statistics we are looking for in these plots, it is possible to pull out a lot of features at once (distribution of population sizes, which populations end up large and which small, etc.). One feature we look for particularly in these plots is a protection effect early on, where mid-level populations escape predation because ladybugs are concentrated on higher populations, allowing the mid-level populations to ‘slip past’ the repellor between the two attractors and reach the high attractor, while those initial high populations are reined in by predation, and along with many initial low populations, reach the low attractor, creating the bimodal distribution we see in the field.

Figure 3 shows the aphid populations on 40 plants as the model runs over 30 days. Each individual line is the population on one plant. The protection effect described above can easily be seen; at about day 10 all the initially high populations begin to drop as predation is concentrated on them, and by day 16 almost all of them have been overtaken by initially smaller populations. Figure 4 shows the aphid populations on all 107 plants in the 2007 time series data. Although it is slightly more difficult to visually track individual plants in the time series data, the protection effect is also evident in this plot.

Figure 5 shows ladybug numbers on each plant for the same model run as figure 3. You can easily see why predation started having significant effects on aphids around day 10 as ladybugs come rushing in at that point. This sudden influx is probably due to retention of ladybugs as aphid number gets high enough to limit diffusion, and then conspecific attraction creates a positive feedback, bringing in more ladybugs. After about day 15, however, there is a sudden slowing of ladybug influx. This is probably both because retention drops as ladybugs eat a lot of aphids, and because attraction is

saturating, so the rate that new LB come in no longer increases as LB number increases, but an increasing LB number *does* still increase diffusion. Later in the run the difference in distribution is evident; as expected ladybugs are much more evenly distributed than aphids; ladybug numbers at day 30 range by about three-fold, while aphid populations range by several hundred-fold (compare final numbers in Fig. 3 and Fig. 5). Figure 6 shows field ladybug numbers on all plants and days. It is difficult to follow due to frequent changes in ladybug number on all plants but shows a decent match to the model in terms of magnitude of total ladybug immigration.

A histogram of aphid populations from the model run at day 25, Figure 7, clearly shows a bimodal distribution. Compared with the observed field distribution, Figure 8, we see that the size of the modes does not match perfectly, but the bimodality is obvious in both.

Statistical Signatures

Although the aphid and ladybug number plots are an important first step, and careful observation can reveal a lot, it is also easy to be misled by plots that seem to look good. For example, in a prior iteration of the model the aphid populations seemed to show a beautiful protection effect which was repeated; every 10 days or so the current high populations would crash and the lower populations would take their place, making for a beautiful oscillation. This plot certainly looked good, but further analysis revealed the system exhibited neither cubic density dependence (i.e. bi-attractor/repellor) nor any of the expected skewness trends, nor a bimodal distribution. This model also made questionable assumptions about aphid population growth and some other things that did

not represent a strictly field-derived understanding as the current model does. Many of these things are difficult or impossible to actually ‘see’ in the population plots, the shape of density dependence in particular would be hard to deduce. For these reasons, and to obtain a more accurate comparison, we ran the same statistics on the model outputs as on the field data to look for some of the drivers of diffusive instability.

Essentially we are looking to see if several characteristics are present which would lead to the bimodality we observe; this is a way of verifying that the bimodality is not a coincidence, but rather an expected feature of the system. Principle among these characteristics is a cubic density dependence, leading to the two-attractor structure; having two attractors is the most obvious way to get two modes. Other characteristics help confirm that diffusive instability is at play, namely that ladybugs (being faster diffusers) are more evenly distributed than aphids. We also check for a pattern of increasing skewness of aphid and ladybug numbers with time as we found in the field (though, consistent with diffusive instability, the magnitude of ladybug skewness is smaller). This suggests that the skewness is being actively created by the system dynamics, rather than being leftover from initial conditions and evening out with time.

Figure 9.1 shows the density dependence calculated once per day for all days of the model run, but none of the possible models we tried to fit to it actually fit (linear, quadratic, cubic) for obvious reasons; it clearly has two dynamics operating. The relatively straight line with a negative slope above the x-axis and the more diffuse curve below the axis clearly cannot be explained simultaneously. When we refer back to Figure 5 and consider that ladybugs are almost not present in the system until day 10, and do not reach semi-stable populations until about day 15, we see that there are two different

scenarios at play throughout the model run. If we plot density dependence for days 15-29 we see, in Figure 9.2, a beautiful cubic density dependence with two attractors separated by a repellor. The attractors lie at approximately four and 5000 aphids, with the repellor at about 1200 aphids. As can easily be seen in the figure, the cubic fit best describes the data, with an R^2 of 0.7756 ($R^2=0.6294$ for the quadratic fit, and $R^2=0.1613$ for the linear fit) and p values for all four parameters that are nearly zero (on the order of 10^{-80}). Comparing this with the density dependence observed in the field, Figure 10, we find a very similar result with the attractors in nearly the same place, although the repellor is lower in the field (at about 200 aphids).

As seen in the field, and helping to explain ability of very high populations to escape being driven to the lower equilibrium by predation, the model also demonstrates undermatching. The more aphids there are on a plant, the lower the relative predation pressure; higher aphid populations have fewer ladybugs per aphid. Figure 11 shows this to be a power law relationship because it is clearly a linear relationship on a log-log scale. The fit is very strong with R^2 of 0.9938 and near zero p-values. Figure 12 shows the same relationship from the field, although the intercept is not quite right in the model.

One signature in the field which came through only weakly in the model was an indication that ladybugs do successfully concentrate on higher aphid populations (even if less so than they “should”). Plotting $\text{Log}_{10}(\text{ladybugs})$ against $\text{Log}_{10}(\text{aphids})$ should result in a positive slope. Figure 13.1 shows that linear regression on this data from the model (averaged across days 15-30) for each plant does result in a significant positive slope ($p \sim 10^{-4}$); however, it is only weakly explanatory ($R^2=0.31$). The apparent nonlinearity of the data in Fig 13.1 seems to be due to these variables being bidirectionally causal; while

ladybugs are weakly explained by aphids, aphids are also explained by ladybugs. This bidirectional causality has some interesting implications further explored below in discussion (with reference to Fig 13.2). Figure 14 shows the same data from the field where aphids are a stronger explanatory variable for ladybugs ($R^2=0.45$).

The third signature we see in the field and the model is the skewness of the distribution of both aphids and ladybugs. Both increase with time in the field, but skewness of aphids is greater. In the model skewness takes a little while to sort itself out, as with the other system characteristics, before ladybugs arrive. But running the model for 40 days, and looking at days 15 through 40, it is clear that there is an upward trend in skewness of aphid distribution. Figure 15 shows aphid skewness for days 15-40 with a linear regression ($R^2=0.87105$, however $0.05 < p < 0.10$). Figure 16 shows the same trend in aphid skewness in the field; though the intercept is much higher in the field.

Figure 17 shows ladybug skewness for days 15-40. Ladybugs took even longer to sort themselves out, skewness oscillates in days 1-15 and continues oscillating into this plot, until almost day 25. The second (green) regression is fit across days 25-40 only (the first is across days 15-40). Although the improvement in fit is only marginal (R^2 of 0.6580 for green instead of 0.6018 for red), the change in dynamics at day 25 is obvious, and the second regression also has a positive rather than a negative slope. In the field ladybug skewness increases with time, and it appears that once the model run has sorted itself out, it also does in the model. Figure 18 shows the same trend in ladybug skewness in the field, but once again, the intercept predicted by the model is low.

Figure 19 shows model ladybug and aphid skewness on the same graph, confirming that aphid skewness is greater (at least once ladybugs have ‘sorted themselves

out'). For comparison, Figure 20 shows field skewness of ladybugs and aphids. Interestingly, in the field we also see that initially the relationship is much less distinct; for at least the first five days, neither is obviously greater than the other. The field seems to take some time to 'sort itself out' as well.

Discussion

Given the number of factors not included in our model it has a very rich behavior with many remarkable similarities to the field system. All of the statistical signatures investigated in the field appeared in the model (with more or less strength and accuracy) despite the fact that none of these were explicitly programmed into the model, which is strictly based on insect behavior. Although admittedly some of the signatures were not so strong, the cubic density dependence and the ladybug-to-aphid ratio vs. aphid number were both very strong, with the density dependence also demonstrating a remarkable degree of accuracy.

Ultimately the goal of emulating the field on a computer, though, is not to see if we can, but to gain insight into how the field is working by seeing what factors create similar signatures. In this regard the similarity of the field and the model results is a boon and offers a window into the workings of a complex system whose mechanisms would be very difficult to untie by simple observation. Although the model described is our best explanation of the system, it certainly is not the only possibility. Field work led to several possible model structures, each slightly different, and none of which stood out as much better than the others until we ran some of the statistical comparisons. It cannot be denied that this model still has significant differences from what was observed in the field, but

even these allow for some insight into what is *not* being driven by the factors we did include, and what possible factors could be added to increase the accuracy of the model. That said, some of the similarities between the model and reality are remarkable and merit much consideration.

Space in our system

The natural history of our system immediately suggests that continuous space is not the appropriate approach; the discrete nature of yucca plants and the inhospitable (to aphids) nature of the interstitial (non-yucca) space suggest some patch-based approach. An island approach might be workable, but the rapid distance decay of ladybug sensory capability and flight likelihood suggest that proximity plays an important role. We chose to construct the model as patches in euclidean space, which is how we see the field (plants in a set of spatial coordinates), but upon considering the behavior of ladybugs, and the functioning of the model, this may not be the way ladybugs see the field.

Sometimes we struggle to see network space in natural systems, even though we operate in network space all the time. Denver and Cripple Creek are two population centers, ‘patches’ if you will, near Colorado Springs (where this study is based). Although in euclidean space Cripple Creek (a small mining and gambling town in the mountains) is about one third the distance from Colorado Springs that Denver is, it only takes marginally longer to drive to Denver due to the strength of the connection (i.e. quality of the highway system and topography). Furthermore, although both in euclidean distance and driving time Denver is at least slightly further away, it has considerably more influence on Colorado Springs than Cripple Creek because it is a much larger

population center. This is not to say that proximity plays no role; New York City is considerably larger than Denver, but many times more distant, and certainly has much less influence on Colorado Springs than Denver.

The possibility that the ladybugs see the field the way we see our world seems strong. The nature of conspecific attraction means that the effect of a plant on its neighbors will be much stronger if that plant has a large number of ladybugs on it than if it has few or none. The model clearly illustrates this point; all redistribution of ladybugs within the system is based on conspecific attraction. A plant with zero ladybugs will never be chosen as a destination for a ladybug from within the system. Of course, there is a constant influx of ladybugs from outside the system onto all plants, so no plant ever has zero ladybugs (in the non-discrete, average of the probability distribution sense of ladybugs), but those with fewer are markedly less visited.

This all suggests that a sort of evolving network structure may be at play; as ladybug numbers on each plant change and the relative attractiveness between plants changes with them, certain connections become more traveled while others are ignored. As a plant gains ladybugs the process has a positive feedback; more ladybugs on a plant mean even more will arrive and so on. Meanwhile a plant with a great many aphids on it may be ignored because the ladybugs do not detect prey directly while in flight. This is one of the ways that an aphid population can escape past the repellor on the cubic density dependence and approach the high attractor. Of course, as the population grows very large the random arrivals (from outside the system) will be retained on the plant (i.e. engage in area-restricted search) (see Kareiva & Odell, 1987), which will start the

positive feedback and bring more ladybugs to the plant, but the time lag of this process may be significant.

Ladybug Distribution and Diffusive Instability

The time lag in ladybugs' preytaxis resulting from this roundabout method of detecting their prey works well to produce diffusive instability. Recall that ideal free distribution (IFD) is the counter to diffusive instability, allowing (if achieved) essentially non-spatial predator-prey-dynamics to take place in a spatial setting. Very strong and/or rapid preytaxis would push ladybugs towards IFD. Also recall that for diffusive instability to operate the prey must activate the predator, and in this system where reproduction of ladybugs is minimal on the relevant time scale (and not included in the model), preytaxis is the only way for prey to activate the predator. Ladybug preytaxis appears to be neither too strong nor too weak, fostering diffusive instability.

Diffusion, on the other hand, operates constantly with no time lag. Although retention, the mechanism for preytaxis, does curb diffusion off of high aphid plants, it is never reduced to zero. By our parametrization, a ladybug arriving on a plant with 16,000 aphids (the largest population ever observed in the field, quite rare) would depart on average 133 minutes after arrival, as compared with 17 minutes for a plant with no aphids (doubling to 34 minutes at 2500 aphids, a more frequently observed aphid count). Given that aphids are *much* less mobile, most being flightless, and their tendency to aggregate (Turchin & Kareiva, 1989) disinclines them from wandering by foot, it is readily evident that diffusion of ladybugs is much faster. This leads to another hallmark of diffusive

instability: undermatching that can be seen *very* clearly in Figure 11 (similar in the field, Figure 12).

By definition to achieve IFD ladybugs would need to all experience equal payoff (prey consumption rate) on their respective plants. For this to be the case the slope of the regression in Figures 11 and 12 would actually need to be positive, because the type II functional response of ladybug predation indicates that at lower aphid populations ladybugs achieve lower payoff per aphid. To equalize, payoff competition would need to be considered and lower competition on low aphid plants would allow ladybugs there to achieve equal payoff to those on higher aphid plants with more competition or, disregarding competition, as we do in the model, *all* ladybugs in the system would have to be on the highest aphid-population plant to maximize their payoff on a type II functional response. Clearly neither of these is the case, rather quite the opposite; ladybugs are more heavily concentrated (in terms of ladybug/aphid ratio) on low aphid populations; ladybugs are clearly undermatching the distribution of aphid populations.

Another way of thinking about the same thing is the comparative skewness of the aphids and ladybugs. Skewness measures how far from normally distributed a population is; a bimodal distribution has very high skewness. If ladybugs were to approximately achieve IFD, we would expect them to be at least as skewed as aphid populations to achieve a similar distribution (i.e. concentrating on the high populations). Instead we find in the field and the model that ladybugs are consistently less skewed than aphids (Figures 19 and 20). One way to think about this is that ladybugs are relatively evenly distributed on an aphid density topography with is *not* even. This implies that where there are troughs or valleys in aphid density ladybug density does not dip as much, and where there

are peaks in aphid density ladybug density does not rise as high. Again this is consistent with undermatching.

Development of two attractors, one repeller and bimodality

Outstanding among the similarities between the model and the field is the cubic density dependence. We might consider how the model went from our parametrized density dependence to the cubic function it demonstrates. Recall that the first 7 days of the model run are essentially predator-free (refer back to Fig. 5). So Fig. 9.3 shows a close approximation of density dependence of the system without ladybugs (before their arrival). Not surprisingly, it also shows a close approximation of the log linear density dependence which we programmed into the model (which is overlaid for reference: the thicker purple line). The linear regression in this figure (red line) does not line up with our parametrized density dependence, primarily because of the daily immigration of aphids. This immigration was necessarily excluded from our plant caging experiment because the screen allowed neither ladybugs nor winged aphids through; furthermore it is only at very low populations that the difference is significant. Although the cubic fit on this plot seems to fit remarkably well, this is probably not because of an actual cubic density dependence; rather there are two dynamics to explain at once, and the cubic fit is simply better able to follow the data. Without ladybugs what we would really expect is a straight line with one up turned end (at the low populations where immigration makes a difference). In this case regression is ‘tricked’ into steepening the line to follow the low populations with a high growth rate, but careful observation shows that the parametrized density dependence (purple line) actually describes the data very well past about $10^{1.4}$ or

25 aphids. Below 25 aphids we see a predictable increasing positive departure from the parametrized density dependence as the effect of a three-aphid-per-day immigration becomes larger relative to the on-plant population.

Around day 7 ladybug immigration into the system starts to take off, but their numbers do not stabilize until about day 14. It is a little more difficult to display the nature of density dependence during this transition; note those points which are in Fig. 9.1 (all days) that are not in Fig. 9.2 or Fig 9.3. Essentially the system transitions from log linear to cubic density dependence. The most notable part of that transition is the ‘drop’ from linear density dependence to the cubic line which can be seen in Fig. 9.1 centered above $\log_{10}(\text{Aphids})=3$ as several vertical series of points ‘falling’ towards the cubic density dependence. These series of points represent distinct plants, and we can “see” ladybug numbers on each of them increasing as the density dependence drops away from the predator-independent line towards the predator-influenced curve (we see these ladybugs implicitly through their influence).

From day 15 on (Fig 9.2) the cubic density dependence becomes quite apparent. This is strikingly clear evidence of the operation of a diffusive instability. The linear regression is included in Fig 9.2 mainly for consistency, nonlinearity is abundantly clear. While the quadratic fit to the data seems good, there are two important issues with it. First it simply does not fit the data as well as the cubic ($R^2 \sim 0.63$ as opposed the cubic for which $R^2 \sim .78$), and it can easily be seen that while the very largest populations do not fall far from the fit curve, they are clearly trending downwards, which the quadratic fails to capture. More importantly, a concave up quadratic density is essentially impossible; an indefinite positive (not to mention increasingly positive) growth rate as population

increases implies an attractor at infinity--this is not possible. Finally, comparison to Fig. 10 shows that the cubic fit is not only the most common form seen in the field, but the cubic found from the model actually matches the x-intercepts (equilibria) found in the field quite closely.

Consistent with Nakao & Mikhailov's (2010) expectation for Turing patterns in a network (or indeed any system with a diffusive instability), and obviously explained by the two-attractor density dependence, we find a bimodal population distribution. As in the field the bimodality is not crystal clear all the time; the slow and sometimes inaccurate method of prey location by ladybugs, among other factors, makes the whole system a little "messy." Figures 7 and 8 show days from the model and the field when the bimodality was quite clear. Checking other days reveals that in the model bimodality was reasonably evident most of the time (10 days) that the system was operating under diffusive instability (the last 16 days). In the field, probably due to the greater number of confounding factors inherent to any natural system, the bimodality was only significant on 8 out of 30 days. In any case, in both the field and the model, skewness of aphids was significant and increased with time, which implies that the systems (both natural and simulated) were dynamically generating this skewness; it was not merely the result of random initial perturbations.

Bidirectional causality and implications for equilibria

One figure (13) which was meant to be a fairly simple demonstration that, despite the drawbacks of their methods, ladybugs are able to find aphids, has led to some unexpected insights. Figure 14 shows a power law at play in the field, the moral of which

is: ladybugs can find aphids. This figure shows the shows the average number of ladybugs on each plant across all 30 days as explained by the average number of aphids (both logged). The positive slope is expected, because the activator (aphids) does indeed activate the inhibitor (ladybugs); in turn this is because ladybugs do indeed demonstrate prey-taxis.

Figure 13.1 was intended to further reinforce the match between the model and the field, a goal which it achieved, demonstrating a significant positive slope: an overall trend of ladybugs to find aphids. However, the nonlinearity of the data could not be ignored, the apparent *downward* trend of ladybug numbers from about 3 to 300 aphids (.5 to 2.5 on the logged axis) being particularly perplexing. Figure 13.2, separating out each day (rather than averaging across all days on each plant) seemed only to complicate the picture. A sharp downward slope is evident (along the blue dashed line) at the left hand side, and a strange shift in dynamics seems to appear from nowhere in the right half of the data. Animating the figure (a service I am unable to provide in a static file) to step through the days in order, populating the graph with data points in the order they were created, proved revealing. The perplexing issues arise from the fact that the two variables plotted here are bidirectionally causal.

It also appears that the dynamics are strongly affected by the ‘memory’ of individual patches (plants). If it appears that this graph is a collection of 40 independent (although bound by similar trends) data series that is because it is; each line or curve of points that appears to belong to a series is a single plant. All patches do not tend towards a common curve, rather each plant seems to create its own curve, although usually parallel to the curves of several other plants but not appearing to converge. The primary

influence on each point seems to be where that same plant was the day before, not where other plants are nor a single common attractor.

We had assumed that the trends present should be explainable by aphids; after all the ladybugs ought to find the curve along which they are happy and stay there. However, as I have repeatedly explained, ladybugs do not operate with perfect knowledge or ideal prey taxis. This is abundantly clear given the preponderance of evidence that ladybugs are unable to achieve IFD. Indeed, the focus of this paper is the effects which ladybugs have on aphids, so it would be folly to assume that ladybugs and aphids are not bidirectionally causal (as is the case with any activator-inhibitor system); while aphids certainly explain ladybugs to some extent, ladybugs must also explain aphids.

In light of this the points along the blue dashed line in Figure 13.2 begin to make sense. From an aphid explanatory perspective it is perplexing that with increasing aphid number we observe decreasing ladybug number. However, it makes perfect sense from a ladybug explanatory perspective: with decreasing ladybug number, more aphids survive. Animating the figure revealed that all the points on the blue dashed line were from the final days of the model run; the relatively flat, spread-out series in the left side of the graph started out near the dramatic steepening of the data and then moved to the left (decreasing aphid population), ending up on or near the blue line. Arriving at the line they all suddenly stopped decreasing in aphid population and stayed there. This line is the low attractor in the cubic density dependence; referring back to Figure 9.2 the similarities are distinct enough to pick out individual plants as the same in the two graphs; we see the same plants start near the repeller and traverse the negative growth rate portion of the density dependence down to the low attractor. It appears that the variation around the

point attractor estimated by the cubic fit in Figure 9.2 can be explained almost entirely by ladybug number. The slope of this line attractor makes sense; we would expect that as ladybug number decreases, the equilibrium population of aphids would increase.

Although the relationship appears to be quite linear in the range observed, it evidently does not hold true if extended to the x-intercept, or the equilibrium population of aphids expected with zero ladybugs. That intercept falls very close to 10^2 aphids, much lower than the actual equilibrium in the absence of ladybugs, which is larger than 10^4 (refer to the purple line in Figure 9.3 for the parametrized density dependence without predation). A final implication of the stability at this attractor is that ladybug emigration/immigration has equilibrated as well, a feature whose cause may require further study.

The second feature is nearly invisible without animation but becomes obvious when animated. To the left of the red dashed line (which I drew in) all the series (plants) moved down and to the left with time (decreasing aphid population and ladybug number) while to the right of that line all plants move up and to the right (increasing aphid population and ladybug number). This line is quite a stiff divider of dynamics; the above rule is followed in 39 of 40 cases, the lone exception being a plant which barely moved in either direction. It can be seen just above the red dashed line at about 10^3 aphids; it appears in the figure as almost a single point (careful analysis showed that it did increase in aphid number on 5 out of the 16 days operating under cubic density dependence, although in all of those cases the increase was nearly imperceptible). This line is the repeller in the cubic density dependence. Again, it appears that most of the variability around the point repeller estimated in Figure 9.2 is explained by ladybug number, given the excellent adherence to expected sign of growth rates on either side of the repeller line

(much better than with the repellor point). The high attractor has not been estimated in part because no populations approached it as closely as they did the low attractor, but I would also not expect the high attractor to be so clearly explained by ladybugs given that it is driven primarily by aphid population growth.

Conclusions

This model proved illuminating on the workings of the *Y. glauca*, *A. helianthi*, *C. septempunctata*, *H. convergens* host-herbivore-predator system. By conditions set forth in several previous articles (Kareiva, 1990; Holmes, et al., 1994; Turchin, et. al., 1998; Nakao & Mikhailov, 2010) it seems clear that a diffusive instability is operating in this system, leading to a classic Turing pattern in a hybrid stepping-stone/network space. It is safe to say that even without a number of major pieces of the natural history, we were able to capture several essential characteristics of this system, illustrating the potential for robust field-derived spatial ecology models in the spirit of, and building on the work of Kareiva & Odell (1987). Finally, the possibility of strong explanatory effects from an inhibitor spatially distributed in a classic manner for diffusive instability on non-point equilibria of activators was shown.

Continuing work

This work leaves much room for further exploration. Further empirical model development calls for the possible inclusion of several factors we left out: other species/life stages (checkered fly beetles, ants, ladybug larvae), senescence of the yucca

flowering stalk at the end of the season, and interference due to ladybug number on plant (i.e. competition), to name a few. Further analysis and refinement of those factors we included could always help, particularly of ladybug in-flight decision-making and their functional response.

For further analysis the model could be simplified and streamlined in several ways. Non-dimensionalizing the model would be a start. In addition, simplifying the structure--particularly the redistribution of ladybugs, possibly using an adapted network structure which could evolve with strength of connections between plants, ignoring very weak connections to reduce processing time could ease analysis considerably.

Within the current or a modified model framework, further analysis could be conducted on several aspects. Adjusting initial conditions to observe behavior above and below both attractors would be interesting. The density dependence also clearly calls for multiple regression, explaining growth rate with both aphid population and ladybug number. Some current analyses, particularly the power law relationships (Figures 11 and 13) and the density dependence might benefit from vector field analysis. Further study of which variables might explain variation in the route taken through these vector fields would be interesting as well (for example, what causes plants to take the distinct parallel routes they do to the low attractor in Figure 13.2?).

Addendum

A1. Explanation of Density Dependence Graphs

Understanding density dependence graphs is critical in population ecology and the reading of this paper. The first thing to note is that time is not on either axis, it is a mistake to think that a population progresses from left to right on these graphs, an individual population can (and will) move back and forth along its density dependence line/curve. The x-axis (horizontal) is current population size (number of individuals), and this is used to explain the current *per capita* growth rate which is on the y-axis (vertical). When the line or curve is above the x-axis it indicates a positive growth rate, below the x-axis a negative growth rate (i.e. population decline).

The most interesting and important feature of these graphs is the position and type of equilibria they show. Any time the line or curve passes through the x-axis that is an equilibrium (because at the x-axis growth rate=0, so a population of that size will stay that size; it is in equilibrium). There are two types of equilibria: attractors and repellers. The equilibrium in Figure 1.1 is an attractor, it can be identified because to the left of the equilibrium point (x-axis intercept), at lower population than equilibrium, the growth rate is positive, so population will increase to the equilibrium, while to the right of the equilibrium point, at higher population than equilibrium, growth rate is negative, so population will decline back down to equilibrium. Attractors always pass through the x-axis with a negative slope.

Repellers, like the middle one in Figure 1.2, pass through the x-axis with a positive slope, and following the same logic it can be seen that populations above or below the equilibrium point will go *away* from it, hence ‘repellor.’ In natural systems repellers do not act as practical equilibria; no population will be stable exactly at that

point, because random events will push it above or below that point and then it will 'fall' away from the repeller, much as a marble could hypothetically be balanced on top of a smooth sphere, but it is highly unlikely in reality.

Figure Legends

Figure 1 Density Dependence Examples

Figure 1.1: p. 68

This is an example of linear density dependence; carrying capacity (equilibrium) is at $N=3$

Figure 1.2: p. 68

This is an example of cubic density dependence. The low attractor is at $N \sim 0.5$, the repeller is at $N \sim 2.7$, and the high attractor is at $N \sim 4$.

Figure 1.3: p. 69

This figure demonstrates how cubic density dependence can be derived for prey with an undermatching predator (the prey population is on a log scale). The red line is the prey's density dependence in the absence of predators (linear). The blue line is the product of a type II functional response and an undermatching predator curve (i.e. rate of consumption per predator times number of predators), all divided by prey number. This yields per capita predation rate on prey. Subtracting predation rate (blue) from predator-free density dependence (red) we obtain cubic density dependence (green).

Figure 2 Ladybug redistribution

Figure 2.1: p. 69

This figure shows all the possible destinations a ladybug could select as it leaves the red plant (plant 'j' in the model) in a simplified system (note that flying back to the red plant is an option).

Figure 2.2: p. 69

This figure shows all the possible sources of redistributing ladybugs arriving at the green plant (plant 'i' in the model) in a simplified system (note that the green plant can be a source for itself, if a ladybug leaves but chooses to return).

Figure 3 Model Aphid Populations: p. 70

This figure shows the aphid populations as produced by the model on each (of 40) plants over the course of a 30 day model run.

Figure 4 Field Aphid Populations: p. 70

This figure shows the aphid populations as recorded in the field on each (of 107) plants over the course of a 30 days.

Figure 5 Model Ladybug Populations: p. 71

This figure shows the ladybug populations as produced by the model on each (of 40) plants over the course of a 30 day model run.

Figure 6 Field Ladybug Populations: p. 71

This figure shows the ladybug populations as recorded in the field on each (of 107) plants over the course of a 30 days.

Figure 7 Model Distribution of Aphids: p. 72

This figure shows the distribution of aphid population sizes (on a log scale) as produced by the model on day 25 of the model run

Figure 8 Field Distribution of Aphids: p. 72

This figure shows the distribution of aphid population sizes (on a log scale) as recorded in the field on day 15.

Figure 9 Model Aphid Density Dependence

Figure 9.1: p. 73

This figure shows aphid density dependence as produced by the model, calculated every day for all 30 days of the model run. Linear, quadratic, and cubic regressions are shown in red, blue, and green (respectively).

Figure 9.2: p. 73

This figure shows aphid density dependence of aphids only from days 15-29 of the model run. Note the excellent fit of the cubic density dependence.

Figure 9.3: p. 74

This figure shows aphid density dependence only from days 1-7 of the model run. Note the linearity of the data.

Figure 10: p. 74

This figure shows the best fit curve of the density dependence every day for aphids in the field. Most days cubic density dependence is observed, corroborating the data from the model.

Figure 11: p. 75

This figure shows ladybug/aphid ratio plotted against aphid number (both logged) from the model output (days 15-30). It can be seen that as aphid number increases, ladybug/aphid ratio decreases; this demonstrates how aphids experience safety in numbers due to undermatching by ladybugs. The strength of the linear regression is obvious.

Figure 12: p. 75

This figure shows the same data as Figure 11, but from field data.

Figure 13

Figure 13.1 p. 76

This figure shows average ladybug number on a plant plotted against average aphid number on that plant (both logged) as produced by the model (days 15-30). It can be seen that overall there is a positive trend suggesting that ladybugs are able to find aphids, but the trend is weak and the data obviously nonlinear.

Figure 13.2 p. 76

This figure shows the same data as Figure 13.1 but instead of averaging aphid and ladybug numbers, every day is included (days 15-30). The dashed red line was found to be the repeller from the cubic density dependence; all plants to the right of it have increasing aphid populations with time while all plants to the left of it have decreasing aphid populations with time. No aphid populations cross this line during the course of the model run. The dashed blue line was found to be the low attractor from the cubic density dependence. Several aphid populations approached it and then stayed at it.

Figure 14: p. 77

This figure shows the same data as Figure 13.1 but from field data, here the nonlinearity is not observed, but evidence that ladybugs are able to find aphids remains.

Figure 15: p. 77

This figure shows aphid skewness from the model output (days 15-40) showing a gradual increasing trend.

Figure 16: p. 78

This figure shows aphid skewness from field data, showing a steeper increase.

Figure 17: p. 78

This figure shows ladybug skewness from the model output (days 15-40). The red regression line is for all points shown, while the green regression line is only for days 25-40.

Figure 18: p. 79

This figure ladybug skewness in the field showing a definite increasing trend.

Figure 19: p. 79

This figure shows aphid and ladybug skewness on the same graph, showing that once ladybugs have 'sorted themselves out' aphid skewness is consistently higher than that of ladybugs.

Figure 20: p. 80

This figure shows the field skewness of aphids and ladybugs where aphids are clearly more skewed.

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Table 1

Parameter	Description	Value & Dimensions
α	Immigration of aphids	3 aphid*day ⁻¹
κ	Slope of log linear density dependence	-0.2113 aphid ⁻¹ *day ⁻¹
r_0	y-intercept of aphid growth rate	0.8521 day ⁻¹
λ	Maximum feeding rate of ladybugs	65 aphid*day ⁻¹
h	Half saturation constant for ladybug feeding	238 aphid
μ	Diffusion rate of ladybugs off a plant	40.61 day ⁻¹
σ	Reduction in diffusion rate with additional aphids	4.07*10 ⁻⁴ aphid ⁻¹
δ	Rate of decay with distance of ladybug diffusion	0.95 m ⁻¹
Φ	Rate of attractiveness of ladybug	30.53 ladybug ⁻¹
ϵ	Rate of decay of attraction with distance	1 m ⁻¹
c	Saturation constant for ladybug attraction	0.5 ladybug ⁻¹
g	Attractiveness of non-yucca/leaving system	8.16 unitless
ω	Rate of attraction of ladybugs from outside systems	10 day ⁻¹
ψ	Diffusive immigration of ladybugs from outside system	0.5 ladybug*day ⁻¹
n	Number of plants in model (variable, user set)	40 in our model runs

Table 2

Model Density Dependence-All Days							
Figure 9.1	co-efficient	Value	p-value	R ²	Varbl order	Variables	Form
Linear Regression (Red Line)							
	a	-0.112776	~10 ⁻²³	0.0802467	{x,y}	{log(aph),rt}	y=a*x+b
	b	0.390471	~10 ⁻³⁷				
Quadratic Fit (Blue Curve)							
	a	0.0335806	0.0163	0.171057	{x,y}	{log(aph),rt}	y=a*x ² +b*x+c
	b	0.0266272	0.6512				
	c	0.275723	~10 ⁻⁶				
Cubic Fit (Green Curve)							
	a	0.0873398	~10 ⁻⁶	0.186956	{x,y}	{log(aph),rt}	y=a*x ³ +b*x ² +c*x+d
	b	-0.576814	~10 ⁻⁷				
	c	1.01887	~10 ⁻⁶				
	d	-0.200854	0.080				
Model Density Dependence-Days 15-29							
Figure 9.2	co-efficient	Value	p-value	R ²	Varbl order	Variables	Form
Linear Regression (Red Line)							
	a	0.0695618	~10 ⁻²⁴	0.161328	{x,y}	{log(aph),rt}	y=a*x+b
	b	-0.260802	~10 ⁻⁴²				
Quadratic Fit (Blue Curve)							
	a	0.145308	~10 ⁻⁷⁹	0.62939	{x,y}	{log(aph),rt}	y=a*x ² +b*x+c
	b	-0.521471	~10 ⁻⁶⁴				
	c	0.168484	~10 ⁻¹²				
Cubic Fit (Green Curve)							
	a	-0.137558	~10 ⁻⁶⁷	0.775595	{x,y}	{log(aph),rt}	y=a*x ³ +b*x ² +c*x+d
	b	1.0137	~10 ⁻⁸³				
	c	-2.11086	~10 ⁻⁹⁶				
	d	0.891727	~10 ⁻⁷⁷				
Model Density Dependence-Days 1-7							
Figure 9.3	co-efficient	Value	p-value	R ²	Varbl order	Variables	Form
Linear Regression (Red Line)							
	a	-0.353499	~10 ⁻¹⁸⁶	0.952424	{x,y}	{log(aph),rt}	y=a*x+b
	b	1.24623	~10 ⁻²⁵²				
Quadratic Fit (Blue Curve)							
	a	0.102411	~10 ⁻¹²²	0.999101	{x,y}	{log(aph),rt}	y=a*x ² +b*x+c
	b	-0.720225	~10 ⁻¹⁹⁵				
	c	1.53183	~10 ⁻³⁰¹				
Cubic Fit (Green Curve)							
	a	-0.055077	~10 ⁻¹⁵⁹	0.999934	{x,y}	{log(aph),rt}	y=a*x ³ +b*x ² +c*x+d
	b	0.406472	~10 ⁻¹⁹¹				
	c	-1.22806	~10 ⁻²⁵⁶				
	d	1.77574	~10 ⁻³⁷⁹				
Model Power Law (Ladybug:Aphid Ratio)-Days 15-30							
Figure 11	co-efficient	Value	p-value	R ²	Varbl order	Variables	Form
	a	-0.977986	~10 ⁻⁷⁰⁶	0.993778	{x,y}	{log(aph),log(lb/aph)}	y=a*x+b
	b	0.713997	~10 ⁻³⁵⁰				
Field Power Law (Ladybug:Aphid Ratio)							
Figure 12	co-efficient	Value	p-value	R ²	Varbl order	Variables	Form
	a	-0.6801		0.7455	{x,y}	{log(aph),log(lb/aph)}	y=a*x+b
	b	-0.5641					
Model Power Law (Ladybugs v. Aphids)-Days 15-30							
Figure 13	co-efficient	Value	p-value	R ²	Varbl order	Variables	Form
Linear Regression-Days 15-30 Plant Averages							
13.1	a	0.0537373	0.00018574	0.310887	{x,y}	{log(aph),log(aph)}	y=a*x+b
13.1	b	0.687065	~10 ⁻²⁰				
Linear Regression-Days 15-30 (no averaging) Note: this regression not shown in figure							
13.2	a	0.0220135	~10 ⁻¹²	0.0748679	{x,y}	{log(aph),log(lb)}	y=a*x+b
13.2	b	0.713997	~10 ⁻³⁵⁰				

Table 2

Field Power Law (Ladybugs v. Aphids) Plant Averages							
Figure 14	co-efficient	Value	p-value	R ²	Varbl order	Variables	Form
	a	0.34104		0.4506	{x,y}	{log(aph),log(lb)}	y=a*x+b
	b	-0.5732					
Model Aphid z score of Skewness-Days 15-40							
Figure 15	co-efficient	Value	p-value	R ²	Varbl order	Variables	Form
	a	0.0625659	~10 ⁻¹²	0.87105	{x,y}	{day,skewness}	y=a*x+b
	b	-0.245018	0.093				
Field Aphid z score of Skewness-All Days							
Figure 16	co-efficient	Value	p-value	R ²	Varbl order	Variables	Form
	a	0.3875	<0.0005	0.5578	{x,y}	{log(aph),log(lb/aph)}	y=a*x+b
	b	12.588					
Model Ladybug z score of Skewness-Days 15-40 (Red line)							
Figure 17	co-efficient	Value	p-value	R ²	Varbl order	Variables	Form
	a	-0.115243	~10 ⁻⁶	0.601772	{x,y}	{day,skewness}	y=a*x+b
	b	4.41475	~10 ⁻⁸				
Model Ladybug z score of Skewness-Days 25-40 (Green line)							
Figure 17	co-efficient	Value	p-value	R ²	Varbl order	Variables	Form
	a	0.00927365	0.000137	0.657986	{x,y}	{day,skewness}	y=a*x+b
	b	0.254306	0.000685				
Field Ladybug z score of Skewness-All Days							
Figure 18	co-efficient	Value	p-value	R ²	Varbl order	Variables	Form
	a	0.265	0.001	0.3133		{day, skewness}	y=a*x+b
	b	7.1049					

Figure 1.1: Linear Density Dependence

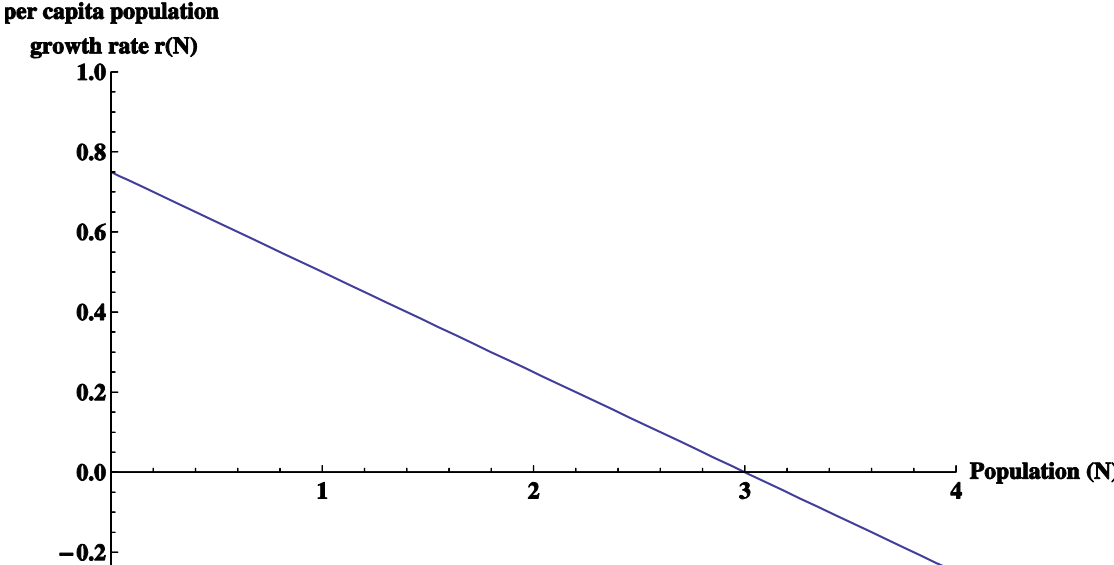


Figure 1.2: Cubic Density Dependence

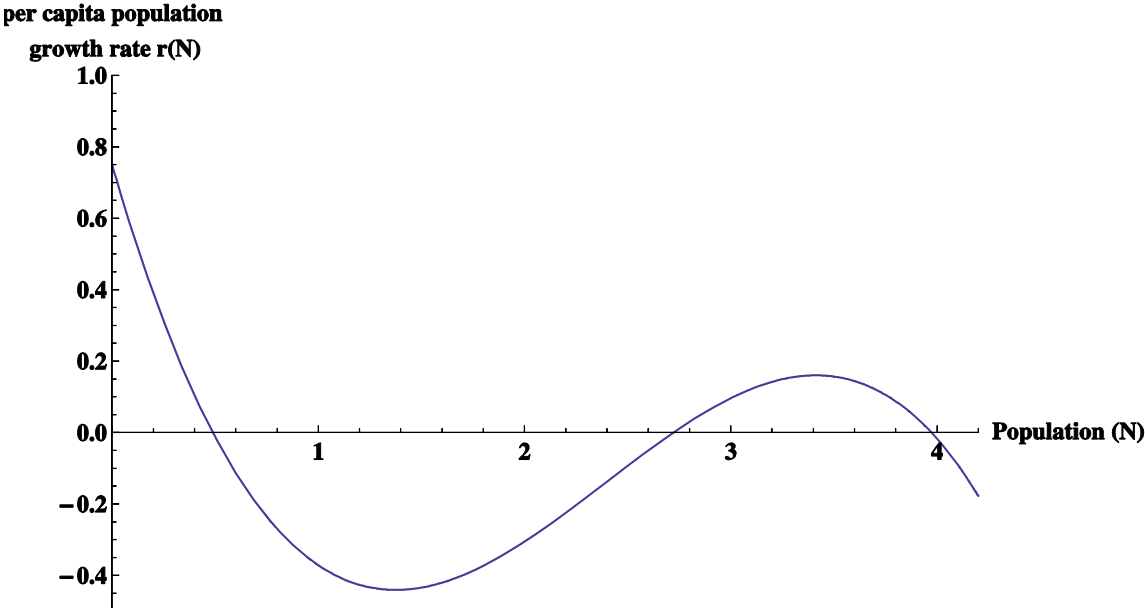


Figure 1.3: Deriving Cubic Density Dependence

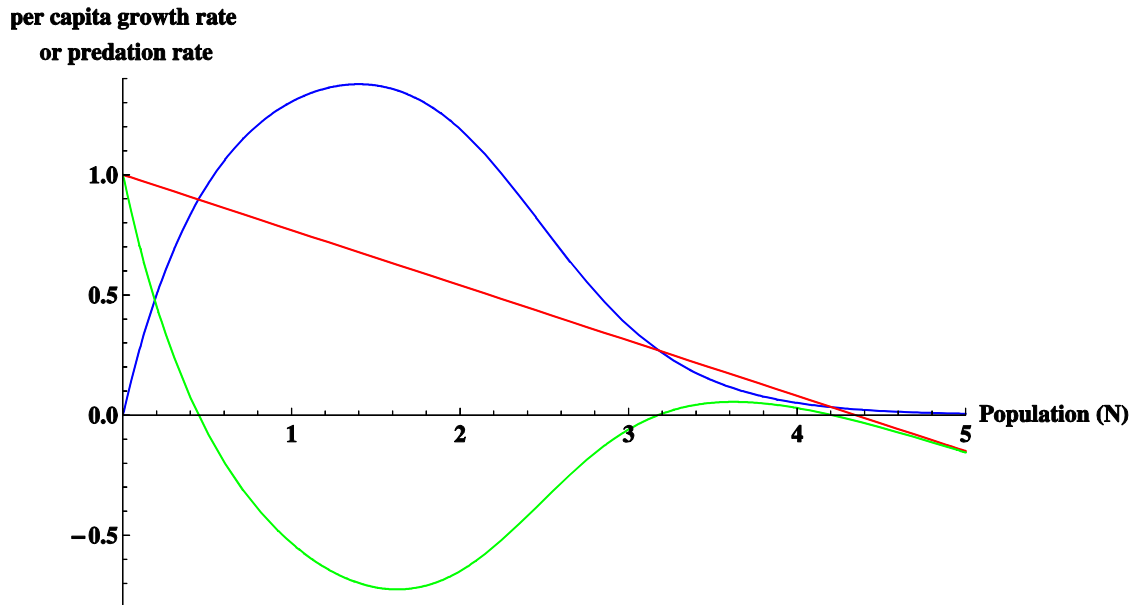


Figure 2.1: Possible Destinations

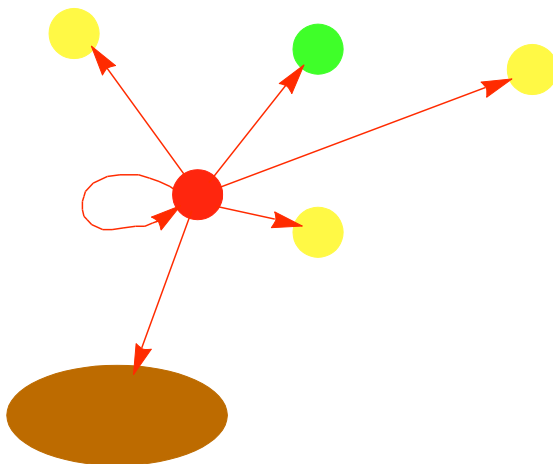


Figure 2.2: Possible Sources

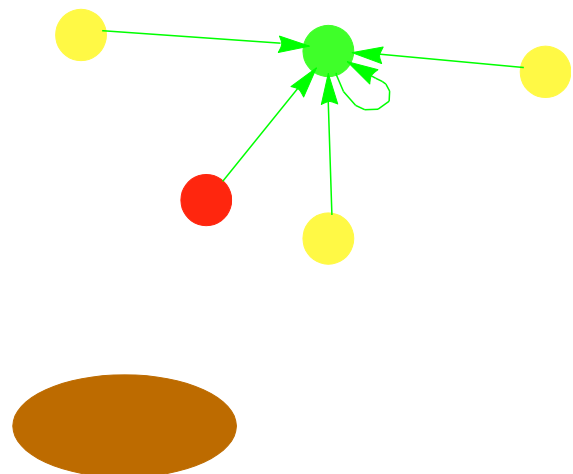


Figure 3: Model Aphid Populations

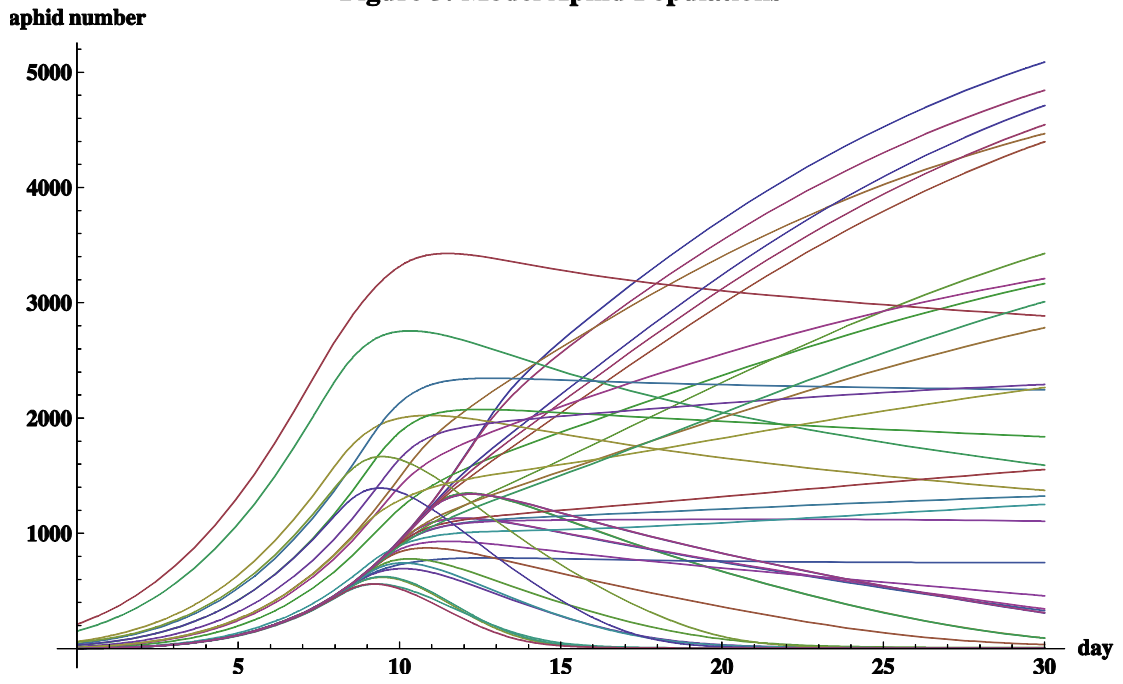


Figure 4: Field Aphid Populations

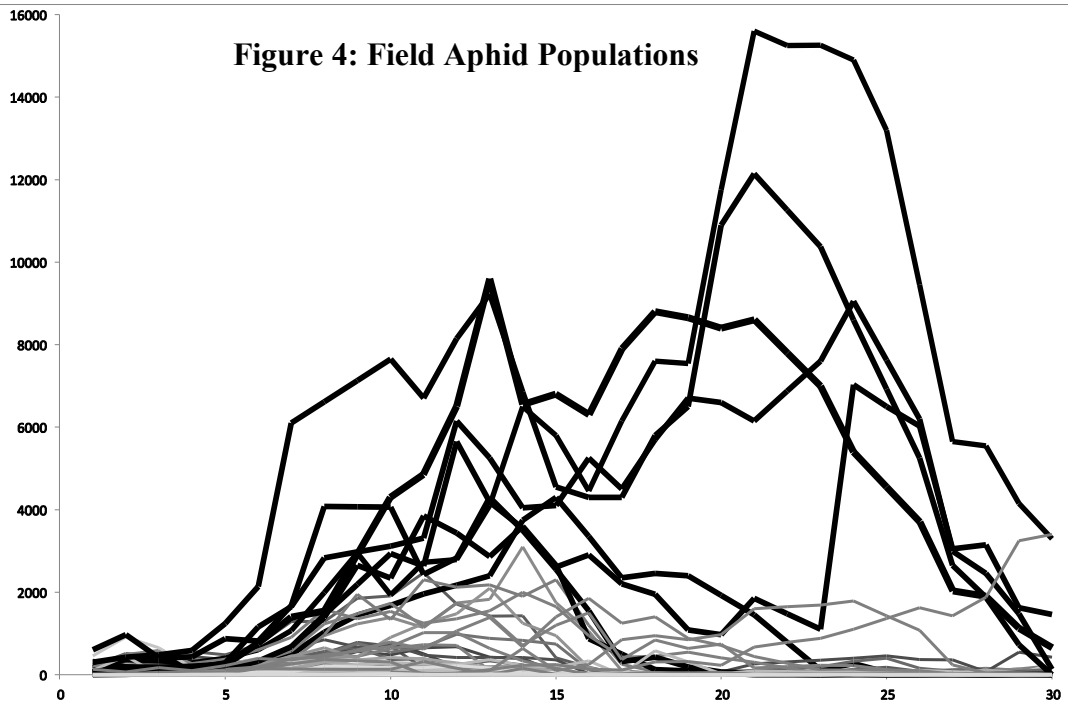


Figure 5: Model Ladybug Numbers

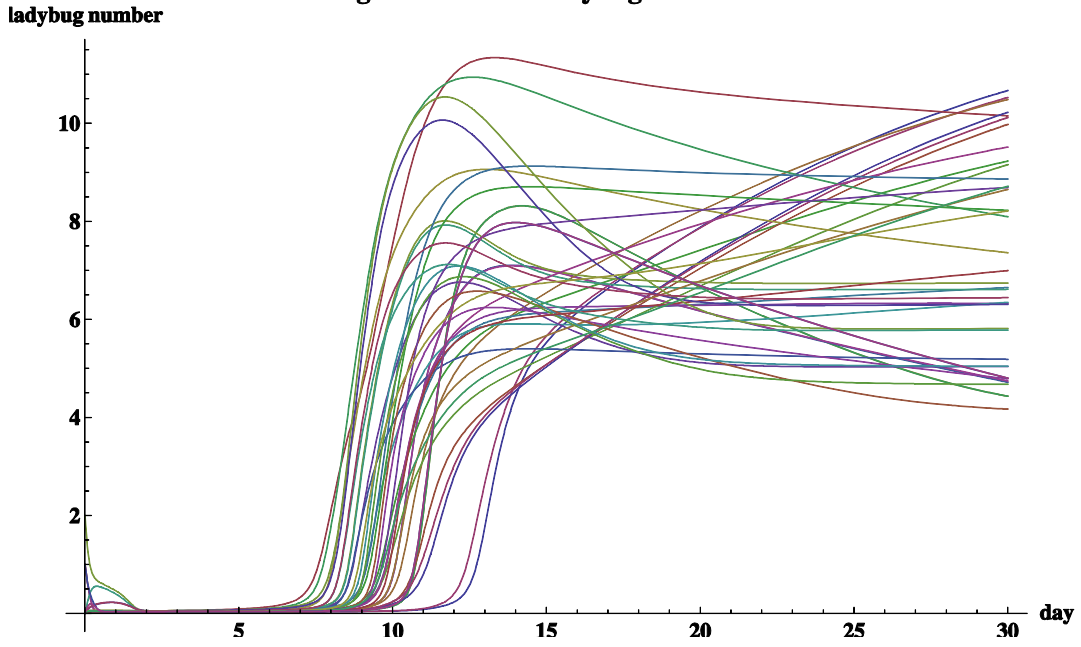


Figure 6: Field Ladybug Numbers

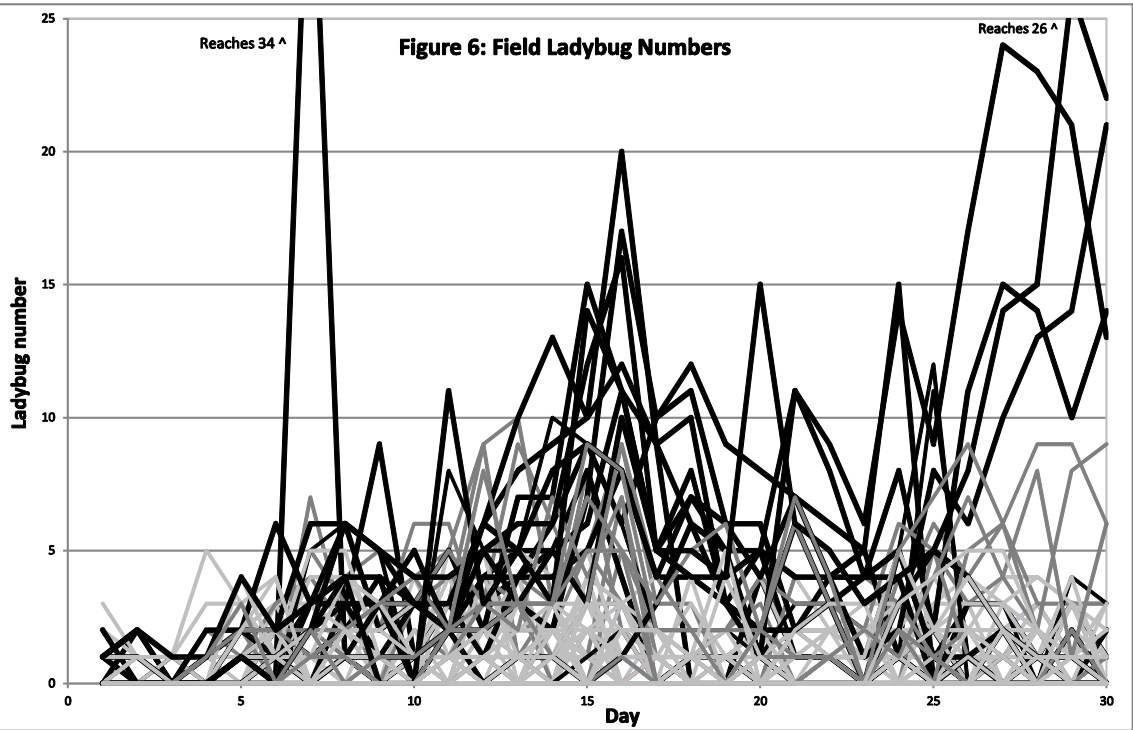


Figure 7: Model Distribution of Aphid Populations Day 25

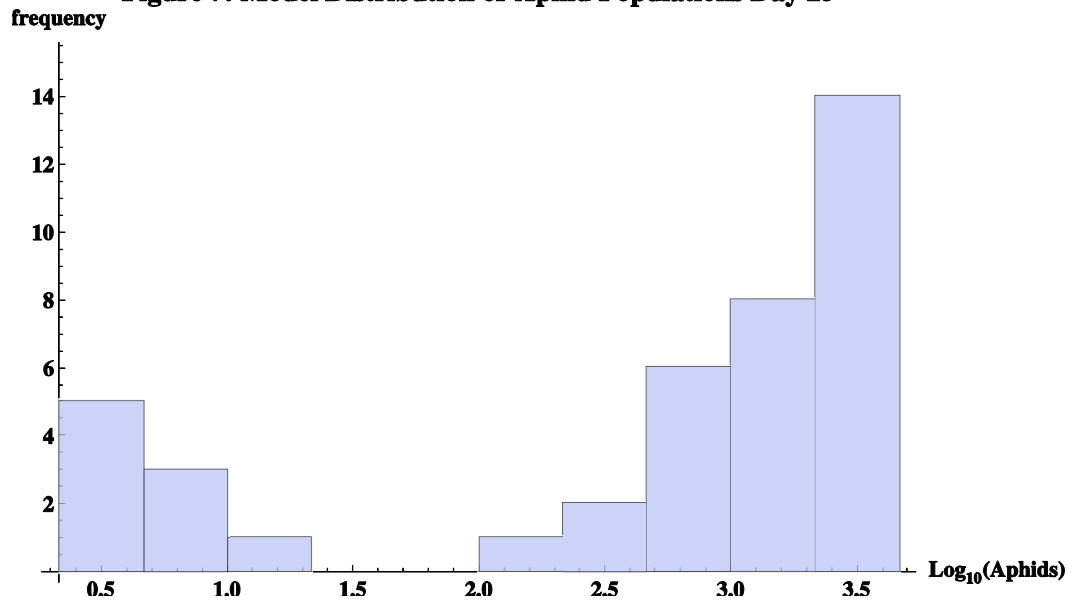


Figure 8: Field Distribution of Aphid Populations Day 15

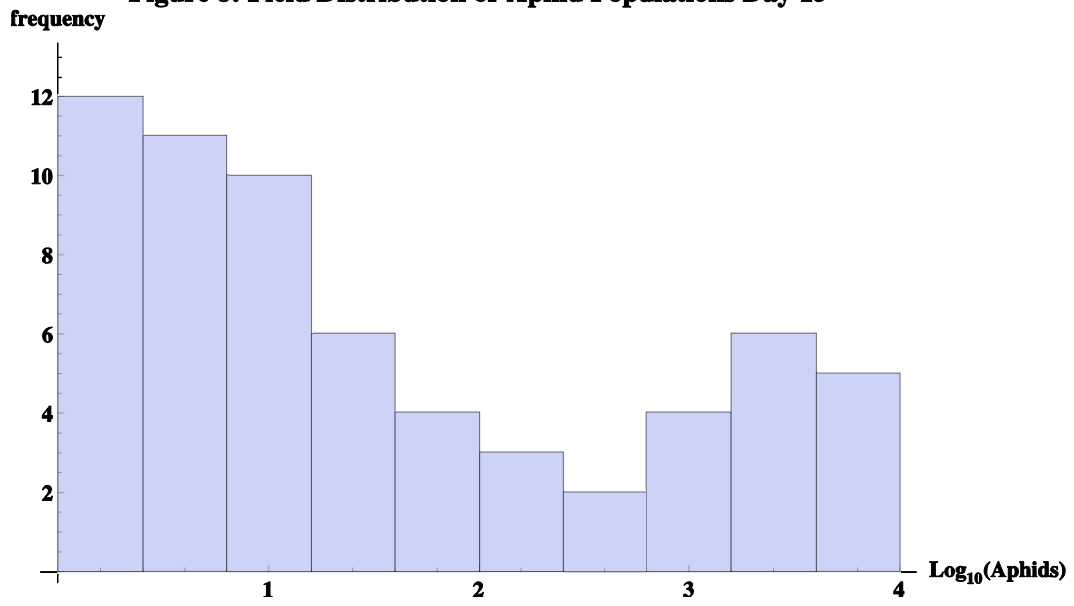


Figure 9.1: Aphid Density Dependence All Days

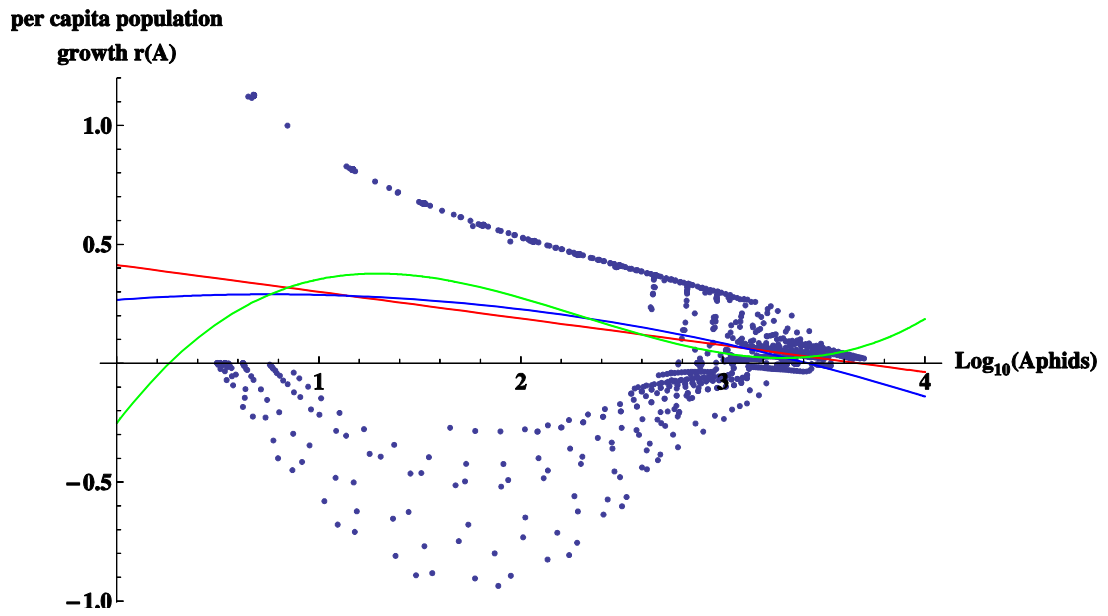


Figure 9.2: Aphid Density Dependence Days 15–29

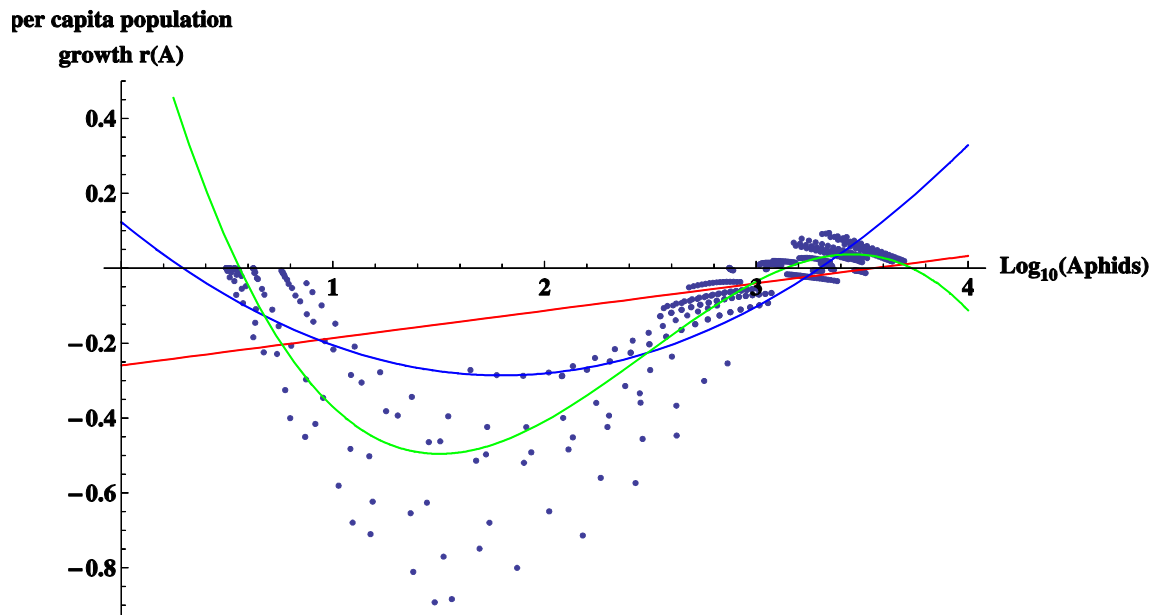


Figure 9.3: Aphid Density Dependence Days 1–7

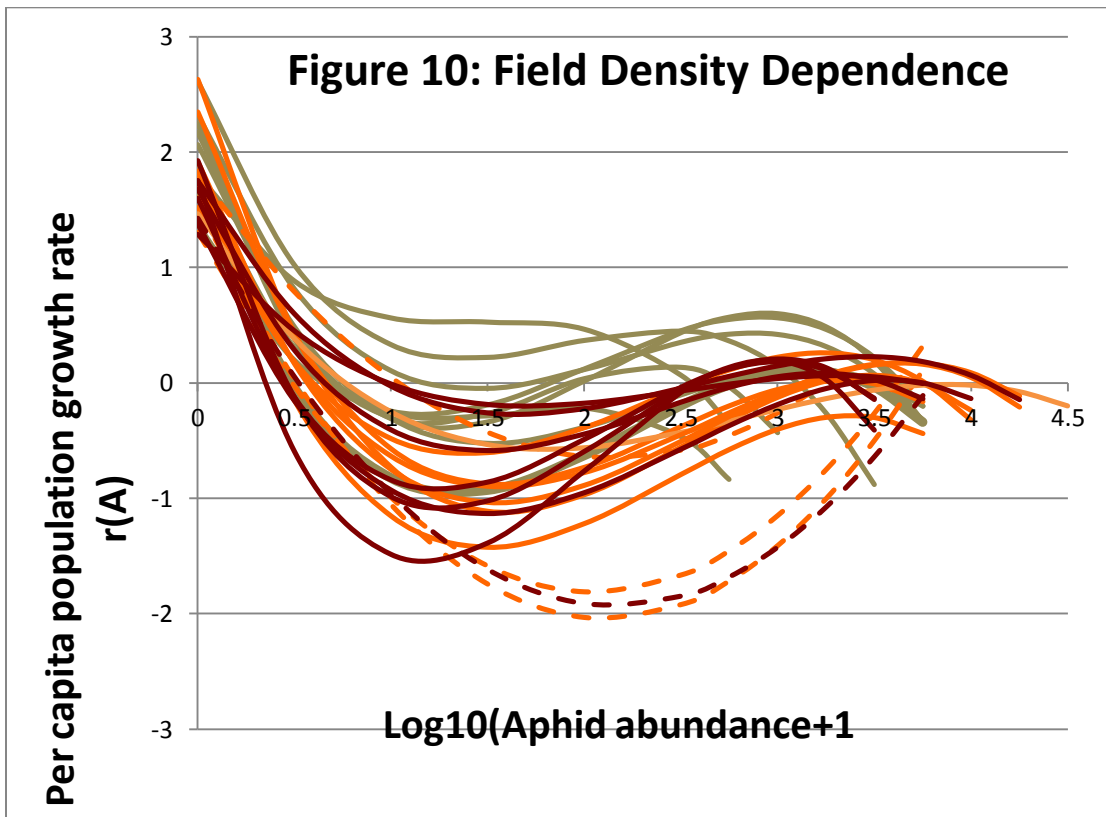
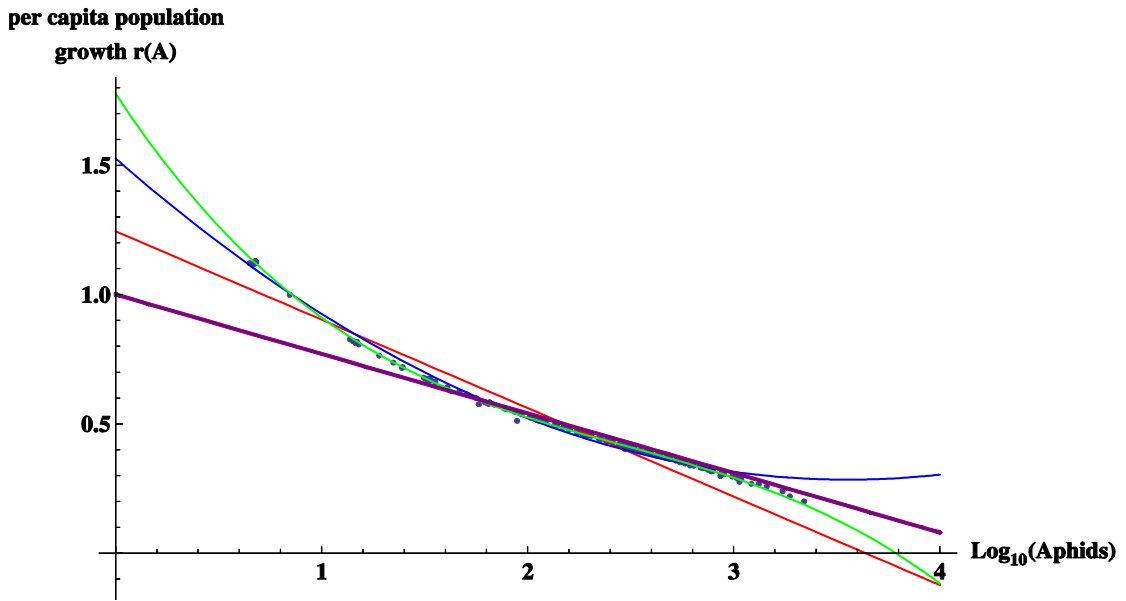


Figure 11

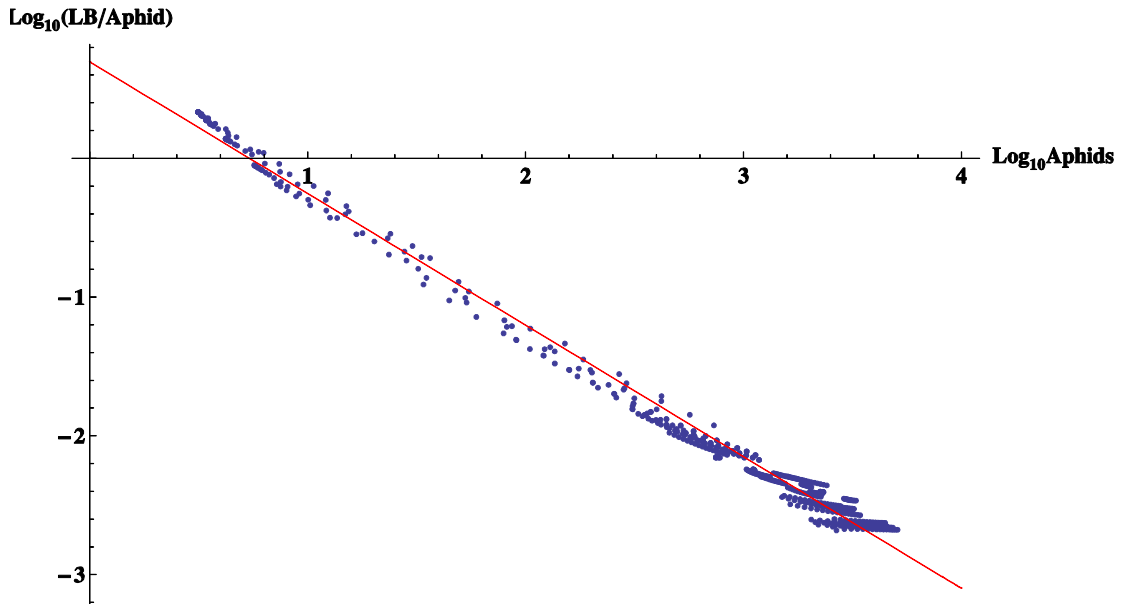


Figure 12

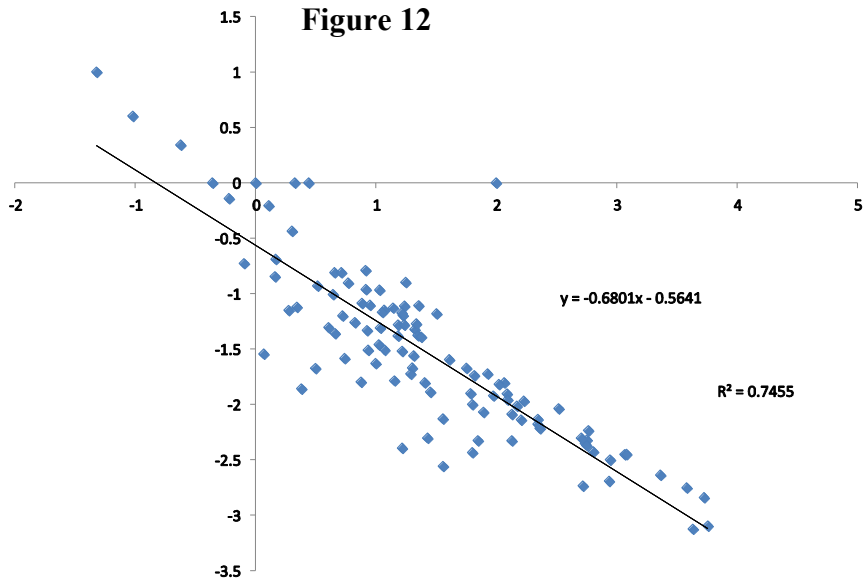


Figure 13.1

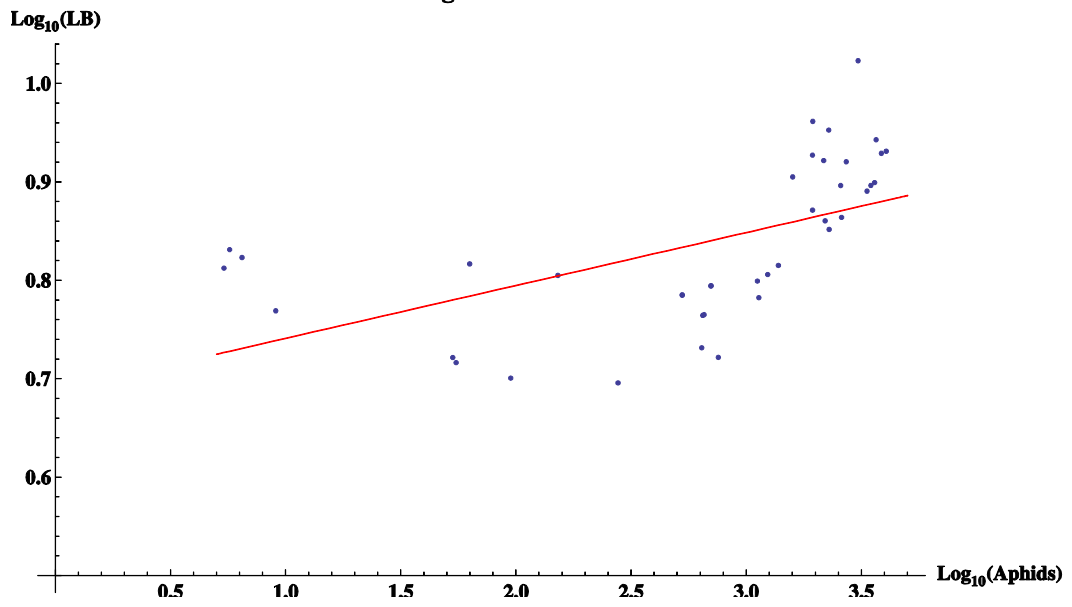
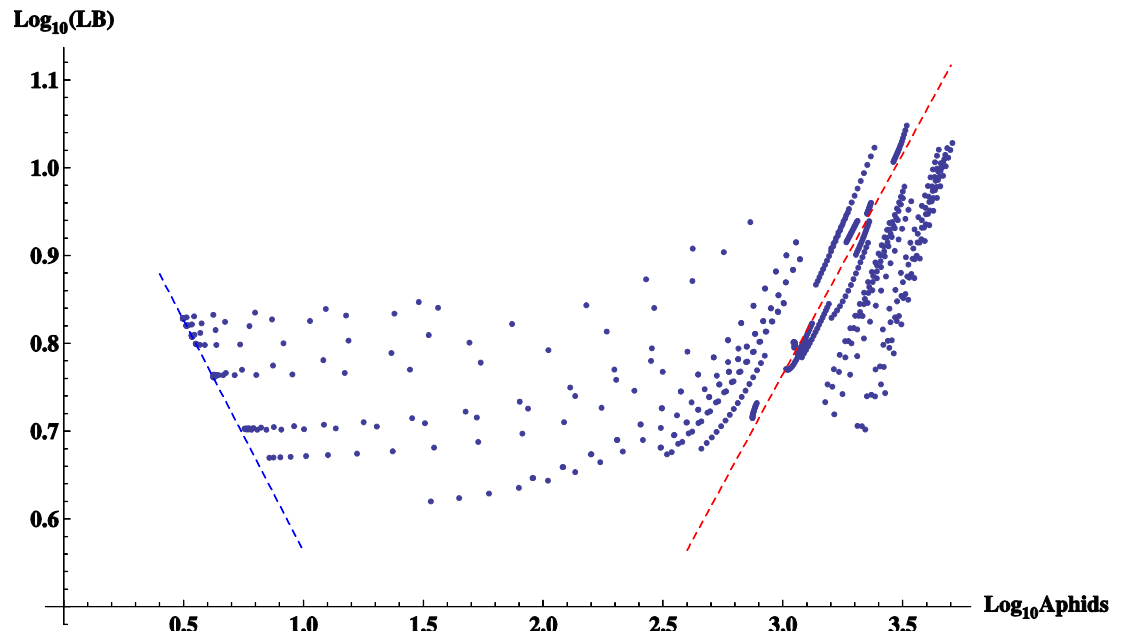


Figure 13.2



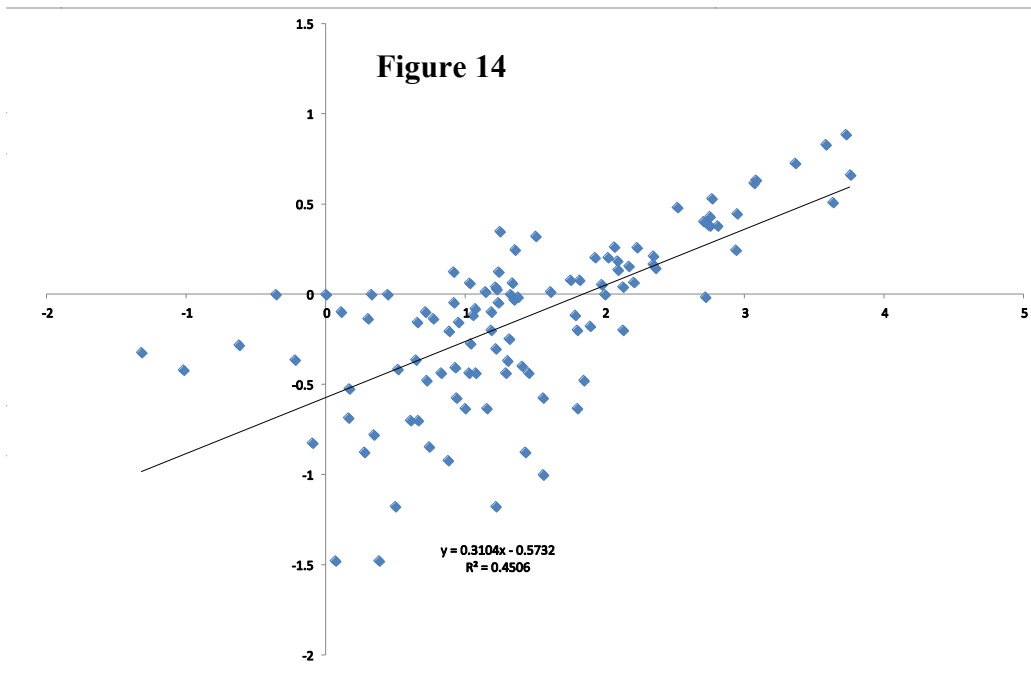


Figure 15

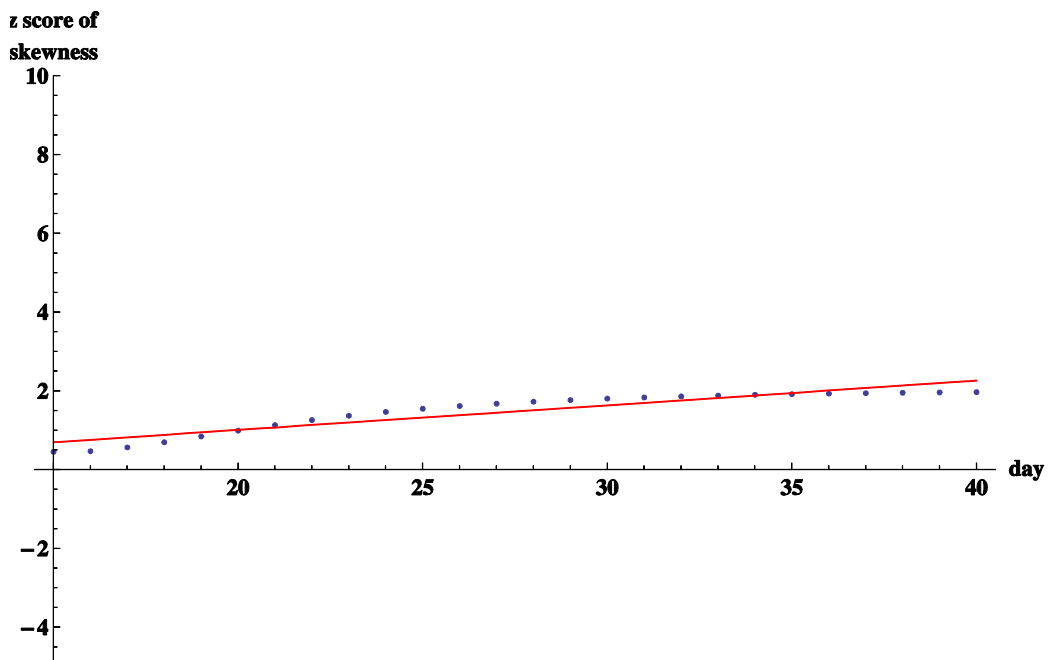


Figure 16

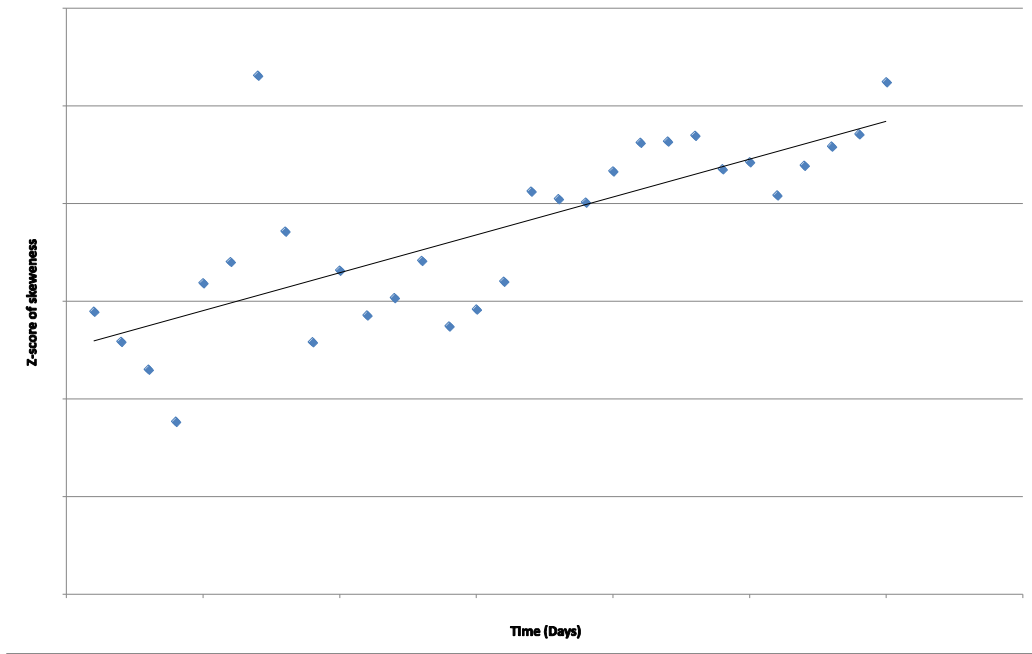


Figure 17

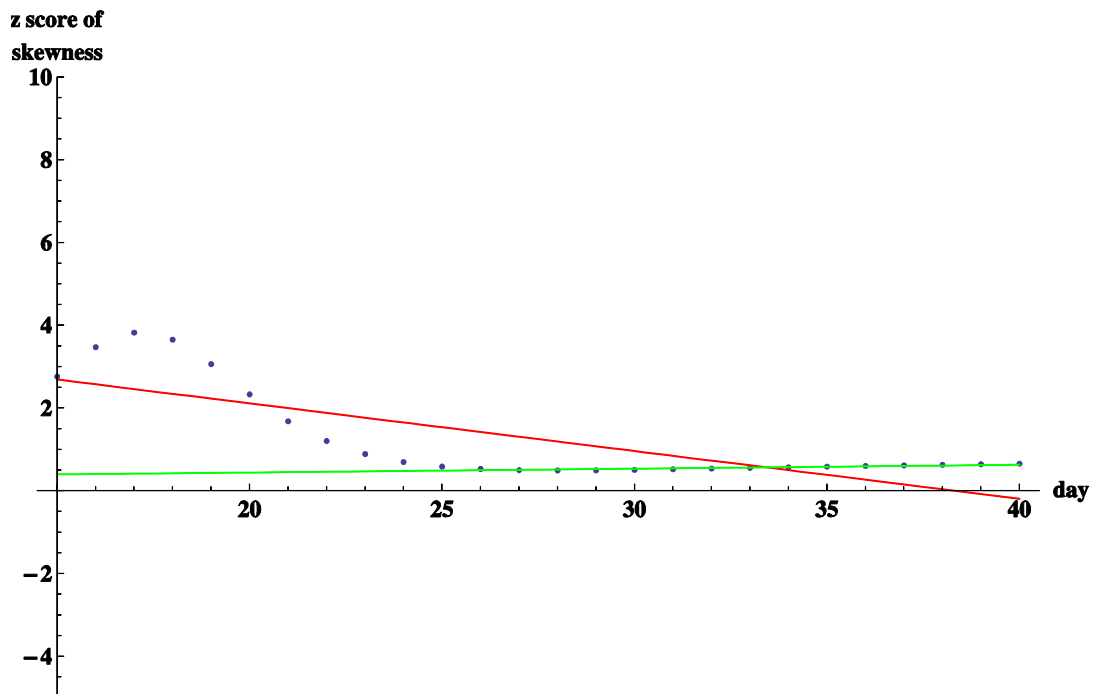


Figure 18

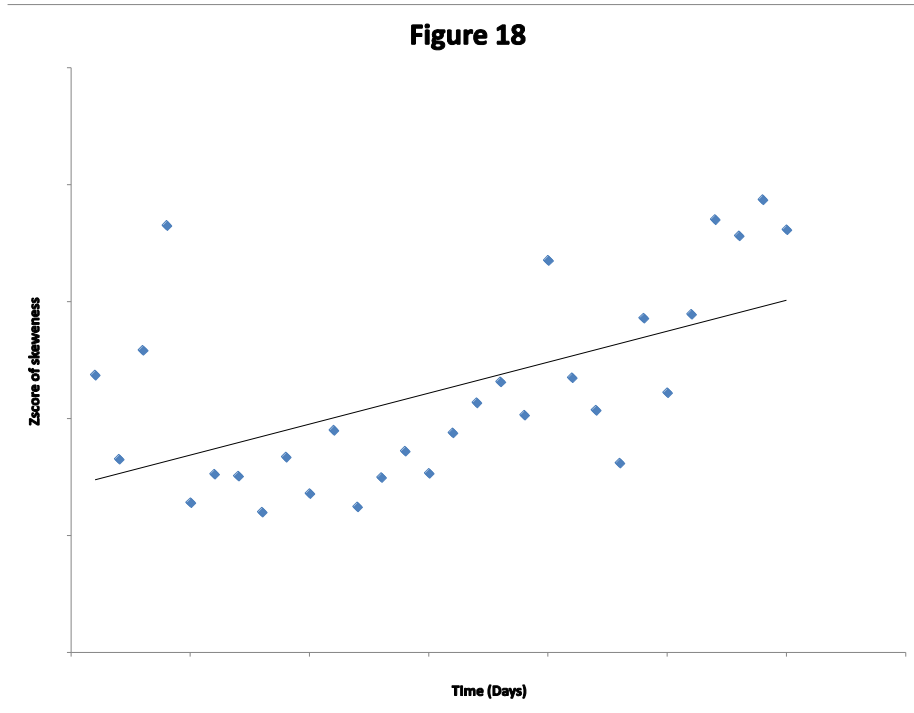


Figure 19

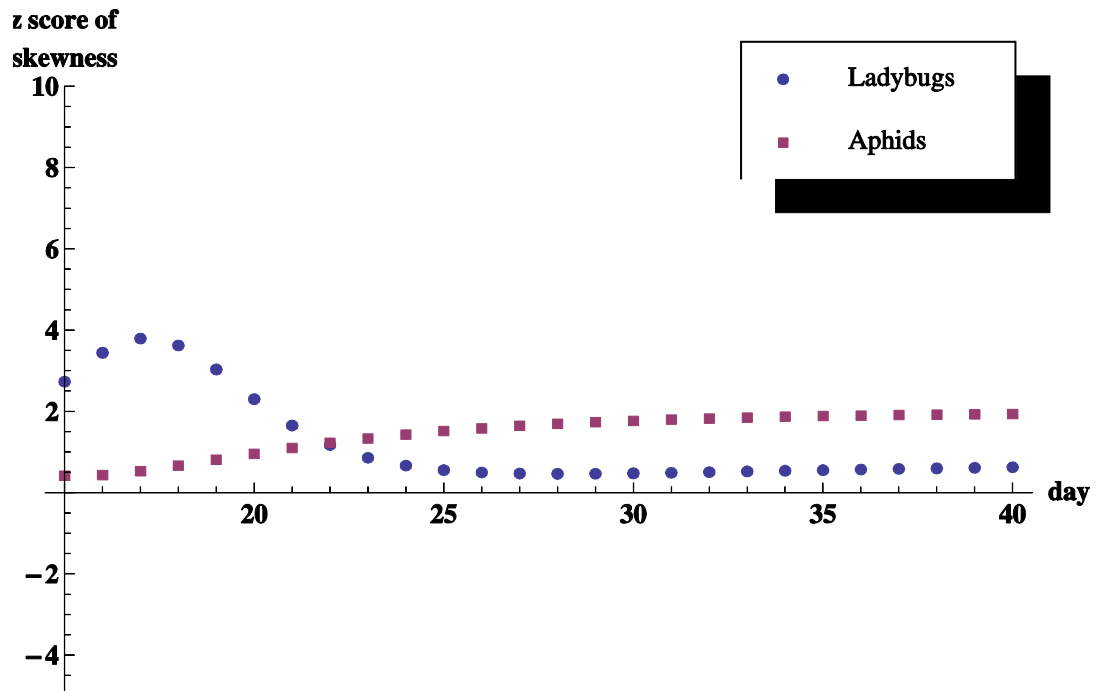


Figure 20

