The use of simulation modeling to evaluate the mechanisms responsible for the nutritional benefits of food-for-protection mutualisms

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A B S T R A C T

In some mutualisms, a plant or insect provides a food resource in exchange for protection from herbivores, competitors or predators. This food resource can benefit the consumer, but the relative importance of different mechanisms responsible for this benefit is unclear. We used a colony-level simulation model to test the relative importance of increased larval production, increased worker foraging and increased worker survival for colony growth of fire ants, *Solenopsis invicta*, that consume plant-based foods. Increased food for larvae had the largest effect on colony growth of *S. invicta* followed by decreased worker mortality. Increased foraging rate had a small effect in the simulation model but data from a small laboratory experiment and another published study suggest that plant-based foods have little or no effect on foraging rates of *S. invicta*. Colony growth steadily increased the longer plant-based food was available and colonies were most responsive to plant-based food in the early summer (i.e., June). Our results demonstrate that population level simulation modeling can be a useful tool for examining the ecology of mutualistic interactions and the mechanisms through which species interact.

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1. Introduction

Mutualisms are widespread among plants and animals (Boucher et al., 1982; Bronstein, 1994). These associations typically involve one species exchanging resources (e.g., food or nesting areas) or services (e.g., defense or cleaning) with another species. The most common types of mutualisms (e.g., mycorrhizal associations, pollination, and food-for-defense mutualisms) can play important roles in shaping the structure and diversity of ecological communities and can also influence the spread and impact of invasive species (Smith et al., 1997; Johnson and Steiner, 2000; Richardson et al., 2000; Helms and Vinson, 2002; Ness and Bronstein, 2004; Lach, 2007). Recent evolutionary models and syntheses have greatly advanced our understanding of the evolution and maintenance of mutualisms (Boucher et al., 1982; Bronstein, 1994; Bronstein et al., 2006); however, these advances would not have been possible without empirical data and ecological modeling of the costs and benefits of mutualistic associations in model systems (e.g., Addicott, 1986; Bronstein and McKey, 1989).

One of the most ubiquitous mutualisms involves food-for-protection mutualisms in which consumers ingest resources from a plant or animal and, in exchange, protect the plant or animal from herbivores, predators or competitors (Stadler and Dixon, 2005; Wackers et al., 2005). Common types of food products in these mutualisms include: floral and extrafloral nectar produced by plants and honeydew produced by hemipterans, including aphids, mealybugs and scales (Bluthgen et al., 2004; Bronstein et al., 2006). These food resources typically contain small amounts of amino acids and relatively large amounts of carbohydrates (Gottsberger et al., 1984; Bluthgen et al., 2004). In some animals, the mechanisms through which consumers benefit from these food resources is clear. For example, in parasitoid wasps, females that consume extrafloral nectar have greater longevity and, hence, more time to locate and parasitize herbivores (Wackers et al., 2005). However, in other animals, the mechanisms contributing to the benefit are less clear. For example, colonies of red imported fire ants, *Solenopsis invicta* Buren, are over 50% larger when they have access to honeydew but it is unclear if this is due to the effects of honeydew on larval production, worker foraging rate or worker survival (Helms and Vinson, 2008; Wilder et al., in review).

Food resources provided by mutualists (e.g., honeydew, floral nectar and extrafloral nectar; hereafter: "plant-based food resources") have been hypothesized to benefit consumers through three different mechanisms (Stadler and Dixon, 2005; Wackers et al., 2005). First, the amino acid content of these plant-based

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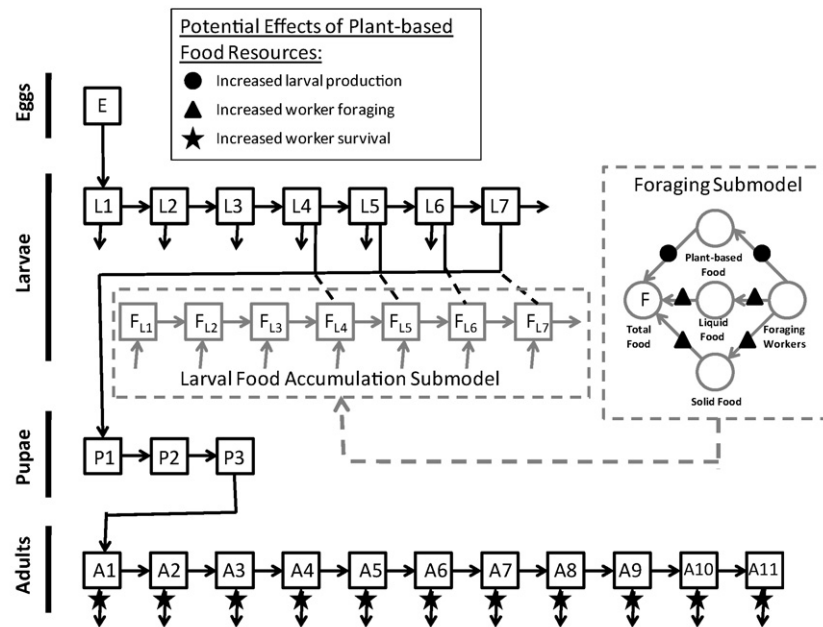
Fig. 1. Simplified diagram of the model simulating the dynamics of a single colony of red imported fire ants. All life stages in a young (non-reproducing) colony are represented and individuals pass from one box to the next in a 5-day time step. At larval stages 4–7 (L4–L7) individuals can mature to pupae if they have accumulated enough food in the parallel "Larval Food Accumulation Submodel". Arrows leaving boxes without connecting to another box represent mortality. Arrows entering into boxes in the "Larval Food Accumulation Submodel" represent allocation of food to different life stages of larvae from the "Total Food" part of the "Foraging Submodel". The proportion of the "Total Food" allocated to a larval developmental stage is equal to the proportion of the total number of larvae in that developmental stage. Circles, triangles and stars indicate the pathways through which plant-based food resources (i.e., nectar, extrafloral nectar and honeydew) can affect the fire ant colony.

resources may increase the production of offspring (Mevi-Schutz and Erhardt, 2005). For example, in the map butterfly, *Arashnia levana*, females produce 50% more eggs when fed a nectar mimic containing amino acids compared to nectar with only sugars (Mevi-Schutz and Erhardt, 2005). Second, the carbohydrates in plant-based food may provide a source of energy to increase activity and foraging of consumers (e.g., the fuel for foraging hypothesis; Davidson, 1997; Stadler and Dixon, 2005; Koptur, 2005; Grover et al., 2007; Kay et al., 2010). For example, in the Argentine ant, *Linepithema humile*, workers are over twice as active when provided with carbohydrates (Grover et al., 2007; Kay et al., 2010). Third, the carbohydrate content of plant-based food may increase the longevity of consumers. This occurs in many species of parasitoid wasps and flies, as well as some predatory arthropods (Wackers et al., 2005, 2008). Separate studies have provided support for each of these three mechanisms in a range of species. However, a more thorough understanding of the evolution and maintenance of mutualisms require a more quantitative and comprehensive study that simultaneously evaluates the effects of mutualistic interactions on multiple components of fitness.

The purpose of this study was to use simulation modeling to examine the relative importance of the three mechanisms (i.e., increased larval production, increased foraging activity and/or increased survival) through which plant-based foods could contribute to increased colony growth of a widespread invasive ant, the red imported fire ant (*S. invicta*). Using empirical data and published sociometric data for *S. invicta* (Tschinkel, 1993, 2006), we constructed a colony-level simulation model of the dynamics of a *S. invicta* colony during a single annual cycle. The simulation model allowed us to isolate the effects of the three mechanisms alone and in combination on colony growth of *S. invicta*, which would be nearly impossible to do with laboratory or field experiments. In addition, we used the simulation model to explore how changes in the timing or duration of plant-based foods affected colony growth in *S. invicta*.

2. Materials and methods

2.1. Laboratory experiment

We conducted a laboratory experiment to collect empirical data for the model on the effects of artificial extrafloral nectar on foraging activity and worker survival in *S. invicta*. Colonies of *S. invicta* were excavated from the campus of Texas A&M University (College Station, Brazos County, TX, USA) in March 2009, reduced to a standard size (i.e., 2 queens, 50 brood and 1 g, ca. 1200, workers) and maintained under laboratory conditions (see Wilder and Eubanks, 2010 for details). We randomly assigned colonies to 2 treatments that were provided with a 5 ml vial of either: water ($n = 12$) or artificial nectar ($n = 26$). The artificial nectar mimicked the nutritional composition of extrafloral nectar of *Passiflora* spp., which has a nutritional content similar to many other plant-based resources (Lanza, 1991; Bluthgen et al., 2004). The vials with the experimental treatments were replaced twice each week.

Sixteen days after the laboratory colonies were established, we conducted an experiment to measure the foraging activity of workers feeding on crickets. Single pre-weighed male and female crickets, *Acheta domesticus* (L.), were skewered on an insect pin and placed 10 cm from the ant nest. We collected data on three measurements of foraging behavior: the number of ants recruiting to crickets after 20 min and after 150 min, and the dry mass of cricket removed after 24 h. Two sample *t*-tests were used to compare the foraging behavior between colonies provided with water and nectar.

Twenty-eight days after the laboratory colonies were established, we collected and counted the number of dead worker ants in each colony. *S. invicta*, like many other ants, will place dead worker ants in one or more piles away from the nest. The time period after which we collected dead ants (28 days) was too short for the experimental treatments to have affected the number of worker ants in the colonies because the duration of larval growth and pupation is approximately 30 days at 32 °C (Tschinkel, 2006). Two sample *t*-

tests were used to compare the number of dead workers between colonies provided with water and nectar.

2.2. Colony-level simulation model

We created a staged-structured model of the dynamics of a colony of *S. invicta* over a complete annual cycle (Fig. 1). We chose to model the dynamics of a relatively young colony (i.e., approximately 50,000 workers) for several reasons. First, net annual growth in small colonies is relatively low (e.g., 5000–10,000 net workers per year; Tschinkel, 2006) and any change in this net growth could have important effects on the success of the colony. Second, small colonies typically invest few or no resources in the production of sexual offspring, which makes them less complicated to model (Tschinkel, 2006). Finally, the dynamics of a small colony may provide some insight into colony growth of both social forms of *S. invicta* because differences between the two forms become greater in larger colonies (i.e., differences in the production of sexuals and the accumulation of queens as polygyne colonies grow in size; Vander Meer et al., 1992; Tschinkel, 2006).

2.3. Model description

Our simulation model was constructed using the program STELLA 7.0.1 (High Performance Systems, Inc., Hanover, NH, USA) (Costanza, 1987). All life stages present in a young colony were represented in the model (egg, larvae, pupae and adults) (Fig. 1). A time step of 5 days was used in the model and each life stage was divided into 5-day bins depending upon the duration of the life stage. The model was run for 73 time steps (i.e., 365 days) and during each time step the individuals in a given bin moved to the next sequential bin or exited the model through a mortality sink. The parameters and equations used in the model are presented in Appendix A and B.

The main portion of the model consisted of a chain of bins representing the life stages of *S. invicta* (Fig. 1). Eggs were produced and added to the first larval bin. This interval encompassed the estimated egg production rates of a monogyne colony (1 queen) or a polygyne colony with 8 queens (Vander Meer et al., 1992). Egg laying rate was adjusted seasonally according to seasonal natality rates observed for colonies of *S. invicta* in the field (Tschinkel, 1993). To summarize the seasonal changes, egg production was 0 until 45 days into the model, gradually increased to a maximum rate on day 170, decreased to 90% of maximum by day 225 and then decreased to 0 again by day 320 (Tschinkel, 1993).

We used 7 larval development bins in the model. The final 4 larval bins all had connections to the first pupal bin to allow individuals to move to pupation at various times depending upon food availability. Biologically, this means that larvae could mature into pupae only between 20 and 40 days of age depending upon food availability and that any larvae that did not mature within 40 days of age died due to starvation (Tschinkel, 2006). Food availability for a given cohort of larvae was tracked using a parallel "larval food accumulation submodel" (Fig. 1). The larval food accumulation submodel consisted of 7 bins each of which corresponded to one of the 7 bins in larval development. As a cohort of larvae passed into a bin in the larval development chain, a certain quantity of food moved into the parallel larval food accumulation bin. The amount of food that was added to a given larval food bin was equal to the total amount of food collected by foragers during a time step multiplied by the proportion of all larvae that were in the corresponding larval development bin. In the 4–7 larval development bins, some larvae matured into pupae while the rest moved to the next larval development bin, or died if they moved beyond the 7th larval development bin. The number of larvae that developed during a time step was equal to the total mass of food in a bin divided by

the mass of food required for the development of a single larva (Appendix A). Any food that was used to allow larvae to mature was then subtracted from the larval food bin.

There were 3 pupal bins and 11 adult worker bins. Cohorts moved sequentially through pupal bins with minimal mortality. While some investigators distinguish between "minor" and "major" workers in *S. invicta*, there is actually a continuous range in the size of workers and small colonies typically have a small percentage of larger workers (Tschinkel, 1993). Our simulation of adults was based on an "average" worker. Seasonal daily mortality rates of adult workers were based on values from Tschinkel (1993). To summarize the seasonal changes, daily mortality rate was 0.27% at day 45, increased to 2% by day 105, peaked at 3.78% at day 255, decreased to 2.21% at day 270 and was not distinguishable from 0% after day 313 (Tschinkel, 1993).

A foraging submodel was created to control the amount of food entering the colony based on field data (Tennant and Porter, 1991; Tschinkel, 2006). Foraging workers could harvest 3 types of food resources: solid food (e.g., insect parts), liquid food (e.g., hemolymph from insects) or plant-based food resources (i.e., nectar, extrafloral nectar or honeydew) (Tennant and Porter, 1991; Tschinkel, 2006). Plant-based food resources could only be harvested in simulation runs that tested how these food resources affected colony growth; in control runs workers could only harvest solid and liquid food. In addition, plant-based food resources were only available from time steps 30 to 42 (i.e., late May to late July) in simulations in which they were included unless otherwise noted, which was done using a function in the modeling program Stella. The seasonal availability of plant-based food resources simulated an early summer peak in plant flowering or an ephemeral increase in the number of honeydew-producing hemipterans. The seasonal rate of food harvest had the same seasonal pattern used for egg laying rate.

Plant-based food could result in 3 independent effects in the simulation model, which we manipulated sequentially and simultaneously (Fig. 1). Plant-based foods could increase the quantity of food used by larval ants for growth, increase the proportion of workers that were foraging, and decrease the mortality rate of worker ants. We used a range of values for each of these variables to examine their relative impact on colony growth. We also ran simulations to examine how the seasonal timing of plant-based food affected colony growth and how the duration that plant-based food was available affected colony growth.

2.4. Model evaluation and sensitivity

The seasonal dynamics of our simulation model match those of natural populations of *S. invicta* (reviewed in Tschinkel, 1993) with an annual low population size in May and June and an annual peak in population size in October and November (Fig. 2). Colony size of *S. invicta* peaks in the fall as a result of high brood production throughout the summer and reaches an annual low in early summer as older workers produced the previous year begin to die off before it is warm enough for high brood production to offset these mortality losses (Tschinkel, 2006). The net gain in colony size in the simulation model (5295 workers) is also consistent with the net gain in number of workers for similar-sized colonies in nature (i.e., 5000–10,000 workers, Tschinkel, 2006).

We conducted a sensitivity analysis by examining the change in colony size with a 10% increase or decrease in several important parameter values (Table 1). There was nearly no change in colony size with a 10% change in egg laying rates. There was only a slight change in colony size with a 10% change in the proportion of workers returning with solid and liquid food. The change in colony size was proportional to the change in parameter value for seasonal worker mortality rate, proportion of workers foraging and grams
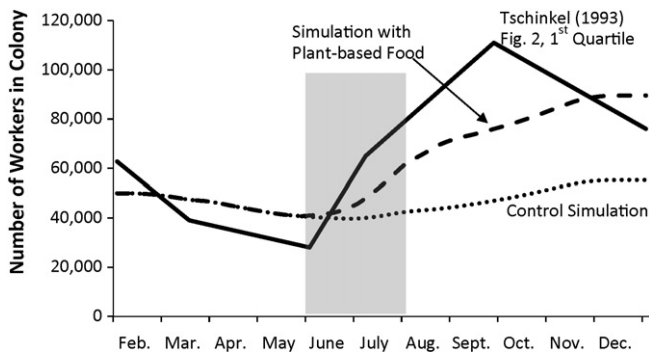
Fig. 2. Annual simulated dynamics of red imported fire ant colonies with no access to plant-based food resources (control simulation) and with access to these resources (with a 49.5% reduction in mortality and 22.5% of plant-based food used for larval growth). Data from Tschinkel (1993) are plotted for comparison of simulations with data from natural populations. The shaded rectangle indicates the period of time during which resources (i.e., nectar, extrafloral nectar or honeydew) were available during the simulations with plant-based food resources.

of food required per larvae. The values for seasonal worker mortality rate and proportion of workers foraging were calculated from large data sets from the field (Tschinkel, 2006). The grams of food required per larvae for development was calculated from a controlled laboratory study (Macom and Porter, 1995). Hence, we are confident the values used for these parameters are realistic. In addition, all of our model simulations used the same values for these parameters, which means that the comparisons among model simulations are sound even if the parameter values differ slightly from values in the field.
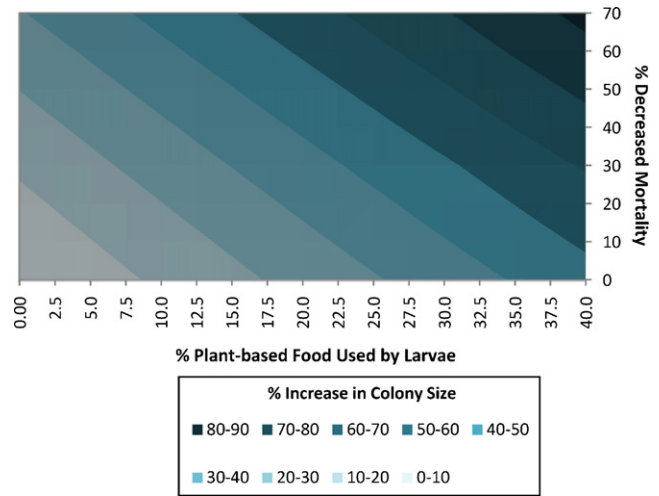
2.5. Simulations

We first used the model to separately examine the effects of variation in each of the three potential mechanisms on colony growth of S. invicta. Increases in each of the mechanisms resulted in a positive linear effect on the percent increase in colony size of S. invicta. A 0.1 increase in the proportion of plant-based food used for larval growth had a much larger effect on percent increase of S. invicta (11.7% increase in colony size) than a 0.1 decrease in mortality rate with plant-based food (4.1% increase in colony size) and a 0.1 increase in the proportion of workers foraging (3.3% increase in colony size).

Our laboratory experiment provided quantitative estimates of the effects of plant-based food on worker mortality rates of S. invicta. All experimental colonies started with 1192 ± 62 (mean ± 1 SE) fire ants. After one month, 210 ± 27 fire ants had died in the colonies with water while 105 ± 16 fire ants died in colonies with access to artificial nectar ($t_{33} = 3.60$, $p = 0.001$). Using these data, we calculated that access to plant-based food resulted in a 49.5% decrease in the mortality rate of fire ants.

We also tested for an increase in the proportion of workers foraging. However, there was no significant effect of artificial nectar

Fig. 3. Graph depicting the combined effect of the percent of plant-based food for larval growth and percent decrease in worker mortality on colony growth of *Solenopsis invicta*. Gradations in color indicate changes in colony size. For reference, the average change in colony size in empirical studies (Helms and Vinson, 2008; Wilder et al., in review) was a 49.4% increase.

on the foraging activity of fire ants (i.e., number of ants that recruit) to insect prey after 20 min (treatment effect: $F_{1,20} = 0.27$, $p = 0.61$; colony as a covariate: $F_{16,20} = 1.86$, $p = 0.09$) and 150 min (treatment effect: $F_{1,21} = 3.56$, $p = 0.07$; colony as a covariate: $F_{16,21} = 4.41$, $p = 0.0009$). In fact, the data show a non-significant tendency for less recruitment to insect prey after 150 min when fire ants have access to artificial nectar, contrary to the predictions of the "fuel for foraging" hypothesis. After 24 h, fire ants with access to artificial nectar harvested significantly less cricket biomass than fire ants that only had access to water (treatment effect: $F_{1,21} = 11.23$, $p = 0.003$; colony as a covariate: $F_{16,21} = 4.80$, $p = 0.0005$). Given that our results and those of another study (Macom and Porter, 1995) did not support the hypothesis that plant-based foods increase foraging of S. invicta, we did not consider this mechanism further.

Combined, the remaining two mechanisms had a slightly non-linear effect on the percent increase in colony size of S. invicta (percent increase in colony size = $0.409 \times$ percent decreased mortality + $1.164 \times$ percent larval food + $0.0027 \times$ percent decreased mortality $\times$ percent larval food; Fig. 3). Using the increase in S. invicta colony size from two empirical experiments (a 49.4% increase on average; Helms and Vinson, 2008; Wilder et al., in review) and our estimate of decreased worker mortality, we were able to calculate the estimated proportion of plant-based food used by larvae (i.e., 22.5% of the mass of plant-based food). All remaining simulations used the decrease in mortality rate that was calculated from our laboratory experiment (0.495) and the proportion of plant-based food used by larvae (0.225) that was calculated using the empirical data and model. Using these values, the seasonal dynamics of an S. invicta colony in the simulation was very

Table 1
Results of a sensitivity analysis to examine how a 10% increase or decrease in several important parameters in the simulation model affected the final colony size of red imported fire ants. Sensitivity analysis was conducted using a deterministic version of the model.
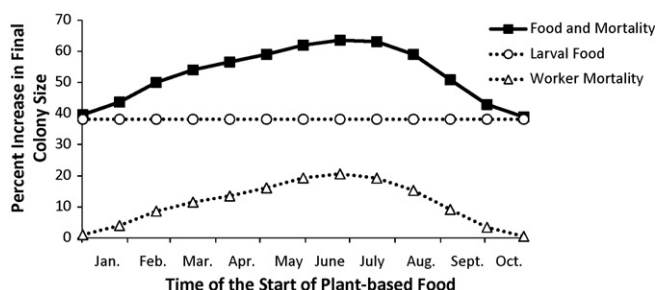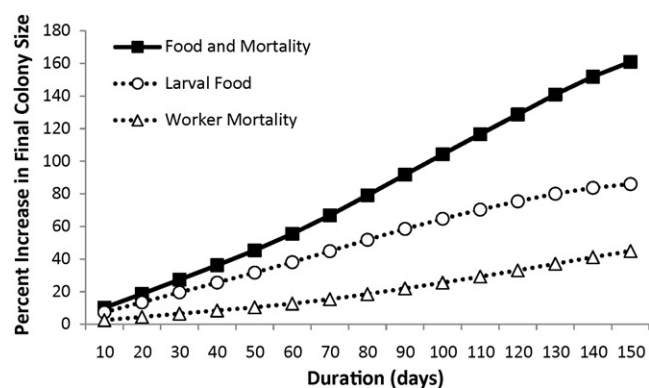
	Change in final colony size with a	
	+10% Change in parameter value	−10% Change in parameter value
Egg lay rate	0.06%	−0.08%
g Food required per larvae	−9.65%	12.77%
Proportion of workers foraging	11.44%	−10.57%
Proportion of foraging workers returning with liquid food	4.44%	−4.29%
Proportion of foraging workers returning with solid food	6.82%	−6.49%
Seasonal daily mortality rate	−9.83%	10.90%

Fig. 4. Relationship between the timing of plant-based food supplements and the percent increase in final colony size of *Solenopsis invicta*. Plant-based food was available for 60 days in all of these simulations. Simulations were conducted by separately using the effects of plant-based food on larval growth or worker mortality, adding the separate effects of larval growth and worker mortality, and simultaneously manipulating larval growth and worker mortality.

Fig. 5. Relationship between the duration during which plant-based food was available to colonies of *Solenopsis invicta* and the percent increase in final colony size. Plant-based food was started at day 90 (April) in the model. Simulations were conducted by separately using the effects of plant-based food on larval growth or worker mortality, adding the separate effects of larval growth and worker mortality, and simultaneously manipulating larval growth and worker mortality.

similar to empirical data on the seasonal dynamics of similar-sized colonies in the field (Fig. 2 and Tschinkel, 1993).

We next examined how the seasonal timing of plant-based food resources affected colony size of *S. invicta*. There was a distinct seasonal effect of plant-based food on colony growth (Fig. 4). Plant-based resources had the lowest effect on colony size when they were available in January (40% increase) and December (39% increase) and the largest effect on colony size when they were available in June (64% increase). When we separated the two mechanisms, increasing food available for larval growth had a similar effect on colony size regardless of the time of year while decreasing worker mortality showed a seasonal pattern similar to the simulation with both mechanisms (Fig. 4).

Increasing the duration that plant-based food was available had a positive effect on colony size of *S. invicta*. While this effect appeared non-linear, it was very closely approximated by a linear function (Fig. 5; $R^2 = 0.99$; percent increase in colony size = 1.05 × number of days plant-based food was available).

3. Discussion

Our simulation model provided insight into the mechanisms through which plant-based foods contribute to greater colony size of an invasive ant. Increased food for larvae and worker survival appear to be the main mechanisms through which plant-based foods contribute to increased colony size of *S. invicta*. Colonies of *S. invicta* do not appear to increase foraging when consuming plant-based foods both in our experiment and in the study of Macom

and Porter (1995). Even if plant-based food did increase foraging, our model suggests that it would only have a small effect on colony growth. The proportion of plant-based food used by larvae affected colony growth far more than the other two mechanisms. This parameter is very difficult to estimate in live colonies. However, our simulation model, with empirical data on colony growth and worker survival, allowed us to estimate the proportion of plant-based food that is used for larval growth. These simulations provided quantitative data on how mutualisms may benefit colony growth of an invasive ant.

The duration and timing of plant-based foods also had a strong effect on colony growth in *S. invicta*. Increasing the duration over which plant-based resources were available had a nearly linear positive effect on colony growth. There was a unimodal relationship between the time of year that plant-based food was available and *S. invicta* colony growth. The early summer peak in the benefit of consuming plant-based food corresponds to the peak time of year for colony growth in the field (Tschinkel, 2006). The early summer is also the time that hemipteran populations peak in the field (Chapin et al., 2001). The correspondence between the timing when sources of plant-based foods had the largest effect on *S. invicta* colony growth and when hemipterans are most abundant in the field is likely a coincidence driven by abiotic conditions (i.e., increased population growth in the spring as temperatures increase), which happens to be mutually beneficial for ants and hemipterans.

Interestingly, our estimate of the proportion of plant-based food that is used for larval growth was much higher than we expected. Animal growth has long been thought to be nutrient-limited (e.g., nitrogen, phosphorus, amino acids; House, 1962). Calculations based on our model suggest that larval ants use 22.5% of plant-based food for growth; yet, plant-based foods contain less than 1% amino acids by mass and are primarily composed of carbohydrates (Bluthgen et al., 2004). This suggests that the carbohydrates in plant-based foods provide an important source of food for carnivorous *S. invicta* and is consistent with recent empirical studies of diet selection and growth that show strong effects of carbohydrates on carnivorous ants (Dussutour and Simpson, 2008, 2009; Cook et al., 2010). Carnivorous ants strongly regulate their intake of carbohydrates and show significantly higher brood production when their diet of insect prey is supplemented with carbohydrates (Dussutour and Simpson, 2008, 2009; Cook et al., 2010). Carbohydrates may be an important component of the diet of ants because they provide an easily digested form of energy to support the high activity level of workers and metamorphosis of larvae (House, 1962; Tschinkel, 2006; Dussutour and Simpson, 2008).

The fuel for foraging hypothesis suggests that access to plant-based resources, which are high in carbohydrates, provides workers with extra energy to increase foraging for insect prey (Koptur, 2005; Stadler and Dixon, 2005; Wackers et al., 2005; Kay et al., 2010). Several studies have shown that carnivorous ants consume more insects on plants when they have access to honeydew (Kaplan and Eubanks, 2005; Grover et al., 2008). However, colonies in our laboratory experiment showed lower foraging for insects when *S. invicta* had access to artificial nectar. In addition, Macom and Porter (1995) showed that when colonies of *S. invicta* were supplemented with carbohydrates, they decreased their foraging on insect prey to maintain a constant total caloric intake. These results may actually not be contradictory. While ants increase their foraging for insects on plants they may decrease their foraging for insects on the ground and, hence, show an overall decrease in the amount of insect prey consumed (Kaplan and Eubanks, 2005; Styrsky and Eubanks, 2007; Grover et al., 2008). Instead of using high-carbohydrate plant-based resources to fuel foraging, ants may be using these resources to fuel competition and aggression with other ants (Grover et al., 2007; Kay et al., 2010).

Plant-based food resources can have large effects on the growth of small colonies of *S. invicta* (this study; Helms and Vinson, 2008; Wilder et al., in review); however, larger colonies could benefit even more from consuming these resources than small colonies. Small colonies of both monogyne and polygyne *S. invicta* typically invest little or no resources in the production of winged sexuals and have similar egg laying rates (Vander Meer et al., 1992; Tschinkel, 2006, 1993). However, larger monogyne, and to some extent polygyne, colonies can invest a large proportion (i.e., up to 50% in monogyne colonies) of their daily energy budget in the production of sexuals in the spring (Ross and Keller, 1995; Vargo, 1996; Tschinkel, 1993). This seasonal investment in sexuals causes larger colonies of *S. invicta* to experience greater spring declines in worker number compared to smaller colonies (Tschinkel, 1993). The high-carbohydrate content of plant-based food resources may be especially important to larger colonies producing sexuals by providing energy to invest in sexual production (i.e., female sexuals are 49% lipid by mass) and by increasing worker survival to reduce the large spring declines in colony size (Tschinkel, 1993).

S. invicta is responsible for substantial ecological and economic damage in its invasive range in the Southeastern US (Porter and Savignano, 1990; Pimentel et al., 2000). While much is known about the biology of *S. invicta* (e.g., Lofgren et al., 1975; Tschinkel, 2006), the factors responsible for the rapid spread and high densities of *S. invicta* in its invasive range remain unclear (Porter and Savignano, 1990; Porter et al., 1997). Several studies have shown that *S. invicta* frequently consumes nectar, extrafloral nectar and honeydew in their invasive range in the Southeastern US and that consumption of honeydew increases colony size (Helms and Vinson, 2002, 2003, 2008). Our simulations suggest that any control efforts that remove sources of plant-based food (e.g., extrafloral nectaries or hemipterans) and reduce the duration that these resources are available to *S. invicta* will slow their colony growth especially if sources of plant-based food are removed in early summer months. Mutualism and facilitation may be important factors aiding the success and spread of a wide range of invasive species and simulation modeling may prove to be a useful tool for exploring the dynamics of these interactions (Simberloff and Von Holle, 1999; Richardson et al., 2000; Simberloff, 2006; Lach, 2003; Tillberg et al., 2007).

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2010.03.010.

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