

**Modeling the impact of an exotic invasive on community structure:  
Predation on lepidopteran larvae by the European paper wasp,  
*Polistes dominulus*, in Eastern Massachusetts**

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## Abstract

The spread of exotic invasive species is an increasing threat to biodiversity and ecosystem functioning worldwide. Exotic invasives negatively impact community structure, although the degree to which they do this is poorly understood for recent introductions. It is therefore essential to elucidate the role that invaders play in new ecological communities. Ecological modeling can be used to form testable predictions of the impact of exotic invasives. The European paper wasp, *Polistes dominulus*, was first found in Eastern Massachusetts in the mid 1970s, and has since established populations across the United States. *P. dominulus* and its native congener, *P. fuscatus*, primarily rear brood on lepidopteran larvae, putting the two wasp species in competition and their shared prey species under increased predation pressure. We constructed an individual-based model of wasp foraging and nesting behavior to predict the impact of *P. dominulus* predation on lepidopteran prey populations. Our model uses location-specific weather data and local demographic data on *P. dominulus* nest growth, along with published data on foraging and nest building in *Polistes* wasps, to make targeted predictions of the number of lepidopteran larvae killed by individual *P. dominulus* nests in invaded communities. Final nest size and number of larvae killed were strongly, positively correlated in our model output. Fitting a linear regression model to these data provided us with an equation that can be used to estimate the amount of caterpillar prey consumed by *P. dominulus* nests in Eastern Massachusetts. These predictions can be combined with information on *P. dominulus* nest density and prey preference to better identify how much prey is being consumed in a given area, and which prey species are most at risk from invasive wasp predation. Ultimately, our model serves as a foundation upon which we will continue to build a more generalizable model

to predict the impact of paper wasp predation on community structure across the global range of *Polistes*.

## **Introduction**

The spread of exotic invasive species is an increasing threat to biodiversity and ecosystem functioning worldwide (Gaudet and Keddy 1988, Pimentel et al. 2000, Clavero and García-Berthou 2005, Molnar et al. 2008, Kenis et al. 2009, Guénard and Dunn 2010). Over half of all recent animal extinctions are due the effects of invasive species (Clavero and García-Berthou 2005). Human activities such as global trade and transport facilitate the dispersal of exotic species outside their native range (Ricciardi 2007, Primack 2010). Species are classified as “invasive” when they rapidly spread, increase in abundance, and have negative consequences on the biota of their new habitats (Lowe et al. 2000, Davis 2009, Wilson et al. 2009). In Executive Order 13112, President Bill Clinton defined invasive species as “an alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health (Clinton 1999).

These consequences take a variety of forms. Pimentel et al. (2000) report that the 50,000 exotic species in the United States cause approximately \$137 billion per year in major environmental damage. Invasive agricultural pests reduce crop yields and can cause significant economic losses (Gould and Jeanne 1984, Furlong and Zalucki 2010, Herlihy and Van Driesche 2013). These losses can be inflicted directly via herbivory, as seen in the cabbage white butterfly, *Pieris rapae* and the European corn borer moth, *Ostrinia nubilalis* (Gould and Jeanne 1984; Mencarelli, Accinelli and Vicari 2012). Economic damage may also be affected indirectly via the vectoring of microbial crop diseases, such as sour rot disease dispersal by the European paper

wasp, *Polistes dominulus* (Madden et al. in review). Exotic invasives may physically alter habitat in their new ranges such that it becomes uninhabitable for native species (Gooden et al. 2009). Additionally, invasive species may displace native congeners who share similar habitat and prey resources (Gamboa et al. 2002, Primack 2010). Exotic invasive predators can decimate local prey populations; for example, the brown tree snake, *Boiga irregularis*, nearly eliminated the bird population of Guam following its introduction to the island (Lowe et al. 2000, Gooden et al. 2009, Perry and Vice 2009). Because of our changing landscapes – changes anthropogenic and otherwise – it is vital to collect data on the behavior of all animals. Studying the behavior and ecology of biological invaders provides crucial insight into the impacts that these species can have on the community structure of invaded areas (Holway and Suarez 1999, Gamboa et al. 2002, Liebert et al. 2006).

One way that we can learn more about the behavior and ecology of invasive species is through ecological modeling. Ecological models range from simple equations to complex computer programs that simulate the biology and behavior of organisms, as well as the properties of their environment (Jackson et al. 2000, Grimm et al. 2006, Clerc et al. 2009, Elphick et al. 2010, McLane et al. 2011). These models serve as “hypothesis-generators” by allowing us to predict changes in a community or population, and then test our predictions against biological data (Clerc et al. 2009, Jackson et al. 2000). Modeling can be essential in scenario planning, where wildlife managers and decision makers must make conservation policies despite great uncertainty (McLane et al. 2011). Ecological models have been used to pursue questions ranging from predator-prey interactions (Hammond et al. 2007, Clerc et al. 2009, Flaxman et al. 2012) and population dynamics (Keeler et al. 2006, Venter and Witkowski 2013), to the movement and

dispersal of organisms (Russo et al. 2006, Tenhumberg et al. 2006) and disease dynamics (Philips and Puschendorf 2013).

Modeling has been especially useful in describing the behavioral dynamics of social insect colonies. Behavioral ecologists have modeled social insects nest choice (Pratt et al. 2005), reproductive strategies (Starks and Fefferman 2006, Macevicz and Oster 1976) and foraging behavior (Sumpter and Pratt 2003, Oster 1976). Ecological modeling has been successfully used to study the spread of exotic invasive species (Keeler et al. 2006), including invasive social insects such as the red imported fire ant (Keith and Spring 2012).

We have the opportunity to study, predict and manage the spread of an exotic invader in the United States in the European paper wasp, *Polistes dominulus*. Native to the Mediterranean, *P. dominulus* was first found in Massachusetts in the mid 1970's, (Eickwort 1978), and has since established populations as far west as California (Liebert et al. 2006). *Polistes* wasps begin to build their namesake paper nests in the early spring using plant fibers and proteinaceous secretions in their saliva (Pardi 1951); their saliva also contains a diverse array of fungi and bacteria, some of which might help with structural integrity (reviewed in Madden and Starks, in prep). *P. dominulus* seem to preferentially nest on man-made structures, which may provide hospitable micro-climates with respect to biotic and abiotic factors (Turillazzi and West-Eberhard 1996). *P. dominulus* have been observed to nest on new structures before related, neighboring wasp species (Cervo et al. 1999, Starks pers. obs.). However, *P. dominulus* may still compete for space with local paper wasp species - in some areas of Michigan, *P. dominulus* appears to have completely replaced the native congener, *Polistes fuscatus* (Gamboa et al. 2002).

Further, the diets of both *P. dominulus* and *P. fuscatus* consist primarily of lepidopteran larvae during the early phase of the colony cycle, when wasp larvae are being reared (Rabb 1960,

Gamboa et al. 2002). *P. dominulus* is more productive than *P. fuscatus*, creating a greater number of workers earlier in the season, due to their shorter development time and smaller body size (Gamboa et al. 2002). The earlier emergence of workers may allow *P. dominulus* to begin exploiting resources before *P. fuscatus* (Gamboa et al. 2002). In eastern Massachusetts, both *P. dominulus* and *P. fuscatus* live in close proximity – we found nests of the two species adjacent to each other on the eaves of the same building at the field site in the present study (Corey pers. obs). In addition, we have observed *P. dominulus* nests - but no *P. fuscatus* nests - on a new building at the same field site (Starks pers. obs). This readiness to exploit new habitat, along with a generalist diet and complex social structure, makes *P. dominulus* an adept invader (Liebert et al. 2006).

Ecological models have been used to study a range of behaviors in *P. dominulus*, including alternative nest founding strategies (Starks and Fefferman 2006), reproductive skew (Nonacs, Liebert and Starks 2006), and colony growth (Karsai, Péntzes and Wenzel 1996). However, despite extensive information on foraging and feeding in *Polistes* wasps (Suzuki 1978, Suzuki 1980, Suzuki 1981, Richter 2000, Karsai and Hunt 2002, Kudo 2002, Mead and Pratte 2002, Armstrong and Stamp 2003a and 2003b, Kudo and Shirai 2011, Brown et al. 2012) a model that makes quantitative predictions of the prey required to support a given population of *P. dominulus* has not yet been created, to our knowledge. Since lepidopteran larvae may face increased predation risk in communities invaded by *P. dominulus* (especially where *P. fuscatus* is sympatric), ecological modeling can be an important tool in determining the effect of the *P. dominulus* invasion on prey populations.

Lepidopterans play a crucial ecological role as pollinators and prey for insectivores, contributing to the biodiversity and ecosystem services of a given area (Losey and Vaughan

2006, Wallisdevries et al. 2011). Butterflies react delicately to changes in the environment, and therefore also serve as useful bioindicators (Schmitt and Rákosky 2007); this does, however, imply that butterflies may be easily threatened. Though popular interest in butterflies has grown in several countries, to the point that it has become a significant political force, stronger conservation efforts must still be made (New et al. 1995). Maintaining lepidopteran biodiversity may not always be preferred, however. Exotic lepidopteran crop pests can inflict serious economic burdens on farmers (Gould and Jeanne 1984; Mencarelli, Accinelli and Vicari 2012). These exotic lepidopterans may become successful invaders due to a lack of predators and pathogens in their new ranges, known as the enemy release hypothesis (Kambo and Kotanen 2013). In these cases, biocontrol via introduced predators such as *Polistes* wasps may be necessary (Gould and Jeanne 1984, Furlong and Zalucki 2010).

*Polistes* wasps are primitively eusocial insects – individuals of different reproductive castes and developmental stages are therefore simultaneously present on their nests (Pardi 1951). In this study, we constructed an individual-based model in order to most accurately represent the complex interactions and behaviors of a paper wasp nest, specifically their foraging for lepidopteran larvae (Jackson et al. 2000). Individual-based models are computer simulations in which the properties of a population emerge from the traits of individuals (Stillman and Goss-Custard 2009). Our model simulates the development and foraging activities of *P. dominulus* nests over the course of the colony cycle. It is informed by our own field data and the natural history of *Polistes* wasps. In the present study, we use our model to predict the impact of *P. dominulus* on community structure in Eastern Massachusetts by quantifying the expected number of lepidopteran larvae consumed by individual *P. dominulus* colonies of a given size over the course of the colony cycle.

## **Methods**

### ***Nest Surveys***

Weekly surveys of 19 *P. dominulus* nests at the Great Brook State Farm in Carlisle, MA were taken from June 6<sup>th</sup> to September 5<sup>th</sup>, 2013. All nests were located underneath overhangs on the exterior of the same building. Photographs were taken weekly and later used to count the number of cells in each nest. Nest growth had already begun on our first survey date. We assumed that nests were established on May 7<sup>th</sup>, 120 days (the average length of the *P. dominulus* colony cycle) before the final survey date, in order to standardize our data (Turillazzi 1980). We hand-counted cell number from photographs. Nest growth was considered to have stopped if there was no increase in nest cell count for two weeks. This is a conservative estimate, as cells can be re-used (Pardi 1951). The date of the last survey in which cell number increased was used as the final date of nest growth. Rate of nest growth was calculated by dividing the final nest cell count by the number of days of nest growth.

One colony was identified as hypergynous (initial cell count = 208, with 13 adults on the nest), in which multiple foundresses re-use a nest that had been constructed and occupied in the previous colony cycle (Liebert et al. 2008). Average rates of nest growth  $\pm$  standard deviation (cells added/day) were used to determine the rate of nest cell building in the model, although data from the hypergynous nest were not included in these parameter calculations. Our model currently only simulates single-foundress colonies, and will ultimately include multiple-foundress colonies, but will not simulate the establishment of hypergynous nests. Field data on final nest size served as a biological check for our model output.

### ***Weather Data***

Temperature (°F) and precipitation data for Bedford, MA were collected from the National Climatic Data Center (NCDC). Hourly measurements were recorded at the Lawrence G. Hanscom Field Airport (14702/BED) for the years 2005-2013. *P. dominulus* typically forage between 1000 and 1500 hours and in the absence of rain (Armstrong and Stamp 2003b), and when temperatures are above 68°F. We therefore recorded the number of “foraging-positive hours” (in which conditions were appropriate for *P. dominulus* foraging) between 1000 and 1500 hours for each day in the months of May-August from the years 2005-2013. In a given simulation, our model randomly selects the number of foraging-positive hours for a given date from one of these 9 years. This process adds environmental stochasticity from weather to our predictions (Aznar et al. 2013).

### ***Model Design***

In order to form quantitative predictions of the impact of *P. dominulus* on lepidopteran populations in invaded communities, we constructed an individual-based model (IBM) for the development of an individual paper wasp colony over the course of the colony cycle. The model was coded in Python 3. Model parameters were determined from our own nest surveys (see above, “*Nest Surveys*”) and previously published data on *Polistes spp.* (Table 1).

Our individual-based model functions as a simulation of daily foraging activities performed on and off a single foundress *P. dominulus* nest over a 123-day colony cycle from May 1<sup>st</sup> to August 31<sup>st</sup> (Fig. 1). Throughout each day, the foundress builds nest cells, lay eggs, and forages (under adequate conditions). Workers take up the task of foraging upon eclosion. At the end of the model run, the final size of the nest (in number of cells), total number of

caterpillars killed by that nest, and number of adult wasps (workers and reproductives) that eclosed are given.

### ***Data Analysis***

Statistical analyses of field data were performed in Microsoft Excel for Mac 2011. We used R Studio 0.98.490 to perform statistical tests on our model outputs. A linear regression model was fit to the predicted number of lepidopteran larvae killed as a function of final nest size (in number of cells). We used Spearman's rank correlation test to determine correlation between model parameters and outputs (Table 4).

## **Results**

### ***Field Data***

The average initial nest size of the *P. dominulus* colonies from our study population in Carlisle, MA was  $52.7 \pm 43.17$  cells (Table 2). Excluding the hypergynous nest from this analysis lowered the average initial nest size to  $44.1 \pm 21.80$  cells; these nests reached an average final size of  $74.8 \pm 36.14$  cells, at a rate of  $0.83 \pm 0.552$  cells per day (Table 2).

### ***Model Output***

We compiled data from 10,000 runs of our model to evaluate its output and predict the number of lepidopteran larvae killed by individual, single foundress *P. dominulus* nests in Eastern Massachusetts over the course of the colony cycle. The average final nest size from our model was  $86.7 \pm 35.24$  cells; an average of  $522.0 \pm 184.13$  lepidopteran larvae were killed per nest over the course of one colony cycle (Table 3). A linear regression model relating final nest size (x) and number of caterpillars killed (y) takes the equation  $y = 4.659x + 117.910$

(Spearman's rank correlation test,  $\rho = 0.903$ ,  $S = 16101572340$ ,  $p < 0.0001$ ) when fit to our data (Fig. 2).

We used the best-fit line determined from linear regression analysis of our model to estimate the number of caterpillars killed by our study population in Carlisle, MA over the 2013 colony cycle. We also predicted the number of caterpillars killed by these nests using previously published data (Suzuki 1980, Armstrong and Stamp 2003a, Brown et al. 2012) to compare to our model output (Fig. 3). Using the best-fit line, the 19 *P. dominulus* nests killed an estimated total of 9552 caterpillars over the course of the colony cycle, with a mean of  $501.2 \pm 223.35$  caterpillars per nest; using only previously published data, an estimated total of 5595.5 caterpillars were killed, with a mean of  $294.5 \pm 171.62$  caterpillars per nest (Fig. 3).

Correlations between our model outputs were tested in order to evaluate interactions between model parameters (Table 4). Final nest size was closely, positively correlated with the number of caterpillars killed per nest, nest building rate, and the number of workers that eclosed over the course of the colony cycle. Nest building rate was closely, positively correlated with the number of caterpillars killed per nest, and the number of workers eclosed. The number of days that the queen lived (queen age) was weakly correlated with all other parameters that were examined, except for the number of reproductives that eclosed over the course of the colony cycle (Table 4).

## **Discussion**

Ecological models serve as “hypothesis generators” that let us form testable predictions of natural phenomena (Jackson et al. 2000). Our individual-based model allows us to predict the number of lepidopteran prey consumed by individual *P. dominulus* colonies in invaded

communities in Eastern Massachusetts over the course of the colony cycle. Regression analysis of our model outputs shows a significant positive correlation between the final size of a *P. dominulus* colony (in number of nest cells) and the number of caterpillars killed by those wasps over the course of a colony cycle (Fig. 2). Linear analysis for our model outputs provides us with a best-fit line whose equation (Fig. 2) can be used to estimate the number of lepidopteran larvae killed by a *P. dominulus* colony of a given size.

This equation can therefore serve as a practical, efficient tool for predicting the impact of *P. dominulus* in the field. An observer need only count the number of cells in a given nest and input that value into the best-fit line equation in order to estimate how many lepidopteran larvae have been killed by that nest. This can be safely and efficiently done by taking photographs of *Polistes* nests from a distance and counting the number of cells from the photographs.

Throughout the course of the summer, we were able to complete weekly surveys of our field population in under an hour, and then review the photos later on. This can be an especially useful technique when a large number of *Polistes* nests are being studied. A survey of nests in a given area, then, can elucidate the impacts of the *P. dominulus* population on prey species in its community. However, the presence of cryptic wasp nests in a community will lead to an underestimation of prey consumption.

By combining our predictions for individual nests with information on local *P. dominulus* nest density, we can also answer the question, “what number of lepidopteran prey is required to support a given population of *P. dominulus*?” This population can be defined in both numbers of wasps and the area that they inhabit. *Polistes chinensis* has an average foraging distance of 120 meters<sup>2</sup> (Suzuki 1978), so our model can therefore be used in making spatial predictions about predation effects on local lepidopteran populations (Flaxman, Lou and Meyer 2012). By

mapping where particular nests are located in an area, we can project “depredation spheres,” or areas in which lepidopteran larvae are at risk of being consumed by *Polistes* wasps. We can then specify areas where predation is higher or lower depending on the number and size of nests in the area.

Even greater accuracy may be achieved by combining these predictions with data on local lepidopteran populations in New England, including density and growth rate. For example, Van Driesche, Nunn, and Pasquale (2003) found the density of *Pieris napi* eggs on hostplants in Craftsbury, Vermont to be 0.229 eggs/m<sup>2</sup> during the middle of the *Polistes* colony cycle. The related species *P. rapae* lay an average of 152.2 eggs per adult individual (Crawford et al. 2013); while this is only a fraction of the number of prey we predict are consumed by the average *P. dominulus* nest in Eastern Massachusetts, we also must know how many *Pieris spp.* are present in an area in order to evaluate the degree to which wasp predation impacts this population.

We can then further gauge relative impact on different lepidopteran species based on *P. dominulus* prey preferences (Armstrong and Stamp 2003b). We have observed *P. dominulus* consuming larvae of *Vanessa cardui*, *Vanessa atalanta*, *Junonia coenia* and *P. rapae* – all species currently present in Massachusetts (Massachusetts Butterfly Club pers. comm.) – in laboratory prey preference tests (Corey pers. obs). If we are able to determine *P. dominulus* prey preferences for local lepidopterans, we may be able to predict not only the number of larvae killed, but also which species constitute a given percentage of those kills.

It is therefore of crucial importance for maintaining lepidopteran biodiversity in Massachusetts that we accurately assess the impacts of predation on prey populations and determine if prey species are at risk of extinction due to overpredation (New et al. 1995). The ranges of different butterfly species in Massachusetts have shifted due to climate change, with

southerly species expanding northward and northerly species receding from their native ranges (Breed et al. 2013). Declines in southerly species may primarily be due to factors other than climate change (Breed et al. 2013); our model provides us with a means of evaluating if wasp predation may be such a factor.

We believe that our model provides biologically reasonable output in its current iteration, although it does deviate from our expectations. To serve as a check for our model, we calculated the expected number of lepidopteran larvae that are killed by an average *P. dominulus* nest by using previously published data (Suzuki 1980, Armstrong and Stamp 2003a, Brown et al. 2012). We estimated that 379.9 lepidopteran larvae are killed over the course of the colony cycle by the average *P. dominulus* nest. By dividing this number by the average nest size of *P. dominulus* colonies living under natural prey conditions found in Armstrong and Stamp 2003a, we can make a simple prediction that 3.58 caterpillars will be killed per cell in a nest. The mean number of lepidopteran larvae killed per nest as predicted by our model was  $522 \pm 184.13$  larvae.

The greater number of lepidopteran mortality as predicted by our model may be influenced by the programmed rules governing foraging. *P. dominulus* in poorly-fed colonies have been observed to forage at temperatures of 23°C (73.4°F), while wasps with greater food resources available do not forage, likely because of the risk of not making it back to the nest on a cool day (Armstrong and Stamp 2003b). It is possible, then, that our model output represents an overprediction of lepidopteran larvae killed, as wasps in the model foraged so long as temperature was above 68°F and there was no rain, which may be a temperature at which only *Polistes* in severe need of food forage.

The data used in our literature-based predictions, except for average nest size, were also used as parameters in our model (Table 1), which aids in explaining the relative closeness of our

two different predictions. However, our model output includes environmental stochasticity as determined by accessing a dictionary of weather data from Bedford, MA from the past 9 years (NCDC 2005-2013). The number of lepidopteran larvae killed per day in our calculations in the model is also affected by the number of workers present on the nest – the greater the number of workers on the nest, the more larvae are killed that day (Table 1). Since brood mortality in our model is triggered by random number generation compared to a fixed parameter (Suzuki 1980), the population of brood that develops into adults, and therefore the number of lepidopteran larvae killed, becomes more variable.

We used weather data from Bedford, Massachusetts (NCDC 2005-2013) to inform our current predictions, although we aim to make our model adaptable for other invaded communities where weather data for the colony cycle are available. Since weather conditions (in foraging-positive hours) are a central source of environmental stochasticity in our model, our predictions will be most accurate when data for the area in question are used. The United States National Climatic Data Center (NCDC) gathers quality-controlled weather data from weather stations in all 50 states, as well as U.S. territories. Given the spread of *P. dominulus* across the nation (reviewed in Liebert et al. 2006), we can use these data to form predictions targeted to specific invaded environments that are informed by local climate. By using our model to form predictions for different climates, we may better understand how weather patterns affect *Polistes* foraging, and can better anticipate how these wasps may be affected by climate change.

Further, the process of building our model has elucidated what information we need on *P. dominulus* in order to make increasingly accurate predictions of prey impacts. Our model parameters are based on data gathered from a number of *Polistes* wasp species, including *P. dominulus*, *P. fuscatus* and *P. chinensis* (Table 1). These concessions were made out of

necessity, as some important data that needed to be used in our model (for example, foraging success rate) have yet to be gathered, to our knowledge, for *P. dominulus*; this information is, however, available for other *Polistes* wasps (Table 1). Given the differences in biology and behavior of these wasp species (Reviewed in Liebert et al. 2006, Gamboa et al. 2002), the most accurate model for *P. dominulus* should only include information on *P. dominulus*.

Future studies may therefore attempt to gather this information, and continue to build upon the foundation that we have set with our model by incorporating more facets of *Polistes* foraging and nesting behavior. Although models are by necessity a simplification of reality (Jackson et al. 2000) we have gathered extensive literature, both on *P. dominulus* and other *Polistes* species, that will allow us to build far greater levels of behavioral complexity into our model. It is our hope to see our model expanded such that it is as biologically accurate as possible. Ideally, our model will be able to be used to predict prey impacts of *Polistes spp.* foraging across the globe, so long as sufficient foraging and weather data are available.

One of the first components that should be added to our model are alternative nest founding strategies for the foundresses in our model. *Polistes* foundresses use several alternative nesting behavioral strategies, and the expected frequencies of these strategies in a population have been determined (Starks and Fefferman 2006). Single foundresses establish nests individually, while multiple foundresses may establish dominant-subordinate relationships to build a nest together and rear brood (Pardi 1951). “Sit-and-wait” adopter wasps wait for a nest to be abandoned (Starks 1998), while usurper wasps will eject a lone foundress from her nest and take over her developing workforce (Starks and Fefferman 2006). Both adopters and usurpers destroy all eggs and young larvae on their new nest, while allowing older larvae and pupae to eclose and serve her and her offspring (Starks 1998, Starks and Fefferman 2006). The frequency

of these alternative strategies varies depending on wasp species – compared to *P. fuscatus*, rates of multiple founding in *P. dominulus* are significantly higher, and rates of intraspecific nest usurpation are significantly lower (Gamboa et al. 2002). Since these alternative strategies affect the rate of development and size of the nest's population, and therefore the amount of lepidopteran prey consumed, it is important that these behaviors be represented in our model.

Our model currently uses field data for invaded habitat in Carlisle, MA to determine the rate of nest growth. Without a season's worth of field data on nest growth, though, we must use another source to inform this parameter. In order to make immediate predictions in areas that have not been extensively surveyed, we may base the rate of nest-building on the average rate for the desired *Polistes* species.

Prior studies have shown that there is considerable pressure for *Polistes* colonies to produce the first wave of workers as quickly as possible, likely due to high colony failure rate associated with foundress mortality (Miyano 1980, Mead et al. 1994). Social wasps consume (Rossi and Hunt 1988) and store supplies of honey in cells on their nest (Strassman 1979) as a nutrient source. In *P. chinensis*, honey availability is shown to affect the frequency of larval cannibalism – honey-limited colonies had significantly higher rates of cannibalism (Kudo and Shirai 2011). In order to better model food needs in adult wasps and rates of larval cannibalism (which in turn affects the availability of nest cells and therefore nest building rate), nectar foraging and storage should be built into our model. The current larval mortality rate used as a parameter in our model (Table 1) is believed to result primarily from cannibalism (Suzuki 1980), but this does not factor in nest cells used for nectar storage.

Sensitivity analysis of ecological models reveals which processes and coefficients in the model most affect the observed results (Jackson et al. 2000). Although we tested for correlations

between parameters (Table 4), we were not able to test how these relationships change when the values of these parameters are adjusted. The correlations between these parameters matched what we expected; for example, since the number of workers determines how many foragers hunt for lepidopteran larvae, the number of caterpillars killed in a model run should be closely, positively correlated with the number of workers (Table 4).

Sensitivity analysis will be essential not just in testing the accuracy of the model, but also in using the model to generate new hypotheses. Our model can be used to test hypotheses beyond prey consumption by *Polistes* wasps over the course of the cycle. For example, since the number of foraging trips made in a given day in the model depends directly on suitable weather conditions, our model can be used to examine how climate change may affect wasp foraging behavior and therefore community structure. If average temperatures increase in an invaded area with climate change, we can expect that wasps will forage more, and more lepidopteran larvae will be consumed. However, if climate change leads to greater rainfall, we may see a decrease in the expected number of lepidopteran prey consumed. These hypotheses can then be tested in the field by studying *Polistes* foraging activity over seasons in a given area.

Ultimately, our individual-based model serves as the foundation upon which to build a more complete simulation of *Polistes* foraging and nesting behavior, which may be used to determine the impacts of *Polistes* wasps on community structure as accurately as possible. We've used the first iteration of this model to form location-specific predictions for how the presence of exotic invasive *P. dominulus* affects lepidopteran populations in eastern Massachusetts. We aim to develop our current model into a tool that can be used across *Polistes* species and habitats to predict the impacts of wasp predation on prey populations and

biodiversity, in order to determine how exotic invasive *Polistes* wasps affect community structure.

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## Tables

Table 1. Parameters used in our individual-based model for predicting the number of lepidopteran larvae killed by an individual, single foundress *P. dominulus* colony over the course of the colony cycle (March 1<sup>st</sup> – August 31<sup>st</sup>).

Parameter	Value	Species	Source
Day 1 of Colony Cycle	May 1st	<i>P. dominulus</i>	Gamboa et al. 2002
Duration of Colony Cycle	4 months	<i>P. dominulus</i>	Turillazzi 1980
Foraging Time Frame	1000 - 1500 hours	<i>P. dominulus</i>	Armstrong and Stamp 2003a
Foraging Conditions	Temperature $\geq$ 68°F, No Rain	<i>P. dominulus</i>	Armstrong and Stamp 2003b
Foraging Positive Hours	0-5 per day (randomly chosen from data dictionary)	n/a	NCDC 2005-2013
Max Payload Capacity (Worker)	0.0140 g	<i>P. dominulus</i>	Brown et al. 2012
Max Payload Capacity (Foundress)	0.0173 g	<i>P. dominulus</i>	Brown et al. 2012
Age Brood = Egg	0-11 days old	<i>P. dominulus</i>	Pardi 1951
Age Brood = Larvae	11-27 days old	<i>P. dominulus</i>	Pardi 1951
Age Range = Pupae	27-39 days old	<i>P. dominulus</i>	Pardi 1951
Age at Eclosion	40 days old	<i>P. dominulus</i>	Pardi 1951
Larval Mortality Rate	5.6% chance death/day	<i>P. chinensis</i>	Suzuki 1980
Worker Foraging Rate	1.9 foraging trips/hour	<i>P. dominulus</i>	Gamboa et al. 2002
Foraging Success Rate	35% per trip	<i>P. fuscatus</i>	Gould and Jeanne 1984
Caterpillars Killed/Hour	0.0140 g max payload x 1.9 foraging trips/hour x 0.35 success rate x 0.90 prey used for only one prey ball x # foraging positive hours	<i>P. dominulus</i> & <i>P. fuscatus</i>	Suzuki 1980 Gould and Jeanne 1984; Gamboa et al. 2002; Armstrong and Stamp 2003a; Armstrong and Stamp 2003b
Chance Workers Return from Foraging	81% per day	<i>P. dominulus</i>	Starks and Peters 2002
Foundress Longevity	87 $\pm$ 26 days	<i>P. dominulus</i>	Gamboa et al. 2002
Nest Building Rate	0.28 - 1.38 cells/day (randomly chosen in range)	<i>P. dominulus</i>	Field Data (Carlisle, MA)
Max Egg Laying Rate	3 eggs/day	<i>P. dominulus</i>	Mead et al. 1994
Start of Oophagic Period	Day of first hatching (Day 12)	<i>P. dominulus</i>	Mead et al. 1994
Duration of Oophagy	6-10 days (randomly chosen in range)	<i>P. dominulus</i>	Mead et al. 1994
Max Oophagy Rate	Max of 3 eggs/day	<i>P. dominulus</i>	Mead et al. 1994
Start of Reproductive Emergence	August 1st (Day 93)	<i>P. fuscatus</i>	Reeve et al. 1998

Table 2. Mean values ( $\pm$  standard deviation) of *P. dominulus* nest growth data from our field site at the Great Brook State Farm in Carlisle, MA (n = 19). Values in parentheses do not include data from the hypergynous nest, and were used as parameters in our model where applicable (Table 1). Nests were considered to be growing until there was no change observed in number of cells between survey weeks. Nests were assumed to be founded on May 7<sup>th</sup>, 120 days (the length of the colony cycle) before the final survey date (Turillazzi 1980).

	<b>Initial Nest Size (# cells)</b>	<b>Final Nest Size (# cells)</b>	<b>Nest Growth (cells/day)</b>	<b># Days Growth</b>
<b>Mean</b>	52.7 (44.1)	82.3 (74.8)	0.90 (0.83)	98.8 (98.8)
<b>Std. Dev.</b>	43.17 (21.80)	47.94 (36.14)	0.620 (0.552)	24.51 (25.23)

Table 3. Summary of model outputs for single foundress *P. dominulus* nests in Eastern Massachusetts over the course of one colony cycle (May 1<sup>st</sup> – August 31<sup>st</sup>, n = 10,000 nests), using the parameters listed in Table 1.

	<b>Final Nest Size (# cells)</b>	<b>Caterpillars Killed</b>	<b>Workers Eclosed</b>	<b>Reproductives Eclosed</b>
<b>Mean</b>	86.7	522.0	30.0	27.0
<b>Std. Dev.</b>	35.23	184.13	12.13	12.22

Table 4. Correlation of model outputs for single foundress *P. dominulus* nests in Eastern Massachusetts after one colony cycle (May 1<sup>st</sup> – August 31<sup>st</sup>, n = 10,000 model runs) All tests performed using Spearman’s rank correlation test. Spearman’s  $\rho$  and p-values are given, with p-values in parentheses.

<b>Output Parameter</b>	<b>Final Nest Size (cells)</b>	<b>Caterpillars Killed/Nest</b>	<b>Nest Building Rate (cells/day)</b>	<b>Queen Age (days)</b>	<b>Workers Eclosed</b>
<b>Final Nest Size (cells)</b>	---	---	---	---	---
<b>Caterpillars Killed/Nest</b>	0.903 (p < 0.0001)	---	---	---	---
<b>Nest Building Rate (cells/day)</b>	0.990 (p < 0.0001)	0.885 (p < 0.0001)	---	---	---
<b>Queen Age (days)</b>	0.048 (p < 0.0001)	0.039 (p < 0.0001)	0.004 (p = 0.680)	---	---
<b>Workers Eclosed</b>	0.964 (p < 0.0001)	0.913 (p < 0.0001)	0.970 (p < 0.0001)	0.001 (p = 0.885)	---
<b>Reproductives Eclosed</b>	0.673 (p < 0.0001)	0.596 (p < 0.0001)	0.665 (p < 0.0001)	0.554 (p < 0.0001)	0.637 (p < 0.0001)

## Figures

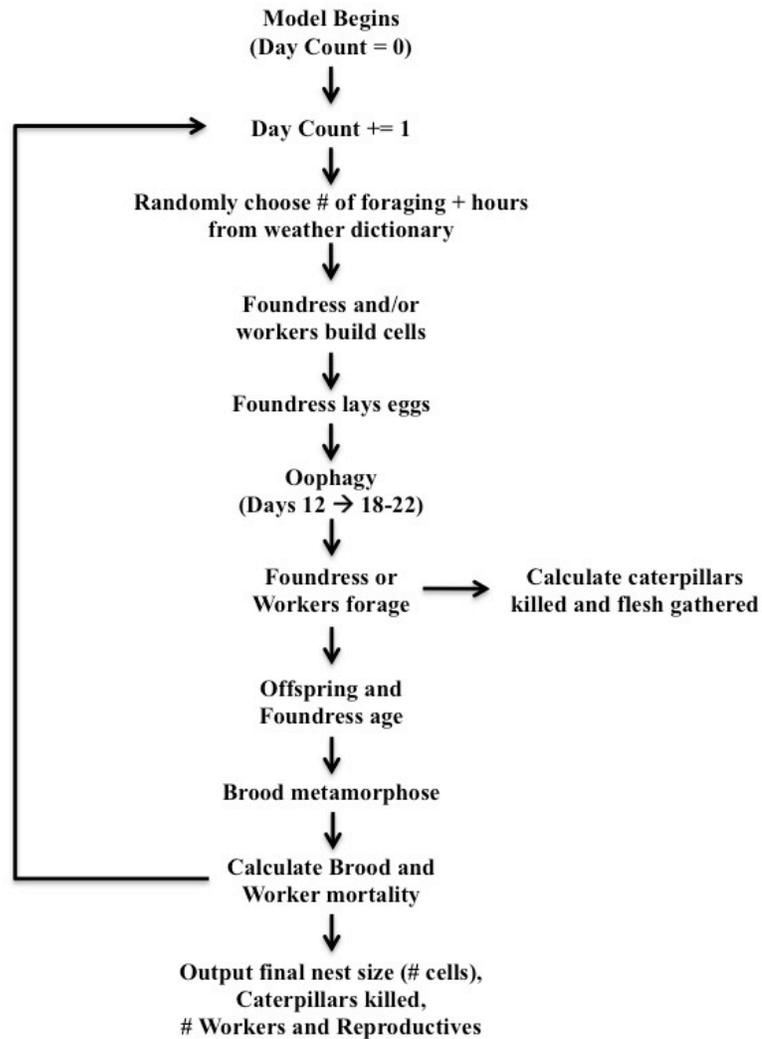


Figure 1. Schedule of events in a single day of our individual-based model. The model runs for 123 days, from May 1<sup>st</sup> to August 31<sup>st</sup>. Parameters governing the above behaviors are given in Table 1.

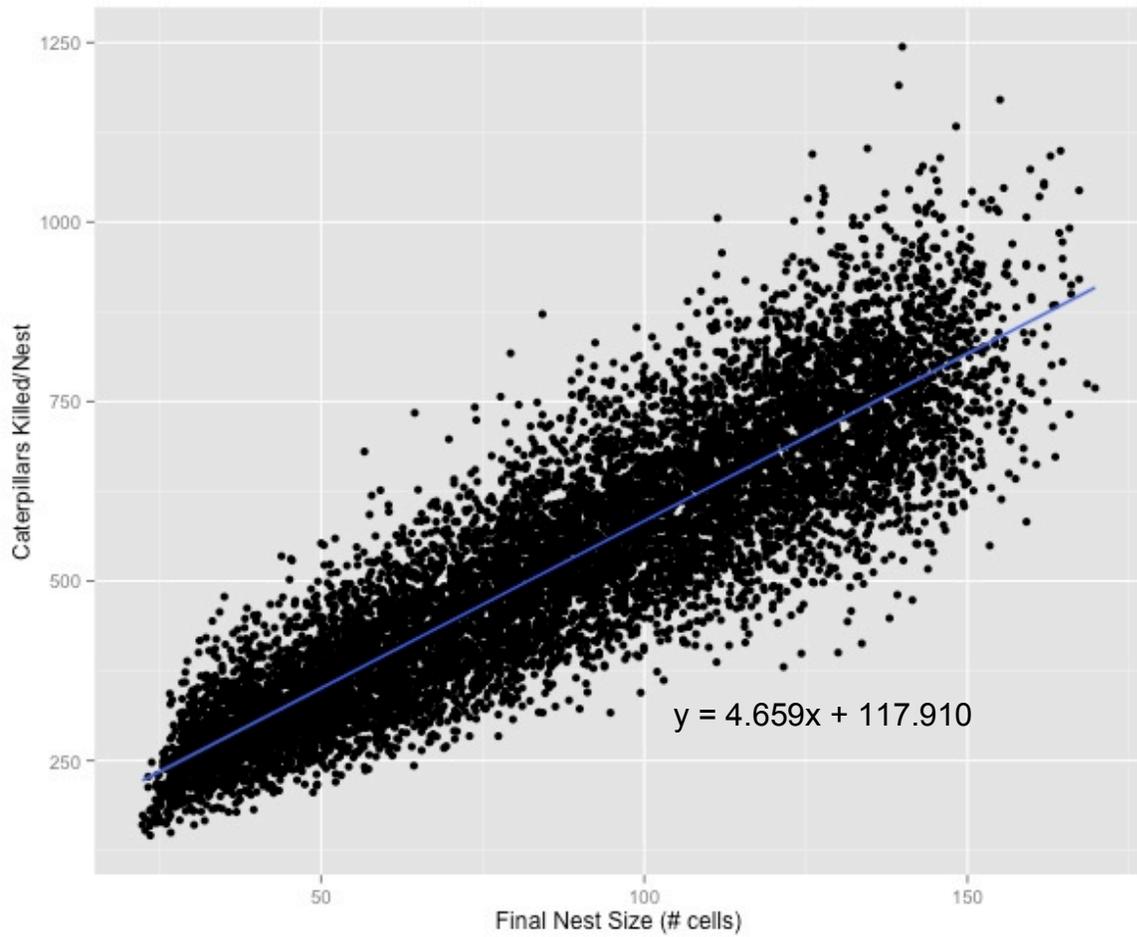


Figure 2. Final nest size and number of lepidopteran larvae (caterpillars) killed by individual, simulated *P. dominulus* colonies over the course of the colony cycle (May 1<sup>st</sup> – August 31<sup>st</sup>, n = 10,000 nests). The number of lepidopteran larvae killed per nest is significantly, positively correlated with final nest size (Spearman's rank correlation test;  $\rho = 0.903$ ,  $S = 16101572340$ ,  $p < 0.0001$ ).

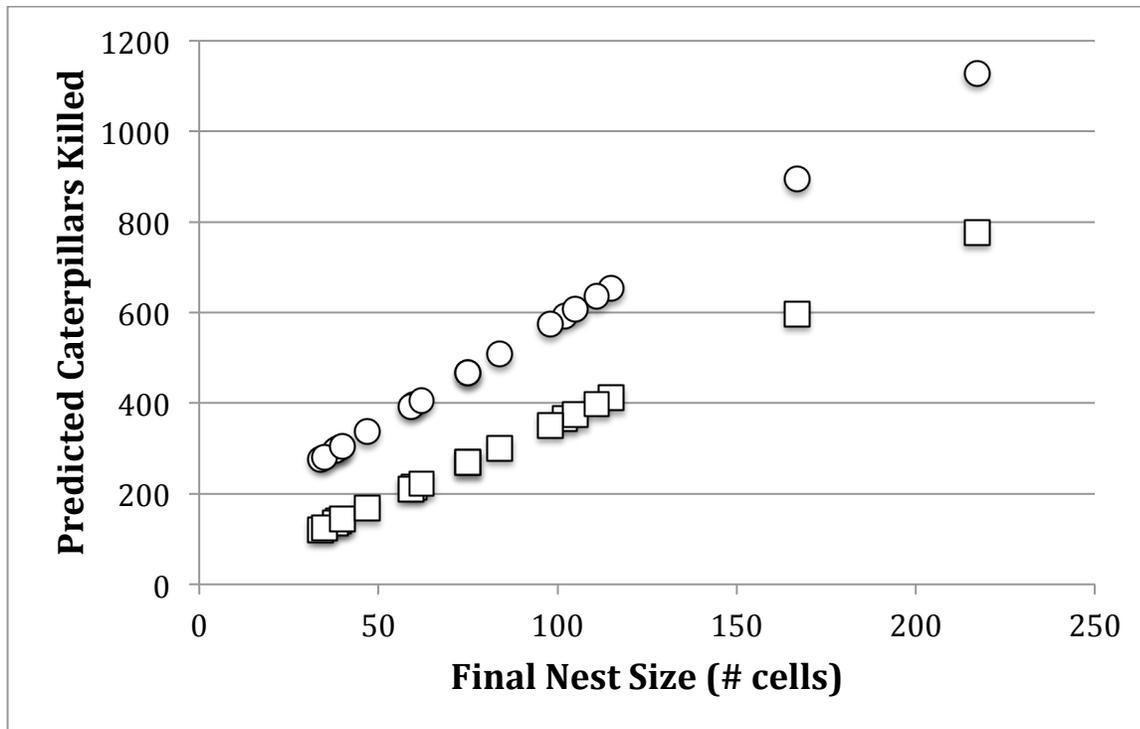


Figure 3. Predicted levels of predation by *P.dominulus* colonies at our field site at the Great Brook State Farm in Carlisle, MA during the 2013 colony cycle (May 1<sup>st</sup> – August 31<sup>st</sup>, n = 19). Each point represents an individual nest; circles represent kills predicted using the best-fit line from our model, and squares represent kills predicted using previously published data on *Polistes* foraging and nest growth. Our model predicts that the study population killed an estimated total of 9,552 caterpillars over the course of the colony cycle (mean = 501.2 ± 223.35 caterpillars/nest), while the literature predicts a total of 5,596 caterpillars killed (mean = 294.7 ± 171.62 caterpillars/nest).

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