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Comparisons of Two Symmetric Density Function Solutions of Aphid Population Growth Models

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Abstract

Aphids are among the world's most devastating crop pests, and their population trajectories in field crops are characterized by rapid boom and bust, under the influence of bottom up (host plant) and top down (natural enemy) forces. Theoretical development in aphid growth trajectory modeling has recently advanced quite significantly, and the logistic and normal probability density functions have been found to provide analytical solutions to mechanistic models of the aphid population growth dynamics. The logistic or hyperbolic secant squared model captures a growth trajectory shaped by negative feedback of the aphid population on itself, due to the accumulation of adverse effect on its host plant and the coupling with natural enemies (bottom up as well as top down effect), while the normal model can be derived on the basis of a relationship between intrinsic growth rate and the host plant phenology. In this paper, we fit both models to a large number of observed aphid population trajectories and explore model properties. It is shown that, despite the diverging mechanistic underpinnings of the model, the generated growth curves, as fitted to the data, are very similar, as are characteristics, such as the height of the peak, the time of the peak and the accumulated area under the curve. Both models are useful workhorses for capturing aphid growth dynamics, but fitting one or either model cannot be used as evidence for the underpinning mechanisms, as different underpinning mechanisms result in similar population dynamics.

1 Introduction

The logistic growth model is classic in ecology (Renshaw 1991) and has been widely used for decades to describe the growth of “any local population whose numbers are determined by the stock of some non-expendable resource” (Andrewartha, 1951, p. 157). Such populations reach a positive equilibrium size, commonly called the carrying capacity. However, local populations of overlapping generations of aphids, as well as numerous other insect species, collapse in size rather than moving towards some positive carrying capacity. Andrewartha (1951) suggests that such populations become extinct because their “numbers depend on the amount of some diminishing or expendable resource” and/or because their predecessors increase the likelihood of a “predator, . . . the recurrent use of an insecticide, or of other environmental forces which eventually lead to local extinction” (Andrewartha 1951, p. 158).

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Recently, two mechanistically based models with relatively simple analytical solutions have been developed to describe the size over time of aphid populations which eventually collapse. The hyperbolic secant squared (or HSS) model was developed by Prajneshu (1998) and Matis et al. (2007a), and the Normal model was developed by Williams et al. (1999) and Costamagna et al. (2007). The parameter sparseness and high degree of process aggregation in each of these models is a strength, as their concise formulations make them useful as descriptions of processes and amenable to parameter fitting. The models differ in their mechanistic underpinning. One model is based on the idea that the use of resource during the history of the population will limit its further growth. The other model is based on the empirical finding in several species of aphid that bottom-up effects of the plant cause the intrinsic rate of increase of the aphid population to decline with plant age, due to effects of survival, development rate and reproduction of the individuals (Williams et al., 1999). Each of these models has been fitted previously to aphid data, but we are not aware of any comparative fittings of the two models.

The purpose of this paper is to gain a better understanding of the two models by comparing their properties and their goodness-of-fit to common data sets on various aphid species. Section 2 develops the mechanistic basis for each of the two models and outlines their solutions. Section 3 describes data on the greenbug (*Schizaphis graminum*), the mustard aphid (*Lipaphis erysimi*), and the soybean aphid (*Aphis glycines*). The results of fitting the two models to these data are discussed in Section 4. Section 5 contains suggestions for the practical application of the two models as well as suggestions for further research.

2 Model Development

For all subsequent models, we let $N(t)$ denote the population size at time t , with initial value $N(0) = N_0$ and with derivative N' .

2.1 Normal Model - For Linearly Decreasing Growth Rate r

Costamagna et al. (2007) develop a generalized model in which the intrinsic rate of increase, denoted r , is a time-varying function. This recognizes, for example, that the “host plant advances in phenological age” and hence that r might diminish over time. Their model could be written as

$$N' = r(t)N \tag{1}$$

with

$$r(t) = r_{\max}(1 - ct), \tag{2}$$

where r_{\max} denotes the intrinsic rate of increase at $t = 0$ and c the slope of the simple linear function. They cite empirical evidence (Williams et al. 1999) which shows that the natural rate of increase for aphids on sugar beet decreased over time.

We note that the solution to (1) and (2) may be written in the convenient user-friendly, nonlinear form

$$N(t) = \exp \{a_0 + a_1t - a_2t^2\} \tag{3}$$

where

$$\begin{aligned} a_0 &= \log \{N_0\} \\ a_1 &= r_{\max} \\ a_2 &= cr_{\max}/2 . \end{aligned} \tag{4}$$

The mechanistic parameters in (2) are immediate from (4) as

$$\begin{aligned} N_0 &= \exp \{a_o\} \\ r_{\max} &= a_1 \\ c &= 2a_2/a_1 . \end{aligned} \tag{5}$$

Letting N_{\max} and t_{\max} denote the predicted size and time of the peak count, one can show

$$\begin{aligned} t_{\max} &= c^{-1} \\ N_{\max} &= \exp \{a_0 + a_1^2/(4a_2)\} . \end{aligned} \tag{6}$$

Costamagna et al. (2007) recognize that the solution in (3) and (4) could also be written as a scaled Normal curve. One convenient form for this Normal is

$$N(t) = N_{\max} \exp[-g^2(t - t_{\max})^2], \tag{7}$$

where N_{\max} and t_{\max} are direct model parameters relating to the peak, and g is a parameter related to spread. The paper shows that model (7) fits soybean aphid data well.

The paper also notes that the Normal curve in (7) is a scaled form of the Normal density function. The mean μ and standard deviation σ , which describe the center and spread, of the underlying Normal distribution are

$$\begin{aligned} \mu &= t_{\max} \\ \sigma &= (\sqrt{2}g)^{-1} . \end{aligned} \tag{8}$$

The area under the curve, or AUC, also called the cumulative density, $F(\infty)$, is an endpoint variable of interest. Integrating model (7), we note that

$$AUC = F(\infty) = \sqrt{\pi}N_{\max}/g. \tag{9}$$

The mechanistic parameters in (2) may be obtained from the parameters in (7) as

$$\begin{aligned} c &= (t_{\max})^{-1} \\ r_{\max} &= 2g^2t_{\max} \\ N_0 &= N_{\max}/\exp[g^2t_{\max}^2]. \end{aligned} \tag{10}$$

2.2 Hyperbolic Secant Squared Model - For Cumulative-Size Dependent Growth

The hyperbolic secant squared, or HSS, model is developed in Matis et al. (2007a, 2008a). The model assumes that the per capita death rate is a function of cumulative past size, denoted

$$F(t) = \int_0^t N(s)ds. \tag{11}$$

The assumption on the rate of change is accordingly

$$N' = (\lambda - \delta F)N \tag{12}$$

where λ and δ are birth and death rate coefficients. Prajneshu (1999) recognizes that this equation has an analytical solution. Matis et al. (2007a) give the user-friendly solution

$$N(t) = 4N_{\max}e^{-b(t-t_{\max})} [1 + e^{-b(t-t_{\max})}]^{-2} \quad (13)$$

in which N_{\max} and t_{\max} again denote the size and time of peak count, and b is an approximate birthrate. Matis et al. (2008a) note that the solution may be written as

$$N(t) = N_{\max} \operatorname{sech}^2 [b(t - t_{\max})/2], \quad (14)$$

which leads to its alternative “hyperbolic secant squared” (HSS) name. The model has been shown to provide a good description of data on the pecan, mustard and cotton aphids.

This model, like the Normal, is symmetric. It is a scaled form of the sech^2 (also called the logistic) distribution (Johnson and Kotz 1970, p. 244) which density is known to be greater in the tails than the Normal. Therefore the sech^2 distribution has a larger coefficient of kurtosis than the Normal. Using properties of the sech^2 distribution, the center and spread of the curve may be expressed in terms of the mean μ and standard deviation σ using the parameters in (13) and (14) as

$$\begin{aligned} \mu &= t_{\max} \\ \sigma &= \pi / (\sqrt{3}b). \end{aligned} \quad (15)$$

We show in Matis et al. (2007a) that the cumulative density, $F(\infty)$, obtained by substituting (14) into (11) is

$$AUC = F(\infty) = 4N_{\max}/b. \quad (16)$$

The paper also shows that the mechanistic parameters in (12) may be obtained from the regression parameters in (13), defining

$$d = \exp(bt_{\max}), \quad (17)$$

as

$$\begin{aligned} \lambda &= b(d - 1)/(d + 1) \\ \delta &= b^2/(2N_{\max}) \\ N_0 &= 4dN_{\max}(1 + d)^{-2}. \end{aligned} \quad (18)$$

Because d in (17) is usually large, it follows from (18) that parameter b estimated in model (13) is an accurate approximation of birthrate parameter λ in (12).

In order to compare this model with the Normal model, we utilize a property from Matis et al. (2008e). The per capita growth rate for this model, found by differentiating (14) and dividing by N , is

$$N'/N = -b \tanh [b(t - t_{\max})/2]$$

which is a decreasing function. The corresponding per capita rate for the Normal is the simple linear function $r(t)$ in (2).

Johnson and Kotz (1970, p. 54) note that “a particular form of the logistic distribution (i.e. HSS model) is very close to a Normal distribution.”. However, there is no apparent simple mathematical relationship between the parameters of models (3) and (13), whereby one could easily transform a predicted HSS model to the Normal counterpart, or vice versa. Therefore, we will examine correspondences between the HSS and the Normal models empirically for a number of data sets. Descriptions of the data sets follow.

3 Experimental Data

3.1 Data on Greenbug (*Schizaphis graminum*)

Data set 1 consists of data gathered by the Texas Agricultural Experiment Station on greenbug abundance at various irrigated and dryland sorghum fields in a study from 1988 through 2000. Twentyseven (27) fields were included in the study. In each field, 144 plants were sampled approximately weekly. The complete data set is given in Michels (2007). We have previously analyzed the 27 cases with a different objective under the simplifying assumption that all sampling intervals were one week in length (Matis et al. 2008d). These data are reanalyzed in Section 4, with each individual case fitted to models (3) and (13) using the exact sampling intervals measured in days.

We regard this first data set as the primary one, as it was gathered under the varied environmental conditions produced over the 13 year period at six different locations with two irrigation treatments. However, we also analyze two additional sets of greenbug data, called data sets 2 and 3, for this paper. Michels et al. (2002) report on experiments to study the effects of irrigation regimes and of plant density on greenbug abundance on sorghum at the Bushland Experiment Station in Texas. Data set 2 consists of 30 random plots on which greenbug abundance was observed on nine sampling dates in 1999, and data set 3 consists of another 30 random plots observed on seven dates in 2000. We analyzed these 60 additional plots to compare the results for the greenbug under the homogeneous conditions with the heterogeneous conditions of data set 1.

3.2 Data on Mustard Aphid (*Lipaphis erysimi*)

We have previously fitted the HSS model to a smaller data set, called data set 4, on the mustard aphid (Matis et al. 2007a) and will use these data now for model comparisons. Studies were conducted at the Haryana Agricultural University in India from 1983-1990 on the effects of the mustard aphid on three different *Brassica* varieties, namely *B. campestris* (rapeseed), *B. juncea* (mustard), and *B. napus* (winter rape). These were studied for 4, 6, and 3 years respectively. Each data point represents the mean of 30 plants. In the absence of more exact information, the samples are assumed to have been gathered on exact weekly intervals.

3.3 Data on Soybean Aphid (*Aphis glycines*)

The Normal model has been previously fitted to a limited data set on the soybean aphid (Costamagna et al. 2007). Four experiments were conducted in Michigan to study the population dynamics under field conditions in predator exclusion cages. Two of these experiments, one in 2004 and the other in 2005, had sampling designs which included observations during the decreasing phase of the abundance curve, and hence are suitable for this investigation. Both of these experiments were conducted at the Kellogg Biological Station using sleeve cages. Sampling was performed approximately weekly by counting the total number of aphids on all the enclosed plants in the sleeve cages. The reported counts are expressed as the mean number of soybean aphids per plant. This data set is included, despite there being only two suitable cases, as the experiment excluded predators and hence provides a contrast to the previous open field greenbug and mustard aphid experiments.

4 Results

We wish to compare both the goodness-of-fit and the corresponding parameters for the two models. For subsequent use, the parameters of the HSS model will be denoted $N1_{\max}$, $t1_{\max}$, $\sigma1$, and $F1(\infty)$, whereas these for the Normal model are $N2_{\max}$, $t2_{\max}$, $\sigma2$, and $F2(\infty)$. Models (3) and (13) were fitted to each case using the nonlinear least squares option in SPSS (2002) assuming additive, normally distributed errors.

4.1 Results for Greenbug Data

4.1.1 General Description of Fitted Models in First Data Set

Both the HSS and the Normal models described the data well for all 27 cases in the first data set. The most representative case is arguably case 15, which is illustrated in Fig. 1A. Its estimated peak size, $N1_{\max} = 111.6$, is the median value for all 27 cases of the HSS model. The modified R^2 for nonlinear models (1-Residual SS/Corrected SS), as given by SPSS and used subsequently as a comparative measure, is $R^2 = 0.999$, which is also the most common R^2 value. The Normal model has peak size $N2_{\max} = 111.4$, which is very close to its median value, and an $R^2 = 0.999$.

Fig. 2 illustrates four of the more extreme cases of the 27 total cases. Fig. 2A graphs case 3 with the largest $N1_{\max}$ for the HSS model (comparable Normal model values in parenthesis) of 2228 (1951), and Fig. 2B gives case 17 with the smallest value of $N1_{\max}$ of only 1.53 (1.55). Figs. 2C and 2D portray cases 18 and 26 with the largest spread, of $\sigma1 = 15.3(12.3)$, and the smallest spread, of $\sigma1 = 2.5(2.7)$, respectively. As one might expect, the largest and smallest estimates of $F(\infty)$ are given in Fig. 2A and 2B, with estimates of 17692 and 14.3 aphid-days.

The *smallest* value of R^2 for all 27 cases is $R^2 = 0.68$ for case 18 in Fig. 2C, and the next smallest is $R^2 = 0.70$ for case 17 in Fig. 2B. These two lowest cases result from atypical fluctuation, possibly sampling error, resulting from the low counts. The next lowest is $R^2 = 0.84$, and the median value is $R^2 = 0.97$. These results indicate that, in general, both models fit these greenbug data very well, whether the peak is high or low, sharp or broad. The fitted curves are remarkably close to one another.

4.1.2 Comparison of Goodness-of-Fit

The HSS model generally fitted the data a bit better than the Normal model, as it provided a better fit in 19 of the 26 cases (one case was tied). The best comparative HSS fitting is case 16 in Fig. 1, for which the ratio of error mean squares, EMS1/EMS2, another comparative goodness-of-fit measure, is 0.23. The best relative fitting for the Normal is given in case 8 in Fig. 3A, for a ratio of 1.71 in EMS's. In general, even though the ratio of EMS's varies from 0.23 to 1.71, the residuals for both models are tiny and virtually unobservable visually.

4.1.3 Comparison of Center and Spread

As both models are symmetrical, it is not surprising that the centers of the curves, i.e. the t_{\max} values, are always very close, never exceeding a difference of 1 day. The Normal $t2_{\max}$ exceeds $t1_{\max}$ for the HSS model in 14 of the 27 cases, with the largest difference being 0.89 days, for case 14 illustrated in Fig. 3B, and the smallest being -0.66 days, illustrated for case 13 in Fig. 3D. Fig. 4A gives the scatterplot of the comparative t_{\max} data. We use regression through the origin, without error assumptions and hence without any subsequent inference, as a data analytic technique to compare

the relative sizes of the two t_{\max} 's using the estimated slope. The regression equation is

$$t1_{\max} = 1.000t2_{\max},$$

with unadjusted $R^2 = 1.000$, indicating very close agreement.

The spread of the HSS model, $\sigma1$, exceeds the spread of the Normal model, $\sigma2$, in 22 of the 27 cases. The ratio $\sigma1/\sigma2$ is smallest (0.80) in case 17 illustrated in Fig. 2B, and is largest (1.08) in case 8 portrayed in Fig. 3A. Although the spread is generally larger for the HSS model, this increase is likely a function of the larger tail area, hence the bulk of the curve, within one standard deviation of the center, is always quite close to one another. Fig. 4B displays the scatter plot of $\sigma1$ vs $\sigma2$. The regression equation is

$$\sigma1 = 1.129\sigma2,$$

with unadjusted $R^2 = 0.996$, indicating a general 13% increase in the spread of the HSS model compared to the Normal model.

4.1.4 Comparison of Key Endpoints

The HSS model generally has a higher peak size than the Normal model, as $N1_{\max}$ exceeds $N2_{\max}$ in 22 of the 27 cases. The largest proportional increase in peak size given by the HSS is $N1_{\max}/N2_{\max} = 1.59$ illustrated for case 8 in Fig. 3A. This is much larger than the rest, as the next largest ratio is 1.22 given for case 22 in Fig. 3C. The smallest ratio is 0.98, illustrated for case 17 in Fig. 2B, which indicates that in all five cases where the Normal model had a larger peak, the increase was very small. Fig. 4C gives the scatter plot of $N1_{\max}$ vs $N2_{\max}$ for all 27 cases. The regression through the origin has equation

$$N1_{\max} = 1.138N2_{\max}$$

with unadjusted $R^2 = 0.996$, which indicates a rough 14% increase in peak size for the HSS as compared to the Normal model.

The cumulative density, $F1(\infty)$, of the HSS model exceeds $F2(\infty)$ of the Normal model in 26 of the 27 cases. The largest value of the ratio $F1(\infty)/F2(\infty)$ is 1.28 for case 8 in Fig. 3A, and the smallest is 0.92 for case 14 in Fig. 3B. Fig. 4D illustrates the scatterplot for these two densities. The estimated regression line is

$$F1(\infty) = 1.035F2(\infty),$$

with unadjusted $R^2 = 0.999$, indicating an average 3.5% increase for the cumulative density of HSS over the Normal model.

4.1.5 Results from Data Sets 2 and 3

Data sets 2 and 3, each gathered at a single location in a given year, did not have the wide variation in population sizes exhibited in data set 1. The peak counts for the second data set, gathered in 1999 which was a relatively cool year with about average rainfall, ranged from 0.9 to 27.5/plant, and the comparable counts in 2000, a dry summer with about average temperature, ranged from 1.1 to 54.3/plant. Nevertheless the results for these data sets are similar qualitatively to those in data set 1.

For 1999, the HSS model provides a better fit in 14 of 27 cases, with three ties, and in 2000, the HSS model fits better in 21 of 28 cases, with two ties. These results are tabulated in Table 1, which also gives the comparative estimated regression slopes and their standard errors for comparing the HSS model to the Normal model for each of the four response variables. The results for 1999 indicate

that, on average, the HSS model in comparison with the Normal model had *increases* in peak size of 16.0% (se=7.5), in cumulative density of -1.6% (3.0), in time of peak of -0.8% (0.4), and in spread of 11.9% (2.8). The corresponding results for 2000 show that the HSS model had increases in peak size of 12.9% (3.3), in cumulative density of 3.9% (1.3), in time of peak of 0.1% (0.2), and in spread of 10.5% (1.4).

4.1.6 Summary of Greenbug Comparisons

In general, both the HSS and the Normal models fit all the greenbug data well. Though the differences are generally very small, the HSS model provided a better fit in 67%, i.e. 54 of the combined 81, cases. The three greenbug data sets in Table 1 were gathered under differing circumstances, and hence it seems remarkable that the three estimated slopes are so close to one another within each of the four measures. Pooling the 87 combined cases, the HSS model is estimated to have a peak size which is 14.2% larger, a cumulative density which is 1.9% larger, a time of peak size which is nearly equal (within -0.3%), and a spread which is 11.7% larger than the comparable Normal model.

4.2 Results for Mustard Aphid Data

4.2.1 General Description of Fitted Models and Goodness-of-Fit

All 13 fitted HSS models are illustrated for the mustard aphid in Matis et al. (2007a). For present purposes, we note only some extreme cases. The maximum peak is $N1_{\max} = 985$ and the minimum is $N1_{\max} = 12.4$. The largest spread is $\sigma1 = 2.93$ and the smallest is $\sigma1 = 0.75$. The error mean square, EMS, was smaller for the Normal model for seven of the 13 cases. The largest ratio EMS1/EMS2 was 2.33 and the smallest was 0.78. As before, though the ratio varied from 0.78 to 2.33, the residuals are tiny for both models. Both of these two models fit this data also as well as any unimodal model could be expected to fit.

4.2.2 Comparison of Center and Spread

The center of the HSS model, $t1_{\max}$, exceeded the center of the Normal, $t2_{\max}$, in nine of the 13 cases, however the differences are small. The largest difference in absolute value occurs when $t2_{\max}$ exceeds $t1_{\max}$ by 0.24 wks. The scatter plot in Fig. 5A has regression equation

$$t1_{\max} = 1.000t2_{\max}.$$

The spread of $\sigma1$ for the HSS model was larger than $\sigma2$ for the Normal model in all 13 cases, with the largest ratio, $\sigma1/\sigma2$, of 1.23. The scatter plot of the standard deviations in Fig. 5B has regression equation

$$\sigma1 = 1.149\sigma2,$$

indicating a mean increase of about 15% in the spread of the HSS model.

4.2.3 Comparison of Key Endpoints

The peak for the HSS model, $N1_{\max}$, exceeded that of the Normal model, $N2_{\max}$, for 12 of the 13 cases, however the differences were small, with the largest ratio $N1_{\max}/N2_{\max}$ of 1.04. The scatter plot in Fig. 5C illustrates these data, which have regression equation

$$N1_{\max} = 1.017N2_{\max},$$

indicating a roughly 2% increase in the peak size for the HSS model.

The cumulative density for the HSS model, $F1(\infty)$, exceeded that for the Normal model, $F2(\infty)$, in 12 of the 13 cases. The largest $F1(\infty)/F2(\infty)$ ratio is only 1.09, and the smallest is 0.96. The scatter plot in Fig. 5D which illustrates the data has regression equation

$$F1(\infty) = 1.047F2(\infty),$$

for an estimated increase of about 5% in $F1(\infty)$ over $F2(\infty)$. All of the slope estimates for the comparative mustard aphid curves are listed in Table 1.

4.3 Results for Soybean Aphid Data

The two soybean aphid data sets together with their respective fitted HSS and Normal models are illustrated in Fig. 6, and the parameter estimates are given in Table 2. In each case, the two fitted models are very close to one another, with the HSS providing the better fit in one case and the Normal in the other. Following the pattern of the previous comparisons, the HSS model in both cases has a larger center (t_{\max}), spread (σ), peak size (N_{\max}) and cumulative density ($F(\infty)$) by averages of, respectively, 0.4%, 13.8%, 2.6% and 2.7%.

5 Discussion and Conclusions

5.1 Overall Model Comparisons

The principal objective of this paper is to compare the two mechanistic models, both of them symmetric and relatively easy to fit to data, for describing aphid population growth curves. Outstanding among our findings is that, despite their completely different mechanistic formulations and analytical solutions, both models fit each of the combined 102 data sets well, whether the peak is high or low, sharp or broad, early or late.

Though both of the models fit the data well, there are distinct qualitative differences in the fittings. These distinct characteristics include:

1. The HSS model tended to fit better for these data. In cases where the EMS were unequal, the HSS model has the better fit in 61 of the 96 cases. This may be due to the fact that almost all of the experimental data were gathered in open field conditions.
2. The centers of the fitted curves were always very close to one another, with the slopes relating the t_{\max} of each model near 1.00 for each data set. However, the spread of the HSS model is larger than that of the Normal in 85% of the cases, with an estimated average increase of 12%.
3. The peak size, N_{\max} , for the HSS model is estimated to be 14.2% larger than the Normal for the greenbug data, but only 1.7% larger for the mustard aphid data. This apparent species effect is confounded with a difference in sampling design. Therefore, further study with different data is required before this possible species effect could be confirmed.

In summary, although there is no analytical relationship between the parameters of the two models, the parameters from either model can be predicted quite well from the parameters of the other model within any experimental setup.

One might expect to distinguish theoretically between the two mechanistic models based on their per capita rate functions, in (2) and (19) respectively, which have different shape characteristics. To

investigate this, we return to the two model in our representative case in Fig. 1A. The parameters for the HSS model from (14) are $N_{\max} = 111.63$ aphids, $t_{\max} = 43.56$ days and $b = 0.355/\text{days}$, with $\sigma = 5.11$ days and $F(\infty) = 1258$ aphid-days. The parameters for the Normal model from (7) are $N_{\max} = 111.36$ aphids, $t_{\max} = 43.55$ days, and $g = 0.157/\text{days}$, with $\sigma = 4.50$ days and $F(\infty) = 1257$ aphid-days.

The two per capita rate functions are illustrated in Fig. 1B. The estimated rate for the Normal from (2) is

$$r(t) = 13.67 - 0.230t,$$

whereas the estimated rate for the HSS model from (19) is

$$r(t) = -0.355 \tanh(0.178t - 7.732).$$

The rate functions are very close to one another for the time period $35 < t < 50$, during which period most of the changes in population size occur. Consequently, the models are difficult to separate empirically, as the large differences in the functions occur only in the extreme ranges for which there are virtually no data. This explains why, as Johnson and Kotz (1970) note, that this “logistic distribution is very close to a Normal distribution”.

In a perfect world of applications, one might expect the soybean aphid data with its predator exclusion cages to be fitted better by the Normal model, and the open field data for the greenbug and mustard aphid, without being protected from predators, to be fitted better by the HSS model. Such, however, is not the case with our data, and it would seem like data from a more powerful sampling design, perhaps even with daily observations in the extreme tail areas, are required to discriminate empirically between the two mechanistic models.

5.2 Model Generalizations

As noted, both of the models investigated in this paper are symmetric, and also relatively easy to fit to data. The following two skewed models for population growth have also been developed as generalizations of these symmetric models, 1) A “power-law” model, which is left-skewed from a delayed feedback migration mechanism, by raising F in (20) to an integer > 1 (Matis et al., 2007b), and 2) An immigration model, which is also left-skewed from adding initial immigration in (20) prior to the onset of the birth (i.e. λN) component (Matis et al., 2008b).

Though one or both of these biological phenomena, and numerous others as well that would tend to skew the population growth curve, are undoubtedly in force, their effects may be manifested visually through only one or two data points in a typical sampling design consisting of weekly collections. Also, each of the above skewed models adds at least one additional parameter, which makes the precise estimation of the parameter defining skewness more difficult. Even though small residuals in the fitted model may suggest that the underlying growth curves are likely to be skewed, the simpler symmetric models in this paper may fit the data adequately for the purpose of subsequent statistical analysis of designed experiments, as e.g. in Matis et al. (2006, 2008c).

Research is in progress to investigate the application of the symmetric models, with slight modifications if needed, for the analysis of population data from other species. Research is also in progress to develop skewed models which are robust and also user-friendly for data analysis.

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Table 1: Comparisons of Goodness-of-Fit and of Estimated Regression Slopes (with standard errors) for Time of Peak, Spread, Size of Peak, and Cumulative Density of HSS vs. Normal Abundance Models for Various Aphid Data Sets.

Data Set	1	2	3	4
Aphid Species	Greenbug	Greenbug	Greenbug	Mustard Aphid
Location	N. Texas	Bushland, TX	Bushland, TX	Haryana, India
Years	1988-2000	1999	2000	1983-1990
Number of Cases	27	30	30	13
% HSS better fit than Normal	73%	52%	75%	46%
Slope for Time of Peak	1.000(.001)	0.992(.004)	0.999(.002)	1.000(.003)
Slope for Spread	1.129(.015)	1.119(.028)	1.105(.014)	1.149(.010)
Slope for Size of Peak	1.138(.014)	1.160(.075)	1.129(.033)	1.017(.003)
Slope for Cumulative Density	1.035(.004)	0.984(.030)	1.039(.013)	1.047(.006)

Table 2: Error Mean Squares (EMS) and Parameter Estimates for Center (t_{\max}), Spread (σ), Peak Size (N_{\max}) and Cumulative Density ($F(\infty)$) from Fitting HSS and Normal Models to Two Soybean Aphid Data Sets.

Year	Model	EMS	t_{\max}	σ	N_{\max}	$F(\infty)$
2004	HSS	5.51×10^6	44.10	7.92	33451	5.84×10^5
	Normal	7.90×10^6	44.06	6.80	32773	5.59×10^5
2005	HSS	1.21×10^6	36.99	6.71	57964	8.59×10^5
	Normal	0.54×10^6	36.75	6.04	56177	8.51×10^5

Figure 1: Analysis of a representative case: greenbugs (*Schizaphis graminum*) in Etter Irrigated fields in 1994. A. Observed mean greenbug counts with fitted curves (HSS = solid line; Normal = dashed line). B. Estimated per capita rate functions for population size change, for $25 < t < 60$.

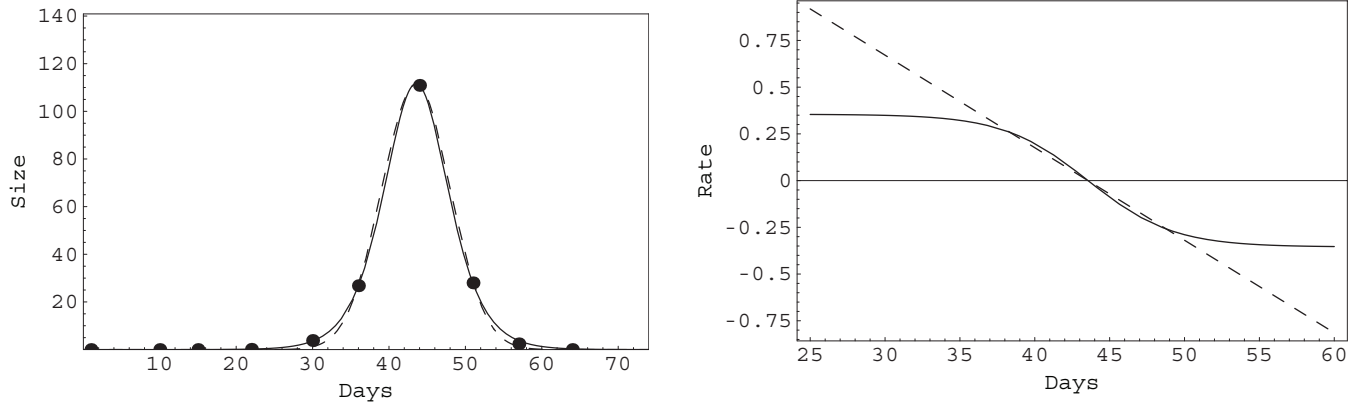


Figure 2: Extreme cases of observed greenbug counts with fitted curves (HSS = solid line; Normal = dashed line). A. Largest peak - case 3. B. Smallest peak - case 17. C. Largest spread - case 18. D. Smallest spread - case 26.

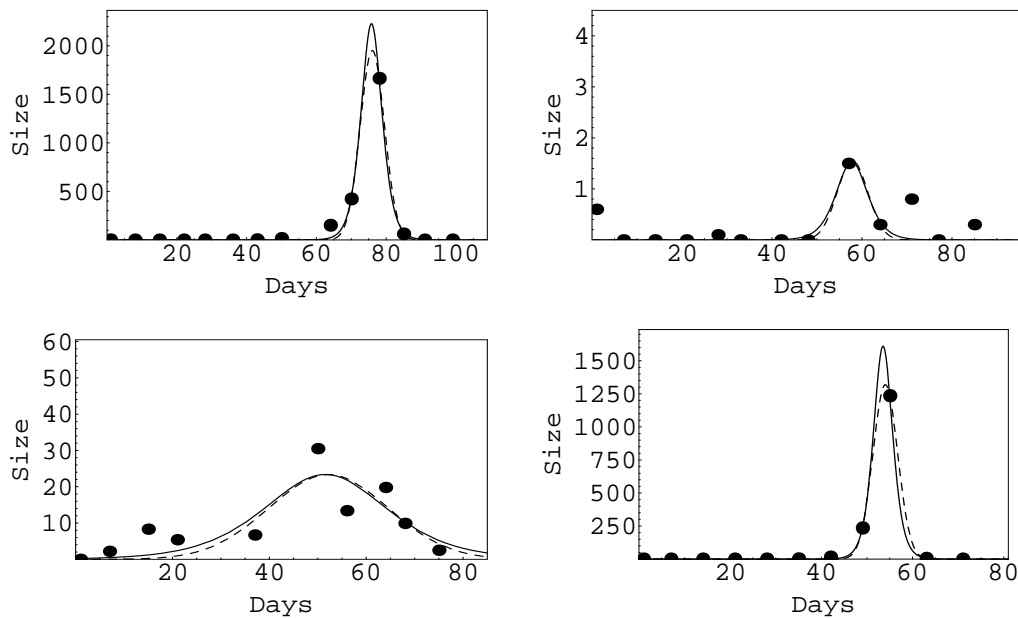


Figure 3: Extreme comparative cases of model fittings of observed greenbug data (HSS = solid line; Normal = dashed line). A. Largest reduction in peak by Normal - case 8. B. Largest increase in center by Normal - case 14. C. Second largest reduction in peak by Normal - case 22. D. Largest decrease in center by Normal - case 13.

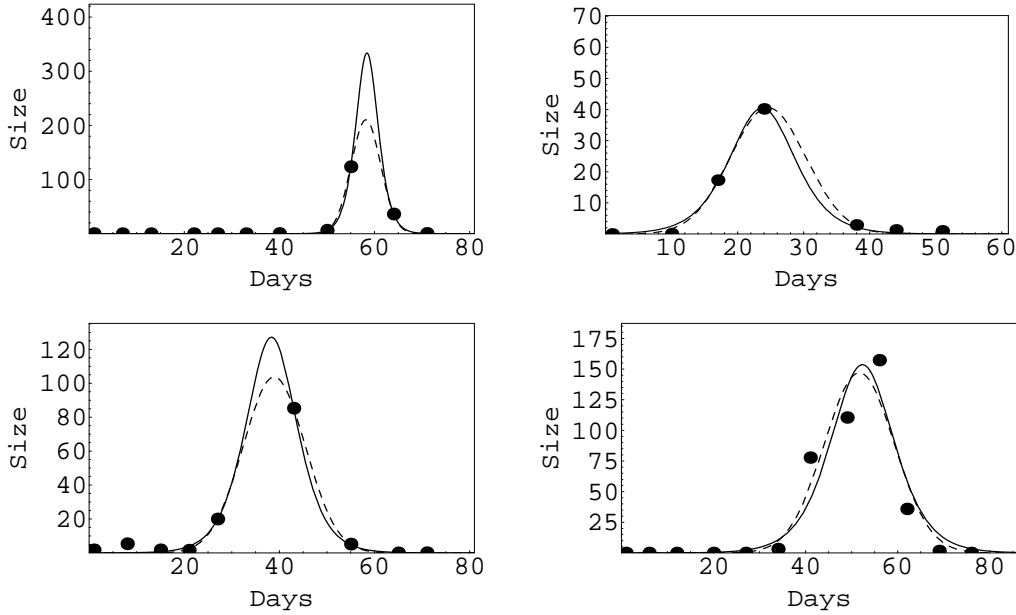


Figure 4: Scatter plots with estimated regression lines for corresponding parameter estimates for HSS vs Normal models for greenbug data set 1. Dashed line indicates slope 1. A. Time of peak. B. Spread. C. Peak size. D. Cumulative density.

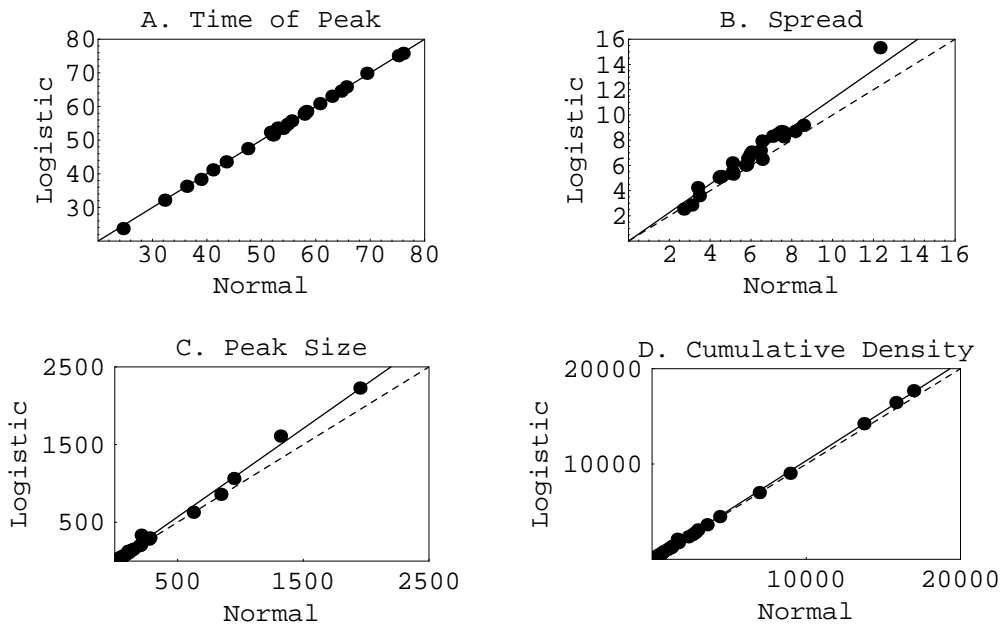


Figure 5: Scatter plots with estimated regression lines for corresponding parameter estimates for HSS vs Normal models for mustard aphid data. Dashed line indicates slope 1. A. Time of peak. B. Spread. C. Peak size. D. Cumulative density.

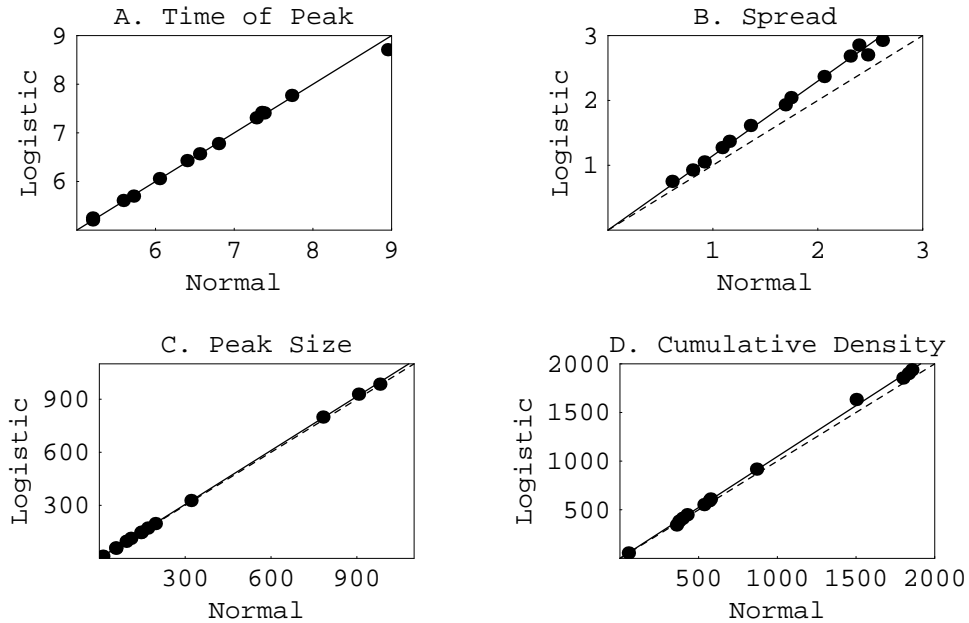


Figure 6: Observed soybean aphid counts with fitted curves (HSS = solid line; Normal = dashed line). A. Data for 2004. B. Data for 2005.

