

Combining Stochastic Models with Experiments to Understand the Dynamics of Monarch Butterfly Colonization

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Submitted December 17, 2004; Accepted July 15, 2005;
Electronically published October 4, 2005

ABSTRACT: Stochastic models are of increasing importance in ecology but are usually only applied to observational data. Here we use a stochastic population model to combine experimental and observational data to understand the colonization of old fields by monarch butterflies *Danaus plexippus*. We experimentally tested for density dependence in oviposition rates when predators were excluded, and we measured predation rates under natural conditions. Significance tests on the resulting data showed that both oviposition and predation were density dependent but could not show how oviposition and mortality combine to determine egg densities in nature. We therefore used our data to calculate the Akaike Information Criterion to choose between a nested suite of stochastic models that differed in their oviposition and mortality terms. When we simply fit the models to the observational data, the best model assumed density independence in both oviposition and predation. When we instead first estimated the oviposition rate at low density from experimental data, however, the best model included density dependence in oviposition, and a model that included density dependence in both oviposition and predation performed nearly as well. This result is consistent with our experiments and suggests that experiments can enhance the usefulness of stochastic models in ecology.

Keywords: *Asclepias syriaca*, density-dependent immigration, density-dependent mortality, *Danaus plexippus*, Akaike Information Criterion, stochastic model.

Over the last few decades, recognition of the importance of stochasticity in ecological processes has driven rapid growth in the use of stochastic models in ecology (Bailey 1964; Nisbet and Gurney 1982; Dennis et al. 1991; Ren-

shaw 1991; Morris and Doak 2002; Allen and Allen 2003; Lande et al. 2003; Taper 2004). Many models, however, are used only to analyze univariate, observational time series data (but see Stacey and Taper 1992; Dennis et al. 1995). In contrast, field ecologists often attempt to explain observational data using experiments, and the data in question, whether experimental or observational, are often multivariate (Hairston 1989). Here we attempt to combine these two approaches by using experimental and observational data on the colonization dynamics of monarch butterflies (*Danaus plexippus*) to parameterize stochastic models. By using experimental data to estimate a key model parameter and then fitting other model parameters to observational data, we are able to show how predation and oviposition combine to determine the dynamics of monarch colonization.

In considering monarch colonization, our work addresses the importance of the relationship between dispersal and local interspecific interactions in determining the distribution of organisms in space, an issue of fundamental importance in ecology (Tilman and Kareiva 1997; Law et al. 2000). Spatial structure and dispersal are widely known to modulate competition (Pacala and Levin 1997; Holmes and Wilson 1998; Bolker and Pacala 1999) and predation (Kareiva and Odell 1987; Ives et al. 1993; Hochberg and Ives 2000) and can strongly influence mate-finding success (Veit and Lewis 1996; Fujiwara and Caswell 2001; Knowlton 2001). Because monarchs recolonize North America each summer (Brower 1995), and because larvae are much less mobile than adults (Dethier 1959; Dethier and MacArthur 1964; Jallow and Zalucki 2003), local densities of monarch larvae are likely to be determined by the interplay between oviposition by mobile adults and predation on sessile eggs. Because monarchs actively select the host plants on which they oviposit (Zalucki and Kitching 1982*b*; Zalucki and Suzuki 1987), in preliminary natural history observations, we expected monarch eggs to be clumped on the most suitable plants (Stamp 1980). Instead, we observed that monarch eggs are typically found by ones and twos per plant and only rarely reach higher per plant densities. In our research, we there-

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fore asked, Why are monarch eggs so rarely found in clumps?

In using both observational and experimental data to address this question, we avoid the classic problem in spatial ecology of attempting to infer mechanisms from observational data alone (Jones 1977; Pielou 1977; Pollard et al. 1987; Singer and Thomas 1992; Stenseth et al. 1998). Because our models are stochastic, they can easily be combined with field data on monarch colonization to construct likelihood functions, which in turn can be used in statistical model choice criteria to measure the strength of evidence for the mechanisms in each model (Royall 1997; Taper 2004). Our data analysis efforts thus focus on using data to choose between different mechanistic models, an approach that has several advantages over tests of statistical significance. First, rather than merely assessing whether there is a statistically significant effect of a particular mechanism, we can directly quantify the strength of evidence that our data provide for that mechanism relative to other mechanisms. We are thus able to go beyond statistical significance to consider biological significance. Second, the models make probabilistic predictions and thus can be used to forecast monarch colonization dynamics. Nevertheless, because the model choice approach requires that we restrict ourselves to particular functional forms, for example, to describe the effects of density on predation, we also present the results of significance tests of general effects. Significance tests have the complementary advantage that they allow us to directly quantify the reliability of our experimental results in the form of error probabilities. These probabilities allow us to test whether we have erroneously adopted our data as evidence for, or against, a given mechanistic hypothesis (Mayo 1996, 2004). Reassuringly, these tests agree with the results of our model choice procedures.

The models that we use are based on hypotheses about the mechanisms determining the dispersion of monarchs in the field, which were in turn generated from a combination of our own field observations and data from the literature. For example, monarchs lay their eggs only on milkweeds in the genus *Asclepias*, and their eggs are laid singly rather than in masses (Zalucki and Kitching 1982b). Some butterfly species are known to use visual (Traynier 1984) and chemical (Feeny et al. 1989) cues to avoid conspecific or conspecific eggs (Rothschild and Schoonhoven 1977; Chew and Robbins 1984; Klijnsstra 1986), thereby preventing the accumulation of singly laid eggs on host plants. Variability in preferences within species, however, is large, and individual butterflies are known to vary in their preferences for particular host plant characteristics (Singer and Parmesan 1993). For monarchs in particular, the response of individuals to oviposition stimulants (Baur et al. 1998; Haribal and Renwick 1998) is partly influenced

by the species-wide preference for intermediate cardiac glycoside concentrations (Zalucki et al. 1990), but there are also strong individual preferences for particular plant ages, heights, and conditions (Zalucki and Kitching 1982b). The wide dispersion of monarch eggs in the field may thus simply reflect variation in host plant preferences among individual females (Rothschild et al. 1978; Price and Willson 1979). On the other hand, monarch eggs and larvae are consumed by many predatory arthropods, including ants (Calvert 1996), hemipterans, coccinellids, spiders, wasps (Koch et al. 2003), lacewing larvae, and mites (reviewed in Prysby 2004). If such predators act in a spatially density-dependent manner by responding either directly to monarch density or indirectly to host plant damage (Heinrich 1979; Bergelson et al. 1986; Bergelson and Lawton 1988; Shiojiri et al. 2002), then predation would tend to reduce spatial clumping, and so it could also explain the wide dispersion of monarch eggs.

We therefore asked, What is the importance of female oviposition behavior relative to predation in maintaining the wide dispersion of monarch eggs? In practice, answering this question became an effort to determine the importance of density dependence in oviposition and predation (Taper and Gogan 2002). Specifically, if individual female monarchs have similar preferences for host plant characteristics but avoid existing eggs, then oviposition rates should be density dependent and should therefore play an important role in maintaining wide egg dispersion. Wide egg dispersion may alternatively be maintained by density-dependent predation (De Moraes et al. 1998) or by a combination of density dependence in both oviposition and predation. Finally, if oviposition rates are low and density independent, then widely dispersed eggs may simply reflect low oviposition and predation rates. This latter scenario may arise from differences among individual females in host plant preferences.

To evaluate these different possibilities, we combined observations, experiments, and models. We designed our field experiments to detect density dependence in oviposition and egg predation in monarch populations in the field. Specifically, we recorded oviposition and mortality rates under natural conditions and used experiments to measure monarch oviposition behavior at high egg density and oviposition rates at low egg density. Because we were able to track each individual egg and larva, we were able to virtually eliminate observation error, a common source of false positives in tests for density dependence in stochastic population models (Shenk et al. 1998; McCallum et al. 2000). This enhanced our ability to use models to disentangle the mechanisms determining observed egg densities (Hilborn and Mangel 1997; McCallum 2000). Next, to make inferences about the presence of density-dependent effects in our data and to infer the relative

importance of oviposition behavior and predation in determining monarch egg dispersions, we used stochastic “immigration-death models.” These models produce probabilistic population-level predictions from the probabilities of immigration and mortality events (Jacquez 1996; Matis and Kiffe 2000). Furthermore, because our experiments yielded data suitable for both univariate and multivariate models, we were able to compare the merits of the two in terms of parameterization effort versus information yield. In terms of the model classification scheme of Cox (1990), we used mechanistic models designed to explain observations in terms of specific processes. Because we used likelihood to choose between these models, our work represents an application of the principle of scientific evidence contained in the law of likelihood (Royall 1997, 2004).

Methods

Our field work was carried out using common milkweed *Asclepias syriaca* in old fields in Allegan County, southwestern Michigan, near the Kellogg Biological Station at approximately 42°N, 85°W. *Asclepias syriaca* is the most common milkweed in the midwestern United States (Hartzler and Buhler 2000) and is a preferred monarch oviposition host (Malcolm et al. 1989; Wassenaar and Hobson 1998). Our experiments thus took place under typical conditions for monarchs in the midwestern United States.

We carried out two complementary experiments. First, in an oviposition experiment, we directly tested whether female monarchs avoid existing eggs when ovipositing. Second, in a colonization experiment, we compared oviposition rates between unmanipulated control plots and experimental plots from which we removed eggs daily (“egg removal” plots). The colonization experiment thus yielded data on immigration rates at both natural egg densities and low egg densities as well as on egg predation rates at natural densities. We used our natural history observations and the results from the oviposition experiment to guide the construction of a set of models that made different assumptions about monarch colonization dynamics, and we used the data from the colonization experiment to choose between these models.

As a model choice statistic, we used the Akaike Information Criterion (AIC). The AIC can be viewed as a likelihood-based statistic that has been extended to allow for consideration of multiple hypotheses or models (Taper 2004). The foundation of likelihood-based model choice is the law of likelihood, which states that if the probability of the data x under hypothesis A is greater than under competing hypothesis B, symbolized as $P_A(x) > P_B(x)$, then the data provide more evidence for hypothesis A than for

hypothesis B. In practice, this law provides a strong argument in favor of the use of likelihood ratios as a measure of the strength of the evidence in favor of one model over the other (Royall 1997, 2004). Likelihood approaches are appropriate in our research because we want to know not simply whether a particular mechanism is operating, but how important different mechanisms are relative to each other.

To emphasize the usefulness of experimental data for explaining observational data, we incorporated the AIC into each of three different fitting methods. In the first method, we simply estimated all the model parameters from the observational control plot data and used the AIC to choose the best model (Burnham and Anderson 2002). In the second method, we first estimated the base immigration rate I_B , the oviposition rate at zero egg density, using the data from the experimental egg removal plots. We then fixed I_B at this experimental value, estimated the remaining parameters from the control plot data, and repeated the AIC calculation to again choose the best model. The difference between these two methods is that the first attempts to estimate I_B from plots in which the egg density was well above 0 while simultaneously estimating the other parameters as well. In contrast, in the second method, we estimated I_B from plots in which the egg density was nearly 0, thereby estimating I_B under more appropriate conditions while reducing the number of parameters being estimated from the control plots. The second method thus uses pseudolikelihood to make it easier to distinguish the effects of density-dependent oviposition or predation from those of a low base immigration rate I_B . Pseudolikelihood is known to work well when the uncertainty in the independently estimated parameter is not too high (McCullagh and Nelder 1989). Moreover, it is important to remember that the control data set is larger than the experimental data set, because the control data include both egg counts and mortality and because there were more control plots than experimental plots. Fitting the models simultaneously to both the control and experimental data therefore gave the same results as fitting the models to the control data alone (K. L. S. Drury and G. Dwyer, unpublished data). Pseudolikelihood in contrast gave us greater power to distinguish between models.

In the third method, we extended the second method to allow for uncertainty in I_B . In so doing, we developed what is, to our knowledge, a new method of plotting model uncertainty, which we call the model selection uncertainty profile. To create this plot, we first bootstrapped values of I_B from our egg removal data, and then as in the second method we fit the remaining parameters to the data from the control plots. Our response variable in this method was the frequency with which each model was chosen as the best model as a function of I_B . To construct the model

selection uncertainty profile, we therefore calculated Δ_i , the difference between the AIC_c values for model i and the best model, as a measure of the strength of the evidence (Taper and Gogan 2002) in favor of each model. We then plotted the Δ_i for each model against I_B to show how the strength of evidence in favor of each model varied with I_B .

Oviposition Experiment

Female monarchs that have only a single plant available will lay ≈ 50 eggs/day on that plant (Altizer et al. 2004). The fact that such densities are not observed naturally, however, is not evidence in itself for egg avoidance, because females take flight after laying each egg, a readily observable alternative explanation. To directly test for this possibility, we performed an experiment in which we manipulated the availability of egg-free milkweed plants for individual caged females. Our cages were 1-m³, 32 × 32-mesh lumite cubes supported by aluminum frames. The experimental female monarchs were collected locally from our study area. The first step in the experiment was to enclose an adult female for 24 h in a cage with one milkweed plant. On the following day, we removed the female and counted the number of eggs on the plant, marking all leaves that bore eggs using loops of grass (see "Colonization Experiment"). Next, we rearranged the cage so that it encompassed both the original milkweed with the eggs on it and three other nearby milkweeds. Each of these latter three plants had previously been excluded, and each was confirmed to have no eggs. A new female was then placed in the cage for 24 h and allowed to choose oviposition sites from among all four plants. We repeated the entire experiment twice using entirely new butterflies and plants each time. In this way, we were able to compare the number of eggs laid on the plant that already had eggs with the number laid on the plants that did not already have eggs. In addition, we compared the number laid on leaves that already had eggs with the number laid on leaves that did not already have eggs.

Colonization Experiment

Our colonization experiment was designed to test for density dependence in monarch oviposition rates and egg mortality rates. In this experiment, we created a 3 × 3 grid of contiguous 2 × 2-m plots, with each plot containing nine milkweed plants, and we randomly assigned each plot to either the control treatment ($n = 6$) or the egg removal treatment ($n = 3$). At the beginning of the experiment, we searched all plants within the plots and removed all monarch eggs and larvae. In the control plots, we then allowed eggs to accumulate at natural rates for

the duration of the experiment. Each day, we tied a blade of grass around the petioles of leaves bearing new eggs to distinguish them as preexisting on subsequent days. In rare cases when there was more than one egg on a leaf, we tied more than one blade of grass so that all eggs had a corresponding marker. We used grass because it was a ubiquitous component of the field. Indeed, the grass was often taller than the milkweeds and entirely surrounded them, suggesting that this technique had no effect on natural oviposition processes.

We censused the eggs in our colonization experiment at approximately 5 p.m. each evening. By that time, the plots were shaded by nearby trees, and so by then the adults that were typically present earlier in the day were rare or absent. Our censusing activity therefore had little effect on oviposition. Moreover, because control and egg removal plots were randomly assigned within milkweed patches, the disturbance caused by censusing affected all plots equally and therefore did not create differences between the two plot types.

In a few instances, eggs hatched, and our grass markers then served equally well to identify the resulting larvae, because first- and even second-stage larvae or "instars" rarely leave their natal leaf (K. L. S. Drury, personal observation). High mortality rates are not unusual for monarch eggs (Zalucki et al. 1990), and during our 12-day experiment nearly all mortality occurred at the egg stage. Early instars that disappeared were counted among the dead (Prysky 2004), and in the few instances when later instars were involved, we counted them as lost if we could not find them. Even when larvae are not visible, they leave distinctive evidence of their presence in the form of characteristic leaf damage and droppings, or "frass." It was therefore generally straightforward to relocate larvae unless they had been eaten.

In the experimental egg removal plots, we removed all new eggs from each plot on each of the 12 days of the experiment. Although it is possible to simply remove an egg and still leave the leaf intact, we instead chose to entirely remove each egg-bearing leaf because of the possibility that eggs might leave behind nonvisual cues such as pheromones (Roitberg and Prokopy 1981; Klijstra 1986). The average number of leaves on plants in nearby transects was 15.7 ($n = 109$, $SE = 0.47$), so that roughly 140 leaves were available per plot. Although anecdotal observations suggested that the removal of leaves had no effect on oviposition, it is possible that it reduced oviposition rates slightly by reducing the absolute number of oviposition sites or by simulating herbivory (Bergelson and Lawton 1988), although mechanical herbivory is generally less effective at inducing plant defenses than natural herbivory (Hartley and Lawton 1987; Agrawal 1998). Nevertheless, one of our main conclusions from this experi-

ment is that oviposition rates were higher in the egg removal plots than in the control plots, and if leaf removal did have an effect on oviposition, the result would almost certainly have been a reduction in oviposition (Oyeyele and Zalucki 1990). Because the point of the experiment was to demonstrate higher oviposition in the experimental plots, the error introduced by removing leaves therefore had a conservative effect on our results and is unlikely to have affected our conclusions. Leaf removal is also unlikely to have increased oviposition rates, because the plants that we removed leaves from were already selected by monarchs for oviposition, and they prefer plants with intermediate levels of defensive compounds (Oyeyele and Zalucki 1990). If leaf removal increased the levels of these compounds, they would at best remain as attractive or, more likely, become less attractive if levels increased too much, a response that would again have a conservative effect on our results. Moreover, as we describe in “Results,” our oviposition experiment showed that females avoid eggs at the scale of the leaf rather than at the scale of the whole plant, suggesting that the effects of leaf removal in our colonization experiment were probably not strongly affected by induced defenses at the scale of an entire plant. Similarly, in other insect-plant interactions, it has been shown that the act of oviposition (Hilker and Meiners 2002) or even insect footsteps on foliage (Bown et al. 2002) can trigger plant responses. The act of oviposition may therefore have induced a defensive response, although we suspect that any such response would have been less than that caused by leaf removal, which again is unlikely to have affected our conclusions. Additional monarch oviposition studies are nevertheless needed to confirm this point.

In the control plots, in which eggs were not removed, egg densities were instead reduced by mortality and hatching. Because eggs were marked, we were able to record these losses with virtually complete accuracy because when larvae hatch, they leave behind visible pieces of egg, whereas eggs that are consumed by predators are completely removed. Although some small number of eggs may have been removed by predators before we could mark them, the number of predation events that we observed between census events was small, and so such losses were probably trivial. In any case, losses were the same for all plots and treatments. In the control plots, we therefore calculated the mortality rate m_t on day t as the difference between the number of eggs x_{t-1} present on day $t-1$ minus the number of eggs x_t present on day t :

$$m_t = x_{t-1} - x_t. \quad (1)$$

Note that hatched eggs were recorded as being present if the caterpillar was found. These data provided us with a means of testing for density dependence in the egg pre-

duction rate. This is crucial because a slowing in the population growth rate of eggs with time could be due to either density-dependent oviposition or density-dependent predation.

Statistical Analyses: Significance Tests

Our main statistical emphasis was on using our data to quantify the strength of evidence in support of different mechanistic models of monarch colonization by calculating the AIC for each of several models. In addition, however, we used significance tests to test whether particular mechanisms should be included in our models. To test whether existing eggs affected oviposition decisions in the oviposition experiment, we used a χ^2 test that compared the number of eggs on egg-bearing plants or leaves with the number of eggs on non-egg-bearing plants or leaves. To test for density dependence in the egg mortality data and thus for density-dependent predation, we carried out a Spearman’s rank order correlation test on the relationship between per capita mortality in each plot, m_t/x_{t-1} , and the number of eggs, x_{t-1} . Finally, to test for differences in the rate of oviposition into control and egg removal plots, we used repeated-measures ANOVA to compare the number of eggs in the experimental plots with the number of eggs in the control plots over time.

Statistical Analyses: Mechanistic Models

After an initial colonizing period of 4 days, the average number of monarch eggs and/or larvae in our unmanipulated control plots was 6.75 (SE = 0.52). In populations this small, the chance events known as “demographic stochasticity” can play an important role in determining the density of eggs. We therefore used models that explicitly take demographic stochasticity into account. Population size in conventional deterministic models is usually interpreted as a representation of the average across stochastic realizations. In contrast, stochastic models like ours generally keep track of the entire probability distribution of population sizes. Such models can be expressed most compactly by using the Kolmogorov forward equations, which in our case take the general form (Matis and Kiffe 2000)

$$\begin{aligned} \frac{dp(x, y, t)}{dt} = & I(x-1)p(x-1, y, t) \\ & - (I(x) + D(x))p(x, y, t) \\ & + D(x+1)p(x+1, y-1, t). \end{aligned} \quad (2)$$

In the jargon of stochastic modeling, equation (2) is known as an “immigration-death model,” because immigration

and death are the two processes assumed to affect $p(x, y, t)$, the probability that there are x eggs and y cumulative deaths at time t . We follow both egg counts and cumulative mortality because doing so provides greater power to resolve oviposition and mortality processes than would following counts alone. This is a crucial distinction because, for the observational data sets to which such models have usually been applied, counts are usually all that is available. Consequently, to highlight the increased statistical power that results from using both count data and mortality data, we used equation (2) first with counts only and second with both counts and mortality. Because in our case immigration is equivalent to oviposition, $I(x)$ is the probability per unit time that a monarch lays an egg. The parameter $D(x)$ is the death rate, the probability per unit time that a monarch egg is eaten by a predator. Note that both immigration and death are functions of the number of eggs x that are present. To test alternative hypotheses about the underlying mechanisms generating our data, we compared different model forms for both immigration and death. The density-dependent oviposition rate is

$$I(x) = I_B e^{-\alpha x}, \quad (3)$$

which collapses to the density-independent form $I(x) = I_B$ when $\alpha = 0$. When $\alpha > 0$, then the probability of an oviposition event $I(x)$ will decline as the number of eggs in the plot increases. The density-dependent death rate is

$$D(x) = x(\beta + \gamma x), \quad (4)$$

which collapses to the density-independent form $D(x) = \beta x$ when $\gamma = 0$. A density-dependent death rate then implies that the per capita probability of a predation event increases with density x . This is essentially equivalent to assuming that predators concentrate their efforts in areas in which eggs are clumped, so per capita egg mortality is higher at higher egg densities. Although, strictly speaking, the model does not require $\alpha, \beta \geq 0$, in practice we expect that they will be. Density-dependent mortality as in equation (4) could alternatively be expressed as an exponential, similar to equation (3) but with opposite sign. We have instead chosen a quadratic because of its similarity to the well-known logistic equation.

Because equation (2) describes a set of ordinary differential equations, we were able to solve for $p(x, y, t)$ using a standard numerical solution technique for differential equations, a fourth-order Runge-Kutta algorithm (Press et al. 2002). A practical problem with equation (2), however, is that it is infinite in each dimension. This is because there may be a nonzero probability of unrealistically high numbers of eggs and deaths, even if such numbers are

highly unlikely. This problem can be solved by truncating the system of equations at some large upper bounds, x_{\max} and y_{\max} , before solving (Matis and Kiffe 2000). If the upper bounds are large enough, the resulting numerical solutions will closely approximate the true solutions to equation (2). In practice, we discovered that the best-fitting parameters gave values of $p(x, y, t)$ that approached 0 quite rapidly with increasing x and y . For example, the largest cumulative number of deaths was 21 in plot 2 on day 12, and so truncating our system of equations at $x_{\max} = y_{\max} = 25$ gave best-fitting parameter values that were almost identical to the values that we found by instead truncating at $x_{\max} = y_{\max} = 30$. The system of 25×25 equations, however, of course required substantially less computing time, and so that is the bound that we used in practice.

Because the model predicts the entire distribution of eggs and cumulative deaths over time, the model prediction $p(x, y, t)$ can be used in a likelihood function to quantitatively compare different model forms to the data. Specifically, suppose that our likelihood function is $L(\theta | (\mathbf{x}, \mathbf{y}))$, where \mathbf{x} and \mathbf{y} are vectors of eggs and cumulative mortality indexed by time. Note that the data are thus constant in the sense that they have already been observed. The value of the likelihood is then determined by the values of the parameters, as expressed by the vector of parameter values θ ; in particular, the parameters can be varied until the best-fit values are found (Edwards 1992). We can then write $L(\theta | (\mathbf{x}, \mathbf{y}))$ as

$$L(\theta | (\mathbf{x}, \mathbf{y})) = \prod_{i=1}^n \prod_{t=1}^T p(x_{i,t}, y_{i,t} | \theta, x_{i,t-1}). \quad (5)$$

Here, i is the plot number, n is the total number of plots, t is the census day, and T is the number of days in the experiment. Also, $x_{i,t-1}$ is the observed number of eggs in plot i at the previous day's census, day $t - 1$. We thus write $p(x_{i,t}, y_{i,t} | \theta, x_{i,t-1})$ to show that we use the model to iterate forward from the observed number of live eggs x_i in plot i at the previous census day $t - 1$ to the number of live eggs $x_{i,t}$ and dead eggs $y_{i,t}$ in that plot on census day t . This procedure explicitly takes autocorrelation between x_{t-1} and x_t into account, whereas simply iterating forward from $t = 0$ does not (Dennis and Taper 1994). Also, note that we can vary the form of the model to consider different assumptions about oviposition and mortality, notably whether oviposition and mortality are density dependent, according to equations (3) and (4), respectively. Finally, notice that in $p(x_{i,t}, y_{i,t} | \theta, x_{i,t-1})$ we do not condition on $y_{i,t-1}$ because eggs $x_{i,t}$ and mortality $y_{i,t}$ on day t are assumed to be independent of mortality $y_{i,t-1}$ on day $t - 1$.

Use of equation (5) as written assumes that the processes in our plots were spatially independent. Our natural history observations of monarch egg dispersion suggested that it is unusual to find more than a few eggs per plant but also that the occurrence of eggs on one plant did not affect the probability that we would find eggs on nearby plants. More importantly, if our plots were strongly spatially correlated, the eggs that were present in our control plots also would have affected the adjacent experimental egg removal plots, thereby eliminating any treatment effects. The fact that we observed treatment effects suggests that the assumption of independence is justified. More generally, if the assumption had been violated, we could have modified our models to allow for dispersal between plots while otherwise using the same model-fitting methods.

Having formulated a likelihood function for our data, we then compared the density-dependent and density-independent forms of immigration and mortality by minimizing the negative log likelihood \mathcal{L} of equation (5) using a nonlinear-fitting routine, the downhill (or Nelder-Mead) simplex algorithm (Press et al. 2002). In practice, this fitting routine chooses a vector of parameters, solves for $p(x_{i,p}, y_{i,t} | \theta, x_{i,t-1})$ for each plot on each census day according to equation (2), calculates the likelihood according to equation (5), and then repeats the process for a new set of parameter values. By systematically varying the parameter values, the algorithm eventually finds the minimum of the negative log likelihood, which occurs at the same parameter values as the maximum of the likelihood function. To ensure that the simplex did not simply find a local minimum, we repeated the procedure using a grid-search algorithm instead of the downhill simplex and obtained very similar results.

Having calculated the maximum likelihood for each model, we then compared the models using the corrected AIC_c , which provides an objective means of ranking candidate models that have different numbers of parameters (Burnham and Anderson 2002). The AIC_c for the i th model, A_i , is calculated by the formula

$$A_i = 2\mathcal{L}(\theta_i | (x, y)) + 2K_i + \frac{2K_i(K_i + 1)}{(n - K_i - 1)}. \quad (6)$$

In equation (6) K_i is the number of parameters in model i , n is the number of data points, (x, y) is the data, and θ_i is the vector of parameters for model i . This form is termed “corrected” because it allows for small sample sizes, meaning cases for which $n/K_i < 40$ (Burnham and Anderson 2002).

One of the useful features of the AIC_c is that one can go beyond merely choosing the best model to quantify the relative support that the data provide for each model using

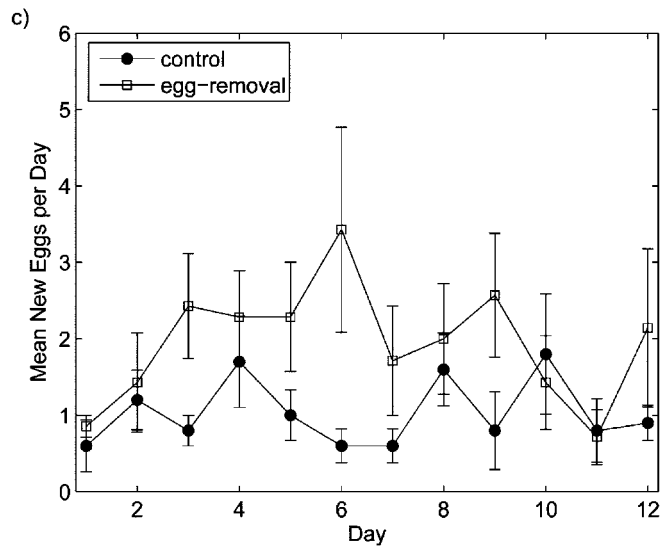
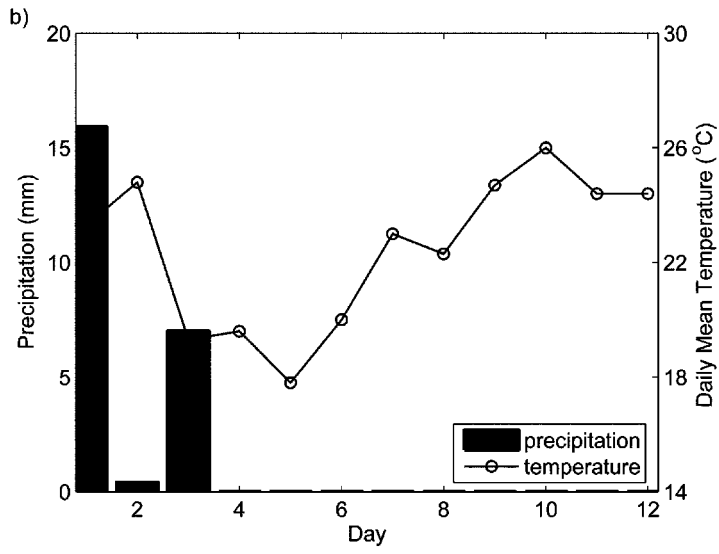
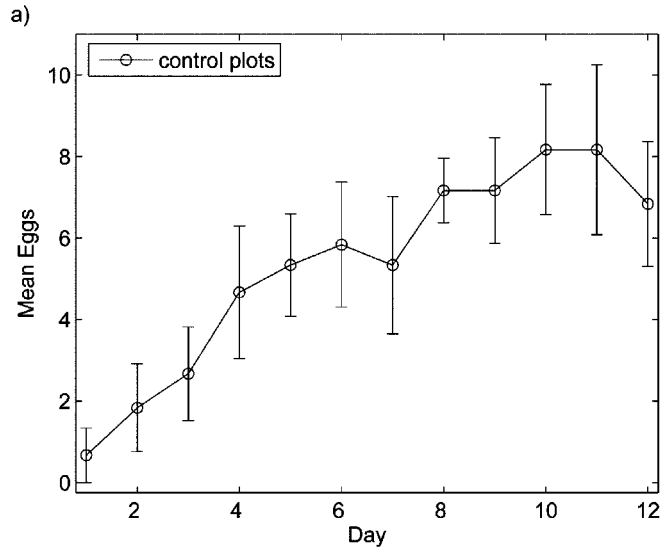
Akaike weights. If Δ_i is the difference between the i th model and the best model, then the weight w_i for the i th model is

$$w_i = \frac{\exp(-\Delta_i/2)}{\sum_{r=1}^R \exp(-\Delta_r/2)}. \quad (7)$$

The w_i can thus be interpreted as a measure of the relative support, scaled between 0 and 1, of the i th model given the data and the other candidate models (Burnham and Anderson 2002). Moreover, the ratio of the weight of model i to the weight of the best model provides a measure of the support for model i relative to the best model. An important point is that when the best-fit values of the density dependence parameters α , β , and γ are 0, the data provide no evidence for density-dependent effects, and the more elaborate models collapse to density-independent models.

For our purposes, the advantage of the AIC approach is that it allows us to quantify the strength of evidence that our data provide for each model, through the Δ_i statistic, the difference between the AIC_c for the i th model and the AIC_c for the best model. The Δ_i has a useful connection to Royall’s (1997) strength-of-evidence approach in the following sense. Royall argued that the ratio of the likelihoods of two hypotheses provides a useful measure of the strength of evidence for one hypothesis over another. Because the Δ_i is the difference of two log likelihoods, it is equivalent to the log of the ratio of the two likelihoods, except that each likelihood is adjusted to include a penalty term based on how many parameters it requires and how many data points are available to estimate the parameters. The Δ_i is thus effectively an AIC-based measure of Royall’s strength of evidence (Taper 2004). Values of $\Delta_i \geq 2$ are said to provide strong evidence for one model over another, while values of $\Delta_i \geq 5$ are said to provide very strong evidence (Taper and Gogan 2002).

We can thus use Δ_i values to quantify the strength of evidence for different processes. For example, we can evaluate the evidence for density dependence in oviposition and mortality by comparing the Δ_i values for models that include density dependence with the Δ_i values for models that do not. Note that while the results of the oviposition experiment inform us about monarch behavior, by itself that experiment could not tell us about the importance of density-dependent oviposition relative to density-dependent mortality in determining the dispersion of monarch eggs. More generally, significance tests allow us to test for the occurrence of either density-dependent oviposition or mortality but do not provide information about the relative magnitudes or even co-occurrences of these pro-



cesses. Comparing the Δ_i values of models with various combinations of density-dependent oviposition and predation, however, provides a quantitative comparison of the evidence for each and hence allows for inferences about the relative importance of each process.

Estimating the Base Immigration Rate

Our three methods of fitting the models to the data correspond to estimating the base immigration rate I_b in three different ways. First, we simply fit I_b to the control plot data along with the other parameters in the model. Second, we took advantage of our experimental egg removal data by first using the average value of I_b from the egg removal plots as an estimate of the base oviposition rate and then fitting the remaining parameters, α , β , and γ , to the observational data. Third, we took uncertainty in I_b into account by bootstrapping 150 values of I_b (Efron and Tibshirani 1993) and then refitting the model to the control plot data for each new value of I_b . To bootstrap I_b , we repeatedly sampled egg counts from our data until we had as many counts as in the original data, calculated a value of I_b based on the sample, and repeated 150 times.

Results

Oviposition Experiment

In the first trial, the first female, which had access to only one milkweed, laid 46 eggs on 16 of the 27 leaves available. When that female was removed and the three additional egg-free plants were included, the second female laid a total of 45 eggs. Of these, none were laid on leaves with existing eggs, although seven of the 45 were laid on egg-free leaves of the first female's plant. The χ^2 tests showed that this second female did not distinguish between the first, egg-bearing plant and the egg-free plants ($\chi^2 = 1.06$, $df = 1$, $P = .30$) but that she did prefer leaves without eggs ($\chi^2 = 6.86$, $df = 1$, $P = .009$). In the second trial, the first female, which again had access to only one milkweed, laid 53 eggs on eight of the 15 available leaves. The second female, which again had access to three additional egg-free plants, then laid 62 eggs, none of which were laid on leaves with existing eggs, although 12 were on egg-free leaves of the original plant. The χ^2 tests showed

that, like the first female, this second female did not distinguish between plants with eggs and plants without eggs ($\chi^2 = 2.14$, $df = 1$, $P = .14$) but did distinguish between leaves with eggs and leaves without eggs ($\chi^2 = 10.19$, $df = 1$, $P = .001$). Our direct test for density dependence in oviposition thus suggested that female monarchs prefer milkweed leaves that do not already have eggs on them.

Colonization Dynamics

In our control plots, where both oviposition and predation occurred, the number of eggs per plot appeared to saturate over time (fig. 1a) as extremely high egg predation over the 3–5-day egg stage balanced colonization by new eggs. Figure 1b shows precipitation and average daily temperature during the 12 days of the study from July 23 to August 3, 2001. Visual comparison of the oviposition and weather data suggests that temporal fluctuations in temperature and rainfall are not likely to provide explanations for the temporal pattern of oviposition. Spearman's rank order correlation tests for egg removal data and temperature ($\rho = -0.51$, $n = 12$, $P = .09$) and precipitation ($\rho = -0.24$, $n = 12$, $P = .46$) are consistent with this interpretation, as are linear regressions (temperature: $P = .15$; precipitation: $P = .19$). Repeated-measures ANOVA confirmed that the oviposition rate in the egg removal plots was significantly higher than the rate in the control plots ($F = 5.631$, $df = 1, 11$, $P = .031$; see fig. 1c), suggesting that oviposition was density dependent, as in our oviposition experiment. In addition, however, a Spearman's rank order correlation test between per capita mortality rate and existing egg density (fig. 2) showed that there was a statistically significant effect of density on per capita mortality ($\rho = 0.376$, $n = 58$, $P < .002$), suggesting that predation was also density dependent. This effect is all the more striking because our analyses used data recorded at the scale of our 4-m² plots, whereas butterfly egg predators presumably search at the scale of individual plants. Note that the large variance in per capita mortality at small population sizes in figure 2 (e.g., at $x(t-1) = 2$ and 4) is expected, because at such population sizes each individual that dies represents a large proportion of the population. Chance variation in the fates of individuals thus leads to a larger variation in mortality rates at smaller population sizes than at larger population sizes.

Figure 1: Monarch oviposition data from an old field in southwest Michigan between July 23 and August 3, 2001. *a*, Mean number of eggs and/or larvae (± 1 SE) in six control plots accumulating under natural conditions. *b*, Precipitation (primary Y-axis) and the mean of temperature readings during each day (secondary Y-axis) as recorded by the Kellogg Biological Station Long-Term Ecological Research site located at 42°24'33"N, 85°22'18"W, approximately 16 km from the field site. Neither precipitation ($P = .19$) nor temperature ($P = .14$) was significantly correlated with oviposition rates in egg removal (uncrowded) plots. *c*, Mean number of new eggs (± 1 SE) per day in six control plots and in three experimental (egg removal) plots from which all eggs were removed daily.

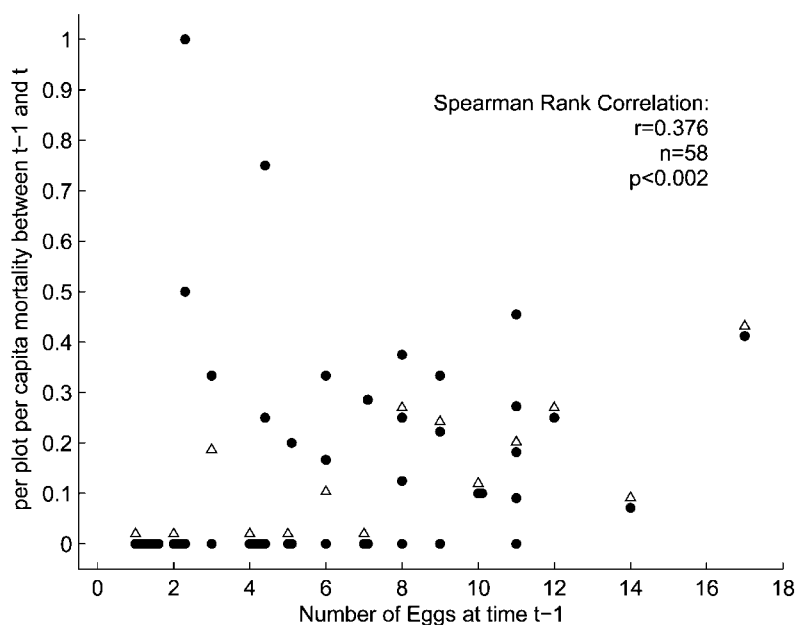


Figure 2: Per capita mortality (*circles*) in each plot between day $t-1$ and day t versus egg number per plot on day $t-1$. Multiple per capita mortality values at a given egg count are indicated by a slight offset in the horizontal direction. The occurrence of a small number of high mortality rates at low density is expected because at small population sizes, each mortality event represents a larger proportion of the population. Also, those few high mortality rates are more than compensated for by multiple zero values at low densities, which is illustrated by the triangles showing median per capita mortality for each egg number.

Fitting the models to the observational egg count data from the control plots, however, produced only weak support for density dependence in either oviposition or predation (table 1). Moreover, notice that in table 1, the negative log likelihoods in this case were the same for all models. This is because the models fit to the one-dimensional, eggs-only data almost always collapsed to the simple, density-independent oviposition/density-independent mortality model. That is, for both the best-fitting density-dependent oviposition model and the best-fitting density-dependent predation model, the parameters affecting density dependence were near 0. Each model was thus effectively reduced to the density-independent model, and so the strength of evidence for density-dependent oviposition or density-dependent predation in both cases is effectively 0. The method used to calculate the base immigration rate I_b had no effect (table 1). The estimate of the immigration rate (see table 2) obtained by fitting I_b to the control data was almost certainly an underestimate, because when we bootstrapped I_b from the egg removal data, for only 6% of the bootstrapped base immigration rates did the one-dimensional data require nonlinear immigration and mortality to explain the data in the control plots. This result is in stark contrast to our experimental results.

In contrast, fitting the models to the two-dimensional data set, which includes both egg counts and cumulative mortality, provided much more support for density-dependent effects, especially when we used an independent estimate of the base immigration rate I_b . First, however, we simply fit I_b , as well as the other parameters, to the control data. In that case, the model with density-independent oviposition and predation provided the best explanation, but the model with density-independent oviposition and density-dependent predation performed nearly as well. Again, however, the density-dependent oviposition parameter was effectively 0 in all models, and so the density-dependent oviposition models collapsed to the density-independent oviposition models. When we instead used an independent estimate of I_b , by calculating it from the experimental egg removal plots, the best-fitting model instead included density-dependent oviposition and density-independent predation. Moreover, for the model that included density dependence in both processes, the Δ_i value, the difference in AIC_c from the best model, was only 1.24. The strength of evidence against the combination of density-dependent oviposition and density-dependent predation was therefore quite weak. The Δ_i values for the models without density dependence in oviposition were in contrast very high (table 1), showing that the

Table 1: Results of one- and two-dimensional model fitting for univariate (egg counts only) and bivariate (egg counts + mortality) monarch colonization data

Data and I_b estimate	Density-dependent oviposition	Density-dependent predation	K	\mathcal{L}	Δ_i	Akaike weight w_i
Egg counts only:						
Fit to data	No	No	2	146.11	^a	.56
	Yes	No	3	146.11	2.16	.19
	No	Yes	3	146.11	2.16	.19
	Yes	Yes	4	146.11	4.42	.06
From experiments	No	No	1	156.76	^a	.55
	Yes	No	2	156.76	2.12	.19
	No	Yes	2	156.76	2.12	.19
	Yes	Yes	3	156.76	4.3	.07
Egg counts + mortality:						
Fit to data	No	No	2	200.93	^a	.39
	Yes	No	3	200.93	2.18	.13
	No	Yes	3	199.94	.2	.36
	Yes	Yes	4	199.94	2.44	.12
From experiments	No	No	1	229.23	11.14	.003
	Yes	No	2	222.60	^a	.65
	No	Yes	2	228.70	12.19	.002
	Yes	Yes	3	222.13	1.24	.35

Note: K = number of parameters including error variance, \mathcal{L} = negative log likelihood, Δ_i = difference between the AIC_c of each model and the AIC_c of the best model.

^a Lowest AIC_c value.

strength of evidence against density-independent oviposition was strong. The combination of the two-dimensional data plus an independent, experimentally derived estimate of the base immigration rate thus provided strong support for density-dependent oviposition and modest support for density-dependent predation. Note that, although a test on the mortality data alone suggested that there was a statistically significant density-dependent predation effect, the results of the two methods of analysis are not necessarily contradictory. This is because the model fitting instead attempts to quantify the importance of density-dependent predation for the control plot data, rather than simply to determine whether the hypothesis of no density-dependent predation can be rejected. Our overall conclusion is thus that, although there may be a statistically significant effect of density on predation, the effect appears to be less important biologically than density-dependent oviposition.

These conclusions were affected only slightly when we used bootstrapping to take into account the uncertainty in the experimental base immigration rate I_b . The top of figure 3 shows the support, based on Akaike weights, for each model versus the bootstrapped values of the base immigration rate I_b . Over the lowest 16% of the range of bootstrapped I_b values, the density-independent oviposition/density-independent predation model was the best, but over the remaining 84% of the range, the density-dependent oviposition/density-independent predation

model was the best, while the density-dependent predation/density-dependent oviposition model performed nearly as well. Unlike the AIC differences Δ_i , however, Akaike weights are not associated with objective rules about the strength of evidence (Taper and Gogan 2002). The bottom of figure 3 therefore instead depicts what we call the model selection uncertainty profile, which shows how Δ_i for each model varies with I_b . This figure shows that, unless I_b is substantially lower than the value calculated from the experimental plots, there is strong to very strong evidence in support of models with density-dependent oviposition. At very low base oviposition rates, however, that density dependence is not necessary to explain the observed egg density. In addition, comparison of the

Table 2: Best-fit parameter values for the one- and two-dimensional models

Dimensions and model	$\hat{\alpha}$	$\hat{\beta}$	$\hat{\gamma}$	Akaike weight
One dimension:				
DI-DI	^a	.3359	^a	1.0
Two dimensions:				
DD-DI	.049	.169	^a	≈.65
DD-DD	.049	.122	.0228	≈.35

Note: Base immigration rate was estimated from the experimental data ($I_b = 2.53$), and the remaining parameters α , β , and γ were estimated from the control plot data. DI = density independent, DD = density dependent.

^a Not included.

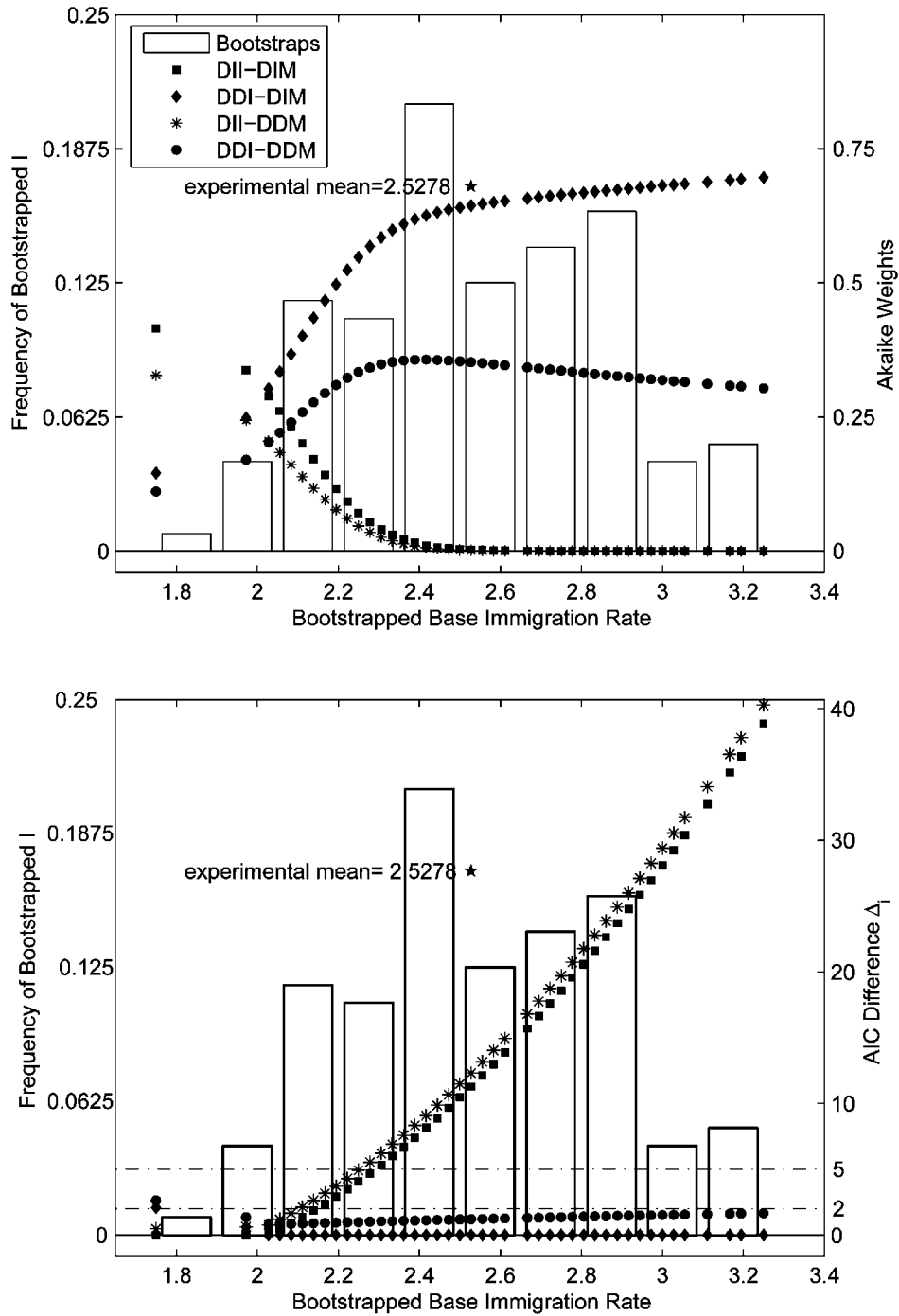


Figure 3: *Top*, plot of Akaike weights for each model superimposed on the histogram of bootstrapped base immigration rates (I_b). For any given value of I_b along the X-axis, the Akaike weights (circles, asterisks, diamonds, squares) sum to 1 across models. *DII* = density-independent immigration (oviposition), *DDI* = density-dependent immigration, *DIM* = density-independent mortality, and *DDM* = density-dependent mortality. Lower values of I_b give more support to density-independent immigration models because nonlinearities were not needed to explain the data. The star indicates the mean of our experimental base immigration data from the egg removal plots. *Bottom*, the model selection uncertainty profile: Δ_i values, the difference between the AIC_c score for each model and the best model, superimposed on the histogram of bootstrapped base immigration rates I_b ; $\Delta_i \geq 2$ is considered to be strong evidence, while $\Delta_i \geq 5$ is considered to be very strong evidence.

top and bottom of figure 3 shows that the lowest values of I_B for which there is strong evidence for density dependence ($\Delta_i \geq 2$) are also the values for which the Akaike weights for the density-dependent models exceed those of the density-independent models.

To quantitatively show the model fit, in figure 4 we have plotted the data along with output for the best model (table 2), which includes density dependence in oviposition but not mortality and which uses our estimate of the base immigration rate I_B from the experimental data. Figure 4a shows the (x_t, x_{t+1}) pairs from our data along with the ninety-fifth percentile contours of the marginal distribution of $x_{t+1}|x_t$ for the model. Said differently, the model contours are the middle 95% of the sum, across all mortalities, of the probability of each possible egg number at time $t + 1$, given that there were x eggs at time t . Similarly, figure 4b shows the (x_t, m_t) pairs that represent egg loss numbers between time t and time $t + 1$, given x eggs at time t . The model prediction lines are again ninety-fifth percentile contours of the marginal distribution, with the difference that each marginal mortality value is summed across all possible egg numbers x_t . The figure thus shows that the best model is able to explain most of the variability in the data, in the sense that only a few data points are outside the ninety-fifth percentile contours of the model.

To compare the shape of the predicted and observed trajectories of eggs and mortality, in figure 5 we have plotted the mode of the best-fit model predictions, along with the sixty-seventh and ninety-fifth percentile contours, against the data for the control plots. As in figure 4, the model again includes density dependence in oviposition but not predation, and base immigration I_B was again calculated from the experimental data. Although in our fitting routines we used the model only to extrapolate from one day to the next, here we extrapolate from the zero eggs/zero mortality conditions (i.e., $x_0 = y_0 = 0$) at the beginning of the experiment to the full distribution of eggs and cumulative mortality events at the end of the experiment. To distinguish among plots, each data point consists of a numeral that corresponds to a particular plot number. The trajectory of these plot numbers through the egg count and cumulative mortality space and time reflects the accumulation of eggs and mortality events. Because here we are extrapolating over a comparatively long interval of time, we do not expect all of the data points to fall inside the contour lines of the model predictions. Nevertheless, the model approximately reproduces the average behavior of the plots, even though we did not fit the data in such a way as to average the data over time. To see this, one can trace the trajectory of each field plot by following that plot's number across time, while comparing the location of the plot number to the mode of the model prediction (the solid circle) along the way. At first, both the individual

plots and the mode of the model increase along the egg number axis as the first colonization events occur. Eventually, however, data and model mode also begin to move along the mortality axis (Y-axis) as mortality events accumulate. The important points are thus that the trajectories of different plots follow roughly similar paths and that these paths are qualitatively similar to the model predictions. These qualitative similarities over longer time-scales suggest that the model captures important features of monarch colonization dynamics, and they give us confidence in the functional forms of density dependence in the model.

Discussion

Experimental Data, Stochastic Models, and Scientific Epistemology

Methods for analyzing univariate time series data that rely on stochastic population models are common in the ecological literature. Nevertheless, such methods have often provided only limited insight into detailed ecological mechanisms (den Boer and Reddingius 1989; Ellner and Turchin 1995; Stenseth et al. 1998; McCallum 2000; Turchin and Ellner 2000; Turchin 2002), albeit with notable exceptions (Dennis and Taper 1994; Zeng et al. 1998; Dennis and Otten 2000; Taper and Gogan 2002). It is thus not surprising that our efforts to choose between models using only our egg time series data likewise failed to identify the mechanisms that determine monarch colonization. Specifically, when we fit the one-dimensional model to the control plot oviposition data, the density-independent oviposition/density-independent mortality model received the most support, irrespective of how we calculated the base immigration rate I_B . Our oviposition experiment, however, suggested that monarchs avoid conspecific eggs, suggesting in turn that oviposition is indeed density dependent. Consequently, when we instead fit the models to the bivariate data, which included both egg counts and mortality counts, the resulting best-fit values of the density-dependent immigration parameter α and the density-dependent predation parameter γ both increased, while the density-independent mortality term β decreased. With the addition of an independent estimate of the base immigration rate I_B , the support for the fully density-independent model dropped to almost 0, and the only models with much support were the density-dependent oviposition/density-independent mortality model and the density-dependent oviposition/density-dependent mortality model (see table 1). Although the former model was the best, the evidence against the latter was weak, suggesting that the data provide strong support for density-independent oviposition and modest support for density-

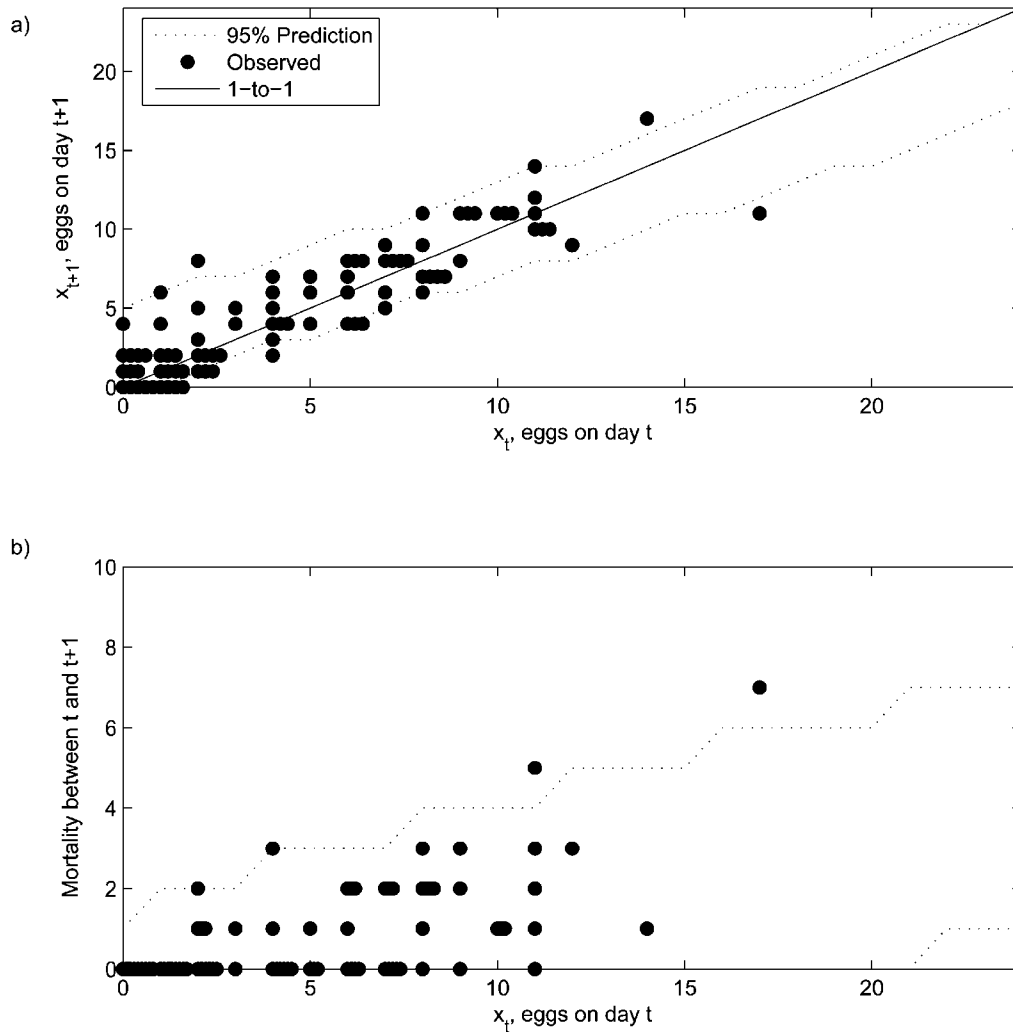


Figure 4: Single-day output of the best immigration-death model compared with the monarch egg and mortality data in the control plots. This model includes density dependence in oviposition but not predation and uses an estimate of the base immigration rate from the egg removal plots. *a*, 95% confidence intervals of model predictions for the marginal distribution of egg number at time $t + 1$ versus egg number at time t with observed values and a one-to-one line of no effect. Multiple observations at the same value are slightly offset in the horizontal direction. For small x_t , model predictions are largely above the no effect line, while for large x_t , model predictions are largely below the no effect line. *b*, 95% confidence intervals of model predictions for the marginal distribution of mortality between t and $t + 1$, given x_t and observed mortality.

dependent mortality. It is important to recall that evidence is necessarily comparative, so arguably we cannot absolutely conclude that immigration and/or predation are density dependent. Instead, we conclude that there is more support for density-dependent than for density-independent processes and that this support is evidence for the mechanisms embodied in the density-dependent models (Taper and Lele 2004). Bootstrapping I_b gave roughly similar results but slightly less strong support for density-dependent effects, because some fraction of the bootstrapped I_b values were small enough that nonlinearity was not needed to explain egg densities.

The two key pieces of data providing inferential power to our analysis were thus the experimentally estimated base immigration rate I_b and the mortality data, the second dimension of our observational data. Without an independent estimate of I_b , low values of the fit parameter I_b were sufficient to explain egg densities. Without mortality data, even with an independent estimate of I_b , high linear mortality provided the best explanation for egg densities. This result was misleading, however, because our experiments suggested that both oviposition and mortality were density dependent. On the other hand, even with the mortality data, our model selection results did not match

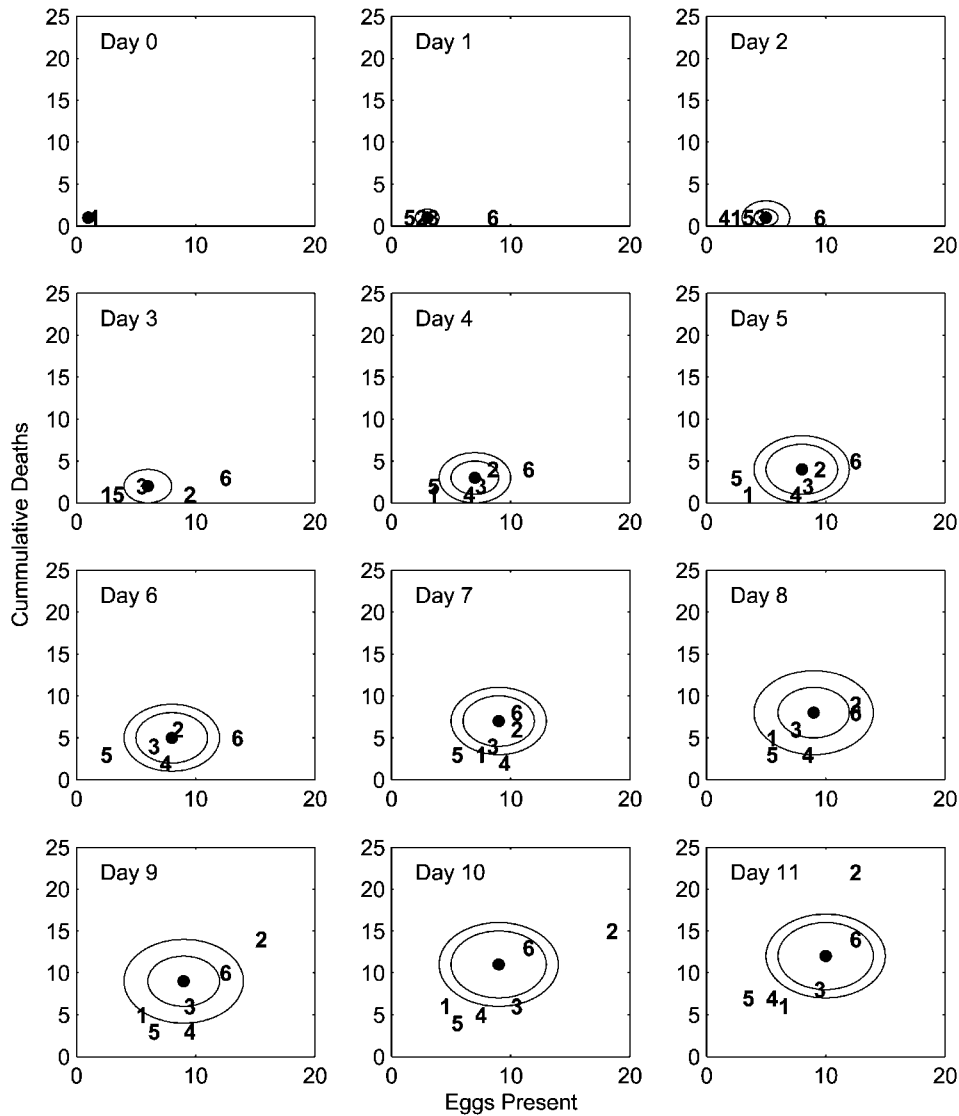


Figure 5: Long-term output of the best immigration-death model. The model is the same as in figure 4, but here we use it to predict the distribution of eggs and mortality over the entire 12 days of the oviposition experiment instead of just one day at a time. The solid circle indicates the model, and the lines indicate the sixty-seventh and ninety-fifth percentiles (the sixty-seventh percentile circle is of course always smaller than the ninety-fifth). The location of the values of eggs and mortality for each plot are shown by locating the plot number at the appropriate point on each graph. Because the model is here making a relatively long-term prediction, we do not expect close agreement between model and data. Instead, the main point is simply that the mode of the model follows a trajectory through time that is qualitatively similar to the trajectories of the individual plots.

our oviposition experiment and correlation results unless we used an independent estimate of I_b .

Our model-fitting efforts thus complemented the results of our significance tests. These tests revealed statistically significant effects of density on both oviposition and per capita mortality. Nevertheless, visual inspection of the data suggests that the effect of density on oviposition (fig. 1c) was quite strong but that the effect of density on mortality was weak (fig. 2). The effects of density-dependent pre-

dation therefore appear to be weaker than those of density-dependent oviposition. The model identification results provided additional support for this conclusion, in that the model with density dependence in both oviposition and predation received less support than did the model with density dependence in oviposition only.

It is instructive to consider the path of inference leading to our conclusions. First, our natural history observations suggested that monarch eggs are typically found at a rate

of one or two per plant, with most plants having none. We rarely found any plants with larger numbers of eggs, and when we did, we found no obvious, consistent characteristics that made those plants preferable for oviposition, such as plant height, number of leaves, developmental stage, distance to nearest neighbor, or presence or absence of other arthropods (K. L. S. Drury, unpublished data). We therefore hypothesized that ovipositing female monarchs avoid existing eggs, a hypothesis for which there is at least anecdotal evidence in the literature (Rothschild et al. 1978; Zalucki and Suzuki 1987; Pilson and Rausher 1988; Calvert 1999). This hypothesis motivated our oviposition experiment, in which we found that, under artificial conditions, females do indeed avoid existing eggs. The importance of this phenomenon under natural conditions and its importance relative to predation were nevertheless both uncertain. We therefore carried out our colonization experiment, which included predation and allowed for natural conditions. The data from our control plots, in which eggs accumulated and were lost according to natural processes, suggested that per plant egg density did appear to saturate as if females were indeed avoiding already laid eggs. Nevertheless, it was possible to explain the data from the control plots using a model with no density dependence, leading to a best-fit value of the base immigration rate I_b that was quite low compared with our experimental estimate. Allowing for mortality data as well gave some support for density-dependent processes, but that support was extremely weak. Indeed, the model fitting provided strong support for density dependence only when we used the experimental egg removal data to estimate the base immigration rate. The combination of observations, experiments, and models thus led to a much deeper understanding of the processes underlying the dynamics of colonization in our control plots than any one approach could have produced alone (Scheiner 2004).

Monarch Oviposition Behavior

The results of our oviposition experiments and our model selection procedures together suggest that monarchs avoid existing eggs when seeking oviposition sites. Monarchs therefore provide an example of an open population with space-limited recruitment (Hyder et al. 2001), with colonization and mortality governed by the density of existing eggs and emigration occurring after pupation. The balance among these processes suggests a roughly constant local monarch density, a pattern that we have observed in many milkweed patches. This is consistent with our intuition, because monarchs possess a suite of characteristics that make them well suited for laying single, widely dispersed eggs. Specifically, monarchs are long-lived for butterflies (Zalucki 1981), they often fly great distances (Ries and

Debinski 2001), they oviposit on a common and widely dispersed host plant (Hartzler and Buhler 2000), and the oviposition period lasts for up to 45 days (Oberhauser 1997), although the oviposition period is often far briefer in Australia (Zalucki and Kitching 1984).

Our results are also in agreement with the literature on monarch ecology. Many authors have commented on the rarity of monarch eggs in milkweed patches (Zalucki and Suzuki 1987; Malcolm et al. 1989; Van Hook and Zalucki 1991; Calvert 1999). Indeed, larvae are so rare that Price and Willson (1979) found no evidence that monarchs exert any selective pressure as consumers of milkweed. Explanations for the proximate cause of this sparse egg dispersion, however, have mostly focused on the importance of host plant foliage quality. For example, as we have described, host plants, including milkweeds, vary in quality (Malcolm et al. 1989; Zalucki et al. 1990; Singer and Parmesan 1993; Singer and Lee 2000), apparency (Floater and Zalucki 2000), and concentration of oviposition stimulants (Zalucki and Kitching 1982a; Haribal and Renwick 1998). Although *Asclepias syriaca* grows in clonal patches (Wilbur 1975; Hartzler and Buhler 2000), the chemical composition of ramets within a clone may vary in response to local environmental conditions such as soil type, moisture, and herbivory history (Price and Willson 1979), which monarchs assess through chemoreceptors on their feet and antennae (Baur et al. 1998; Haribal and Renwick 1998). Even within a host plant species of suitable chemical composition, monarchs discriminate based on patch size, plant density, plant age (Zalucki and Suzuki 1987), and location within the patch (Zalucki and Kitching 1982b). Moreover, preferences for host plant attributes sensu Singer (2000) vary among individual females (Singer and Parmesan 1993; Kuussaari et al. 2000; Hanski and Singer 2001) and are context dependent (Rothschild and Schoonhoven 1977; Singer and Thomas 1992). These individual preferences may therefore partially explain the lack of clumping among monarch eggs. Our data, however, also suggest that active egg avoidance is an important part of monarch oviposition behavior, a type of "herbivore offense" that must be understood along with the more familiar plant defenses in order to understand herbivore-plant dynamics and coevolution (Karban and Agrawal 2002). Although our oviposition experiment considered only a small number of individuals, the results were consistent with such behavior, and our model-fitting results provide yet stronger evidence. The fact that monarch larvae generally perform more poorly on previously damaged plants (Van Zandt and Agrawal 2004) suggests that part of the ultimate explanation for density-dependent oviposition behavior is avoidance of competition with conspecifics. The occurrence of density-dependent predation in our plots, however, suggests that avoidance of predators may also be part

of the ultimate explanation. Of course, our results are limited to a single field site in a single year, and so female preference for individual host plants may be more important under other circumstances than those in our experiments.

The larger significance of this work is that our models may be relevant to monarch conservation. Because the monarch is the only bidirectional migratory insect in North America (Williams 1930), and because the geographic extent of its wintering habitat is highly constrained (Urquhart and Urquhart 1976; Brower et al. 1977; Wasenaar and Hobson 1998), it may potentially be at risk of extinction (Weis et al. 1991; Malcolm 1993; Malcolm and Zalucki 1993; Brower 1995; Thomas et al. 1996; Brower et al. 2002). Monarch populations fluctuate widely in response to large-scale weather patterns (Brower 1995; Swengel 1995), but as we have shown, they are regulated locally by the small-scale decisions of ovipositing females and foraging predators. Both density-independent and density-dependent processes are therefore relevant to monarch population dynamics (Turchin 1995). Indeed, our work clearly demonstrates that there is an upper bound on larval monarch numbers in milkweed patches. Decreases in milkweed abundance that force monarchs to oviposit at higher local densities are therefore likely to lead to fewer monarchs because of density-dependent predation. This is in contrast to much conventional thinking, which has predicted higher colonization success rates when there are greater numbers of propagules (Ebenhard 1991). Furthermore, although much is known about the density-dependent factors leading to emigration of butterflies from patches (Hansson 1991; Kuussaari et al. 1996; Hanski 1999), far less is known about the density-dependent factors affecting immigration into patches. Our results imply that such nonlinearities can be important for monarch population dynamics and should be taken into account in efforts to conserve monarchs. Such effects may currently be of limited importance for North American monarch populations because of the ubiquity of common milkweed but may nevertheless be of significance for the conservation of other egg-avoiding butterflies.

Conclusion

We have shown that stochastic models can play a valuable role in uniting experimental and observational data in ecology. Our results also add to an understanding of butterfly colonization dynamics by providing a clear example of how female monarchs avoid existing eggs, by showing that egg predation increases with egg density, and by quantifying the relative importance of these effects for natural egg dispersals. These nonlinearities have the potential to

affect within-patch density in a way that ultimately leads to a higher fraction of occupied patches.

Acknowledgments

We are grateful to L. Maurer and S. Maurer for permitting us to perform our field experiments on their property. A. Hunter, J. H. Matis, and the members of the Dwyer lab—K. Abbot, P. Fujita, and S. H. Yee—made useful comments on previous versions of the manuscript. M. Coram and S. Lalley of the University of Chicago Statistics Department assisted with our understanding of how to fit stochastic models to data. We thank B. Elder for suggesting that we bootstrap I_B . K.L.S.D. was supported by Department of Education Graduate Assistance in Areas of National Need training grant P200A80129 and National Science Foundation Doctoral Dissertation Improvement Grant DEB-0206687 to G.D. and K.L.S.D. This article began as a chapter of K.L.S.D.'s dissertation, and he would therefore like to thank his committee for helpful comments, including J. Bergelson, S. Lalley, C. Pfister, and S. Venkataramani. The comments of the reviewers, M. Singer and M. Taper, also greatly improved the manuscript.

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Associate Editor: Judith L. Bronstein
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