Ecology, 80(8), 1999, pp. 2750–2761

MODEL SELECTION FOR A SUBTERRANEAN TROPHIC CASCADE: ROOT-FEEDING CATERPILLARS AND ENTOMOPATHOGENIC NEMATODES

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Abstract. Conjecture abounds while evidence is limited concerning indirect protection afforded plants by carnivorous predators in terrestrial ecosystems, apropos of the Hairston-Smith-Slobodkin (HSS) hypothesis. We conducted a field experiment with a suspected trophic cascade. Could an entomopathogenic nematode protect bush lupine by killing root-feeding ghost moth caterpillars? The experiment measured survival of lupine seedlings as a function of density of hatchling ghost moth caterpillars in rhizospheres with or without the entomopathogenic nematode.

We modeled lupine survival with a hierarchical family of "one-hit dose response" models to interpret the results of the experiment. We obtained maximum likelihood estimates of parameters and selected the best-fitting model using the Schwarz Information Criterion (SIC). The best model fit the data closely, and SIC model selection was consistent with classical likelihood ratio test results of models nested in the one-hit family. A parallel analysis performed upon a logistic family of models yielded results of poorer fit but largely consistent with results of the one-hit analysis. Finally, we compared our model-centered approach with the conventional methods-centered approach of logistic regression in statistical packages. While these packages give correct calculations, the implications of hypothesis tests are ecologically obscure in the absence of the explicit representation of models and their hierarchical relationships. For understanding ecological data, building an explicit statistical model of the process and testing parameters can be more informative than accepting the implicit model and testing variables in canned statistical packages.

The ecological implications were that seedling survival decreased exponentially with increasing densities of root-feeding caterpillars, and the entomopathogenic nematode virtually canceled the negative effect of this herbivore upon seedling survival. However, the significance to the broader community of this trophic cascade remains to be demonstrated. This cascade is a module or vignette within the greater food web, and additional interactions affect its influence: intraguild predation by nematode predators, apparent competition from other herbivores of lupine (each with its own natural enemies), and even more complicated interactions through competing plant species all come into play. As well, genetic variation of both the lupine and ghost moth caterpillars affects these interactions. Evidence does not support the inference that protection from ghost moth caterpillars by the entomopathogenic nematode is key to the "green" world of bush lupine.

Key words: Akaike information criterion; binary data; entomopathogenic nematode; indirect interaction; natural enemy; one-hit dose-response; Schwarz information criterion; statistical models; subterranean herbivory.

INTRODUCTION

With its hallmark "green world" metaphor, indirect, top-down control was a seminal idea of trophic ecology that has remained central to population-based theories of food webs (Oksanen et al. 1981, Hairston and Hairston 1993, 1997; carnivores ("natural enemies") suppress herbivore populations and thereby protect plants (Hairston, Smith, and Slobodkin 1960, "HSS"). Although HSS was originally applied to terrestrial food chains, most compelling examples of carnivores that indirectly protect plants are aquatic (Power 1990, Carpenter and Kitchell 1993, Estes and Duggins 1995, Brett and Goldman 1996). For communities on land, opinion is divided. Some authors advocate that simple HSS food chains determine the character of terrestrial ecosystems (Hairston and Hairston 1993), while others emphasize a more diverse set of food webs on land (Pastor and Naiman 1992, Strong 1992, Polis and Strong 1996, Jefferies 1999). Here we focus on a subterranean food chain that has been cited as evidence of HSS (Hairston and Hairston 1997). Herbivorous insects in the soil are ubiquitous (Brown and Gagne 1990),

Manuscript received 12 March 1998; revised 12 October 1998; accepted 14 October 1998.

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and very little is known of the significance of natural enemies in suppressing root-feeders. Our experiment concerned the plant protection afforded by an underground natural enemy of root-feeding insects.

Circumstantial evidence of a trophic cascade

Previous correlations suggested that an entomopathogenic nematode, *Heterorhabditis hepialus,* could indirectly protect bush lupine by killing root-feeding ghost moth caterpillars, which appeared to kill unprotected lupines. *Lupinus arboreus,* bush lupine, is a rapidly growing, nitrogen-fixing, perennial shrub (Maron and Connors 1996) native to the central California coast. Ghost moth caterpillars of *Hepialus californicus* (Lepidoptera, Hepialidae) feed upon lupine roots, are univoltine and largely monophagous at the study site at the Bodega Marine Reserve, Sonoma County, California. Ghost moths, also known as "swifts" or "swift moths," are strong flyers and disperse widely. On the wing, a single moth broadcasts upwards of 2000 small (0.5 mm diameter) eggs around and beneath *L. arboreus* plants (Wagner 1985, Tobi et al. 1993). Hatching within a few weeks, the tiny larvae burrow into the soil and feed upon the exterior of lupine roots. By early summer, larger caterpillars can bore inside to a refuge from natural enemies. Death rates of mature lupines were correlated in space with densities of large ghost moth caterpillars on lupine roots. Roots of dead plants were girdled or deeply bored, presumably by ghost moth caterpillars (Strong et al. 1995). An entomopathogenic nematode, *H. hepialus,* killed ghost moth caterpillars in the soil of the study site (Stock et al. 1996). Where nematode prevalence in lupine rhizospheres was highest, densities of ghost moth caterpillars and annual rates of lupine mortality were lowest (Strong et al. 1996). This evidence was suggestive of an HSS chain, but circumstantial, and the field observations did not resolve the interactions of the nematode, young caterpillars (which are numerous but too small to be seen reliably in field surveys), and seedling bush lupine.

Ecology of an entomopathogenic nematode, Heterorhabditis hepialus

Adults, reproduction, and feeding of entomopathogenic nematodes are restricted to the interior of host insects (Kaya 1990). The nonfeeding "infective juveniles," or third-instar, dauer larvae, live in the soil, search for hosts, and disperse. *H. hepialus* infective juveniles are ~0.55 mm in length. Attracted to CO_2 and other waste gases, they move up to 6 cm/d through moist soil toward an insect (Strong et al. 1996). An infective juvenile enters the host through a spiracle or other orifice, punctures a membrane, then regurgitates the symbiotic bacterium *Photorhabdus luminescens,* which kills the host within 48 h (Forst and Nealson 1996, Bowen et al. 1998). A burgeoning bacterial population then digests the cadaver and provides food for the exponentially growing adult nematode population inside. Although several infective juveniles can invade a host insect, nematodes in the family Heterorhabditidae are hermaphrodites; a single infective juvenile can kill a host and give rise to a full complement of offspring. The symbiotic bacteria produce antibiotics and other antimicrobial substances that protect the host cadaver and the adult nematodes inside from invasion of alien bacteria and fungi from the soil. When the insect cadaver is exhausted of resources, reproduction shunts to infective juveniles, which break the host integument and disperse into the soil. As many as 410 000 *H. hepialus* infective juveniles are produced in a large ghost moth caterpillar (Strong et al. 1996).

We conducted a field experiment that tested interactions in the effects of young ghost moth caterpillars and entomopathogenic nematodes on survival of lupine seedlings. The focus was upon plant protection during the crucial first spring of growth, when seedling bush lupine grow a tap root and are attacked by small caterpillars. "Nematode" refers to the entomopathogenic nematode *H. hepialus.*

Model-centered statistical approach

The binary survival data generated by this experiment had nonstandard features that were not well described by the statistical models in conventional statistical packages. We adapted the one-hit dose-response model (Turner 1975, Janardan 1986) for the statistical analysis. The model has seen extensive use in carcinogenesis and toxicology studies (Krewski and Brown 1981), but has been seldom employed in ecology (Costantino et al. 1998). The model is based on a plausible biological mechanism and might find useful applications in other systems. We accordingly describe the statistical methods here in some detail. Our model-centered approach emphasized customized model construction, model selection, parameter estimation, and model evaluation, in addition to the more traditional pairwise hypothesis tests. The use of an Akaike-type model selection index (Sakamoto et al. 1986) played a crucial role in sorting out the various hypotheses about the interactions between nematodes and caterpillars. Finally, we contrasted this approach with conventional logistic regression in statistics packages.

MATERIALS AND METHODS

Experimental design

The experiment was a randomized, factorial design with four levels of hatchling ghost moth caterpillars (Caterpillars: 0, 8, 16, and 32) crossed with two levels of the entomopathogenic nematode (Nematodes, present or absent) in soil with a single lupine seedling. Each treatment combination had 15 replicates. On 31 March 1995 we transplanted single *L. arboreus* seedlings that had germinated naturally on the study site into 46 cm deep pots with untreated native soil from the study area. Roots were carefully washed of all soil to remove any insects or nematodes. Pots had holes cut in the bottoms to allow the rapidly growing tap roots to exit. Pots were set in holes dug 40 cm deep. A lip of the top 5 cm of the pot was left aboveground to divert surface runoff of rain, to hinder exit of experimental caterpillars, and to deter entry of crawling animals that might carry and introduce entomopathogenic nematodes. Seedlings ranged between 10 and 15 cm in height, and had tap roots roughly equal in length to the height of the stem. All seedlings had been nodulated naturally by the nitrogen-fixing bacteria *Bradyrhizobium* sp. (Bentley and Johnson 1991) before transplantation into the pots. Seedlings averaged 0.62 ± 0.16 g dry mass (mean ± 1 SD, $n = 10$.) The pots were spaced on 1 m centers of a 620-m rectangular grid cleared of bush lupine in the Bay Shore area of the Bodega Marine Reserve. Potted seedlings were assigned haphazardly to positions on the grid before receiving a treatment designation. A handful of lupine leaf litter, previously heated to 60°C to kill any tiny ghost moth caterpillars or entomopathogenic nematodes present, was added for mulch to each pot. Wax-worm assays (Bedding and Akhurst 1975), which reveal the numbers of soil-dwelling infective juveniles that are competent to kill host insects (Koppenhofer et al 1998), failed to detect any *H. hepialus* nematodes in the soil in the pots. On 4 April 1995, hatchling ghost moth caterpillars ~3 mm in length and 20 μg in mass, from eggs laid in the laboratory by field-collected moths, were added randomly to pots in densities of either 0, 8, 16, or 32 caterpillars. These hatchling densities were well within those occurring naturally (Strong et al. 1995).

On 5 April 1995 infective juveniles of *H. hepialus* nematodes were added to one-half of the pots, chosen randomly, in each caterpillar density; the other half of the pots for each caterpillar density lacked the nematode. Nematodes were added at a density of ~1 individual/cm^3 of the top 10 cm of soil in the pot (2250 cm^3 of soil). Thus we added, with a pipette, a solution containing a mean of 2295 ± 160 nematodes (mean ± 1 SD, $n = 30$). This was within the middle two quartiles of field intensity of these nematodes at the study site (Strong et al. 1996). Mortality, height of the plants, and evidence of herbivores were measured twice monthly. Seedlings that died were inspected for root damage and for the silk and debris that are produced by ghost moth caterpillars. The plants were harvested on 13 September 1995; roots were examined for insects, and dry mass and root damage were measured. At harvest, the soil in each pot was assayed with wax worms for *H. hepialus*.

Statistical methods

The data are binary; a seedling's response to the treatments was survival or death. Caterpillars were a quantitative covariate ("dose") with experimentally manipulated values. Of interest is the effect of the caterpillars, the entomopathogenic nematode, and whether the two nematode treatments (+ and 0) produce an interaction in the dose-response function.

Under the one-hit dose-response model (Turner 1975, Janardan 1986), the probability p that a given seedling survives the experiment is an exponentially declining function of the dose of x caterpillars:

$$p = \lambda e^{-\beta x}. \tag{1}$$

Here λ is the background survival probability in the absence of caterpillars, and β is a positive constant. This model is similar to but simpler than the logistic, which has an inflection point; both are appropriate for binary responses. In the one-hit model, a seedling does not survive the experiment if one or more caterpillars finds and feeds substantially upon the plant; one random "hit" kills. Although this model is not packaged explicitly in convenient statistical software, its use is relatively straightforward.

The key assumption behind the exponential function is that caterpillars independently threaten seedlings. Suppose the chance is ϕ that any caterpillar completes the sequence of encountering and feeding that kills the seedling. Then the probability that the seedling avoids this threat and survives is $1 - \phi$. For the combined threat of x caterpillars under the independence assumption, the probability that a seedling survives is

$$[1 - \phi]^x = e^{-\beta x} \tag{2}$$

where $\beta = -\ln[1 - \phi]$. The exponential function does not have the inflection point that might be expected if caterpillars were not independent in their threat to the seedlings (Berryman et al. 1985).

The constants λ and β are unknown parameters that must be estimated from the data. Values of λ and β can, but need not, differ between the two nematode treatments. Thus, the survival probability for a seedling in treatment $i (i = 1$: nematodes present; $i = 2$: nematodes absent) at dose level x_j was taken to be

$$p_{ij} = \lambda_i e^{-\beta_i x_j} \tag{3}$$

with $i = 1, 2$ and $j = 1, 2, 3, 4$ ($x_1 = 0$, $x_2 = 8$, $x_3 = 16$, $x_4 = 32$).

To each nematode treatment i and caterpillar treatment j, 15 seedlings were assigned at random. The number of survivors y_{ij} observed out of 15 seedlings was the outcome of a binomial random variable:

$$P[Y_{ij} = y_{ij}] = \binom{15}{y_{ij}} p_{ij}^{y_{ij}}(1 - p_{ij})^{15-y_{ij}} \tag{4}$$

where p_{ij} is given by Eq. 3.

The fundamental tool for statistical inferences is the likelihood function. The likelihood function $L(\lambda_1, \lambda_2, \beta_1, \beta_2)$ for the unknown parameters λ_1, λ_2, β_1, and β_2 is the joint probability of the independent binomial outcomes for the eight treatment combinations:

$$L(\lambda_1, \lambda_2, \beta_1, \beta_2) = \prod_{i=1}^{2} \prod_{j=1}^{4} \binom{15}{y_{ij}} p_{ij}^{y_{ij}}(1 - p_{ij})^{15-y_{ij}}. \tag{5}$$

TABLE 1. Ten possible submodels (hypotheses) of the one-hit model for the lupine seedling survival experiment.

Hypothesis	Parameters	SIC	G^2_{kl} (df, P)
H_{00}	$\lambda_1 = \lambda_2$, $\beta_1 = 0$, $\beta_2 = 0$	55.3	32.5 (7, <0.001)
H_{01}	$\lambda_1 = \lambda_2$, $\beta_1 = 0$, $\beta_2 \neq 0$	31.2	3.61 (6, 0.73)
H_{02}	$\lambda_1 = \lambda_2$, $\beta_1 \neq 0$, $\beta_2 = 0$	57.4	29.8 (6, 0.001)
H_{03}	$\lambda_1 = \lambda_2$, $\beta_1 = \beta_2 \neq 0$	45.4	17.8 (6, 0.007)
H_{04}	$\lambda_1 = \lambda_2$, $\beta_1 \neq 0$, $\beta_2 \neq 0$	34.1	1.72 (5, 0.87)
H_{10}	$\lambda_1 \neq \lambda_2$, $\beta_1 = 0$, $\beta_2 = 0$	48.8	21.2 (6, 0.002)
H_{11}	$\lambda_1 \neq \lambda_2$, $\beta_1 = 0$, $\beta_2 \neq 0$	33.2	0.84 (5, 0.97)
H_{12}	$\lambda_1 \neq \lambda_2$, $\beta_1 \neq 0$, $\beta_2 = 0$	53.1	20.7 (5, <0.001)
H_{13}	$\lambda_1 \neq \lambda_2$, $\beta_1 = \beta_2 \neq 0$	47.4	15.0 (5, 0.01)
H_{14}	$\lambda_1 \neq \lambda_2$, $\beta_1 \neq 0$, $\beta_2 \neq 0$	37.5	0.29 (4, 0.99)

Notes: The model is $p_{ij} = \lambda_i \exp(-\beta_i x_j)$, where p_{ij} is the probability of a seedling's survival under nematode treatment i and caterpillar dose x_j; λ_i and β_i ($i = 1, 2$) are parameters. SIC = Schwarz information criterion; G^2_{kl} (df, P) = likelihood ratio goodness-of-fit statistic (degrees of freedom, P value for goodness-of-fit test).

Because the likelihood function is a product of sometimes very large and very small numbers, calculations are usually performed with the log-likelihood function given by

$$\ln L(\lambda_1, \lambda_2, \beta_1, \beta_2) = \sum_{i=1}^{2}\sum_{j=1}^{4} \ln\binom{15}{y_{ij}} + \sum_{i=1}^{2}\sum_{j=1}^{4} y_{ij}\ln(p_{ij}) + \sum_{i=1}^{2}\sum_{j=1}^{4} (15 - y_{ij})\ln(1 - p_{ij}). \tag{6}$$

Maximum likelihood (ML) estimates of the unknown parameters are the values of λ_1, λ_2, β_1, and β_2 that jointly maximize L or $\ln L$. We calculated ML estimates by numerically maximizing $\ln L$ using the Nelder-Mead simplex algorithm, which requires a subroutine to calculate the function being maximized. Full computer code and explanations of this surprisingly simple routine are provided by Press et al. (1992:402). The algorithm is a preprogrammed library function in MATLAB (Math Works 1993).

An alternative algorithm for calculating ML estimates for the model can be implemented through standard statistical programs such as SAS (SAS Institute 1990) or SYSTAT (SYSTAT 1996). The algorithm is known as iteratively reweighted least squares (Green 1984). The algorithm "tricks" a nonlinear regression program into maximizing the product-binomial likelihood (Eq. 5) instead of minimizing a sum of squares. Details and an example SAS program are provided in the Appendix to this paper.

Different ecological hypotheses about the effects of caterpillars and nematodes on seedling survival correspond to different model substructures (Table 1). The simplest possibility is that neither nematodes nor caterpillars affected survival of the seedlings, so that $\lambda_1 = \lambda_2$, and $\beta_1 = \beta_2 = 0$; this submodel has just one parameter to be estimated ($\lambda_1 = \lambda_2 = \lambda$, hypothesis H_{00}, Table 1). Another possibility is a potent herbivore but no plant protection from the carnivore, that nematodes did not affect seedling survival but caterpillars did ($\lambda_1 = \lambda_2$ and $\beta_1 = \beta_2 \neq 0$, two parameters (λ, β) estimated, hypothesis H_{03}, Table 1). A more complicated statistical outcome that is ecologically enigmatic is that entomopathogenic nematodes affected the base chance of seedling mortality but had no influence upon the mortality caused by caterpillars ($\lambda_1 \neq \lambda_2$ and $\beta_1 = \beta_2 \neq 0$, three parameters (λ_1, λ_2, β) estimated, hypothesis H_{13}, Table 1). The full four-parameter model is hypothesis H_{14}: $\lambda_1 \neq \lambda_2$, $\beta_1 \neq 0$, $\beta_2 \neq 0$, Table 1. Each hypothesis in Table 1 required a separate maximization of the log-likelihood function, subject to the parameter constraints indicated. In the iterative calculations, the reparameterization $\lambda_i = \exp(-\exp(\theta_i))$, where θ_i is a real number, was helpful for constraining λ_i to be between 0 and 1.

Our models have a nested structure. A single nestedness link from the more general to the more special case is formed by a change from "not equal to" to "equal to" for one parameter relationship (by $\lambda_1 \neq \lambda_2$ changing to $\lambda_1 = \lambda_2$, by $\beta_i \neq 0$ changing to $\beta_i = 0$, or by $\beta_i \neq \beta_j$ changing to $\beta_i = \beta_j$), as depicted as connections in Fig. 1. For instance, H_{01} is a special case of H_{04}, as indicated by a line between them (Fig. 1). For all nested model pairs, classical likelihood ratio test statistics were calculated. Denote by $\hat{L}_{\text{null}}$ the maximized value of the likelihood function for the simpler model, and by $\hat{L}_{\text{alt}}$ the maximized value of the likelihood function for the more complex model. The likelihood ratio statistic for testing the simpler model (null hypothesis) against the more complex model (alternative hypothesis) was computed as

$$G^2 = -2\ln(\hat{L}_{\text{null}}/\hat{L}_{\text{alt}}). \tag{7}$$

If the simpler model generated the data, then G^2 is an outcome of an approximate chi-square distribution with degrees of freedom equal to the number of parameters estimated in the more complex model minus the number of parameters estimated in the simpler model (Kendall and Stuart 1979:246). Note that if $0 < \lambda_i < 1$, the value $\beta_i = 0$ is an interior point of the valid parameter

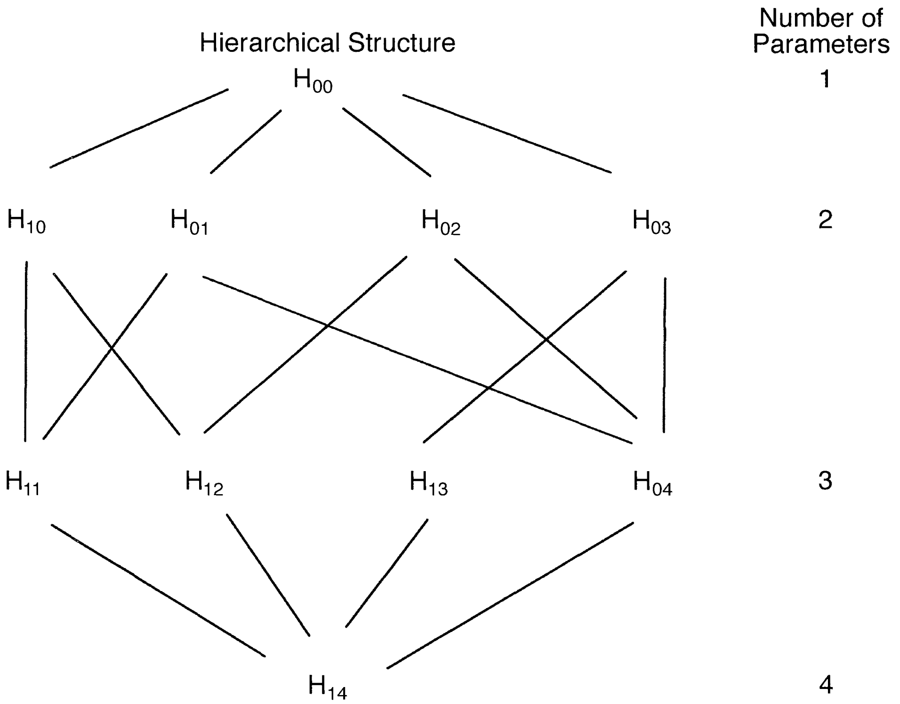

FIG. 1. Model substructure and nestedness of one-hit dose responses in survival of lupine seedlings attacked by ghost moth caterpillars and protected by the entomopathogenic nematode. The probability that a lupine seedling survives the experiment is $p_{ij} = \lambda_i e^{-\beta_i x_j}$, where λ_i and β_i are parameters. For each submodel, the first subscript refers to the equality (H_{0l}) or inequality (H_{1l}) of λ_1 and λ_2, which indicate the overall or intercept values for the two nematode treatments; $i = 1$ is the treatment with nematodes, and $i = 2$ is the treatment without nematodes. The second subscript refers to the relationships of β_i: H_{k0} indicates that $\beta_1 = \beta_2 = 0$; H_{k1} indicates that $\beta_1 \neq 0$, $\beta_2 = 0$; H_{k2} indicates that $\beta_1 = 0$, $\beta_2 \neq 0$; H_{k3} indicates that $\beta_1 = \beta_2 \neq 0$; and H_{k4} indicates that $\beta_1 \neq 0 \neq \beta_2 \neq 0$. Nestedness of the subhypotheses is indicated by lines, with the most general subhypothesis at the bottom (H_{14}).

space for β_i ($p_{ij} = \lambda_i e^{-\beta_i x_j}$ remains <1 for slightly negative values of β_i, and so Eq. 4 remains a valid probability model): the theorem giving the asymptotic chi-square distribution of the likelihood ratio statistic therefore remains valid when testing simpler models with $\beta_i = 0$ vs. more complex models with $\beta_i \neq 0$.

We reported all hypothesis tests as two-sided tests conducted at the 0.05 significance level. The chi-square approximation for the distribution of the likelihood ratio statistic only applies strictly to two-sided tests. Our scientific interests about the β_i values, though, tended toward one-sided alternative hypotheses. For the hypothesis H_{01}, for instance, a value of $\beta_2 > 0$ would be biologically irreconcilable with our modeling framework and our current understanding of the system. For practical purposes, the two-sided tests on the β_i values are serviceable. A two-sided test can be considered as a one-sided test, by the device of rejecting the alternative hypothesis whenever the estimated value of β_i is "on the null side" of its hypothesized null value. The resulting one-sided test is conservative in that the probability of rejecting a true null hypothesis is <0.05.

There are many models to choose from (Table 1), but model selection schemes based on pairwise hypothesis testing do not necessarily select the best model (Sakamoto et al. 1986). We calculated the Schwarz information criterion (SIC) for each model H_{kl} as an index of overall model quality. The SIC for model H_{kl} is given by the following formula (Schwarz 1978):

$$\mathrm{SIC}_{kl} = -2 \ln \hat{L}_{kl} + r_{kl} \ln n. \quad (8)$$

Here $\hat{L}_{kl}$ is the value of the maximized likelihood for model H_{kl}, r_{kl} is the number of parameters estimated in the model, and n is the sample size (in our case, $n = 120$ binary observations). We considered the model with the lowest SIC among the family of models to be the best model. The SIC is sometimes called the "Bayesian information criterion" or BIC, because its original derivation was based on the Bayes factor. However, it has a compelling frequentist interpretation. Selecting the model with the lowest SIC provides an asymptotically unbiased estimate of the number of parameters in the "true" model (see Bozdogan 1987). Note that, unlike the conventional approach of sorting out many hypotheses with hierarchical pairwise comparisons in which submodels alternately assume the role of null and alternative hypotheses, in the SIC approach all hypotheses are considered at the outset to be on a level playing field.

Occasionally some models have SIC values close to that of the model with the lowest value. An informal rule-of-thumb states that one can be indifferent concerning two models for which the difference of the SIC values is <2 (Sakamoto et al. 1986). When the lowest SIC value is substantially lower than the rest of the field, one can be more confident that the selected model provides a better description of the data than all the other models considered.

For each model H_{kl}, we also calculated the likelihood ratio goodness-of-fit statistic:

$$G^2_{kl} = 2\sum_i\sum_j y_{ij}\ln[y_{ij}/(15\hat{p}_{ij})] + 2\sum_i\sum_j (15-y_{ij})\ln\{(15-y_{ij})/[15(1-\hat{p}_{ij})]\}. \qquad (9)$$

Here $\hat{p}_{ij}$ is Eq. 3 with the ML estimates of λ_1, λ_2, β_1, and β_2 substituted, as calculated under model H_{kl}. The goodness-of-fit statistic is algebraically equivalent to Eq. 7, with $\hat{L}_{\text{null}}$ corresponding to the maximized likelihood of the fitted model H_{kl}, and $\hat{L}_{\text{alt}}$ corresponding to Eq. 5 with $y_{ij}/15$ substituted for p_{ij}. The goodness-of-fit test contrasts the fitted model (null hypothesis) with a fully saturated model in which each of the eight binomial distributions gets its own value of p_{ij} that is functionally independent of the other p_{ij}'s. If the null model fits, the calculated likelihood ratio statistic is an outcome from an approximate chi-square distribution with degrees of freedom equal to 8 minus the number of parameters estimated in the null model.

For comparison to the one-hit model, we performed parallel analyses with a logistic model, which takes the survival probability to be

$$p_{ij} = \frac{e^{-(a_i+b_ix_j)}}{1 + e^{-(a_i+b_ix_j)}} \qquad (11)$$

where a_1, a_2, b_1, and b_2 are parameters (compare with Eq. 3). Like the one-hit model, the logistic uses a product-binomial likelihood function (Eq. 5) and requires iterative maximization for calculating ML estimates. Unlike the one-hit model, the logistic function has an inflection point (declining S-shape). Different values of the parameters a_1, a_2, b_1, and b_2 yield a series of hypotheses parallel to those of the one-hit model in Table 1. We calculated ML estimates for the logistic hypotheses directly using the Nelder-Mead algorithm, just as we did for the hypotheses in the one-hit model family.

The various logistic hypotheses can also be fit with standard computer packages (including SAS and SYSTAT); each hypothesis requires a separate fitting. However, these methods-centered approaches use a syntax in terms of "variables" rather than the "parameters" of our model-centered approach. Models are implicit in the methods-centered approach, and this can lead the unwary astray. For our experiment, nematode treatment could be entered as a quantitative indicator variable (0 for absence, 1 for presence, say), and caterpillars would be a quantitative variable (x_j). When performing this type of analysis with statistical packages, one must avoid the temptation to judge the significance of the variables based on the output of a single run containing all the variables; this is equivalent to fitting just one model. Understanding is served by understanding the hierarchical structure of models and fitting them all.

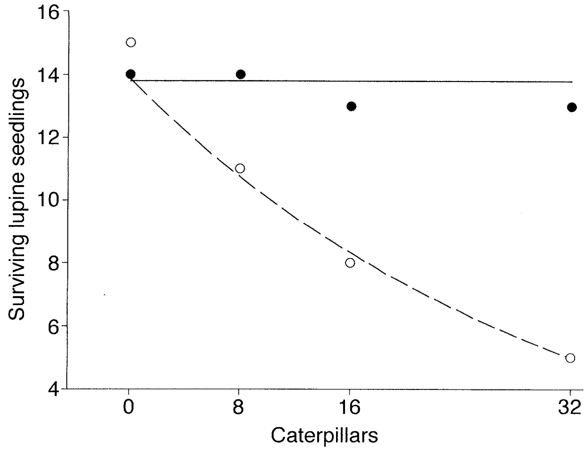

FIG. 2. The experimental outcome of the experiment (circles) and expected values of the best fitting one-hit model (lines). Solid symbols and line indicate the treatment combinations with nematodes; the open symbols and dashed line indicate those without nematodes.

To illustrate how fitting only one model can mislead, we performed a logistic regression with three variables: nematode treatment coded as a quantitative indicator variable (0 or 1, "NEMS"), caterpillar level coded as a quantitative variable (x_j, "CATS"), and an interaction term (the product of NEMS and CATS, "NEMXCAT"). We used SAS PROC LOGISTIC (SAS Institute 1990). We modeled the binary seedling mortality as a function of the main effects NEMS and CATS and the interaction NEMXCAT. We examined the chi-square tests printed on the output to determine significant effects.

RESULTS

By 17 June, ~2 mo after the beginning of the experiment, 47% (24/45) of seedlings had died while growing in treatment combinations with ghost moth caterpillars and no entomopathogenic nematodes, while only 11% (5/45) of seedlings had died in soil containing both the nematode and caterpillars. More ghost moth caterpillars meant fewer survivors of the lupine seedlings in the absence of the nematode (open circles, Fig. 2), but not in its presence (closed circles, Fig. 2). Other than the seedling deaths, little evidence of ghost moth herbivory was to be seen aboveground during the experiment. The tiny hatchling caterpillars disappeared into the soil within hours of their addition, and their activities remained belowground for the duration of the experiment. Four instances of severed root/shoot interfaces, with the dead plant falling to the ground, were observed in the caterpillar treatments over the duration of the experiment, but no ghost moth caterpillars remained by the time we discovered these severed shoots. Only 12 instances of the sawdust-like silk and debris of ghost moths were observed aboveground during careful regular examinations of the plants. No direct evidence of the entomopathogenic nematodes was visible during the experiment; they became indistinguishable to the naked eye even as they were applied to the soil at the beginning of the experiment. The entomopathogenic nematodes that we placed in the soil had low survivorship to September, even though the inoculations lasted long enough to give the clear results of plant protection in the first month of the study. In only 6 of the 60 rhizospheres to which we introduced *H. hepialus* in April did we find this nematode in September when the plants were harvested. *H. hepialus* was found in 1 of the 60 treatment combinations that had lacked this nematode at the beginning of the experiment.

Four models out of the 10 one-hit hypotheses gave adequate fits to the data, according to the likelihood ratio goodness-of-fit tests (Eq. 9) (G^2_{kl}, Table 1). These adequately fitting models are H_{14}, H_{11}, H_{04}, and H_{01}. The other six models fitted poorly. The adequate models have a common structure. In all four, β_2 ($-$nematodes) was positive, indicating the deleterious effect of more caterpillars on lupine survival in the absence of nematodes. Also, β_1 was different from β_2. In H_{01} and H_{11}, the ML estimates of β_1 (+nematodes) = 0, while those for β_2 ($-$nematodes) $\neq 0$. For H_{04} and H_{14}, in which the ML estimates of both β_1 and $\beta_2 \neq 0$, the estimates of β_1 were substantially less than those of β_2. Thus, all of the adequate models described an ecological result in which the entomopathogenic nematode stanched or even canceled the threat of ghost moth caterpillars to lupine seedlings.

The four adequate models have nested relationships: H_{01} is nested within both H_{11} and H_{04}, while H_{11} and H_{04} are in turn each nested within H_{14} (Fig. 1). In pairwise hypothesis tests (Eq. 7), neither H_{11} or H_{04} can be rejected as null (simpler, special case) hypotheses against the more complex alternative hypothesis H_{14} at the 0.05 level of significance. In addition, H_{01} cannot be rejected against either H_{11} or H_{04}. The pairwise results in conjunction with the goodness-of-fit results point to H_{01} as giving the best description of the data with the fewest parameters.

The SIC values for all the models supported the conclusion that H_{01} was the best among all the models considered (Table 1). The SIC value of 31.2 for model H_{01} was lower than that of any of the other models by 2 or more units. The second-best model was H_{11}, with an SIC of 33.2. The six models rejected by goodness-of-fit tests had SIC values higher than 45 (Table 1).

TABLE 2. Maximum likelihood parameter estimates for the four best fitting one-hit model hypotheses from Table 1.

Hypothesis	λ_1	λ_2	β_1	β_2
H_{01}	0.9205	0.9205	0	0.03195
H_{04}	0.9637	0.9637	0.004255	0.03456
H_{11}	0.9000	1.000	0	0.03677
H_{14}	0.9354	1.000	0.002791	0.03677

ML parameter estimates for model H_{01} (Table 2) yielded the following estimate of survival probability for a seedling in the *i*th nematode treatment in the presence of x_j caterpillars:

$$\hat{p}_{1j} = \hat{\lambda} = 0.9205 \qquad (\beta_1 = 0) \tag{12}$$

$$\hat{p}_{2j} = \hat{\lambda}e^{-\hat{\beta}_2 x_j} = 0.9205e^{-0.03195x_j} \tag{13}$$

Multiplying each of these probabilities by 15 gave the estimated expected number of survivors in each treatment. The expected values showed excellent agreement with the observed values (Fig. 2).

Results of our parallel SIC-based analysis of logistic regression models were similar overall to those of the one-hit model; however, the logistic models did not fit as well. Suppose the 10 hypotheses about the parameters a_1, a_2, b_1 and b_2 are labeled in a scheme like that in Table 1, with a_i in the role of λ_i, and b_i in the role of β_i (Table 3). Thus, H'_{00} corresponds to $a_1 = a_2$, $b_1 = 0$, $b_2 = 0$, H'_{01} corresponds to $a_1 = a_2$, $b_1 = 0$, $b_2 \neq 0$, etc. According to goodness-of-fit tests, five logistic models fitted the data adequately (H'_{01}, H'_{11}, H'_{13}, H'_{04}, and H'_{14}, Table 3). The list differs from the corresponding list of adequately fitting one-hit models (Table 1) only in that the logistic model H'_{13} is included (the one-hit counterpart H_{13} did not fit adequately). The logistic model with the lowest SIC was H'_{01} (SIC = 33.0), just as H_{01} (SIC = 31.2, Table 1) was the best one-hit model. The best one-hit model had a lower SIC value than that of the best logistic model. In fact, all four of the adequately fitting one-hit models had lower SIC values than their logistic counterparts.

The results of the methods-centered, "canned" logistic regression exercise were ecologically deceptive in the absence of our hierarchical model (Table 4). Recall that we used SAS PROC LOGIST to perform a logistic regression with two main effects, CATS and NEMS, and an interaction, NEMXCAT. The results detected a significant main CATS effect, but they also indicated that the evidence is at best weak for a main NEMS effect and for the interaction NEMXCAT; neither was significant at the 0.05 level. Indeed, these statistical results appear to be at odds with the distinct nematode effect and an equally distinct interaction in the plot of the data (Fig. 2)! Actually, this particular logistic regression corresponds to fitting the fully parameterized model, H'_{14}. The test for a nematode by caterpillar interaction (significance of NEMXCAT) corresponds to a pairwise hypothesis test of H'_{13} (null) vs. H'_{14} (alternative), as per Eq. 7. Were the hierarchical

TABLE 3. Ten possible submodels (hypotheses) of the logistic model for the lupine seedling survival experiment.

Hypothesis	Parameters	SIC	G^2_{kl} (df, P)
H'_{00}	$a_1 = a_2, b_1 = 0, b_2 = 0$	55.3	32.5 (7, <0.001)
H'_{01}	$a_1 = a_2, b_1 = 0, b_2 \neq 0$	33.0	5.42 (6, 0.49)
H'_{02}	$a_1 = a_2, b_1 \neq 0, b_2 = 0$	56.8	29.2 (6, <0.001)
H'_{03}	$a_1 = a_2, b_1 = b_2 \neq 0$	47.9	20.3 (6, <0.002)
H'_{04}	$a_1 = a_2, b_1 \neq 0, b_2 \neq 0$	37.5	5.10 (5, 0.40)
H'_{10}	$a_1 \neq a_2, b_1 = 0, b_2 = 0$	48.8	21.2 (6, 0.002)
H'_{11}	$a_1 \neq a_2, b_1 = 0, b_2 \neq 0$	37.8	5.41 (5, 0.37)
H'_{12}	$a_1 \neq a_2, b_1 \neq 0, b_2 = 0$	53.1	20.7 (5, <0.001)
H'_{13}	$a_1 \neq a_2, b_1 = b_2 \neq 0$	40.0	7.61 (5, 0.18)
H'_{14}	$a_1 \neq a_2, b_1 \neq 0, b_2 \neq 0$	42.1	4.90 (4, 0.30)

Notes: The model is $p_{ij} = e^{-(a_i+b_ix_j)}/[1 + e^{-(a_i+b_ix_j)}]$, where p_{ij} is the probability of a seedling's survival under nematode treatment i and caterpillar dose x_j, and a_i, b_i ($i = 1, 2$) are parameters. SIC = Schwarz information criterion; G^2_{kl} (df, P) = likelihood ratio goodness-of-fit statistic (degrees of freedom, P value for goodness-of-fit test).

model structure stated explicitly, one could proceed correctly, if not awkwardly, through the full set logistic models with a series of model statements in SAS or another program, to test each link in the hierarchy (Table 1, Fig. 1).

DISCUSSION

Statistical issues

The data in our experiment are by no means unusual; nonlinear effects of treatments upon nonnormal response variables are common in ecological studies. Nonetheless, the experimental results raise questions regarding conventional methods-centered statistical practices in ecology that rely upon canned routines, pairwise hypothesis testing, variables-type syntax, and a limited repertoire of statistical models. Ecological understanding is better served by beginning with a wider variety of statistical models, proceeding through an ecologically informed choice of explicit model candidates, and arriving at the best model through more effective evaluation and parameter testing.

The model-centered approach chooses the model, explicitly, from a range of scientifically reasonable candidates. The focus is on model construction, parameter estimation, model selection, and model evaluation. The model is the mathematical representation of how the variability in the data arose; it is the joint probability distribution used to describe the data (Eq. 5 in our study). When the data values are substituted into the joint distribution, the expression becomes a likelihood function, the fundamental link in statistics between parameters (unknown quantities in the model) and data. Whether one is doing a mark–recapture analysis or an analysis of variance, the analysis rests upon some kind of statistical model. The "variables" syntax of canned packages can obscure the form of the models actually being fitted and lead to confusion about the statistical inferences being drawn. The model is a part of the thinking, a part of the scientific argument, and should not be hidden from view.

The model-centered approach builds realistic statistical models tailored for the applications. Ecological data are often nonstandard and ill suited for off-the-shelf statistical methods. Just as the shoe is cut to fit the foot, and not vice versa, ecological processes should not be shoehorned into ill-fitting statistical models owing to inertia, tradition, or lack of packaged software. Realistic, nonstandard models of ecological processes can help make inferences stronger by harnessing the information in the data more effectively.

Our analyses of the lupine–ghost moth–entomopathogenic nematode experiment illustrates what can be gained with a model-centered statistical approach. Perfunctory use of a canned logistic regression program produced misleading results. Fitting multiple logistic regression models produced only a set of adequately fitting models. As well, the logistic models deemed to be adequate by pairwise tests did not have a consistent structure in terms of meaning. The hypothesis H'_{13} fitted the data (unlike H_{13} for the one-hit case) and was not

TABLE 4. Portion of output resulting from a routine logistic regression (PROC LOGISTIC, SAS Institute 1990) of lupine seedling survival data; analysis of maximum likelihood estimates.

Variable	df	Parameter estimate	Standard error	Wald chi-square	P
INTERCPT	1	2.1758	0.5630	14.9346	0.0001
NEMS	1	0.4166	0.9299	0.2008	0.6541
CATS	1	−0.1001	0.0283	12.5071	0.0004
NEMXCAT	1	0.0745	0.0454	2.6942	0.1007

rejected in favor of H'_{14} by the pairwise test. Hypothesis H'_{13} lacked the caterpillar–nematode interaction of H'_{14}: in H'_{13}, $b_1 = b_2$. Instead, H'_{13}, with a nematode "main effect," accounted for the difference between nematode treatments with different intercept parameters ($\lambda_1 \neq \lambda_2$). Was there or was there not an interaction? The problem was that the logistic regressions used the wrong model, a fact revealed by diagnostic plotting (Fig. 2) and the SIC values (Tables 1 and 3). The one-hit model provided an overall better description of the stochastic mechanisms that generated the data.

Ecological issues

Ghost moth caterpillars readily kill bush lupine. Even a few, very small, early-instar caterpillars caused high mortality to lupine seedlings. The highest number of hatchling caterpillars in the experiments was near the median numbers of large caterpillars observed on roots in the field (Strong et al. 1995: Fig. 4), and thousands of eggs can be laid by an ovipositing moth. Thus, seedling risks commensurate with those in the experiment are probably common in nature.

The experiment also confirmed that hatchling ghost moth caterpillars are quite vulnerable to this subterranean natural enemy. Entomopathogenic nematodes are widespread in both agricultural and natural systems (Hominick and Reid 1990, Gaugler et al. 1997). Because root-feeding insects are common (Brown and Gange 1990), these nematodes are of general ecological significance. A paradox is how the nematode cohort abides the low reproductive value provided by the first, small host insects encountered in the new caterpillar generation in early winter. Powers of discrimination are not known for infective juveniles, which vigorously attack host insects independent of size (Gaugler and Kaya 1990, Gaugler et al. 1997). Small caterpillar hosts yield very few if any infective juveniles, while larger, older caterpillar hosts yield hundreds of thousands of infective juveniles and are clearly the key to population persistence of the nematode (Strong et al. 1996). Infective juveniles, the third instars that dwell in the soil, are the propagules of entomopathogenic nematodes. They disperse to find new hosts and over-summer to perpetuate populations between generations of the univoltine ghost moth populations. Does a fraction of the infective juvenile population somehow delay attack until later in the season when ghost moth caterpillars have grown to large sizes? Alternatively, does the nematode population go through a bottleneck, first attacking the small caterpillars of the year and later recovering in numbers through a subsequent nematode generation that attacks larger caterpillars later in the growing season?

The experiment corroborated earlier field observations of the potential for a trophic cascade (Strong et al. 1996). Indeed, the entomopathogenic nematode can protect lupine seedlings from ghost moth caterpillars under field conditions. In the model that best described the data (H_{01}), ghost moth caterpillars had no effect upon lupine survival when nematodes were present ($\beta_1 = 0$). Of course, the invisibility of the caterpillars and nematodes underground meant that, for this experiment, the second link of the food chain was inferred. This inference is reasonable in light of the high lethality to host insects of entomopathogenic nematodes in general (Kaya 1990) and to the ghost moth in particular (Strong et al. 1996). Although some self-thinning occurs as bush lupine grows from seedlings into mature plants, high densities of germinating seedlings persist into the adult phase to set seed themselves (Maron and Simms 1997). Thus, ghost moth herbivory and the entomopathogenic nematode can have opposite large effects upon adult densities and population dynamics of bush lupine.

However, this potential trophic cascade is but a "module" (Holt and Polis 1997), a "vignette" (Strong 1999) within a less clearly resolved network of additional species in the lupine food web. Two sets of other interactions appear to have particularly high potential for attenuating or otherwise modifying the cascade. First, the nematode suffers extremely high rates of mortality in soils of the study site, with local extinctions at the scale of individual rhizospheres of the host plant (Strong et al. 1996). Intraguild predation upon the entomopathogenic nematode by nematophagous fungi could be the cause of this mortality, lessening the protection that this natural enemy affords the lupine, analogously to the effects of predators that consume predators in other systems (Polis and Holt 1992, Carpenter and Kitchell 1993, Rosenheim 1998). At least 13 species of nematophagous fungi occur in the soils of the study site, some in virtually all samples taken during our yearlong study (Jaffee et al. 1996). The five most abundant of these species all readily killed the entomopathogenic nematode on agar and in soil microcosms (Koppenhoffer et al. 1996). Yet other food web elements are apparent competition (Louda et al. 1990) between ghost moths and the other herbivores of bush lupine (Maron and Harrison 1997, Maron and Simms 1997) and microgeographic, genetic differences in interaction coefficients between lupine, ghost moths, and the nematode (Whipple 1998).

The HSS hypothesis (Hairston et al. 1960) opened wide the conceptual world of indirect interactions to ecology (Menge 1995). The particular indirect interaction featured in HSS is a forceful trophic cascade at the lower end of a simple, unbranched food chain, producing a "green" world with predators protecting plants by suppressing herbivores. Scores of archetypical HSS cascades have been demonstrated in lakes (Carpenter and Kitchell 1993), in flowing waters (Power 1990), and on sea shores (Paine 1992, Estes and Duggins 1995). However, while some authors advocate HSS (indirect plant protection by carnivores) as a unifying element of terrestrial ecosystems (Hairston and Hairston 1993, 1997), other authors have argued that compelling examples are lacking on land (Crawley 1989, Hunter and Price 1992, Strong 1992). Most terrestrial webs, based upon higher plants, are different from exemplary HSS cascades based upon algae. Perhaps the greatest functional distinctions are that higher plants have greater phytochemical protection than algae, and terrestrial herbivores are more specialized than herbivores of the typical aquatic trophic cascade (Polis and Strong 1996).

We would argue, contrary to Hairston and Hairston 1997, that evidence does not support this food chain as an exemplar of HSS. The nematophagous fungi and the other food web connections described above suggest that this lupine food web is more complex than a trophic cascade. This brings into question the idea that lupine thrives because the entomopathogenic nematode suppresses ghost moth caterpillars. It remains to be demonstrated that HSS is a valid model for terrestrial ecosystems.

ACKNOWLEDGMENTS

We thank Kelly Dyer and Dino Garcia-Rossi, who helped harvest the experiment, and Bruce Jaffee, Harry Kaya, John Maron, John Moore, Ellen Simms, Diane Cosgrove, Ed Connor, and Duane Meeter for comments on the ms. Peter Chesson reinforced early suspicions of strange inconsistency between results of conventional logistic regression and the graph of the data. The research was supported by NSF award DEB 9508673 to D. R. Strong and by the Bodega Marine Laboratory visiting Distinguished Research Fellow award to B. Dennis.

LITERATURE CITED

Bedding, R. A., and R. J. Akhurst. 1975. A simple technique for the detection of insect parasitic rhabditid nematodes in soil. Nematologica **21**:109–114.

Bentley, B. L., and N. D. Johnson. 1991. Plants as food for herbivores: the roles of nitrogen fixation and carbon dioxide enrichment. Pages 257–272 *in* P. W. Price, G. W. Fernandes, T. M. Lewinson, and W. W. Benson, editors. Plant–animal interactions. Wiley, New York, New York, USA.

Berryman, A. A., B. Dennis, K. F. Raffa, and N. C. Stenseth. 1985. Evolution of optimal group attack, with particular reference to bark beetles (Coleoptera: Scolytidae). Ecology **66**:898–903.

Bowen, D., T. A. Rocheleau, M. Blackburn, O. Andreev, E. Golubeva, R. Bhartia, and R. ffrench-Constant. 1998. Insecticidal toxins from the bacterium *Photorhabdus luminescens.* Science **280**:2129–2132.

Bozdogan, H. 1987. Model selection and Akaike's information criterion (AIC): the general theory and its analytical extensions. Psychometrika **52**:345–370.

Brett, M. T., and C. R. Goldman. 1996. A meta-analysis of the freshwater trophic cascade. Proceedings of the National Academy of Sciences (USA) **15**:7723–7726.

Brown, V. K., and A. C. Gange. 1990. Insect herbivory below ground. Advances in Ecological Research **20**:1–58.

Carpenter, S. R., and J. F. Kitchell, editors. 1993. The trophic cascade in lakes. Cambridge University Press, Cambridge, UK.

Costantino, R. F., J. M. Cushing, B. Dennis, R. A. Desharnais, and S. M. Henson. 1998. Resonant population cycles in temporally fluctuating habitats. Bulletin of Mathematical Biology **60**:247–273.

Crawley, M. J. 1989. Insect herbivores and plant population dynamics. Annual Review of Ecology and Systematics **34**: 531–564.

Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. Ecological Monographs **65**:75–100.

Forst, S., and K. Nealson. 1996. Molecular biology of the symbiotic-pathogenic bacteria *Xenorhabdus* spp. and *Photorhabdus* spp. Microbiological Reviews, March:21–43.

Gaugler, R., and H. K. Kaya, editors. 1990. Entomopathogenic nematodes in biological control. CRC Press, Boca Raton, Florida, USA.

Gaugler, R., E. Lewis, and R. Stuart. 1997. Ecology in the service of biological control. Oecologia **109**:483–489.

Green, P. J. 1984. Iteratively reweighted least squares for maximum likelihood estimation, and some robust and resistant alternatives. Journal of the Royal Statistical Society **B46**:149–192.

Hairston, N. G., Sr., and N. G. J. Hairston, Jr. 1993. Cause–effect relationships in energy flow, trophic structure and interspecific interactions. American Naturalist **142**:379–411.

Hairston, N. G., Jr., and N. G. Hairston, Sr. 1997. Does food web complexity eliminate trophic-level dynamics? American Naturalist **149**:1001–1007.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist **94**:421–425.

Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. American Naturalist **149**:745–764.

Hominick, W. M., and A. P. Reid. 1990. Perspectives on entomopathogenic entomology. Pages 327–349 *in* R. Gaugler and H. K. Kaya, editors. Entomopathogenic nematodes in biological control. CRC Press, Boca Raton, Florida, USA.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative rolls of bottom-up versus top-down forces in natural communities. Ecology **73**:724–732.

Jaffee, B. A., D. R. Strong, and A. E. Muldoon. 1996. Nematode-trapping fungi in a natural shrubland: tests for food-chain involvement. Mycologia **88**:554–564.

Janardan, K. G. 1986. A Lagrange–gamma multihit dose-response model for risk assessment. Mathematical Biosciences **80**:209–222.

Jefferies, R. L. 1999. Herbivores, nutrients, and trophic cascades in terrestrial environments. Pages 301–332 *in* H. Olff, V. K. Brown, and R. H. Drent, editors. Herbivores: between plants, and predators. Blackwell Science, Oxford, UK.

Kaya, H. K. 1990. Soil ecology. Pages 93–116 *in* R. Gaugler and H. K. Kaya, editors. Entomopathogenic nematodes in biological control. CRC Press, Boca Raton, Florida, USA.

Kendall, M., and A. Stuart. 1979. Inference and relationship. The advance theory of statistics. Volume 2. Fourth edition. Charles Griffin, London, UK.

Koppenhofer, A. M., J. F. Campbell, H. K. Kaya, and R. Gaugler. 1998. Estimation of entomopathogenic nematode population density in soil by correlation between bait insect mortality and nematode penetration. Fundamental and Applied Nematology **21**:95–102.

Koppenhofer, A. M., B. A. Jaffee, A. E. Muldoon, D. R. Strong, and H. K. Kaya. 1996. Effect of nematode-trapping fungi on an entomopathogenic nematode originating from the same field site in California. Journal of Invertebrate Pathology **68**:246–252.

Krewski, D., and C. Brown. 1981. Carcinogenic risk assessment: a guide to the literature. Biometrics **37**:353–366.

Louda, S. M., K. H. Keeler, and R. D. Holt. 1990. Herbivore influences on plant performance and competitive interactions. Pages 414–437 *in* J. B. Grace and D. Tilman, editors. Perspectives on plant competition. Academic Press, New York, New York, USA.

Maron, J. A., and P. G. Connors. 1996. A native nitrogen-fixing shrub facilitates weed invasion. Oecologia **105**:302–312.

Maron, J. L., and S. Harrison. 1997. Spatial pattern formation in an insect host-parasitoid system. Science **278**:1619–1622.

Maron, J. L., and E. L. Simms. 1997. Effect of seed predation on seed bank size and seedling recruitment of bush lupine (*Lupinus arboreus*). Oecologia **111**:76–83.

Math Works. 1993. MATLAB. Math Works, Natick, Massachusetts, USA.

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecological Monographs **65**:21–74.

Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist **118**:240–261.

Paine, R. T. 1992. Food web analysis: field measurements of per capita interaction strength. Nature **355**:73–75.

Pastor, J., and R. J. Naiman. 1992. Selective foraging and ecosystem processes in boreal forests. American Naturalist **139**:690–705.

Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. Trends in Ecology and Evolution **7**:151–154.

Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. American Naturalist **147**:813–846.

Power, M. E. 1990. Effects of fish in river food webs. Science **250**:811–814.

Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery. 1992. Numerical recipes in FORTRAN: the art of scientific computing. Second edition. Cambridge University Press, Cambridge, UK.

Rosenheim, J. A. 1998. Higher-order predators and the regulation of insect herbivore populations. Annual Review of Entomology **43**:421–447.

Sakamoto, Y., M. Ishiguro, and G. Kitagawa. 1986. Akaike information criteria statistics. D. Reidel, New York, New York, USA.

SAS Institute. 1990. SAS/STAT user's guide, version 6. Fourth edition, Volume 2. SAS Institute, Cary, North Carolina, USA.

Schwarz, G. 1978. Estimating the dimension of a model. Annals of Statistics **6**:461–464.

Stock, P., H. K. Kaya, and D. R. Strong. 1996. Identification of *Heterorhabditis* (Nemata: Heterorhabditidae) from California with a new species isolated from the larvae of the ghost moth *Hepialus californicus* (Lepidoptera: Hepialidae) from the Bodega Marine Reserve. Fundamental and Applied Nematology **19**:585–592.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology **73**:747–754.

Strong, D. R. 1999. Predator control in terrestrial ecosystems: the underground food chain of bush lupine. Pages 577–602 *in* H. Olff, V. K. Brown, and R. H. Drent, editors. Herbivores: between plants, and predators. Blackwell Science, Oxford, UK.

Strong, D. R., H. K. Kaya, A. V. Whipple, A. L. Child, S. Kraig, M. Bondonno, K. Dyer, and J. L. Maron. 1996. Entomopathogenic nematodes: natural enemies of root-feeding caterpillars on bush lupine. Oecologia **108**:167–173.

Strong, D. R., J. L. Maron, P. G. Connors, A. V. Whipple, S. Harrison, and R. L. Jefferies. 1995. High mortality, fluctuation in numbers, and heavy subterranean herbivory in bush lupine, *Lupinus arboreus*. Oecologia **104**:85–92.

SYSTAT. 1996. SYSTAT 6.0 for Windows: statistics. SPSS, Chicago, Illinois, USA.

Tobi, D. R., J. R. Grehan, and B. L. Parker. 1993. Review of the ecological and economic significance of forest Hepialidae (Insecta: Lepidoptera). Forest Ecology and Management **56**:1–12.

Turner, M. E. 1975. Some classes of hit-theory models. Mathematical Biosciences **23**:219–235.

Wagner, D. L. 1985. The biosystematics of [Hepialus] F. [s. lato] with special emphasis on the [californicus-hectoides] species group. Dissertation. University of California, Berkeley California, USA.

Whipple, A. V. 1998. Sources of variation in the interactions among the bush lupine (*Lupinus arboreus*), a microbial symbiont (*Bradyrhizobium* sp.), a root-feeding caterpillar (*Hepialus californicus*), and an entomopathogenic nematode (*Heterorhabditis marelata*). Dissertation. University of California, Davis, California, USA.

APPENDIX

Some nonlinear regression packages can be "tricked" into maximizing a product-binomial likelihood, or for that matter any other likelihood from the exponential family of statistical distributions. The trick is to specify an appropriate weight function in the usual Gauss algorithm that depends on the parameters and thus changes in value from iteration to iteration. The resulting "iteratively reweighted least squares" algorithm yields the ML estimates of the model parameters.

For a product-binomial likelihood (Eq. 5), the method uses the binomial counts (y_{ij} values) as the observations on the "dependent" variable, the binomial expected values (np_{ij}) as the model to be fitted, and weights of $1/[np_{ij}(1 - p_{ij})]$ are calculated each iteration. Omitting the weight statement will result in least squares estimates that have inferior statistical properties.

The SAS program listed below fits model H_{01} (Table 1) to the data. The variable y contains the seedling survivor counts, n is the total number of seedlings in each treatment, nemtrt indicates the presence (1) or absence (0) of nematodes, and x is the number of caterpillars. Note that each nematode treatment in model H_{01} requires separate calculation of the survival probabilities (p_{ij}). The Gauss algorithm for nonlinear regression requires derivatives of the expected values (with respect to the parameters) to be specified.

In the output of the program, the final parameter estimates are the ML estimates, and the asymptotic standard errors and correlation matrix are the valid ones obtained from inverting the Fisher information matrix. "Sum of loss" in the output is minus the maximized log-likelihood. The rest of the analysis-of-variance-type table is gibberish.

A separate program would be required for every other model in Table 1.

```
/*---fit one-hit dose-response model to lupine survival data---*/

data:

input y n nemtrt x;

cards:

 14   15   1    0
 14   15   1    8
 13   15   1   16
 13   15   1   32
 15   15   0    0
 11   15   0    8
  8   15   0   16
  5   15   0   32
;

proc nlin nohalve sigsq=1;
parameters lambda=.9 beta2=.3;
if nemtrt=1 then do;
   p=lambda;
   derp1=1;
   derb2=0;
end;
if nemtrt=0 then do;
   p=lambda*exp(-beta2*x);
   derp1=exp(-beta2*x);
   derpb2=-x*lambda*exp(-beta2*x);
end;
model y=n*p;
der.lambda=n*derp1;
der.beta2=n*derpb2;
_weight_=1/(n*p*(1-p));
_loss_=-(1gamma(n+1)-1gamma(y+1)
          -1gamma(n-y+1)+y*log(p)
          +(n-y)*log(1-p))/_weight_;
run;
```