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A Likelihood-Based Biostatistical Model for Analyzing Consumer Movement in Simultaneous Choice Experiments

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ABSTRACT Consumer feeding preference among resource choices has critical implications for basic ecological and evolutionary processes, and can be highly relevant to applied problems such as ecological risk assessment and invasion biology. Within consumer choice experiments, also known as feeding preference or cafeteria experiments, measures of relative consumption and measures of consumer movement can provide distinct and complementary insights into the strength, causes, and consequences of preference. Despite the distinct value of inferring preference from measures of consumer movement, rigorous and biologically relevant analytical methods are lacking. We describe a simple, likelihood-based, biostatistical model for analyzing the transient dynamics of consumer movement in a paired-choice experiment. With experimental data consisting of repeated discrete measures of consumer location, the model can be used to estimate constant consumer attraction and leaving rates for two food choices, and differences in choice-specific attraction and leaving rates can be tested using model selection. The model enables calculation of transient and equilibrium probabilities of consumer-resource association, which could be incorporated into larger scale movement models. We explore the effect of experimental design on parameter estimation through stochastic simulation and describe methods to check that data meet model assumptions. Using a dataset of modest sample size, we illustrate the use of the model to draw inferences on consumer preference as well as underlying behavioral mechanisms. Finally, we include a user's guide and computer code scripts in R to facilitate use of the model by other researchers.

KEY WORDS attraction rate, host selection, leaving rate, movement ecology, transient dynamics

Consumer feeding preference among resources has critical implications for larger ecological and evolutionary patterns and processes. Feeding preference can be a significant driver of ecological specialization, assortative mating, and thus speciation (Linn et al. 2003). Feeding preference of a disease vector for different hosts of a pathogen has important and complex implications for infectious disease spread in both plant and animal host populations (Kingsolver 1987, Zeilinger and Daugherty 2014). In invasion biology, feeding preference has been used to support the biotic resistance hypothesis (Morrison and Hay 2011). In ecological risk assessment, feeding preference is often used to help assess potential nontarget effects of introduced biological control agents (Babendreier et al. 2005) and genetically engineered organisms (Prager et al. 2014).

Consumer preference is also an important process in optimal foraging theory. In optimal patch foraging models, fitness is a function of residence time of the consumer within a patch (Stephens and Krebs 1986). Patch residence time should be a function of both attractiveness and consumption rate of the resource; both of which are fundamental components of feeding preference (Nicotri 1980, Schoonhoven et al. 2005). Optimal patch foraging models are essentially models of consumer movement (Nathan et al. 2008). Describing and understanding the movement of consumers among multiple resources—in other words, relating preference to movement—could help inform optimal patch foraging models.

Within consumer choice experiments or assays—where two or more choices are provided simultaneously to a consumer—feeding preference is inferred from either measures of relative consumption among resource choices (Larrinaga 2010, Morrison and Hay 2011), or measures of initial consumer movement or consumer location (Nicotri 1980, Rovenská et al. 2005, Bakonyi et al. 2006, Zirbes et al. 2011). Measures of consumption and measures of movement provide distinct and complementary information about feeding preference. Measures of consumption may be more relevant for investigating the potential for a consumer to suppress a resource, such as in a test of a potential bio-

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logical control agent (Babendreier et al. 2005). Movement-based measures of feeding preference, however, may incorporate elements of habitat preference (Underwood et al. 2004). As a result, compared with measures of consumption, measures of movement may be more relevant for investigating questions relating to the degree of association of a consumer with different resources, such as in optimal patch foraging models and in investigations into the evolutionary and ecological responses of consumers to novel resources (Linn et al. 2003). Movement can be quantified for any mobile consumer, whereas consumption can be difficult to measure for consumers with haustellate or sucking mouthparts. Moreover, the transient dynamics and equilibria associated with consumer movement behavior can, in some cases, be more revealing about consumer preference than consumption experiments, especially for mobile species. For example, leaving rates are probably related to assessment, handling, and consumption times, and provide a broader perspective than consumption experiments by themselves.

For at least four decades, biologists have debated and refined the design and analysis of consumer choice experiments based on measures of relative consumption, resulting in a rigorous set of methodologies (Manly 1974, 1993; Roa 1992; Horton 1995; Lockwood III 1998; Prince et al. 2004; Underwood et al. 2004; Taplin 2007; Larrinaga 2010). However, design and analysis of choice experiments based on measures of movement have lagged behind. At the same time, recent analyses of organismal movement have made significant advances using state-space models, which link probabilistic statistical models of observations of organismal location to biologically relevant stochastic models of movement (Jonsen et al. 2003, Patterson et al. 2008).

Rigorous analysis of repeated measures of movement within consumer choice experiments have been lacking because frequentist goodness-of-fit tests for repeated-measures multinomial data do not exist. While measures of movement have been used extensively in choice experiments, preference is often inferred from a single movement event, such as a consumer's first choice or location at the end of a trial (Nicotri 1980, Bakonyi et al. 2006, Zirbes et al. 2011). In such cases, the transient behavior of the consumer is ignored, the parameters estimated often have little biological relevance, and the results are difficult to relate in a quantitative manner to larger scale models of movement (e.g., Nathan et al. 2008).

In the present article, we develop a simple, likelihood-based, biostatistical model to analyze repeated measures of consumer location between paired resource choices. The model incorporates all available information on consumer location to and from choices during the trial, but does not require constant observation. Estimated choice-specific attraction and leaving rates are then used to make inferences on preference: higher attraction rates, lower leaving rates, or both, associated with one food choice indicate a greater preference. The model also allows for calculation of transient and equilibrium probabilities of as-

sociation between consumer and resource choices. Using stochastic simulation, we explore elements of the model relevant to experimental design. Finally, using an empirical dataset on herbivorous stink bug preference, we illustrate that the model can be used to draw inferences on consumer preference.

Materials and Methods

Theory and Model Development. In general, movement among potential resource choices is a stochastic process comprising probabilities of movement to (attraction) and from (leaving) a resource item or patch. Following the work of Haccou and Meelis (1992) on statistical analysis of continuous and discrete observations of animal behavior, we modeled the movement of a consumer between two choices as a continuous time, stochastic Markov chain model. In contrast to Haccou and Meelis (1992), we focus only on movements relevant to food choice with the goal of estimating attraction and leaving rates for each choice in a paired-choice experiment. Let $P_j(t_i)$ be the probability that a consumer is feeding on or associated with state j at observation time t_i , where $j = 1, 2, \dots, n$ for an experiment with $n - 1$ food choices and $i = 1, 2, \dots, m$ for m total number of discrete-time observations of consumer location per trial. The probability that a consumer is in the neutral space, i.e., not at a food choice, defined as $P_n(t_i)$, at time t_i is

$$P_n(t_i) = 1 - \sum_{j=1}^{n-1} P_j(t_i). \quad [1]$$

The probability that the consumer is associated with choice j , where $j \neq n$, $P_j(t_i)$, is a function of the probability that the consumer is feeding on food choice j at time $t_i - \Delta t$, defined as $P_j(t_i - \Delta t)$, and the probability that the consumer is in the neutral space at time $t_i - \Delta t$, defined as $P_n(t_i - \Delta t)$. We assume that consumers leave food choice j at a choice-specific constant leaving probability $\mu_j \Delta t$ and move toward food choice j at a choice-specific attraction probability $p_j \Delta t$. We further assume that consumers can only move to a food choice from the neutral space; in other words, a switching event from one choice to the other can be decomposed into two independent events—leaving the first choice and subsequent attraction toward the second choice (Fig. 1). Note that the model assumes that some amount of physical distance exists between choices that could reasonably be considered neutral space; the boundary between neutral space and a choice can at times be vague and researchers should consider this in their experimental design.

The probability that the consumer is at food choice j is

$$P_j(t_i) = (1 - \mu_j \Delta t) P_j(t_i - \Delta t) + p_j \Delta t P_n(t_i - \Delta t) + o(\Delta t) \quad [2]$$

where $o(\Delta t)$ are higher order terms of Δt . As Δt goes to zero, equation 2 becomes

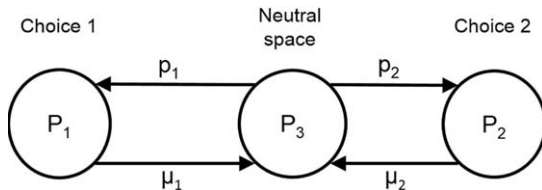


Fig. 1. Conceptual diagram of host plant choice and movement between three locations within a paired-choice experimental arena. The three circles represent the three possible states or locations; the two food choices (choices 1 and 2) and the neutral space between the choices. The arrows represent possible movements between the three locations. P_1 and P_2 = probability that consumers are on choices 1 and 2, respectively; P_3 = probability that consumers are in neutral space; p_1 and p_2 = attraction rates to choices 1 and 2, respectively; μ_1 and μ_2 = leaving rates from choices 1 and 2, respectively.

$$\frac{dP_j}{dt} = -\mu_j P_j + p_j P_n. \quad [3]$$

Combining equations 1 and 3 and considering the special case of an experiment with only two choices, $j = 1, 2$, the system can be modeled as

$$\begin{aligned} \frac{dP_1}{dt} &= -\mu_1 P_1 + p_1 P_3 \\ \frac{dP_2}{dt} &= -\mu_2 P_2 + p_2 P_3 \\ P_3 &= 1 - P_1 - P_2 \end{aligned} \quad [4]$$

where the parameters p_1 , p_2 , μ_1 , and μ_2 are fitted constants (Fig. 1), and P_3 is a special case of equation 1 for a system with only two choices. We substituted the equation for P_3 into the differential equations to produce the following two-equation model of linear, nonhomogeneous differential equations:

$$\begin{aligned} \frac{dP_1}{dt} &= -(\mu_1 + p_1) P_1 - p_1 P_2 + p_1 \\ \frac{dP_2}{dt} &= -(\mu_2 + p_2) P_2 - p_2 P_1 + p_2. \end{aligned} \quad [5]$$

We solved system (5) analytically with respect to t using Kolmogoroff's forward differential equations method (Tijms 2003) to produce a set of three dynamic probability functions $P_1(t_i)$, $P_2(t_i)$, and $P_3(t_i)$

$$\begin{aligned} P_1(t_i) &= -c_1 p_1 e^{\lambda_1 t_i} - c_2 p_1 e^{\lambda_2 t_i} + \frac{p_1 \mu_2}{\mu_1 p_2 + \mu_2 p_1 + \mu_1 \mu_2} \\ P_2(t_i) &= c_1 (\mu_1 + p_1 + \lambda_1) e^{\lambda_1 t_i} + c_2 (\mu_1 + p_1 + \lambda_2) e^{\lambda_2 t_i} \\ &\quad + \frac{p_2 \mu_1}{\mu_1 p_2 + \mu_2 p_1 + \mu_1 \mu_2} \\ P_3(t_i) &= 1 - P_1 - P_2 \end{aligned} \quad [6]$$

where c_1 and c_2 are arbitrary constants and λ_1 and λ_2 are eigenvalues of the system (Supp Material 1 [online only]).

The system of equation 6 describes the probability that the consumer is associated with choice 1 or choice 2 at time t projected from time $= 0$. In an experimental context, a researcher will often want to measure the location of each consumer multiple times over the course of the trials. Given m total observations at times t_i where $i = 1, 2, \dots, m$, then the conditional probabilities of consumer association, P_j , can be calculated for the interval $\tau_i = t_i - t_{i-1}$:

$$\begin{aligned} P_1(\tau_i) &= -c_1 p_1 e^{\lambda_1 \tau_i} - c_2 p_1 e^{\lambda_2 \tau_i} + \frac{p_1 \mu_2}{\mu_1 p_2 + \mu_2 p_1 + \mu_1 \mu_2} \\ P_2(\tau_i) &= c_1 (\mu_1 + p_1 + \lambda_1) e^{\lambda_1 \tau_i} + c_2 (\mu_1 + p_1 + \lambda_2) e^{\lambda_2 \tau_i} \\ &\quad + \frac{p_2 \mu_1}{\mu_1 p_2 + \mu_2 p_1 + \mu_1 \mu_2} \\ P_3(\tau_i) &= 1 - P_1 - P_2 \end{aligned} \quad [7]$$

where c_1 and c_2 are determined by the observed distribution of consumers at time t_{i-1} . The system (7) describe the conditional probabilities of finding consumers in states 1, 2, and 3, given that an observed number of them were found in each state at the beginning of the time interval.

Given N total consumers and that their distribution at time t_{i-1} is $(n_1(t_{i-1}), n_2(t_{i-1}), n_3(t_{i-1}))$, then c_1 and c_2 can be found by solving the initial value problem, where $P_1(t_i) = n_1(t_{i-1})/N$, $P_2(t_i) = n_2(t_{i-1})/N$, and $t = 0$:

$$\begin{aligned} n_1(t_{i-1})/N &= -c_1 p_1 - c_2 p_1 + \frac{p_1 \mu_2}{\mu_1 p_2 + \mu_2 p_1 + \mu_1 \mu_2} \\ n_2(t_{i-1})/N &= c_1 (\mu_1 + p_1 + \lambda_1) + c_2 (\mu_1 + p_1 + \lambda_2) \\ &\quad + \frac{p_2 \mu_1}{\mu_1 p_2 + \mu_2 p_1 + \mu_1 \mu_2}. \end{aligned} \quad [8]$$

Once system (8) is solved for c_1 and c_2 and the solutions are substituted into equation 7, the conditional probability for any time interval and any initial observation can be calculated in terms of the parameters of interest. For the initial conditions of the experiment (i.e., all consumers start in the neutral state), c_1 and c_2 have been calculated explicitly in the appendix. Because of the Markov properties of the model, these sequential conditional probabilities are independent (Tijms 2003).

To derive a likelihood function, let $n_1(t_i)$, $n_2(t_i)$, and $n_3(t_i)$ be the observed number of consumers at each location at observation time t_i . Then $P_1(t_i)$, $P_2(t_i)$, and $P_3(t_i)$ can be modeled as the parameters of a multinomial distribution, so $(n_1(t_i), n_2(t_i), n_3(t_i)) \approx \text{Multinom}(N, [P_1(t_i), P_2(t_i), P_3(t_i)])$, for N sample size and $i = 1 \dots m$ number of observation times per trial. Accordingly, the log-likelihood function at each time point, $\ell(\theta, t_i)$, is the log of the probability mass function for the multinomial distribution (Boos and Stefanski 2013). Summing over all observations produces the following likelihood function:

$$\ell(\theta) = \sum_{i=1}^m \left[\ln \left(\frac{N!}{n_1(\tau_i)! n_2(\tau_i)! n_3(\tau_i)!} \right) + \ln(P_1(\tau_i)^{n_1(\tau_i)}) \right. \\ \left. + \ln(P_2(\tau_i)^{n_2(\tau_i)}) + \ln(P_3(\tau_i)^{n_3(\tau_i)}) \right] \quad [9]$$

where θ is a vector of model parameters p_1 , p_2 , μ_1 , and μ_2 . Note that, whereas $p_j \Delta t$ and $\mu_j \Delta t$ in equation 2 were defined as attraction and leaving probabilities for choice j , respectively, here in system (7) and likelihood function (9), p_j and μ_j are defined as attraction and leaving rates, respectively.

Statistical Inference. From this model, consumer feeding preference can be inferred from differences between the choice-specific attraction and leaving rates. To test for differences in preference between choices, we compared four variants of the likelihood function (9). First, we set both the attraction rates and the leaving rates equal to each other, which we call the Fixed model ($p_1 = p_2$, $\mu_1 = \mu_2$). In the Fixed model, the optimization algorithm is forced to fit one attraction rate and one leaving rate for the data from both choices; the Fixed model represents a null model of no preference. Second, in the Free Leaving model, we set attraction rates, p_1 and p_2 , equal to each other but allowed the leaving rates to vary ($p_1 = p_2$, $\mu_1 \neq \mu_2$). Third, in the Free Attraction model, we allowed the attraction rates to vary but set the leaving rates, μ_1 , and μ_2 , equal to each other ($p_1 \neq p_2$, $\mu_1 = \mu_2$). Finally, in the Free model, we allowed all four parameters to be fit independently ($p_1 \neq p_2$, $\mu_1 \neq \mu_2$). Differences among the maximum likelihood estimates (MLEs) of these four model variants can be tested with Akaike's information criterion (AIC). Models do not need to be nested for AIC (Bolker 2008, Burnham et al. 2011), so all variants can be tested together. Inference can be made either based on the best model—the one with the lowest AIC value—or through model averaging (Burnham and Anderson 2002).

Variances for parameter estimates can be estimated using either the profile method or the normal approximation method, if the MLE is at or near the global minimum (Bolker 2008, Millar 2011). In the normal approximation method, variances are extracted from a variance-covariance matrix that is calculated by inverting the Hessian matrix of the MLE (Bolker 2008), which is often an output of derivative-based MLE algorithms. However, if a parameter estimate is on the boundary of the inequality constraint, then the MLE is unlikely to be at the global minimum and the profile and normal approximation methods for estimating variance are no longer valid. In this case, variances and SEs can be estimated using jackknife methods. Importantly, CIs should not be calculated from jackknife estimates of SE because, in general, their probability distributions are unknown (Efron and Tibshirani 1993).

Finally, parameter estimates can be used to calculate the probabilities, at equilibrium, that a consumer will be associated with the two choices using equations (A12) in Supp Material 1 (online only).

Testing Model Assumptions. The present model assumes that attraction and leaving rates are constant for the duration of the trials, although it is possible to develop more general models with time-varying parameters. The assumption of time-constancy can be interrogated using graphical inspection of $\ln(t_i)$ versus $\ln\{-\ln[S(t_i)]\}$ from Kaplan-Meier survival functions of the attraction rates and leaving rates, where t_i is the time of an attraction or leaving event, and $S(t_i)$ is the proportion of individuals remaining at time t_i . If the data follow the line of best fit, then the attraction or leaving rates are constant (Machin et al. 2006). Also, Machin et al. (2006) note that the y-intercept of the line of best fit provides an estimate of the natural log of the constant hazard rate, $\ln(\lambda)$. This estimate of the hazard rate, λ , can be used as an initial parameter value in the MLE algorithm.

The model also assumes that consecutive consumer choices are independent from previous choices. This assumption can be interrogated with contingency table analyses in which consecutive choices are the factors: first choice versus second choice, second choice versus third choice, etc. (Andow and Kiritani 1984). Note that such an analysis requires following individuals through time. Alternatively, independence between choices can be assessed by examining correlations between model parameter estimates at the MLE. As described in the Statistical Inference section, the variance-covariance matrix can be calculated from the Hessian matrix. When the variance-covariance matrix is scaled to the variances, then the off-diagonal elements of the matrix provide correlations between parameter estimates (Bolker 2008). Contingency table analysis will be invalid when movement event frequencies are too small; namely, when one or more table cells are 0. Estimating correlations between parameter estimates will be invalid when parameter estimates are on a constraint boundary.

Stochastic Simulation. To explore the behavior of the model and maximum likelihood estimation of parameters, we used stochastic simulation to investigate how various dimensions of consumer choice experimental design influence parameter estimation. We simulated consumer location data, $n_1(t_i)$, $n_2(t_i)$, and $n_3(t_i)$, using a Markov stochastic process (Pielou 1969) of model (7). The simulated data were used with the likelihood function (8) to estimate the parameters using the Free model variant.

First, we explored how sample size influences parameter estimation by simulating data at low, medium, and very large sample sizes: $N = 10$, 20, and 1,000, respectively. We also explored how the rate of movement by experimental consumers may influence parameter estimation. Specifically, we hypothesized that, for accurate parameter estimation, the distribution of observation times should match the rate of movement by consumers such that both the transient dynamics and equilibrium are observed. In the slow consumer scenario, we simulated data using each combination of low and high parameter values in which the observation times covered only the transient dynamics; the low and high values were 0.02 and 0.1,

Table 1. True parameter values (p_1 , p_2 , μ_1 , and μ_2) for fast consumers (0.2 and 0.6) and slow consumers (0.02 and 0.1), equilibrium values (P_1^* , P_2^* , and P_3^*), and the time to equilibrium of the model for each PC

PC	p_1	p_2	μ_1	μ_2	P_1^*	P_2^*	P_3^*	Time to equilibrium ^a
Fast consumer true parameter values								
1	0.2	0.2	0.2	0.2	0.33	0.33	0.33	18
2	0.6	0.2	0.2	0.2	0.60	0.20	0.20	12
3	0.2	0.6	0.2	0.2	0.20	0.60	0.20	12
4	0.6	0.6	0.2	0.2	0.43	0.43	0.14	8
5	0.2	0.2	0.6	0.2	0.14	0.43	0.43	35
6	0.6	0.2	0.6	0.2	0.33	0.33	0.33	43
7	0.2	0.6	0.6	0.2	0.08	0.69	0.23	26
8	0.6	0.6	0.6	0.2	0.20	0.60	0.20	30
9	0.2	0.2	0.2	0.6	0.43	0.14	0.43	35
10	0.6	0.2	0.2	0.6	0.69	0.08	0.23	26
11	0.2	0.6	0.2	0.6	0.33	0.33	0.33	43
12	0.6	0.6	0.2	0.6	0.60	0.20	0.20	30
13	0.2	0.2	0.6	0.6	0.20	0.20	0.60	11
14	0.6	0.2	0.6	0.6	0.43	0.14	0.43	8
15	0.2	0.6	0.6	0.6	0.14	0.43	0.43	8
16	0.6	0.6	0.6	0.6	0.33	0.33	0.33	6
Slow consumer true parameter values								
1	0.02	0.02	0.02	0.02	0.33	0.33	0.33	177
2	0.1	0.02	0.02	0.02	0.71	0.14	0.14	99
3	0.02	0.1	0.02	0.02	0.14	0.71	0.14	99
4	0.1	0.1	0.02	0.02	0.45	0.45	0.09	63
5	0.02	0.02	0.1	0.02	0.09	0.45	0.45	389
6	0.1	0.02	0.1	0.02	0.33	0.33	0.33	405
7	0.02	0.1	0.1	0.02	0.03	0.81	0.16	146
8	0.1	0.1	0.1	0.02	0.14	0.71	0.14	255
9	0.02	0.02	0.02	0.1	0.45	0.09	0.45	389
10	0.1	0.02	0.02	0.1	0.81	0.03	0.16	146
11	0.02	0.1	0.02	0.1	0.33	0.33	0.33	405
12	0.1	0.1	0.02	0.1	0.71	0.14	0.14	255
13	0.02	0.02	0.1	0.1	0.14	0.14	0.71	80
14	0.1	0.02	0.1	0.1	0.45	0.09	0.45	63
15	0.02	0.1	0.1	0.1	0.09	0.45	0.45	63
16	0.1	0.1	0.1	0.1	0.33	0.33	0.33	36

^a Time to equilibrium indicates the min. time step where $P_j(t) = P_j^*$ to a precision of 5 decimal places.

respectively (Table 1). This generated 16 different combinations of true parameter values. In the fast consumer scenario, we repeated this process with low and high parameter values that allowed for observation of both transient dynamics and the equilibrium. In this case, the low and high parameter values were 0.2 and 0.6.

Second, we explored how the number of and intervals between per trial observations influenced parameter estimation. We simulated data at low, medium, and high numbers of per trial observation times: $m = 10, 20$, and 40 , respectively. For each level of m , we compared two different interval schemes: when those observations were evenly spaced at a constant interval of 1 time step and when the observations were weighted toward the beginning of the experiment (i.e., front-loaded observations).

To assess the performance of the MLE process, we calculated expected proportional bias as $E((\hat{d} - d)/d)$, where \hat{d} is the maximum likelihood parameter estimate and d is the true parameter value, from 4,000 simulation runs for each true parameter combination (PC). The MLE converged in 100% of the simulations.

Consumer Choice Experiment. To illustrate the practical use of the model, we used data from an experiment conducted to test for feeding preference of nymphs of the herbivorous stink bug species *Eu-*

schistus servus Say and *Nezara viridula* L. (Heteroptera: Pentatomidae) between a cotton plant (*Gossypium hirsutum* L.) that had been damaged by a larval *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae) and an undamaged cotton plant. The study was designed to test the hypothesis that induced plant responses to *H. zea* herbivory influenced stink bug feeding preference (Zeilinger et al. 2011). Briefly, three possible locations of the stink bug were recorded in each trial: on the undamaged plant, on the damaged plant, or in neutral space between plants. We monitored the location of the stink bug at 10, 30 min, 1, 12, 18, 24, and 36 h from the start of the experiment. We focused our observations in the beginning of the experiment, i.e., front-loaded observations because stink bug movement was most likely to occur during this period (A.R.Z, unpublished data). We obtained sample sizes of 15 and 19 for trials with *E. servus* and *N. viridula*, respectively. For model selection, we used AIC corrected for small sample size (AIC_c). Variances and 95% CIs were calculated using the normal approximation method (Bolker 2008, Millar 2011). Parameter estimates and variances were averaged for all models with $\Delta AIC_c < 7$ following Burnham et al. (2011). For more detail on the experimental design see Zeilinger (2011).

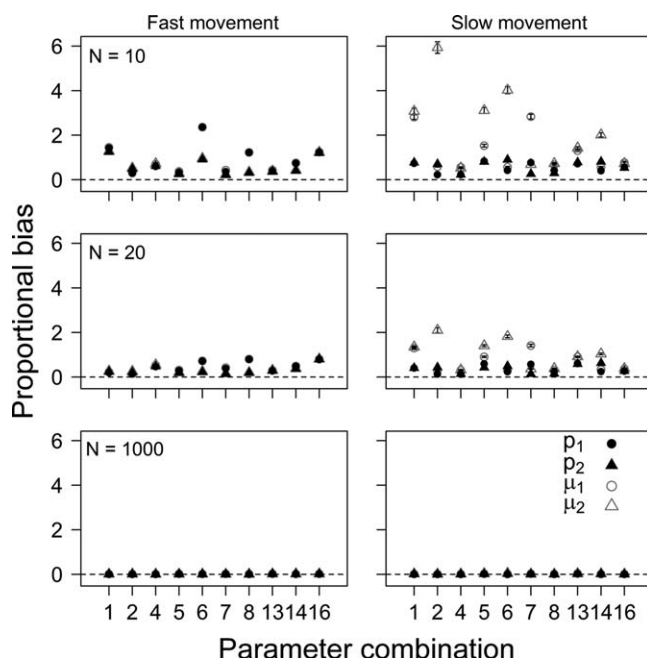


Fig. 2. Sample Size Simulation. Expected proportional bias estimates, $E((\hat{d} - d)/d)$ for rate parameters over a range of sample sizes, $N = 10, 20$, and $1,000$, for 10 unique PCs from 4,000 simulation runs. Left-side panels ("Fast movement") represent combinations of greater true parameter values: 0.2 and 0.6 for high and low values, respectively (see Table 1). Right-side panels ("Slow movement") represent combinations of smaller true parameter values: 0.02 and 0.1. Number of observation times $m = 40$ for each simulation and spaced at 1 time step. These values were within the range of initial parameter estimates from empirical data from trials with herbivorous stink bugs on cotton plants (Zeilinger et al. in review).

All programming was done in R 3.1.0 (R Core Team 2014, Vienna, Austria). To maximize the negative log-likelihood function, we used the `optimx` function (Nash and Varadhan 2011) with the Barzilai–Borwein spectral projected gradient ("spg") optimization algorithm (Varadhan and Gilbert 2009). The spg method was used because preliminary simulations showed that other constrained optimization algorithms, namely L-BFGS-B, did not consistently converge on an MLE (results not shown). For MLE of simulated and empirical data, convergence tolerance was set at 10^{-20} and the number of maximum iterations was set at 10,000. To improve MLE convergence, we used inequality constraints of $10 \geq \theta \geq 0.0001$ and supplied exact gradient functions. Gradient functions were derived in Mathematica 9 (Wolfram Research, Inc. 2012, Champaign, IL) and verified by calculating numerical derivatives with the `grad` function in R (Gilbert 2012). To facilitate the future use of the model, we have developed a user's guide (Supp Material 2 [online only]) and supplied R script for maximum likelihood estimation with the four model variants, model selection, variance estimation using the normal approximation method, and jackknife method, and testing assumptions (Supp Material 3 [online only]). Current R scripts and future revisions and extensions to the model will also be available at: <https://github.com/arzeilinger/Consumer-Choice-model>.

Results

Stochastic Simulation of Sample Size. Some of the 16 PCs were reciprocals, in which the true parameter values were switched between the two choices, and in these cases, bias estimates were switched and equivalent (Supp Fig. 1 [online only]). For example, PC 6 ($p_1 = 0.6, p_2 = 0.2, \mu_1 = 0.6, \mu_2 = 0.02$) is reciprocal to PC 11 ($p_1 = 0.2, p_2 = 0.6, \mu_1 = 0.2, \mu_2 = 0.6$); likewise, p_1 was overestimated in PC 6, whereas p_2 was overestimated in PC 11 (Supp Fig. 1 [online only]). That estimated bias was equivalent between reciprocal PCs indicates that accuracy in parameter estimates between choice 1 and choice 2 were equivalent. Following this, we show only results from the 10 unique PCs (Figs. 2 and 3).

Estimated proportional bias was generally greatest at low sample size ($N = 10$), decreased at intermediate sample size ($N = 20$), and was negligible at very large sample size ($N = 1,000$; Fig. 2). These results suggest that bias was a sampling problem, and not intrinsic to the model and estimation method. Bias estimates were generally positive, indicating that the parameter estimates were greater than the true values (Fig. 2).

Estimated proportional bias also depended on the overall movement rates (Fig. 2). The patterns of bias indicate that low accuracy (high bias) may be because of poor estimation of either the transient dynamics (when the model moves quickly to equilibrium) or equilibrium values (when the model moves slowly to

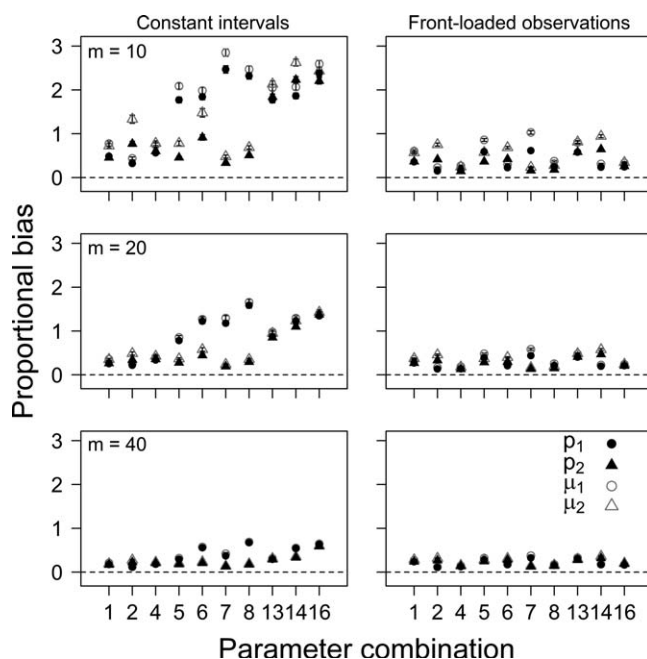


Fig. 3. Number of Per trial Observation Times Simulation. Expected proportional bias estimates, $E((\hat{d} - d)/d)$, for rate parameters over a range of number of per trial observations and intervals between observation times for 10 unique PCs from 4,000 simulation runs. Range of number of per trial observations included $m = 10, 20$, and 40 . Left-side panels ("Constant intervals") represent simulations with constant intervals between observations, with an observation every 1 time step. Right-side panels ("Front-loaded observations") represent simulations with a greater concentration of observations, with shorter intervals, at the beginning of trials. PC numbers correspond to those in Table 1. Sample size, N , for each simulation = 20.

equilibrium). The model requires four degrees of freedom (dfs) to estimate the four parameter values. The equilibria of the three state variables provide two dfs, so the remaining information is in the transient dynamics of the system. We evaluated the time to equilibrium for each PC using equations (A12). Consistent with our hypothesis, the greatest bias estimates occurred with PCs that caused the system to move to equilibrium quickly—PCs 2 and 16—and PCs that caused the system to move to equilibrium slowly—PCs 1, 5, and 6 (Fig. 2; Table 1) relative to the time step and duration of observations. Specifically, all instances of high bias are associated with PCs in which there are insufficient observations of both the transient period and the equilibrium. For instance, under the slow consumer scenario, PCs 1, 2, 5, and 6 take ≥ 99 time steps to reach equilibrium (Table 1) while observations were made up to 40 time steps, excluding any observations of the equilibria. However, when rates of movement were increased—under the fast consumer scenario—the time to equilibrium approached 40 and bias estimates were greatly reduced (Fig. 2; Table 1).

Stochastic Simulation of Per Trial Observation Times. Using the fast consumer scenario, we explored the effects of varying the per trial observation times—both total number and intervals between observations—on parameter estimation. As with the sample size simulation, estimated proportional bias was greatest at a low number of observation times ($m = 10$) and

decreased substantially at intermediate and large numbers of observation times ($m = 20$ and $m = 40$, respectively; Fig. 3).

We also found that the interval scheme—constant intervals of 1 time step or front-loaded observations—affected bias estimates (Fig. 3). Bias estimates tended to be greater when observations were evenly spaced; front-loading observations resulted in consistently small bias estimates (proportional bias < 1) across PCs, particularly for $m \geq 20$.

Consumer Choice Experiment. For the assumption of independent consecutive choices, we tested for independence between first and second choices for *N. viridula* using contingency table analysis; the frequencies of *E. servus* movement were too small for such analysis (Table 2). Consecutive choices made by *N. viridula* nymphs were independent (odds ratio = 0.06; 95% CI = [0.0007, 1.34]; $P = 0.07$). Independence is also supported by correlations between parameter estimates, calculated from the Hessian matrix of the Free Choice model; correlation between μ_2 and p_1 (r_{μ_2, p_1}) was 0.09 and correlation between μ_1 and p_2 (r_{μ_1, p_2}) was 0.14. For *E. servus*, parameter correlations suggested that choices were independent as well; $r_{\mu_2, p_1} = 0.009$ and $r_{\mu_1, p_2} = 0.039$. For the assumption of constant attraction and leaving rates, the data available followed the line of best fit, indicating that the attraction and leaving rates were constant during the experiment (Fig. 4).

Table 2. Contingency tables of the outcomes of consecutive choices made by stink bugs between *H. zea*-damaged and undamaged cotton plants

Species	First choice	Second choice	
		Damaged	Undamaged
<i>E. servus</i>	Damaged	2 ^a	0
	Undamaged	1	1
<i>N. viridula</i>	Damaged	1	4
	Undamaged	6	1
	Second choice	Third choice	
		Damaged	Undamaged
<i>E. servus</i>	Damaged	0	1
	Undamaged	0	0
<i>N. viridula</i>	Damaged	0	3
	Undamaged	2	0

^a Number of stink bug nymphs on the damaged plant for their first choice and damaged plant for their second choice, meaning that the stink bug was observed to have left the damaged plant and to have returned to the damaged plant. Only the first contingency table, between first and second choices, was analyzed.

For *E. servus* trials, the Free Attraction model fit the data best, but all models were good with $\Delta\text{AIC}_c < 7$ (Table 3). Averaged parameter estimates and CIs from these models showed that *E. servus* was significantly

Table 3. Degrees of freedom, information criterion corrected for small sample size (AIC_c) values, and change in AIC_c (ΔAIC_c) for each model variant in the stink bug choice experiment

Stink bug species	Model variant	df ^a	AIC_c	ΔAIC_c ^b
<i>E. servus</i>	Free attraction model	3	56.66	0 ^c
	Free leaving model	3	60.19	3.53 ^c
	Free model	4	60.46	3.80 ^c
	Fixed model	2	62.50	5.84 ^c
<i>N. viridula</i>	Fixed model	2	50.40	0 ^c
	Free attraction model	3	52.65	2.25 ^c
	Free leaving model	3	53.02	2.62 ^c
	Free model	4	55.50	5.10 ^c

^a Degrees of freedom associated with the model variant.

^b ΔAIC_c indicates the change in AIC_c relative to the minimum AIC_c value among model variants. Model variants are ordered according to ΔAIC_c values.

^c Models with $\Delta\text{AIC}_c < 7$ were considered good models and selected for averaging following Burnham et al (2011).

more attracted to undamaged plants than to *H. zea*-damaged plants. Differences in attraction rates had a strong effect in determining preference, whereas leaving rates between choices were indistinguishable (Fig. 5). Based on the model-averaged parameter estimates (Fig. 5), the probability that *E. servus* is associated with undamaged plants is predicted to be much greater than the probability of association with *H. zea*-damaged plants (Fig. 6).

For *N. viridula*, the best model was the Fixed model but once again all four model variants were good with $\Delta\text{AIC}_c < 7$ (Table 3). Using all four models to estimate model-averaged parameter values, we found that *N. viridula* attraction rates and leaving rates were equivalent between undamaged and damaged plants (Fig. 5). At equilibrium, we predict that *N. viridula* will be

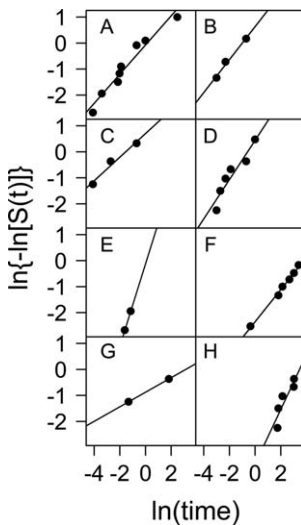


Fig. 4. Graphical inspection of model assumptions: constant attraction rates (A–D) and leaving rates (E–H) for each stink bug species, *E. servus* (A, C, E, and G) and *N. viridula* (B, D, F, and H), on undamaged cotton plants (A, B, E, and F) and *H. zea*-damaged plants (C, D, G, and H). The variable “time” on the x-axis indicates the time (in hours) when an attraction or leaving event occurred (i.e., when one or more stink bugs moved to a plant or left a plant). The variable “S(t)” on the y-axis indicates the proportion of individuals remaining, i.e., “surviving,” in neutral space or remaining on the plant after the event at time t . Each datum represents the proportion of stink bugs that moved from a choice j at observation time t_i out of the total number of stink bugs at location j at observation time $t_i - 1$. Note that each panel is used to assess one rate parameter; thus each p_j and μ_j must be assessed using different plots. If the data points follow the line of best fit, then the rate is constant.

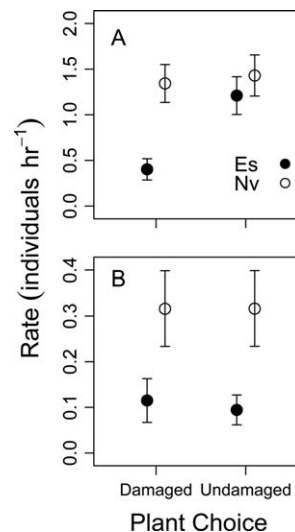


Fig. 5. Model-averaged parameter estimates $\pm 95\%$ CIs for attraction rates (A) and leaving rates (B) for *E. servus* (‘Es’, closed circles) and *N. viridula* (‘Nv’, open circles) trials for undamaged and *H. zea*-damaged cotton plants. Parameter estimates are averaged from good models identified in Table 3.

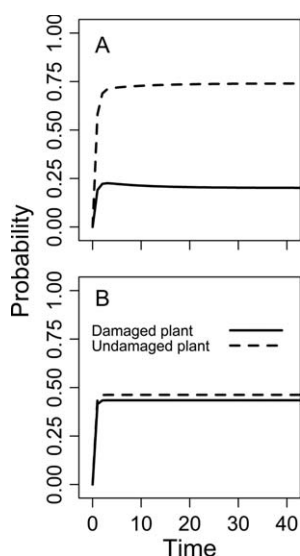


Fig. 6. Predicted dynamics of *E. servus* (A) and *N. viridula* (B) selecting *H. zea*-damaged cotton plants (solid line) and undamaged plants (dashed line), calculated using model-averaged parameter estimates shown in Fig. 5.

equally distributed between undamaged and *H. zea*-damaged plants (Fig. 6).

Discussion

Methods for the design and analysis of consumer choice assays using measures of consumption have been debated and refined for at least four decades (Manly 1974, 1993; Roa 1992; Horton 1995; Prince et al. 2004; Underwood et al. 2004; Taplin 2007; Larrinaga 2010). In contrast, similar attention has been lacking for choice assays using measures of movement. Measures of movement provide distinct and complementary insight into feeding preference compared with measures of consumption; movement-based inferences on preference may be more directly related than measures of consumption to optimal patch foraging models and other classes of movement models (Stephens and Krebs 1986; Patterson et al. 2008). Similar to some state-space models described by (Patterson et al. 2008), we modeled the probability of a mobile consumer being associated with two resource choices as a function of choice-specific attraction and leaving rates. Using repeated measures of consumer location with choice trials, attraction and leaving rates were estimated using maximum likelihood estimation and inferences on the differences of these rates determined by model selection methods. Finally, transient and equilibrium probabilities of association between the consumer and the resource choices can be calculated from the model.

We simulated data to explore the effects on parameter estimation from variation in movement rates, sample size, the number of per trial observation times, and the intervals between observation times. Increasing sample size and increasing the number of observations

generally improved the accuracy of parameter estimates. Greater sample sizes should enhance “valleys” and “ridges” in the likelihood surface, making it easier to find the MLE (Bolker 2008). Increasing the number of observation times and changing the spacing of observations improve the accuracy of parameter estimation because they allow information to be gathered on both transient dynamics and the equilibrium. Accurate parameter estimation depends on multiple observations covering both transient and equilibrium periods of consumer movement. Overall, bias estimates tended to be positive, indicating that parameter estimates tended to be greater than the true values. Importantly, parameter bias was symmetrical between choices, indicating that difference between the choices in parameter estimates relate to real differences in consumer choice rather than artifacts from the model or the MLE procedure.

Our simulations suggest that capturing both transient dynamics and the equilibrium of consumer location are important. We were able to improve accuracy by increasing sample size, increasing the per trial number of observation times, or changing the spacing of observations to better estimate transients and equilibria. From an experimental perspective, increasing the number of observation times and changing their temporal spacing would be more efficient than increasing sample size. In practice, the number of per trial observations and their spacing must be determined by the movement behavior of the consumer(s) under study.

In the analysis of stink bug feeding preference data, we found greater attraction rates toward undamaged plants for *E. servus* relative to *H. zea*-damaged plants and equivalent movement rates between choices for *N. viridula*. The *E. servus* results correspond to PC 2 in the stochastic simulation (Table 1). The simulation results predict that such a PC at a modest sample size, modest number of observation times, and front-loaded observations should result in moderate overestimation of the leaving rate of the less-preferred choice (Figs. 2 and 3). While the leaving rate from the *H. zea*-damaged plant may be overestimated, the implications from the estimated parameters were not affected. Indeed, if it is overestimated, the true effect is even greater than the estimated effect. We expect little bias in the parameter estimates for *N. viridula* and all estimates to be biased equally. In both cases, the predicted biases in the parameter estimates do not alter the interpretation of the results.

Data on the feeding preference of stink bug nymphs between *H. zea*-damaged and undamaged cotton plants largely conformed to the assumptions of the model; stink bug attraction and leaving rates were constant over the duration of the trials and consecutive choices were independent. The number of data points produced from Kaplan–Meier survival analysis will depend on the number of observations and the intervals between observations in relation to mobility of the consumer. In our data on *E. servus*, the number of observations was too few to rigorously test the assumption of constant movement rates. Again, the

number of per trial observations and their spacing should be determined by the behavior of the consumer under study.

The model also assumes that movement choices are sequentially independent, violation of which will not necessarily invalidate parameter estimates and model selection. Rather, positive correlation between consecutive choices may inflate attraction rates. For highly mobile consumers, it may be difficult to observe the consumer in neutral space, possibly resulting in more switching events being recorded than leaving-and-returning events and a violation of the independent choice assumption. This could be resolved by increasing the frequency of per trial observations. Alternatively, consider a scenario of extreme choice dependence, where no observations are made of the consumer in neutral space and each attraction rate is exactly equal to the leaving rate from the opposite choice. In this case, $P_3 = 0$ and $\mu_1 = p_2$ and $\mu_2 = p_1$. If parameter γ_{12} is the rate of switching from choice 1 to choice 2 and γ_{21} is the rate of switching from choice 2 to choice 1, then system (4) reduces to

$$\begin{aligned}\frac{dP_1}{dt} &= -\gamma_{12}P_1 + \gamma_{21}P_2 \\ \frac{dP_2}{dt} &= -\gamma_{21}P_2 + \gamma_{12}P_1\end{aligned}\quad [10]$$

and the assumption of independent choice is relaxed. However, using model (10) does not allow one to distinguish between preferences through greater attraction versus lower leaving rates.

The present model defines preference as the balance between choice-specific attraction and leaving rates. A difference in attraction rates between choices indicates that feeding preference is likely influenced by consumer selection behavior (Vinson 1976, Bernays and Chapman 1994, Schoonhoven et al. 2005) and that cues detected from a distance may be important determinants of preference. However, a difference in leaving rates indicates that preference is likely influenced by consumer acceptance behavior and patch giving up times. A wide variety of cues are known to affect acceptance behavior, including visual cues, olfactory cues in the host–food headspace, or surface or internal chemistry (Vinson 1976, Bernays and Chapman 1994). Information on whether preference is determined by attraction rates or leaving rates would facilitate developing hypotheses on the particular mechanisms underlying preference for testing in further research.

The distinction between preference owing to attraction rates and leaving rates can be ecologically valuable. The feeding preference of vectors of plant and animal pathogens can greatly influence pathogen spread (Kingsolver 1987). Theory predicts that the epidemiological importance of preference will depend on disease prevalence but only when preference is determined when selecting a host, i.e., by attraction rates (Sisterson 2008). Preference determined after vector feeding—relating to differences in leaving rates—will have a relatively minor influence on dis-

ease spread. Further, the host manipulation hypothesis predicts that spread of nonpersistent vector-borne pathogens (pathogens that do not enter the circulatory system of the vector) will be greatest if vectors are preferentially attracted to infected hosts but also leave them quickly (Mescher 2012). Thus, our model provides an efficient way to estimate the influence of vector feeding preference on disease spread and test the host manipulation hypothesis using simple feeding preference experiments.

Leaving rates are used widely in optimal patch foraging models, but the assumed processes underlying patch leaving in optimal foraging models differ from those assumed in our model. Here, we assume that leaving-inducing cues are constant over the duration of the experiment. If, however, leaving rates are determined by resource depletion—which is central to optimal patch foraging models (Stephens and Krebs 1986)—then leaving rates will not be constant, but will increase over time, and this will be apparent from tests of model assumptions (e.g., Fig. 4). Indeed, tests of time-constancy in parameters could potentially detect any changes in the resource choices during the experiment that are relevant to preference, including autogenic changes (Manly 1993).

From estimated attraction and leaving rates, the model can be used to calculate transient and equilibrium probabilities that the consumer will be associated with the resource choices tested. Such probabilities could be incorporated into movement and foraging models, or to test the influence of preference in associations of consumer and resource. For example, do innate preferences for different resources or the relative abundance of those resources explain consumer–resource associations in the environment (Spotswood et al. 2013)?

Our consumer movement model described here could also be used to analyze data from repeated measures of consumer colonization of habitat patches. In particular, the method would be well suited for mark–release–recapture data, where individuals are followed to habitat patches (Kuussaari et al. 1996). The model described here provides all of the advantages of state-space models recently developed for movement ecology data: it enables the estimation of states (probabilities of location), biologically meaningful model parameters (attraction and leaving rates), observation error (variance of parameter estimates), and enables statistical inferences from model selection among biologically relevant models (Patterson et al. 2008). The technique can be used for paired-choice experiments of any duration, with any number of repeated observations of consumer location, and any interval scheme between observation times as long as observation times are allocated in both the transient and equilibrium periods. Possible future extensions of the model include time-varying parameters and adaptations to experiments using more than two simultaneous choices or more than one consumer per arena.

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References Cited

- Andow, D. A., and K. Kiritani. 1984. Fine structure of trivial movement in the green rice leafhopper, *Nephotettix cincticeps* (Uhler) (Homoptera: Cicadellidae). *Appl. Entomol. Zool.* 19: 306–316.
- Babendreier, D., F. Bigler, and U. Kuhlmann. 2005. Methods used to assess non-target effects of invertebrate biological control agents of arthropod pests. *BioControl* 50: 821–870.
- Bakonyi, G., F. Szira, I. Kiss, I. Villanyi, A. Seres, and A. Szekacs. 2006. Preference tests with collembolas on isogenic and Bt-maize. *Eur. J. Soil Biol.* 42: 132–135.
- Bernays, E. A., and R. F. Chapman. 1994. Host-plant Selection by Phytophagous Insects, Contemporary topics in entomology. Chapman & Hall, New York, NY.
- Bolker, B. M. 2008. Ecological models and data in R. Princeton University Press, Princeton, NJ.
- Boos, D. D., and L. A. Stefanski. 2013. Essential statistical inference theory and methods, Springer Texts in Statistics. Springer, New York, NY.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: A practical information-theoretic approach, 2nd ed. Springer, New York, NY.
- Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* 65: 23–35.
- Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman & Hall/CRC, London, United Kingdom.
- Gilbert, P. 2012. numDeriv: Accurate numerical derivatives. R package version 2012.9–1. (<http://CRAN.R-project.org/package=numDeriv>).
- Haccou, P., and E. Meelis. 1992. Statistical analysis of behavioural data: An approach based on time-structured models. Oxford University Press, Oxford, United Kingdom.
- Horton, D. R. 1995. Statistical considerations in the design and analysis of paired-choice assays. *Environ. Entomol.* 24: 179–192.
- Jonsen, I. D., R. A. Myers, and J. M. Flemming. 2003. Meta-analysis of animal movement using state-space models. *Ecology* 84: 3055–3063.
- Kingsolver, J. G. 1987. Mosquito host choice and the epidemiology of malaria. *Am. Nat.* 130: 811–827.
- Kuussaari, M., M. Nieminen, and I. Hanski. 1996. An experimental study of migration in the glanville fritillary butterfly *Melitaea cinxia*. *J. Anim. Ecol.* 65: 791–801.
- Larrinaga, A. R. 2010. A univariate analysis of variance design for multiple-choice feeding-preference experiments: A hypothetical example with fruit-eating birds. *Acta Oecol.* 36: 141–148.
- Linn, C., J. L. Feder, S. Nojima, H. R. Dambroski, S. H. Berlocher, and W. Roelofs. 2003. Fruit odor discrimination and sympatric host race formation in *Rhagoletis*. *Proc. Natl. Acad. Sci. USA* 100: 11490–11493.
- Lockwood III, J. R. 1998. On the statistical analysis of multiple-choice feeding preference experiments. *Oecologia* 116: 475–481.
- Machin, D., Y. B. Cheung, and M. K. Parmar. 2006. Survival Analysis: A practical approach, 2nd ed. Wiley, Inc., West Sussex, England.
- Manly, B. F. 1993. Comments on design and analysis of multiple-choice feeding-preference experiments. *Oecologia* 93: 149–152.
- Manly, B. F. 1974. A model for certain types of selection experiments. *Biometrics* 30: 281–294.
- Mescher, M. C. 2012. Manipulation of plant phenotypes by insects and insect-borne pathogens, pp. 73–92. In D. Hughes, J. Brodeur, and T. Frederic. (eds.), Host Manipulation by Parasites. Oxford University Press, Oxford, United Kingdom.
- Millar, R. B. 2011. Maximum likelihood estimation and inference: With Examples in R, SAS and ADMB, 1st ed. Wiley, Ltd, West Sussex, England.
- Morrison, W. E., and M. E. Hay. 2011. Herbivore preference for native vs. exotic plants: generalist herbivores from multiple continents prefer exotic plants that are evolutionarily naive. *PLoS ONE* 6: e17227.
- Nash, J. C., and R. Varadhan. 2011. Unifying optimization algorithms to aid software system users: optimx for R. *J. Stat. Software* 43: 1–14.
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. *Proc. Nat. Acad. Sci. USA* 105: 19052–19059.
- Nicotri, M. 1980. Factors involved in herbivore food preference. *J. Exp. Marine Biol. Ecol.* 42: 13–26.
- Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos. 2008. State-space models of individual animal movement. *Trends Ecol. Evol.* 23: 87–94.
- Pielou, E. C. 1969. An introduction to mathematical ecology. Wiley, Ltd. West Sussex, England.
- Prager, S. M., X. Martini, H. Guvvala, C. Nansen, and J. Lundgren. 2014. Spider mite infestations reduce *Bacillus thuringiensis* toxin concentration in corn leaves and predators avoid spider mites that have fed on *Bacillus thuringiensis* corn. *Ann. Appl. Biol.* 165: 108–116 (doi: 10.1111/aab.12120).
- Prince, J. S., W. G. LeBlanc, and S. Maciá. 2004. Design and analysis of multiple choice feeding preference data. *Oecologia* 138: 1–4.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Roa, R. 1992. Design and analysis of multiple-choice feeding-preference experiments. *Oecologia* 89: 509–515.
- Rovenská, G. Z., R. Zemek, J.E.U. Schmidt, and A. Hilbeck. 2005. Altered host plant preference of *Tetranychus urticae* and prey preference of its predator *Phytoseiulus persimilis* (Acari: Tetranychidae, Phytoseiidae) on transgenic Cry3Bb-eggplants. *Biol. Control* 33: 293–300.
- Schoonhoven, L. M., J.J.A. Van Loon, and M. Dicke. 2005. Insect-Plant Biology. Oxford University Press, USA.

- Sisterson, M. S. 2008.** Effects of insect-vector preference for healthy or infected plants on pathogen spread: insights from a model. *J. Econ. Entomol.* 101: 1–8.
- Spotswood, E. N., J.-Y. Meyer, and J. W. Bartolome. 2013.** Preference for an invasive fruit trumps fruit abundance in selection by an introduced bird in the Society Islands, French Polynesia. *Biol. Invasions* 15: 2147–2156.
- Stephens, D. W., and J. R. Krebs. 1986.** Foraging theory, monographs in Behavior and Ecology. Princeton University Press, Princeton, NJ.
- Taplin, R. H. 2007.** Experimental design and analysis to investigate predator preferences for prey. *J. Exp. Marine Biol. Ecol.* 344: 116–122.
- Tijms, H. C. 2003.** Continuous-Time Markov Chains, pp. 141–186. *In* A First Course in Stochastic Models. Wiley, Ltd, West Sussex, England.
- Underwood, A. J., M. G. Chapman, and T. P. Crowe. 2004.** Identifying and understanding ecological preferences for habitat or prey. *J. Exp. Marine Biol. Ecol.* 300: 161–187.
- Varadhan, R., and P. Gilbert. 2009.** BB: An R package for solving a large system of nonlinear equations and for optimizing a high-dimensional nonlinear objective function. *J. Stat. Software* 32: 1–26.
- Vinson, S. B. 1976.** Host selection by insect parasitoids. *Annu. Rev. Entomol.* 21: 109–133.
- Wolfram Research Inc. 2012.** Mathematica. Wolfram Research Inc., Champaign, IL.
- Zeilinger, A. R. 2011.** The role of competitive release in stink bug outbreaks associated with transgenic Bt cotton (Ph.D dissertation).
- Zeilinger, A. R., D. M. Olson, and D. A. Andow. 2011.** Competition between stink bug and heliothine caterpillar pests on cotton at within-plant spatial scales. *Entomol. Exp. Appl.* 141: 59–70.
- Zeilinger, A. R., and M. P. Daugherty. 2014.** Vector preference and host defense against infection interact to determine disease dynamics. *Oikos* 123: 613–622.
- Zirbes, L., M. Mescher, V. Vrancken, J.-P. Wathelet, F. J. Verheggen, P. Thonart, and E. Haubruge. 2011.** Earthworms use odor cues to locate and feed on microorganisms in soil. *PLoS ONE* 6: e21927.

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