Modeling Predator Preferences

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Abstract

The literature on modeling a predator's prey selection includes many intuitive indices, few of which have both reasonable statistical justification and tractable asymptotic properties. Here, we provide a simple model that meets both of these criteria, while extending previous work to include an array of multiple species and time points. Further, we apply the Expectation-Maximization algorithm to cases where exact counts of the number of prey species eaten in a particular timer period is not observed. A simulation is provided to demonstrate the accuracy of our methods.

1 Introduction

Modeling a predator's food selection was given much attention for a short period of time; see Strauss [1979] and the references within. Many, if not all, of the indices developed, though intuitive, focused on a snapshot in time and only on one prey species, and rarely obtained practical asymptotic properties. This leaves interested practicioners to the most computationally manageable of the techniques, and has completely ignored simultaneous testing across an array of both species and time.

The model presented here maintains tractable asymptotic properties while being general enough to take into account multiple speices and time points. By modeling both time and any number of prey species, we are able to see a more detailed anlyais of the predator's eating preferences. Further, the simplicity of the model allows us to consider predators for which exact tallies of the number of each variety of prey species eaten within any given time period is not observed. Instead, we rely on the researcher being able to DNA sequence the contents of the predator's gut, and make a simple binary conclusion: this predator ate some of that prey species during this time period, or did not. Despite the data's lost information, under certain situations our model is able to accurately estimate the parameters of interest.

2 Methods

2.1 Data

We assume data are collected in the following manner. Traps are dispersed, for T time periods, throughout the habitat of the predator and prey of interest. Prey species, indexed

by $s \in \{1, \ldots, S\}$, are collected in the traps and counted at each time period. The number of prey species s the predator will encounter on average during time period $t \in \{1, \ldots, T\}$ are considered random draws from a Poisson distribution with rate parameter γ_{st}. We further assume that the number of prey species found in the gut of the similarly trapped predators follows a Poisson distribution with rate λ_{st}. Here, the parameter λ_{st} represents the rate at which the predator ate prey species s during time period t. By modeling λ_{st} and γ_{st} we are able to test claims about a predator's eating preferences.

The use of Poisson distributions make the following implicit assumptions: 1) traps independently catch the prey species of interest, 2) predators eat prey species independently, 3) predators eat indepedent of each other.

We denote the number of predators and the numer of prey species caught, in each time period t, by J_t and I_t, respectively. Let $X_{jst} \overset{\text{iid}}{\sim} \mathcal{P}(\lambda_{st})$ represent the number of prey species s that predator j ate during occurrence t, where $j \in \{1, \ldots, J_t\}$. Let $Y_{ist} \overset{\text{iid}}{\sim} \mathcal{P}(\gamma_{st})$ represent the number of prey species s found in trap i during occurrence t, $i \in \{1, \ldots, I_t\}$. Formal statistical statements about the relative magnitudes of the parameters $\boldsymbol{\lambda}$ and $\boldsymbol{\gamma}$ offer insights to the relative rates at which predators eat particular prey species.

We consider five variations on the relative magnitude of $\lambda_{st}/\gamma_{st} = c_{st}$. These five hypotheses each allow c_{st} to vary by time, prey species, both, or neither. Because the five hypotheses are nested, a natural testing order is suggested in Figure 1.

1. $c_{st} = 1, s = 1, \ldots, S; t = 1, \ldots, T$

2. $c_{st} = c, s = 1, \ldots, S; t = 1, \ldots, T$

3. $c_{st} = c_s, s = 1, \ldots, S$

4. $c_{st} = c_t, t = 1, \ldots, T$

5. $c_{st} = c_{st}, s = 1, \ldots, S; t = 1, \ldots, T$

The first hypothesis states that predators and traps sample all prey species at the same rate. One imagines this is the case if the predator simply eats that which comes within its reach, thus suggesting a diet indifferene. The second says that predators sample prey proportionally across all time periods. The third hypothesis says that predators sample different prey species at different rates, but each rate is steady across time. This implies that the predator expresses preferences for one prey species over another, but is unresponsive to changes due to time. Conversely, the forth hypothesis implies that each prey species is sampled similarly within each time period, while the rates across time are allowed to change. The fifth assumes a predator's selection varies by both time and prey species. This would make sense if environmental variables, say weather, or prey availability, and taste were affecting predators' selection strategies.

2.2 Fully Observed Count Data

The likelihood function that allows for estimation of these parameters is as follows. Since we assume X_{jst} is independent of Y_{ist} we can simply multiply the respective Poisson probability density functions, and then form products over all s, t to get the likelihood.
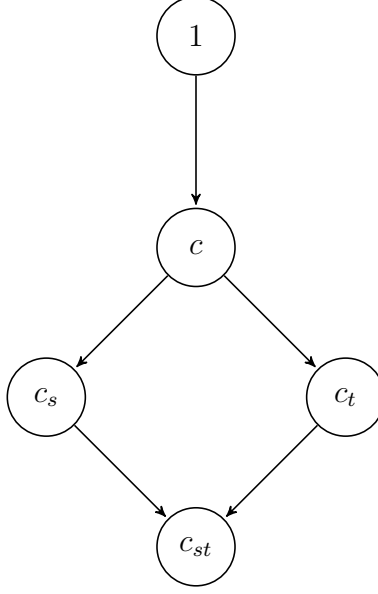
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Figure 1: Hierarchy of hypotheses.

$$L(x_{jst}, y_{ist}|\boldsymbol{\lambda}, \boldsymbol{\gamma}) = \prod_{t=1}^{T}\prod_{s=1}^{S}\left\{\prod_{j=1}^{J_t} f_X(x_{jst}|\boldsymbol{\lambda})\prod_{i=1}^{I_t} f_Y(y_{ist}|\boldsymbol{\gamma})\right\}. \tag{1}$$

Writing all five hypotheses as $\lambda_{st} = c_{st}\gamma_{st}$, we can, in the simplest cases, find analytic solutions for the maximum likelihood estimates of c_{st} and γ_{st}. Under the hypothesis $c_{st} = 1$, and when the data are balanced $J_t = J$, $I_t = I$, and $c_{st} = c$ analytic solutions exist. Namely, these solutions are

$$\hat{\gamma}_{st} = \frac{X_{\cdot st} + Y_{\cdot st}}{J_t + I_t}, \quad \text{and} \quad \hat{c} = \frac{I\sum_{s,t} X_{\cdot st}}{J\sum_{s,t} Y_{\cdot st}}, \quad \hat{\gamma}_{st} = \frac{X_{\cdot st} + Y_{\cdot st}}{I\left(\frac{\sum_{st} X_{\cdot st}}{\sum_{st} Y_{\cdot st}} + 1\right)}$$

respectively, where $X_{\cdot st} = \sum_{j=1}^{J_t} X_{jst}$ and $Y_{\cdot st} = \sum_{i=1}^{I_t} Y_{ist}$.

In all other cases, analytic solutions are not readily available and instead we rely on the fact that the log-likelihood $l(\boldsymbol{\lambda}, \boldsymbol{\gamma}) = \log L$ is concave. We maximize the log-likelihood, using coordinate descent [Luo and Tseng, 1992], by iteratively solving partial derivatives of l, with respect to c_{st} and γ_{st}, set equal to zero

$$\hat{c} = \frac{\sum_{s,t} X_{\cdot st}}{\sum_{t} J_t \sum_{s} \gamma_{st}}, \quad \hat{c}_t = \frac{\sum_{s} X_{\cdot st}}{J_t \sum_{s} \gamma_{st}}, \text{ or } \quad \hat{c}_s = \frac{\sum_{t} X_{\cdot st}}{\sum_{t} J_t \gamma_{st}}, \text{ and } \quad \hat{\gamma}_{st} = \frac{X_{\cdot st} + Y_{\cdot st}}{J_t c_{st} + I_t}.$$

2.3   Unobserved Counts

Many times it may not be possible to count the number of individuals of each prey species that are in a predators gut. Instead, it may only be possible to detect whether or not a predator consumed the prey species during a given period. This is the case in the study

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of ? spiders which relied on DNA sequencing to identify the prey species in a spider's gut contents. Despite this, we can still make inference about the predators preferences for the different prey species by using the EM algorithm to compute maximum likelihood estimates.

We denote the binary random variable indicating that the jth predator did in fact eat at least one individual of prey species s in time period t by $Z_{jst} = 1(X_{jst} > 0)$. The variables are independent Bernoulli observations with success probability $p_{st} = P(Z_{jst} = 1) = 1 - \exp\{-\lambda_{st}\}$. Despite not observing X_{jst}, we can compute maximum likelihood estimates of the parameters $\boldsymbol{\lambda}, \boldsymbol{\gamma}$ through the EM algorithm using the complete data log-likelihood

$$l_{comp}(\boldsymbol{\lambda}, \boldsymbol{\gamma}) = \log f_{X,Y,Z}(\boldsymbol{x}, \boldsymbol{y}, \boldsymbol{z}|\boldsymbol{\lambda}, \boldsymbol{\gamma}) = \sum_{s=1}^{S}\sum_{t=1}^{T}\left[\sum_{j=1}^{J_t}\log f_{X,Z}(x_{jst}, z_{jst}|\boldsymbol{\lambda}) + \sum_{i=1}^{I_t}\log f_Y(y_{jst}|\boldsymbol{\gamma})\right].$$

The density of Y_{jst} is exactly as given above and so we focus on deriving the joint density of X_{jst} and Z_{jst}. With the distribution of Z_{jst} given above, we can compute $f_{X,Z}(x_{jst}, z_{jst}|\boldsymbol{\lambda})$ by noting that $X_{jst} = 0$ with probability 1 if $Z_{jst} = 0$ and that $X_{jst}|Z_{jst} = 0$ has a truncated Poisson distribution with density

$$f_{X|Y,Z,\boldsymbol{\lambda},\boldsymbol{\gamma}}(x_{jst}|z_{jst}) = \frac{\exp\left\{-\lambda_{st}\right\}\lambda_{st}^{x_{jst}}}{(1 - \exp\left\{-\lambda_{st}\right\})x_{jst}!}1(x_{jst} > 0) \quad \text{where}$$

and expected value

$$\mathbb{E}_{X|Y,Z}X_{jst} = \frac{\lambda_{st}\exp\left\{\lambda_{st}\right\}}{\exp\left\{\lambda_{st}\right\} - 1}.$$

The joint density of X_{jst}, Z_{jst} is then

$$f_{X,Z|\boldsymbol{\lambda}}(x_{jst}, z_{jst}) = \begin{cases} \exp\left\{-\lambda_{st}\right\}, & x_{jst} = 0 \text{ and } Z_{jst} = 0 \\ \frac{\exp\left\{-\lambda_{st}\right\}\lambda_{st}^{x_{jst}}}{x_{jst}!}, & x_{jst} > 0 \text{ and } Z_{jst} = 1 \\ 0 & \text{otherwise} \end{cases}.$$

The EM algorithm works by iterating two steps, the E-step and M-step, until the optimum is reached [Dempster et al., 1977, McLachlan and Krishnan, 2007]. Let k index the iterations in the EM algorithm so that $\boldsymbol{\lambda}^{(k)}$ and $\boldsymbol{\gamma}^{(k)}$ denote the estimates computed on the kth M-step. The E-step consists of computing the expectation of l_{comp} with respect to the conditional distribution of X given the current estimates of the parameters

$$Q^{(k)}(\boldsymbol{\lambda}, \boldsymbol{\gamma}) = \mathbb{E}_{X|Y,Z,\boldsymbol{\lambda}^{(k)}}l_{comp}$$

in order to remove the unobserved data. The M-step then involves maximizing $Q = \mathbb{E}l_{comp}$ with respect to the parameters in the model to obtain updated estimates of the parameters,

$$(\boldsymbol{\lambda}^{(k+1)}, \boldsymbol{\gamma}^{(k+1)}) = \underset{(\boldsymbol{\lambda}, \boldsymbol{\gamma})}{\arg\max}\, Q^{(k)}(\boldsymbol{\lambda}, \boldsymbol{\gamma}).$$

These steps are then alternated until a convergence criterion monitoring subsequent differences in the parameter estimates/likelihood values is met.

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The calculation of $Q^{(k)}(\boldsymbol{\lambda}, \boldsymbol{\gamma})$ is not difficult and is given by:

$$
\begin{aligned}
Q^{(k)}(\boldsymbol{\lambda}, \boldsymbol{\gamma}) &= \mathbb{E} \log f_{X,Z|\boldsymbol{\lambda}}(X_{jst}, z_{jst}) + \log f_{Y|\boldsymbol{\gamma}}(y_{ist}) \\
&= \sum_{s=1}^{S} \sum_{t=1}^{T} \sum_{j=1}^{J_t} \mathbb{E} \log f_{X,Z|\boldsymbol{\lambda}}(X_{jst}, z_{jst}) + \sum_{s=1}^{S} \sum_{t=1}^{T} \sum_{i=1}^{I_t} \log f_{Y|\boldsymbol{\gamma}}(y) \\
&\propto \sum_{s,t,j} \left(-\lambda_{st} + z_{jst} \mathbb{E} X_{jst} \log \lambda_{st} \right) + \sum_{s,t} \left(-I_t \gamma_{st} + Y_{\cdot st} \log I_t \gamma_{st} \right) \\
&\propto \sum_{s,t} \left(-J_t \lambda_{st} + z_{\cdot st} \mathbb{E}(X_{jst} | \lambda_{st}^{(k)}, \gamma_{st}^{(k)}) \log \lambda_{st} \right) + \sum_{s,t} \left(-I_t \gamma_{st} + Y_{\cdot st} \log I_t \gamma_{st} \right).
\end{aligned}
\tag{2}
$$

No analytic solution to the M-step exists, however, so we chose to maximize Q with co-ordinate descent [Luo and Tseng, 1992]. In fact, as we only need find parameters that increase the value of Q on each iteration, we forgo fully iterating to find the maximum and instead perform just one step uphill within each EM iteration. Since $Q^{(k)}$ is concave and smooth in the parameters $\boldsymbol{\lambda}, \boldsymbol{\gamma}$, we are able to use the convergence of parameter estimates, $||(\boldsymbol{\lambda}^{(k)}, \boldsymbol{\gamma}^{(k)}) - (\boldsymbol{\lambda}^{(k+1)}, \boldsymbol{\gamma}^{(k+1)})||_\infty < \tau$, for some $\tau > 0$, as our stopping criterion.

As we show in our simulation study, this generalized EM algorithm accurately estimates the parameters when values of λ_{st} are relatively small, such that zeros are prevalent in the data Z_{jst}. In this case, not too much information is lost since estimation of $\mathbb{E} Z_{jst}$ can be estimated well by the proportion of observed zeros. On the other hand, if the predator consistently eats a given prey species, few to no zeros will show up in the observed data and $\mathbb{E} Z_{jst}$ is estimated to be nearly 1. The loss of information is best seen by attempting to solve for λ_{st} in the equation $\mathbb{E} Z_{jst} = 1 = 1 - \exp\{-\lambda_{st}\}$. As the proportion of ones in the observed data increase, we expect λ_{st} to grow exponentially large. When no zeros are present in the data, so that where only ones are observed, the likelihood can be made arbitrarily large by sending the parameter off to infinity.

2.4 Testing

The likelihood ratio test (LRT) statistic is

$$
\Lambda(X, Y) := -2 \log \frac{\sup_{\theta_0} L(\theta_0 | X, Y)}{\sup_{\theta_1} L(\theta_1 | X, Y)},
$$

where θ_0, θ_1 represent the parameters estimated under the null and alternative hypotheses, respectively. It is well known that the asymptotic distribution of Λ is a χ_ρ^2 distribution with ρ degrees of freedom [Wilks, 1938]. When the observations X_{jst} are not observed, we use $L_{obs}(Z, Y)$ as the likelihood in the calculation of Λ.

The degrees of freedom ρ equal the number of free parameters available in the stated hypotheses under question. If we put the null hypothesis to be $H_0 : \lambda_t = c_t \gamma_t$, for all t and contrast this against $H_1 : \lambda_{st} = c_{st} \gamma_{st}$ then there are $\rho = 2(S \cdot T) - S \cdot T - T = S \cdot T - T$ degrees of freedom.

A set of hypotheses is determined by the p-value of the χ_ρ^2 distribution. Hence, with a level of significance, α, the null hypothesis is rejected in favor of the alternative hypothesis if $\mathbb{P}(\chi_\rho^2 > \Lambda) < \alpha$.

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2.5 Testing c_{st}

After determining which model best fits the data, more detail can be extracted through a hypothesis test of the elements of c_{st}, or in vector notation as $\mathbf{c} \in \mathbb{R}^{S \cdot T}$. Let the elements of $\hat{\mathbf{c}}$ be the maximum likelihood estimates, $\hat{c}_{st}$, as found via the framework above. Since $\hat{\mathbf{c}}$ is asymptotically normally distributed, any linear combination of the elements is also asymptotically normally distributed. For instance, let a be a vector of the same dimension of $\hat{\mathbf{c}}$. Then $a^t \hat{\mathbf{c}}$ is asymptotically distrbuted as $\mathcal{N}(a^t \mathbf{c}, a^t \Sigma a)$, where Σ is the covariance matrix of the asymptotic distrbution of $\hat{\mathbf{c}}$.

Suppose, for example, that the hypothesis c_s is determined to best fit the data with s ranging $s = 1, 2, 3$. We can test to see whether or not two species are statistically equally preferred under the null hypothesis $c_1 = c_2$. This hypothesis is alternatively written in vector notation as $a^t \mathbf{c} = 0$, where $a = (1, -1, 0)^t$. Tests of the following form $H_0 : a^t \mathbf{c} = \mu$ against any alternative of interest are then approximate Z-tests. Confidence intervals of any size are similarly, readily obtained.

3 Simulations

Our simulations assume two prey species and five time points, throughout. Of the hierarchy of hypotheses, we generate data under three models: c, c_s, c_t. Sample sizes for both prey species and predator gut count observations are randomly chosen from four overlapping levels: "small" sample sizes are randomly sampled numbers in $[20, 50]$, "medium" $[30, 75]$, "large" $[50, 150]$, and "huge" $[100, 200]$. This is repeated for each level of sample size. We simulate 500 replicate datasets for each of the twelve scenarios above for both types of data, fully observed count data, X_{jst}, and for non-count data, when we observe only a binary response, $Z_{jst} = 1(X_{jst} > 0)$. Each scenario is then fit with the true model that generated the data. All simulations of non-count data use $\tau = 10^{-5}$ as the convergence tolerance. A subset of the examples are provided here; the interested reader is referred to the supplementary materials for the complete simulation results. For the simulations we used the R Core Team [2014] package BatchExperiments by Bischl et al. [2014].

For all simulated data, the true parameter values for the rate at which prey species are encountered in the wild are fixed to be $\gamma_{st} = \pi$, $\forall s, t$. The values of λ_{st} are set with respect to each data generating model. For model $c_{st} = c$, where predator preferences don't vary by either time or species, we put $\lambda_{st} = 2\pi$, $\forall s, t$. Under model c_s, the ratio of rates vary by species only, so we put $\lambda_{1t} = \sqrt{2}$ and $\lambda_{2t} = \pi$. Hence, $c_1 = \sqrt{2}/\pi \approx 0.45$ and $c_2 = 1$. For the last model, c_t, the ratio of rates vary by time t. Here, we put $\lambda_{st} = t$ for $t \in \{1, \ldots, 5\}$.

Figure 2 shows density plots of the estimates of c_s, c when fitting the true model to the fully observed count data generated under models c_s and c. The plots provide evaluations of parameter estimates under each scenario. In the first display, the parameters $c_1 \approx 0.45$ and $c_2 = 1$ are on average, across all 500 simulations, estimated as $\hat{c}_1 = 0.45$ and $\hat{c}_2 = 1.00$, with standard errors of $\text{se}(\hat{c}_1) = 0.03$ and $\text{se}(\hat{c}_2) = 0.06$. The second display provides results for model $c_{st} = c$. Averaging across all 500 simulations, the parameter $c = 2$ is estimated as $\hat{c} = 2.00$. This is further seen in figure 3, where box plots of the parameter estimates, centered at true parameter values, of the correct model fit to data generated from both c_s
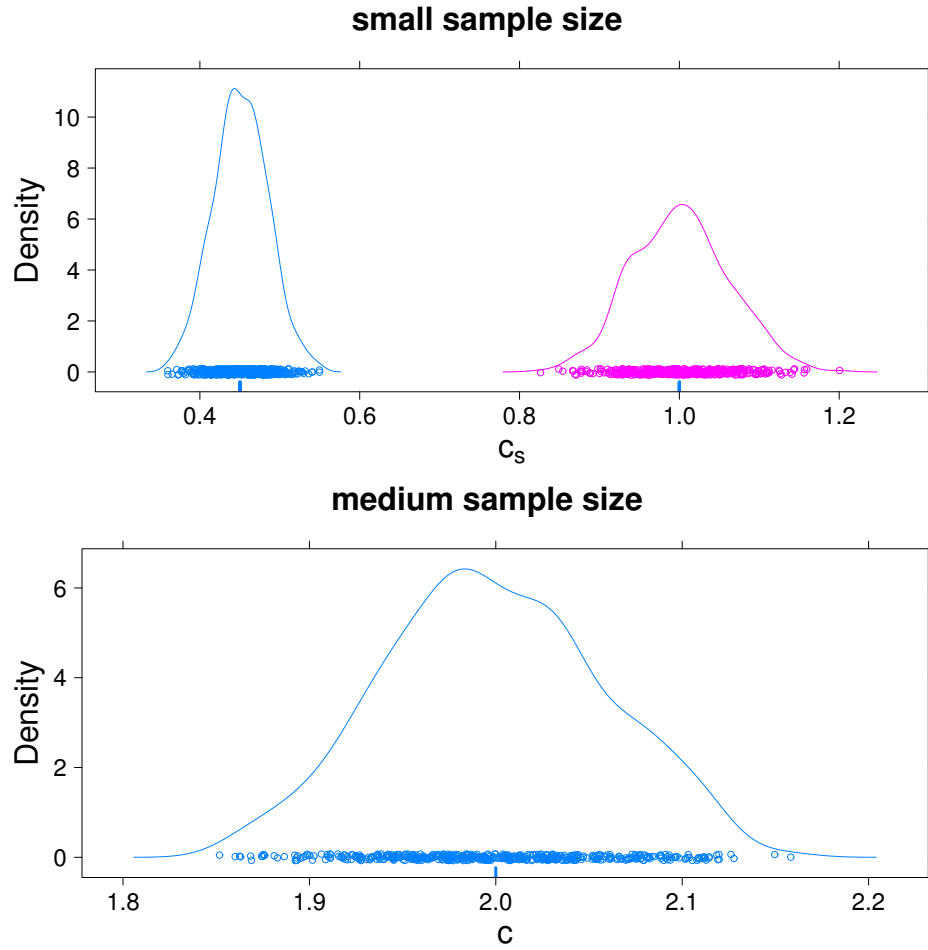
Figure 2: Density plots of all 500 estimates of fitting the true model to the data generated from models c_s, c are shown with sample sizes small and medium, respectively.
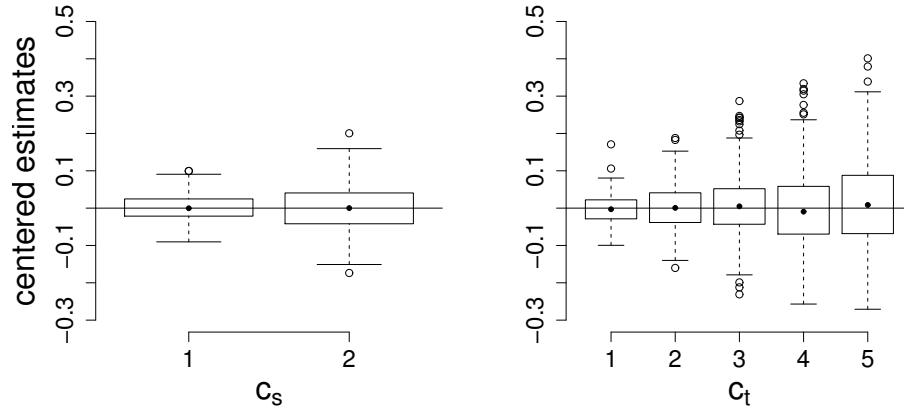
Figure 3: Shown are all 500 estimates, centered at the true parameter values, from fitting the true model to the data generated from models c_s, c_t with sample sizes small and medium, respectively.

and c_t show empirically very little bias.

We next generated data with unobserved counts. As noted above under certain circumstances our unobserved counts model accurately estimates the parameters of interest, and at other times can infinitely over-estimate parameters. To investigate this issue further, we consider the same scenarios mentioned above, but now we reduce all of the count data down to binary observations. For each scenario, we fit the unobserved counts model as if we knew the true underlying model that generated the observed data.

Figure 4 contains density plots for all 500 replications of the data generating models c_s, c_t with small and huge sample sizes, respectively. When data are generated under the model c_s and the true model fit to the non-count data, we find even for the small sample size that point estimates are only very slightly biased. When parameter values are of sufficient size to make zeros in the simulated data less common, the estimates from fitting the correct model to the generated data are occasionally over-estimated. This effect is easily seen in the bottom panel of figure 4 for larger values of c_t despite the increased sample size, but is also seen, less dramatically, in the density plot for the c_s generated data.

The cluster of estimates for c_5 between 3.5 and 4.0 in the bottom panel of figure 4 comes from datasets in which $X_{js5} > 0$ so that $Z_{js5} = 1$ for all j, s. For the data shown in figure 4, this happened 73 times out of the 500 replicated datasets. As mentioned above, the estimate of c_5 is infinite in this case. However, the EM algorithm will always provide a finite estimate for all parameters when it terminates. In this case, we set $\tau = 10^{-5}$ and it just happened that this caused the algorithm to terminate with $\hat{c}_5$ between 3.5 and 4.0 in all cases. To confirm that this is due to the arbitrary choice of τ, we repeated the algorithm with smaller values of τ for several datasets. As expected, $\hat{c}_5$ increased without bound as we refit the model with increasingly small values of τ.

The over-estimation of parameters, a symptom of the loss of information due to the unobserved counts, can also be seen with box plots of the 500 point estimates centered at their respective true parameter values. Figure 5 contains box plots of the same scenarios in
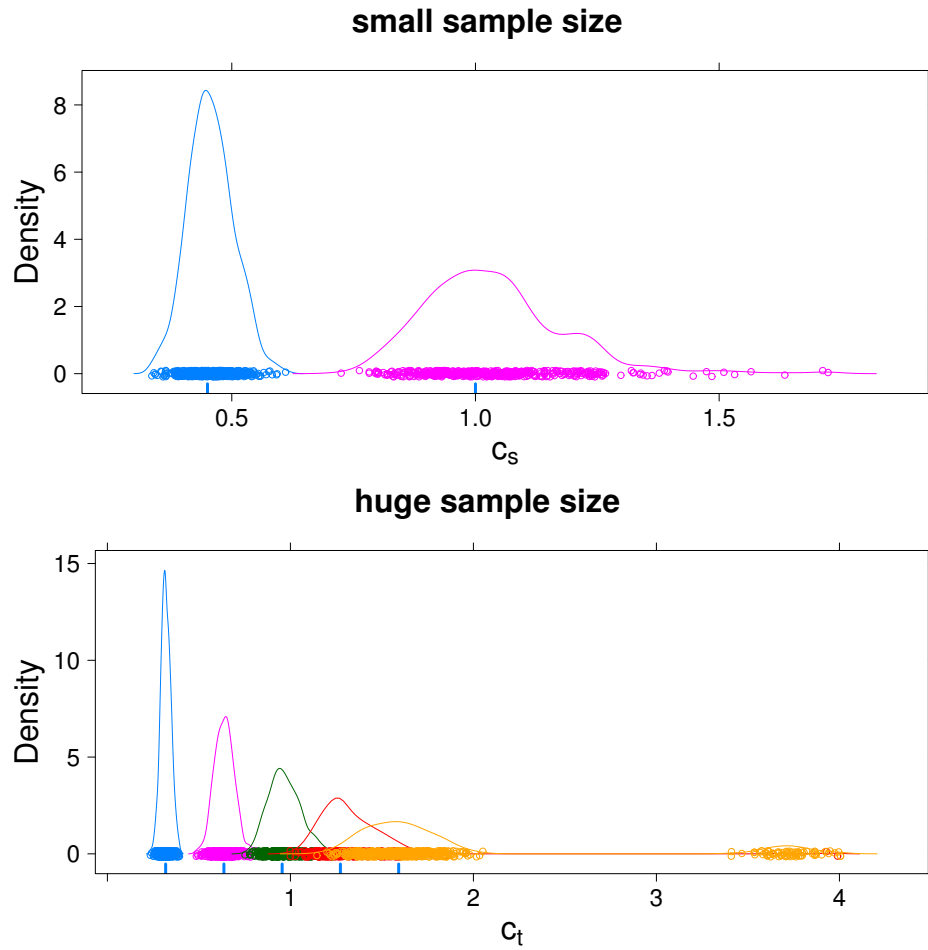
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Figure 4: Density plots of all 500 estimates of fitting the true model to the data generated from models c_s, c_t, when counts are not observed, are shown with sample sizes small and huge, respectively.
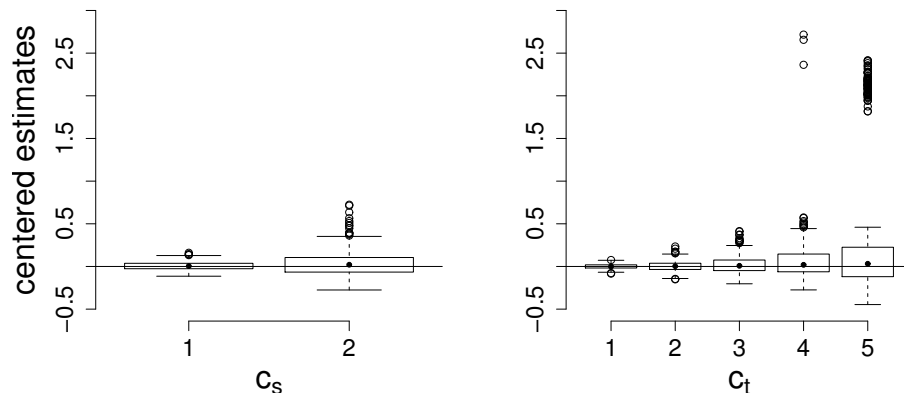
Figure 5: Shown are all 500 estimates, centered at the true parameter values, from fitting the true model to the data generated from models c_s, c_t, when counts are not observed, with sample sizes small and huge, respectively.

Figure 4. For the 73 cases in which $Z_{js5} = 1$ for all j, s under model c_t with the huge sample size, the bias is infinite since parameter estimates will, theoretically, be infinite. The finite bias shown in these plots is due to the finite estimates provided by the termination of the EM algorithm. Thus, conditional on a mixture of 0s and 1s in the data the corresponding estimators are unbiased, but when no 0s exist in the data the theoretical bias is infinite.

4   Real Data

We analyze a dataset that was collected to investigate the eating preferences of the wolf spider, genus *Schizocosa*, towards the prey orders *Diptera* and *Collembola*. Predators were collected in traps within the deciduous Berea College Forest in Madison County, Kentucky, USA and had their gut-contents analyzed to determine whether or not the spiders ate any *Diptera* or *Collembola* within each time period. The left panel of figure 6 plots the percentage of spiders that had the prey in their guts across time. Prey were also collected in traps from the same area. These data were collected for each month from October 2011 to March 2013. On average, 69 spiders, and 111 and 297 *Diptera* and *Collembola*, respectively, were caught in each time period. The range of the sample sizes, across all 18 months is, 11 to 181 for caught spiders, from 7 to 322 for trapped *Diptera*, and from 101 to 755 for trapped *Collembola*. The right panel of figure 6 plots the total number of each order that was caught during each time period.

These data provide an example of our hierarchy of hypotheses. First, tested model $c_{st} = c$ against $c_{st} = c_s$, to determine whether or not the wolf spider has different preferences for the two orders *Diptera* and *Collembola*. With, one degree of freedom, this likelihood ratio test indicated, $p-value < 0.0001$, that two parameters, one for each order, fits these data better than one parameter for both. Similarly, we tested whether or not there was a significant effect across time by testing model $c_{st} = c$ against $c_{st} = c_t$. Here, the likelihood ratio test,
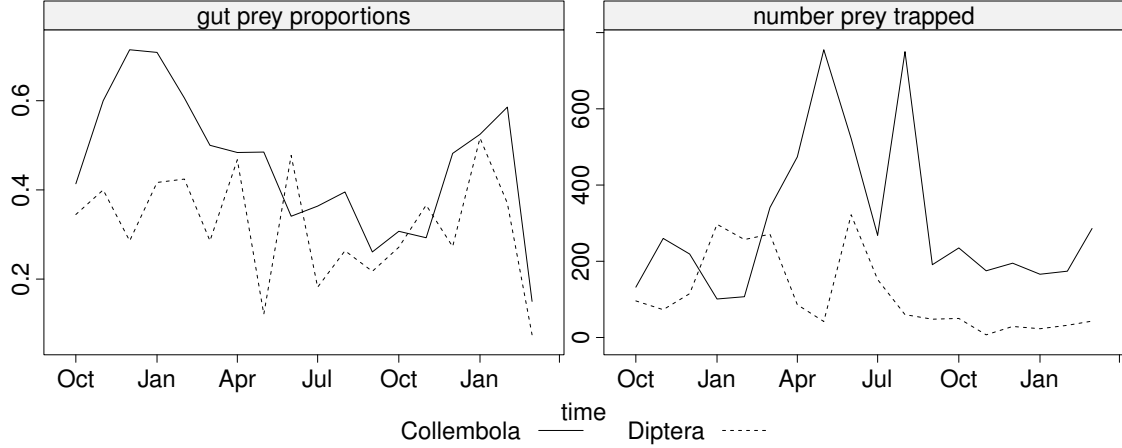
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Figure 6: For both *Diptera* and *Collembola*, the plots show the proportion of spiders with these orders found in their guts, and the number of these orders trapped in each time period.

with 17 degrees of freedom, implies that the wolf spiders of the Berea College Forest eat these prey orders at different rates across the months of the year, $p - value < 0.0001$. In fact, we find that the most parameter rich model, $\lambda_{st} = c_{st}\gamma_{st}$ fits these data better than is expected by chance, $p - value < 0.0001$. Model c_{st} estimates 72 parameters in total; since, in this case, there are two prey of interest and 18 time periods, it takes 36 parameters to estimate each c_{st} and γ_{st}. Figure 7 plots the point estimates and confidence intervals of c_{st}, for both prey across all time periods.

With point estimates of c_{st} under the model $\lambda_{st} = c_{st}\gamma_{st}$, we can test any number of linear contrasts. For instance, $c_{1t} = c_{2t}$, for $t \in \{1, \ldots, 18\}$. Using a level of significance of 0.05, and after making a Bonferroni multiple comparisons adjustment, the data can not say that the two prey are differently preferred in October, November, and December of 2011 and for March and July of 2012.

5   Discussion

The model developed here allows practicioners to determine predators' preferences by testing simultaneously across an array of multiple prey species and time. This is acheived via a simple, but statistically powerful, likelihood ratio test. Further testing of the ratio of rates for which predators eat to encounter prey species allows researchers to make specific conclusions about predators' preferences. For instance, rates acros time can be estimated to make statements about seasonal effects on a predator's eating habits, or relative rates across species groups allows for statements about the preferences for different species.

When counts of predators' gut contents are not fully observed, and instead only a binary response indicating the existence of the prey species in the gut is observed, we are able to treat the counts as missing data. By modelling all of the observed data, both the binary responses and the number of prey species caught, and the missing count data, we are able to use the EM algorithm to extract as much information from the data as possible. Though
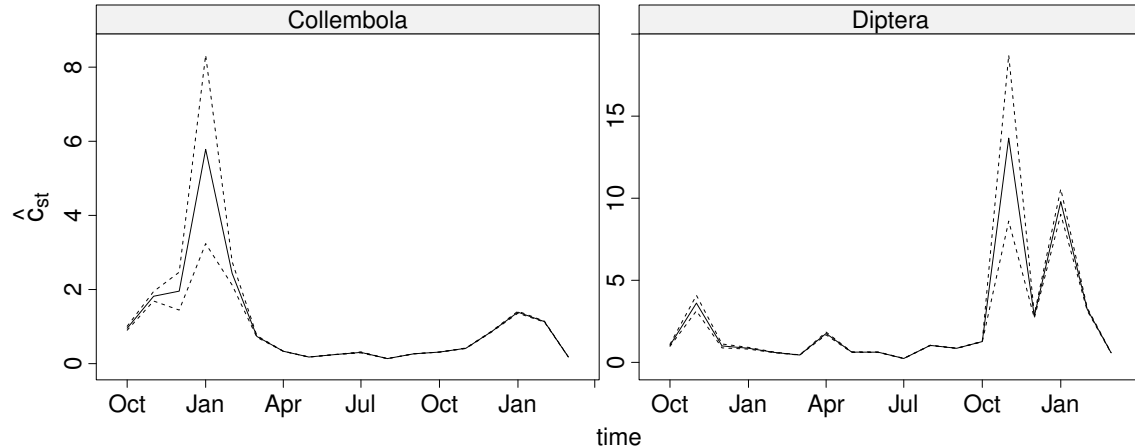
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Figure 7: One plot for each prey order displays the point estimates and confidence intervals as estimated from the model c_{st}.

this is nice in theory, in practice the success of this modification to our original model is limited by the magnitude of the unknown parameters λ_{st}.

Further developments of our model could be beneficial. Taking into account other environmental variables that might effect a predators' eating habits, such as rain or temperature, say, might be advantageous.

An R package, named `spiders`, is available on CRAN at `http://cran.r-project.org/web/packages/spiders/index.html` and fits all the methods discussed above.

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