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Generalist consumption modelling and prey switching: A case study of insectivorous bats in cacao plantations

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Abstract

Predation is essential in the regulation of ecosystems, with predators having a profound effect on the population dynamics of their prey. The consumption of a predator per unit time as a function of prey availability, known as their functional response, has a rich research history within ecology. Furthermore, this functional response can indicate whether a predator is likely to switch from its preferred prey as its availability decreases. Generalist predators feed on multiple prey species and switch between alternative prey. This introduces a significant challenge when modelling predator-prey relationships. Traditionally, studies have focussed only on the relationship between a generalist predator and a single species of its prey. However, excluding all possible prey from their consumption analysis results in misleading conclusions on the effect generalist predators have on the populations of their prey. Therefore, developing consumption models that take all prey species into account can provide an accurate understanding of the predator's functional responses and the conditions under which they exhibit prey switching.

Using Bayesian methods, we fitted a multi species functional response (MSFR) model to consumption data of a generalist insectivorous bat, *Rhinolophus alcyone*, feeding on five orders of arthropods. Data on arthropod abundance and consumption, via DNA metabarcoding, was collected from sixteen cacao plantations of varying vegetation structure. Comparing the results of the MSFR model to a single species approach demonstrates the importance of including all possible prey when investigating the consumption of a generalist predator. Focussing on one taxon resulted in unfeasibly large parameter values, which would generate misleading conclusions on the predator-prey relationship. Using the MSFR, the proportion of orders within the predicted diet were close to that of the real diet, ascertained through DNA metabarcoding. Results of the model demonstrate a high degree of prey

switching within the system, with evidence for a type III functional response between the predator and three of the five orders. Furthermore, the resulting parameter estimates of the model are used to predict the diet of the predator under changing prey fields. Finally, no evidence was found to suggest that vegetation structure of the plantations influences the diet composition of the predator.

These models have the potential to be extended to better describe generalist predator-prey relationships and assess the impacts of habitat structure on these. In addition, the resulting fully fitted model can be used in dynamic ecosystem models to investigate the stable states and biodiversity/ production trade-offs in agroforest ecosystems. Therefore, this approach will prove important in the long-term management strategies and conservation of our ecosystems.

Background

Predation is a fundamental ecological process, playing a vital role in the regulation of populations within ecosystems (Sih, Englund, & Wooster, 1998). Predator-prey interactions have a rich history within ecological research, particularly within ecosystem management and biological control (Ives, Cardinale, & Snyder, 2005). Moreover, there has been a growing interest in the complex relationship between predators and their prey, particularly where generalist predators are concerned. Single species approaches to ecosystem management using predator population abundances as a proxy for lower trophic levels has long been popular. However, these predators are often generalist and their abundance being a function of the availability of multiple prey species makes using single species models inappropriate (Smout et al., 2010). As awareness on the importance of interactions between multiple species continues to grow, multi-species predation models are becoming increasingly popular to predict the outcomes of managed ecosystems (Asseburg et al., 2006; Lindstrom et al., 2009; Yodzis, 1994).

The relationship between a predator's behaviour and their prey has long been of interest. In particular a predator's functional response, where an individual predator changes its feeding rate in response to changes in prey availability (Gascoigne & Lipcius, 2004). One pioneering study by Holling (1959a) proposed that predators will have three types of functional response when interacting with their prey (fig.1). Type I, being the simplest of the three, assumes that predation will increase linearly with prey abundance. Eventually consumption reaches a

maximum where it will then become constant, due to the physiological bounds of ingestion (Yodzis, 1994). This response assumes that the time taken for the predator to consume the

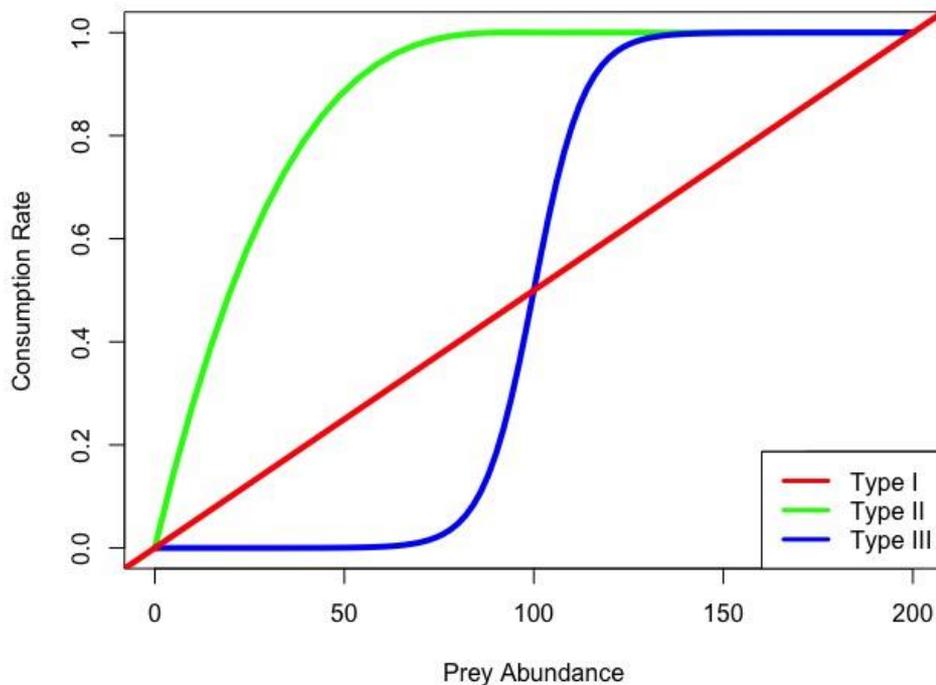


Figure 1. Hollings three functional responses, demonstrating how predators respond to increased prey abundances under the three different responses.

prey is negligible, giving the linear shape. In a Type II response, the intake rate is slowed by the predators ability to handle and process its prey, and assumes that a predators ability to search for, and process, food are mutually exclusive. In this scenario, high densities of prey result in lower proportions of prey being consumed, as predators can locate prey quickly and spend more time handling them. Finally, the type III response is similar to type II, in that high densities of prey result in a lower number of prey being consumed. However, under this response, at low prey densities the number of prey consumed is much lower than that of type II, before increasing rapidly, giving the response a sigmoidal shape (Sinclair et al., 2008). This is due to predators having to learn to search and attack efficiently at such low

densities, as they may not be familiar with the best ways to capture this particular prey.

Furthermore, in the case of generalist predators, the consumption rate of a prey species at low densities is low due to the predator switching their preference to other, more abundant prey (Holling, 1959a).

In particular, Holling (1959b) proposed an equation for a functional response model where a predator preys on a single species of prey.

$$F = \frac{\alpha q}{1 + \alpha t q} \quad (1)$$

In Hollings proposed equation (1) the abundance of prey is denoted by q , with t representing handling time, and α being the encounter rate between the predator and prey species.

However, this model does not account for the fact that encounter rates are likely to change with prey abundance. For example, low densities of prey will likely result in fewer encounters. The relationship between encounter rate and abundance can be expressed as $\alpha q = aN^{m-1}$, when q is proportional to the true abundance of prey. Therefore, Real (1977) expanded the equation to:

$$F = \frac{aN^m}{1 + atN^m} \quad (2)$$

Here, m denotes the form of the predators functional response, with t denoting handling time as in equation (1). When $m=1$, the encounter rate is independent of the abundance of prey.

Once $m>1$, the encounter rate, a , will begin to vary with the abundance of prey available, relating this to N^{m-1} . Here a is a constant of proportionality, and distinct from α in equation

(1). As presented above, equation (2) is a single species functional response model, and can be altered to correspond with the three types of functional responses as proposed by Holling (1959a). Using this equation, a type I (linear) response can be fitted when $m=1$ and $t=0$ (handling time is negligible). Once handling time starts to increase from 0, and m remains at 1, we achieve a hyperbolic curve, suggesting a type II response. Finally, once m increases above 1 the shape of the curve achieved will be sigmoidal, a type III response. This indicates the predator is capable of prey switching at low prey densities. Although useful, equation (2) is only relevant when discussing specialist predators, those that are linked with only one prey species. Furthermore, the equation assumes that the number of predators will remain constant, and that the only influence on their functional response is caused by the abundance of one specific prey species (Smout et al., 2010).

However generalist predators, which prey on several species, are common and play an important role within ecosystems and food webs. A predator may switch its preference once a preferred prey species becomes scarce, and therefore becomes more energetically costly to track down. Different magnitudes of a predator's perturbation on one prey species may have the opposite effect on other prey species (Abrams & Matsuda, 1996). For example, an increased preference for one species of prey will allow the population of another to recover, before it eventually becomes preferred again. Therefore, prey switching can have a stabilising effect on predation species, preventing them from both going extinct and proliferating excessively (Jaworski et al., 2013; Oaten & Murdoch, 1975; Symondson et al., 2002). A predator's preference may also be influenced by a prey species nutritional value, as well as the ease of capturing and handling their prey. These preferences may differ between species of generalist predators. For example, Eubanks & Denno (2000) demonstrated that big-eyed bugs deemed prey mobility more important than their preys nutritional value, as they are well

equipped to detect movements of prey, and this strategy may be less costly than randomly moving across plants to detect stationary prey (Desneux & O'Neil, 2008; Higginson & Ruxton, 2015). Furthermore, predators may preferentially attack prey that are an optimal size, with a lower risk of causing injury during prey handling. However, as this prey become scarce, predators may be forced to ambush larger and therefore more dangerous prey (Cooper & Stankowich, 2010; Owen-Smith & Mills, 2007). Therefore, generalist predators play an influential role on the dynamics of a wide range of prey populations within an ecosystem, and modelling their interactions may reveal the extent of this.

Determining the processes underlying the structure of food webs has long been a fundamental problem in ecology (Allesina et al., 2008; Rohr et al., 2010). Generalist predators pose a problem for consumption and food web modelling due to their ability to prey on a wide variety of species, as well as switch their preference when prey availability changes. This introduces dynamical complexity to food webs which single species models, such as equation (2), cannot take into account (Closs, Balcome, & Shirely, 1999; Smout et al., 2010). Their ability to prey on several species means that the abundance of a generalist predator will not be directly associated with any one of its prey species, and therefore their functional response and diet will be driven by the abundances of all their available prey. Generalist predators can have both direct and indirect effects on the populations of their prey species and the strength of these interactions is likely to depend on the preference a predator has for its prey (Jaworski et al., 2013; Lindstrom et al., 2009). Indirect interactions are likely triggered through a generalist predator's ability to switch their prey preference, with the abundance of one species of prey associated with the abundance of others within the ecosystem (Jaworski et al., 2013; Oaten & Murdoch, 1975; Smout et al., 2010; Symondson, Sunderland, & Greenstone, 2002). Additionally, prey switching introduces direct interactions amongst prey species,

adding to the complexity (Abrams & Matsuda, 1996). For example, this can include competition for space not occupied by the predator, which affects prey species abundance within the ecosystem (Holt & Lawton, 1994). Consequently, there has been a growing realisation that to fully understand the predator-prey relationships, all prey taxa must be considered. Historically, studies investigating the effects of changing prey abundances on generalist predators have only focussed on the link between a single prey species and their predator, however consumption by generalist predators depends on the densities of all available prey species (Schenk & Bacher, 2002; Smout et al., 2010). Therefore, without the context of other prey species, this results in misleading conclusions about a predators functional response to the changing availability of their prey, and would lead to consumption and food web models that are too simple due to their sole reliance on species richness and connectedness (Allesina, Alonso, & Pascual, 2008; Novak et al., 2017; Smout et al., 2010). Deepening our understanding of how generalist predators prey switching influences the composition of food webs will prove beneficial in conservation and management of vulnerable ecosystems, within both terrestrial and marine habitats (Lindstrom et al., 2009). Therefore, accurately modelling these interactions is becoming increasingly necessary as we aim to monitor and maintain the health of our ecosystems.

As habitat conversion and degradation is on the rise, and agriculture continues to intensify (Tschardt et al., 2005), it is imperative to understand the effects this has on important functional groups, such as generalist predators. Food web and consumption models provide key insights into how species diversity and functionality are affected by anthropogenic driven habitat change (De Visser, Freymann, & Olf, 2011). Additionally, previous studies have shown that the functional forms of a predators interaction with their prey is just as important as the surrounding parameter values when determining the outcome of habitat changes that

alter prey availability (Yodzis, 1994). Establishing how this may influence the consumption of predators and the underlying food webs of ecosystems will prove beneficial to management strategies. These are particularly important when investigating the impacts human harvesting has on vulnerable ecosystems, such as fisheries and agroecosystems. Effective management and conservation of biodiversity requires an indepth understanding of both predator and prey populations and how they interact with each other (Dobson et al., 2006). This involves developing models which can accurately predict how a predator will interact with their prey, providing vital knowledge for the development of accurate food webs and trophic interactions (Burgar et al., 2014). Traditionally, management strategies were based on single-species models, which have proven unreliable when dealing with generalist predators due to the lack of context of all available prey. Furthermore, they are unable to describe the consequences of direct and indirect interactions between a generalist predator and their prey (Lindstrom et al., 2009; Smout et al., 2010; Yodzis, 2001). Therefore, there has been an increasing interest in developing a strategy to assess the consumption of generalist predators and how their diet changes with changing prey availability. This approach is known as multispecies functional response (MSFR) modelling and uses Holling's (1959a) three functional responses to evaluate how a predator reacts to changing abundances of their prey. In their paper, Smout *et al.* (2010) adapted equation (2) to develop an MSFR model. To do this they made each parameter prey-specific and specified $m > 1$ to allow preference (a) to change with relative prey abundance.

$$F_i = \frac{a_i N_i^{m_i}}{1 + \sum_{j=1}^n a_j t_j N_j^{m_j}} \quad (3)$$

In this equation, n , denotes the number of prey species, allowing the equation to account for changes in encounter rates of all species. In their paper they demonstrated that understanding a generalist predators MSFR can prove essential when monitoring ecosystems and understanding the interactions between generalists predators and pests or endangered species. Further studies demonstrate the equations successful application to a range of management scenarios, including both marine and terrestrial environments (Asseburg et al., 2006; Lindstrom et al., 2009; Smout et al., 2013; Smout et al., 2014).

Here, we will present a case study to produce a consumption model using equation (3) (Smout et al., 2010) to determine the functional responses of a generalist bat predator to changes in arthropod availability in Cameroonian cacao plantations.

Traditional Cameroonian cacao plantations have shade trees above the cocoa and provide an excellent habitat for harbouring high levels of biodiversity (Aenz et al., 2006; Faria et al., 2006; Rice & Greenberg, 2000; Ruf, 2011; Schroth et al., 2004; Schroth & Harvey, 2007). This strategy is recognised as producing several environmental benefits, particularly the conservation of biodiversity within an agricultural landscape. Within sub-Saharan Africa, cacao farming is replacing traditional forests, making agricultural habitats more readily available to bats (Nkrumah et al., 2016). However, as the demands for cacao continue to rise, farmers are increasingly switching to zero-shade cultivation techniques, driving the loss of vegetative, arthropod and bat diversity within the forests (Rice & Greenberg, 2000; Schroth & Harvey, 2007). This zero-shade, or “full sun” approach, refers to cacao plantations with only one level of canopy storage, the cacao trees. This in contrast to traditional plantations which contain a rich variety of native trees standing above the cacao canopy, providing shade. The use of full sun cultivation has been on the rise since the 1980s, particularly as

replacing shade trees with fertilisers increases yields, making it difficult for those using traditional methods to compete economically (Ruf, 2011). This has important consequences for the fauna residing within these forests, potentially reducing the presence of keystone species. Insectivorous bats provide many essential ecosystem services within tropical agroforests, particularly the suppression of pest insects within plantations (Kalka and Kalko, 2006; Kunz et al., 2011). Changing the vegetation diversity within plantations will have knock-on effects for the arthropod assemblages found there, with the potential for increasing pest presence (Andow, 1991). This in turn will affect the available arthropod abundances for insectivorous bats within the system. Fluctuations in a predator's behaviour, such as deciding what to consume whilst foraging, can directly impact their survival and reproductive success (Nkrumah et al., 2016). Therefore, increasing our understanding of how a predator's diet changes will allow us to predict whether they will persist under different scenarios of habitat change. Furthermore, cacao plantations in Cameroon are becoming increasingly plagued by pest species, such as brown capsids (*Sahlbergella singularis*). As a result, farmers are turning to pesticides and insecticides to keep pests at bay, typically through mass fumigation of their plantations (Sonwa et al., 2008). Therefore, understanding how a generalist predator's foraging decisions are impacted by changes to their habitat may prove important in their conservation and management.

The exact consequences for biodiversity and the functional responses of generalist predators is largely unknown, and will be better understood through the development of consumption models. Therefore, we aim to investigate how the proportions of prey consumed by generalist predators change with changing prey availability. This study will produce a consumption model based on equation (3) to quantify the consumption couplings between a generalist predator in a system with a field of several prey. Using data from cacao plantations with varying vegetation structures, from full-sun (no shade trees) to traditional ("rustic") forests,

the model will be fitted using Bayesian methods. This model can then be used to infer the functional responses of the generalist predator to changes in prey abundances. This research provides important groundwork for developing models that accurately describe the behaviour of predators to changing prey availability. This may prove essential when developing techniques to monitor the effects of habitat change, effectively use biological control methods and predict trade-offs between biodiversity and productivity in agroecosystems.

Methods

Study Area

Cameroon is one of the major cacao producers in West Africa, with up to 75% of rural households producing cacao (Gockowski & Dury, 1999). Cacao plantations in this region vary in their structure, with some farmers opting for the full sun approach. All study sites are located within sixteen cacao plantations in Cameroon, West Africa. These plantations include eight traditional agroforests, six fruit tree and two full sun, all with varying vegetation structures. Data collection was carried out across two field seasons, August-September 2017 and January-February 2018. Within each plantation, the Plant Area Index (PAI) was recorded using a fisheye lens. This information indicates the management of the plantations by the structure of the vegetation.

Study species

Prior to our study insectivorous bats across the sixteen plantations were caught using passive mist netting with 20m x 20m nets. Once individuals were caught, they were identified and released following the production of a faecal sample. Seventeen species of generalist insectivorous bat were caught. However, this study shall focus on the diet of one, *Rhinolophus alcyone* (Halcyon horseshoe bat), as it was caught at all sixteen study sites in high numbers, increasing the chances of successful DNA extraction and diet analysis. This species is found in West Africa, particularly Cameroon, Congo and Senegal. Although common, they are threatened by a loss of habitat resulting from the conversion of land to agriculture (Monadjem, Hutson, & Bergmans, 2017; Monadjem et al., 2017). Furthermore, they forage throughout cocoa plantations of varying vegetation structures (Nkrumah et al., 2016). Insectivorous bats feeding in these ecosystems typically consume a diverse range of

prey, making *R. alcyone* an ideal model predator for generalist consumption modelling (Clare et al., 2011; Nkrumah et al., 2016).

Arthropod Identification

To understand the availability of different arthropod orders at each plantation, data on arthropods abundance were collected during the 2018 season using sweep net sampling- 40 firm sweeps at green vegetation at each plantation. These were then preserved in 100% ethanol at -20°C for later identification within individual tubes for each of the plantations.

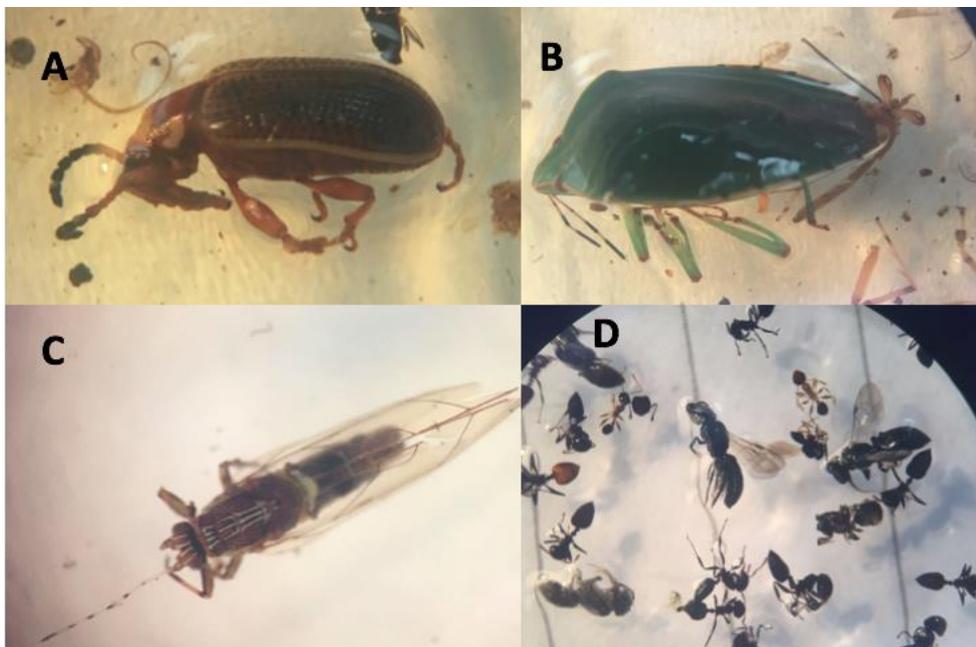


Figure 2. Example arthropods from Cameroon samples. A) Coleopteran, B) Hemipteran and C) Psyllidae, order Hemiptera: Homoptera and D) selection of Hymenoptera

Arthropods were identified to order level following guidelines and descriptions in Chinery (2005). These were Hymenoptera, Arancaea, Coleoptera, Hemiptera, Diptera, Lepidoptera, Orthoptera, and ‘Other’, which included larvae, Blattodea and individuals which could not be confidently identified. Once each sample had been separated into orders, all the individuals present within each order were counted.

DNA Metabarcoding

Diet and consumption data often come from first hand observations of a predator handling and consuming its prey (Smout et al., 2010). Previous studies analysed diet through observational techniques, or more intrusive approaches such as stomach analysis. However, it is not always possible to observe diets due to a variety of factors, including nocturnal species, where darkness makes it difficult to observe which species the predator is consuming (Burgar et al., 2014). Therefore, methods such as DNA metabarcoding may provide a less intrusive, and accurate, alternative. Dietary analysis through metabarcoding involves extracting DNA from faecal samples to determine which taxa were consumed by the predator (Berry et al., 2017). This method was selected due to the difficulty in observing the diets of bats foraging at night within potentially dense plantations, and the approach would avoid fatal captures of bats for stomach content analysis. Furthermore, when using this technique prey are taxonomically described, improving the accuracy of the dietary analysis, where field observations would decrease the accuracy of prey species identifications (Brown et al., 2014).

DNA was extracted from faecal samples using a protocol adapted from Jusino et al., (2017) and the QIAmp DNA Stool Handbook 06/2012 (Technologies, 2012). Following extraction, DNA was amplified through triplicate PCR, using extensive and up-to-date primer sets. Furthermore, an independent primer set, ZBJ, was used, targeting the arthropod mitochondrial cytochrome oxidase c subunit I (COI) gene, which are fragments of approximately 200 base pairs (Lunt et al., 1996; Zeale et al., 2010). Repeating PCR amplifications three times to ensure that false negatives were not discarded should one amplification not be successful. Following this, gel electrophoresis was used to determine the success of each DNA extraction. To do so, each amplified DNA sample was run through a gel alongside a DNA ladder to demonstrate whether DNA of the expected length were

present. This resulted in 81 successful DNA extractions of *R.alcyone* faecal samples across the 16 plantations from the 2017 and 2018 field seasons. The triplicate PCR products of these samples were then pooled in equal volumes and cleaned using carboxyl paramagnetic beads. Successful samples were then sent for metabarcoding to determine the full sequences of the DNA present. Once returned, these were matched with known sequences in GenBank and the Barcode of Life Database (BOLD) to determine which species (or closest known taxon) of arthropod were consumed by each bat within each plantation.

Statistical Analysis

A Bayesian approach was used for producing models of bat consumption within the plantations. The Bayesian Monte-Carlo Markov Chain (MCMC) approach was chosen for several reasons. Firstly, it allowed us to select the most appropriate sampling distribution for our data, without the need for data transformations. Furthermore, the Bayesian approach allows the inclusion of independent information from different sources to be combined in the form of parameter priors (Berger, 2006). All models were developed in RStudio (R Core Team, 2017), using JAGS (Denwood, 2016; Plummer, 2016). The original Smout *et al.* (2010) equation (3) was used with for-loops to allow the model to produce consumption rates using each sample within each farm.

Before attaining the consumption data from DNA metabarcoding, the model was run using simulated data. This allowed us to test the robustness of the model and determine the appropriate number of arthropod orders to use. To test how the model would perform under different scenarios and how many arthropod orders could feasibly be included, we altered conditions to provide scenarios with different numbers of farms and arthropod orders, to determine whether the model could still converge on a sensible posterior distribution for our

given parameters. This analysis was necessary due to only sixteen farms being sampled, which would severely restrict the number of parameters that could be included. Each order would require three parameters: a (preference/ attack rate), t (handling time), and m (the functional response of the predator/ shape parameter). We used additional biological data from previous knowledge and the literature to supply prior distributions for the parameters a , t and m where possible. No prior knowledge was available for both a_i and t_i , therefore, uninformative priors were used. Both priors used a gamma distribution with mean 1 and SD 0.99 (shape=1.01, rate=1), as it would not be possible for handling time to be below 0, and when testing for robustness, gamma priors were found to be the most appropriate for a_i . Similarly, it is not possible for m to have a value below 0, therefore a gamma distribution was also used to exclude negative values from the prior. Furthermore, values of m between 0 and 1 would indicate that attack rates on one species can decrease whilst it's density increases, with the density of all alternative prey remaining the same (Smout et al., 2010). Therefore, the m_i prior had a gamma distribution shifted by 1 to exclude those values, a mean of 2 and variance of 0.9. Finally, a gamma prior was used for the precision of the model, τ (tau), with shape= 4000, and rate= 10. This distribution would constrain the precision of the model to 5%, allowing a large error rate of between 40 and 60%. Here, instead of supplying the model with data on the consumption of each order within each farm, we used equation (3) to generate a matrix of random consumption rates with a standard error of 5%. Additionally, a matrix of randomly generated arthropod availability for each order within the sixteen plantations was created. Under different conditions (number of plantations and arthropod orders), the model was supplied with the simulated data and the MCMC was implemented with two chains using a Metropolis Hastings algorithm (Chib & Greenberg, 1995), using a burn-in period of 10,000 and 10,000 iterations. Once the model was run, diagnostic tools including trace plots and convergence statistics were used to determine the success of

convergence, and whether sensible posterior parameter means were produced. The plot function was then used to plot the ‘real’ data supplied for parameters a , t and m against the posterior means generated by the model. This demonstrated whether the values calculated by the model were at, or close to, the ‘real’ values supplied in the generation of the simulated consumption matrix.

Once satisfied with the simulated model, the real arthropod abundance and predator consumption data could be used. Bat consumption data from the two field seasons were pooled, as using just one would reduce the number of plantations in the model, therefore restricting the number of arthropod orders that could be included. It was determined from the sensitivity analysis that no more than five orders of arthropods could be used in the model. Therefore, arthropod abundance and consumption were grouped into Coleoptera, Diptera, Hemiptera, Lepidoptera as these orders were present in both the arthropod abundance and consumption data. All remaining orders were grouped into the fifth category ‘Others’. Data were supplied to the model in the form of two matrices as before. One with the abundance of each of the five orders within each plantation, as based on the sweep-net samples, and another with the consumption data for each order consumed by each bat, collected from the DNA metabarcoding. The DNA metabarcoding results provide information on the number of sequencing reads attained for each order within individual samples, which can vary greatly in magnitude. Therefore, using these data resulted in the model converging on parameter posteriors that overlapped with the priors, indicating that the priors were uninformative and the consumption data provided no guidance for the model. Previous captive feeding trials have suggested that the percentage of sequencing reads may not be directly proportional to the percentage of each prey item in the diet. However, there is evidence to suggest that the rank-order of species abundance in the diet is preserved (Deagle et al., 2014; Srivathsan et al.,

2016; Thomas et al., 2013). Therefore, assuming a larger signal in the DNA metabarcoding data is correlated with the rank of that order within the predator's diet, the metabarcoding data was transformed to diet proportions. This approach preserved the rank order of the sequencing reads, whilst greatly reducing the variation within the data. The MCMC was then run with the parameter priors, burn-in and number of iterations determined by the sensitivity analysis. The resulting chains were then tested for convergence to ensure that enough iterations had been used, and that the priors were appropriate, by examining diagnostic statistics and trace plots. The Gelman-Rubin statistic was used to determine whether chains had converged successfully, parameters with a summary statistic at or close to 1 were deemed acceptable. Should chains not have converged successfully, the number of iterations was increased until all parameters had a Gelman-Rubin statistic at or close to 1.

Once the MSFR model had been run, 100 draws from the coda list of the model results for each of the parameters were extracted to visualise the functional response of the predator to each of the five orders. To do so, a 200-row matrix with the mean abundance from the sweep net samples for each order, in separate columns, was created. For the order of interest, these means were replaced with a sequence from 0 to the maximum abundance counted in the sweep net samples. The data was then supplied to equation (3), which looped over the 200 possible abundances, this was repeated 100 times for each of the parameter coda draws corresponding to the species of interest. The resulting consumption values of the prey of interest for each of the 100 iterations were then stored in an empty 200x100 matrix. The mean change in consumption rate of the 100 samples was then plotted using `ggplot2` (Wickham, 2009), with the calculated standard deviation for each of the 200 possible abundances, to graphically illustrate the shape of the functional response of the predator to the order of interest. This approach was repeated for each order to produce five functional

response graphs. Similarly, using the original abundance matrix from the sweep net data, the expected consumption rates of the predator to the five orders were calculated and stored in an 81x5 matrix, with each column representing an individual bat from the metabarcoding samples. The columns were grouped according to vegetation structure of the plantation the bat they represented was sampled from, derived from the PAIs of the plantations. PAIs varied between 0.6 and 5, therefore plantations were separated into three groups; PAI <2, PAI between 2 and 3, and PAI >3 to investigate the effect of vegetation structure on the diet of the predator. Wilcoxon rank sum tests were used to compare the mean consumption rates of each order within the three groups. Finally, the effect of certain orders no longer being available to the predator can be predicted. To do so, one order (such as Lepidoptera) was removed out from the predator's diet by setting their abundance to zero within the arthropod availability matrix. The posterior parameter values from the model and new availability matrix were then supplied to equation (3) to produce an expected consumption matrix without an order present. The predicted diets of the predator were then illustrated using the pie chart function.

To compare the effectiveness of an MSFR model against a single species approach, equation (2) was used to fit a single species functional response model to each of the orders. As with the MSFR model, data on abundance and consumption of each order at each of the sixteen farms was supplied in the form of two matrices. Using loops within the Bayesian model, the expected consumption rate of the order at each farm was calculated. The model was fitted with the same priors as the MSFR, and success of chain convergence was also assessed using the Gelman-Rubin statistic and trace plots. The resulting posterior parameters for the two approaches could then be compared to determine which approach was superior. Finally, the maximum handling time, $\frac{1}{t}$, of each order predicted by the two approaches was compared.

Results

Sensitivity Analysis

Sensitivity analysis demonstrates that the model is capable of converging onto appropriate posterior distributions when not over-parameterised. For the sixteen plantations present, we can include five orders of arthropod (including ‘other’) and still obtain reliable results. Each order brought with it three parameters, a , t and m , resulting in fifteen parameters total for the sixteen farms. However, once the number of orders used increased from five, the model became over-parameterised, with chains failing to converge (Gelman-Rubin statistic >1.2), and the resulting posterior distributions being far from their true values, with large standard deviations.

Single-Species Functional Response Model

The posterior mean, standard deviation and credible intervals for the single species functional response models (eq. 2) shown in table 1 demonstrate a large variation in parameter estimates between the orders of arthropod. The highest degree of prey switching was found to occur with Dipterans and ‘others’, suggesting that, at low densities, the predator will switch to other available prey.

Table 1. The posterior means for each arthropod order resulting from the single species model (equation 2). **t** representing handling time, **m** the switching parameter (where $m > 1$ indicates that switching occurs) and **a** the encounter parameter. Gelman-Rubin < 1.02 for each parameter.

Variable	Mean	SD	Lower	Upper
t Coleoptera	4.99	0.39	4.26	5.79
t Diptera	0.0006	0.0006	0.00	0.002
t Hemiptera	1.04	1.04	0.0001	1.24
t Lepidoptera	1.01	0.99	0.0002	3.00
t Others	0.0027	0.0006	0.002	0.0028
m Coleoptera	1.09	0.10	1.00	1.30
m Diptera	4.33	0.45	3.48	5.24
m Hemiptera	1.08	0.08	1.00	1.24
m Lepidoptera	1.09	0.09	1.00	1.30
m Others	43.64	2.21	39.24	47.82
a Coleoptera	1.87	1.17	0.19	4.15
a Diptera	0.002	0.002	0.00002	0.006
a Hemiptera	0.001	0.0007	0.00	0.002
a Lepidoptera	1.02	1.01	0.00	3.01
a Others	>0.0001	>0.0001	>0.0001	>0.0001

However, the posterior **m** means of these groups were unusually large ($m > 3$), with the posterior mean of **a** for each group also being extremely low. Under the single species model, the predator was found to have a weak sigmoidal response ($m < 1.1$) to Coleopterans, Hemipterans and Lepidopterans, providing only weak evidence for prey switching when these orders are present in low abundances. Furthermore, the model predicts the highest encounter rates between the predator and Coleopterans and Lepidopterans, which would result in both orders being high proportions of their predicted diets. Dipterans were predicted a low handling time, despite being one of the most abundant orders in terms of availability, where predators may choose to spend more time handling prey. Finally, ‘Others’ were predicted an extremely low encounter rate parameter, which is unexpected given their availability in both the sweep-net data and their presence in the DNA metabarcoding diet data of the predator (fig. 3).

Multi-Species Functional Response Model

Table 2. The posterior means for each arthropod order resulting from the multi species functional response model (equation 3). **t** representing handling time, **m** the switching parameter (where $m > 1$ indicates that switching occurs) and **a** the encounter parameter. Gelman-Rubin statistic < 1.02 for each parameter.

Variable	Mean	SD	Lower	Upper
t Coleoptera	0.14	0.14	0.00	0.52
t Diptera	0.01	0.01	0.00	0.05
t Hemiptera	0.49	0.61	0.01	2.26
t Lepidoptera	1.75	0.03	1.69	1.81
t Others	0.17	0.15	0.01	0.57
m Coleoptera	1.47	0.28	1.11	2.17
m Diptera	1.39	0.10	1.20	1.59
m Hemiptera	1.60	0.29	1.18	2.29
m Lepidoptera	1.03	0.01	1.01	1.06
m Others	1.18	0.09	1.05	1.40
a Coleoptera	0.14	0.09	0.01	0.34
a Diptera	0.41	0.14	0.20	0.77
a Hemiptera	0.0004	0.0005	0.00	0.00
a Lepidoptera	11.64	2.46	7.67	17.30
a Others	0.15	0.06	0.05	0.28

However, when the MSFR model was fitted (Table. 2, fig. 4), the predator was found to have the weakest sigmoidal response to Lepidopterans (**m** closest to 1), which may be expected, as they were found to be the predators most abundant prey from diet analysis. Their resulting **a** parameter was also extremely high when compared to the other orders, signifying that the predator encounters these most often, resulting in a high attack rate. All other orders had higher values of **m**, demonstrating that the predator's preferences are variable, and that it's likely to switch from these orders at low abundances. This contrasts with the results shown by the single species model (Table 1), where Coleopterans and Hemipterans were predicted to have a very weak sigmoidal functional response ($m < 1.1$), suggesting a low degree of switching. Both the single and MSFR models predicted parameter values of $m > 1$ and $t > 1$ for each of the orders considered, indicating type III responses and a high degree of prey switching is expected within the system.

Using the values from tables 1 and 2, the maximum consumption rate of each order can be calculated using the equation, $\text{consumption}_{\max} = \frac{1}{t}$ (Table 3). The results show a large disparity between the single and MSFR models, particularly with Diptera and ‘Others’. The maximum consumption rates predicted by the single species model for these two orders are much higher than those predicted by the MSFR, and exceeded the abundances counted for each order. The maximum handling time for Coleopterans predicted by the single species model is much higher than the MSFR, which would drastically lower the maximum consumption rate predicted. Both predicted Lepidopterans to have a low maximum consumption rate, which agrees with the abundance data, where Lepidopterans were the least abundant of the orders present.

Table 3. The predicted maximum consumption rates for each order calculated using mean t parameter values from the single and multi-species functional response models (tables 1 and 2).

Order	Single Species FR (Eq. 2)	Multi Species FR (Eq. 3)
Coleoptera	0.2	7.14
Diptera	1666.67	100
Hemiptera	0.96	2.04
Lepidoptera	0.99	0.57
Others	370	5.88

The maximum consumption rates predicted using the MSFR model are within the abundance estimates of each of the orders, which indicates that the results of this approach are likely more reliable than the values attained from the single species models.

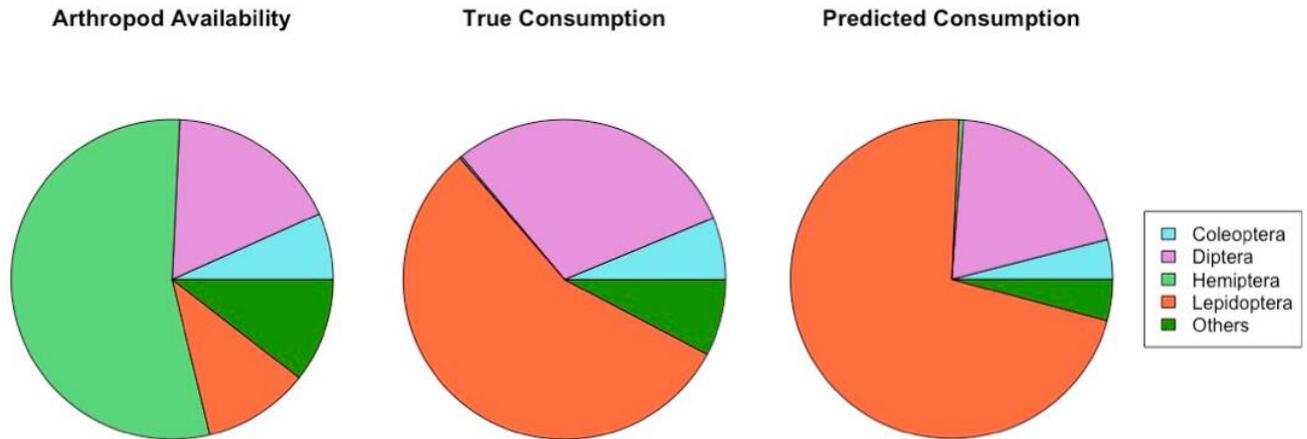


Figure 3. Pie charts demonstrating the proportions of arthropods available to *R. alcyone* in the cacao plantations, the proportions found in their diet and the predicted diet using equation 3. Number of plantations= 16, number of bat samples=81.

Using the values of the posterior means in table 2, the expected consumption rates of each order were determined using equation 3. The model computed expected consumption rates resulting in diet proportions close to that of the true consumption (fig. 3). This demonstrates that Lepidopterans and Dipterans form a large part of the predator's diet. Lepidopterans had the lowest switching parameter (\mathbf{m}), and highest encounter rate (\mathbf{a}), therefore this order made up the largest proportion of the predicted diet. Additionally, Dipterans had a low predicted handling time and high encounter rate, resulting in the order making up a large proportion of the predator's predicted diet, though slightly less than the true diet. Furthermore, both Coleopterans and 'Others' made up similar proportions across the sweep-net data, true and predicted diets. Although Hemipterans were prevalent in the sweep-net data, they made up a very low proportion of the predator's diet, and were therefore low in the predicted diet. This is due to the low encounter rate parameter ascertained by the model, indicating that even though they are present within the plantations, the predator does not encounter them regularly.

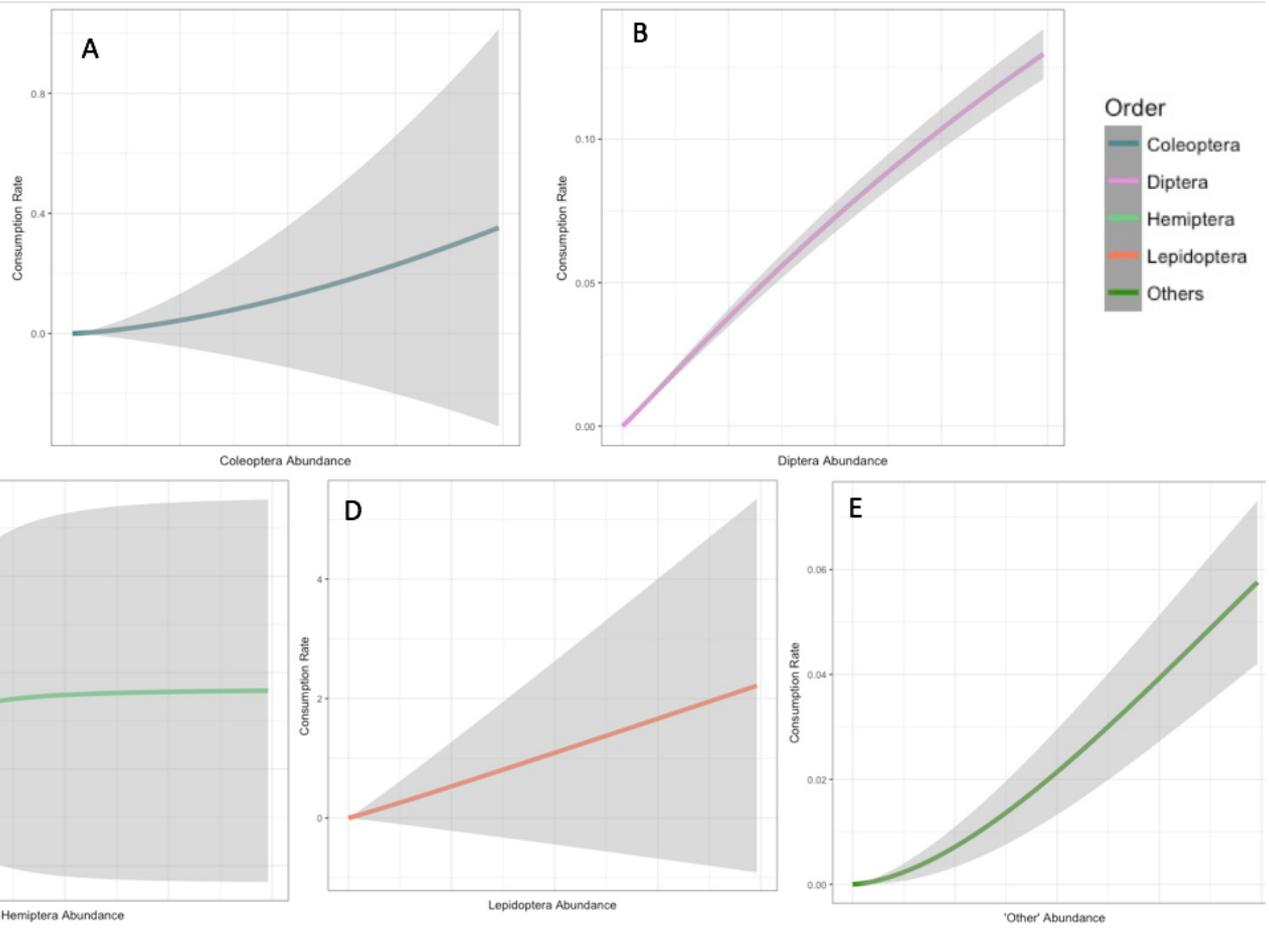


Figure 4. Plots showing the functional response of the predator to increasing abundances of each of the five orders. The standard deviation of the consumption rate is shown by the grey shading. A= Coleoptera, B=Diptera, C=Hemiptera, D= Lepidoptera and E= 'Other' (n=81). A, C and E show a type III functional response, B a type II and D a type I.

The resulting consumption rates were then plotted to visually show which type of functional response the predator exhibits to changing abundances of each of the five orders (fig. 4). The predator shows a type III functional response to Coleopterans, Hemipterans and 'Others', with a slow increase in consumption rate, before increasing rapidly past a certain threshold abundance, shown by the 'kink' in the lines for each. The relationship between the predator and Diptera is a type II functional response, with consumption increasing with abundance, before beginning to level off. Finally, the predator appears to show a type I response to changing abundances of Lepidopterans, with consumption rates increasing linearly with their abundance. These functional responses are largely in accordance with the posterior means of

parameter m for each of the five orders. Hemiptera had the highest posterior value of m , indicating a strong sigmoidal curve, as well as a value of t larger than 0 (Table 2). This information would suggest a type III function response of the predator, which is clearly illustrated by figure 4C, although the standard deviations for the order are very large. The posterior means of m being greater than 1 and large handling times of both Coleoptera and ‘Other’ also indicate a type III response which is illustrated in figure 4A and E. Although with a posterior mean of m greater than 1, the functional response of the predator to Diptera is type II, which is due to the handling time parameter, t , being so close to 0. Finally, the relationship between the predator and Lepidopterans appears to be a type I functional response. However, the handling time parameter is greater than 0, and m parameter indicates a type II or III response (although weakly).

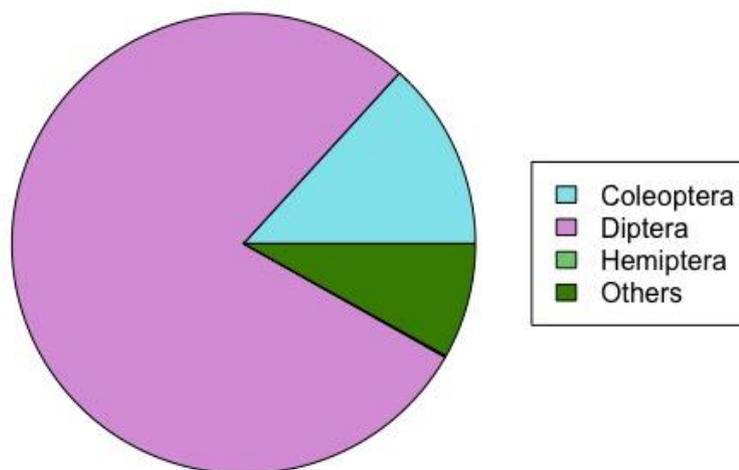


Figure 5. Pie chart showing the diet composition of *R. alcyone* when no Lepidopterans are present. The consumption values were calculated using equation 3, where the abundance of available Lepidopterans was 0.

Using the resulting parameter values and setting the abundance of Lepidopterans to 0, the model can be used to visualise how the composition of the predator’s diet will change should they no longer be available (fig. 5). The results of the model indicate that should conditions

change and Lepidopterans no longer be available, they will replace them with Dipterans in their diet.

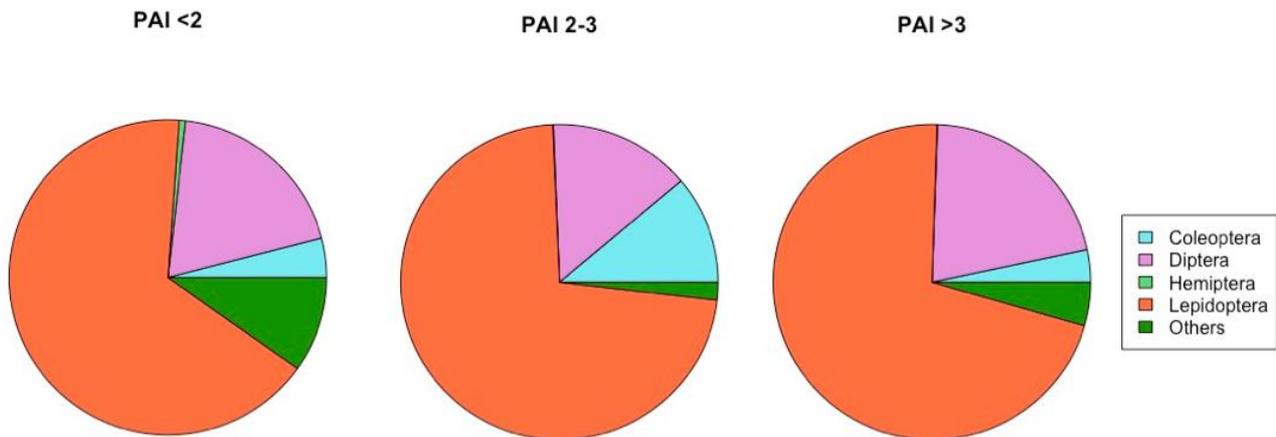


Figure 6. Pie charts demonstrating the diets of insectivorous bat *R.alcyone* when feeding in cacao plantations with different vegetation structures. PAI<2 n=5, PAI 2-3 n=3, PAI>3 n=7.

Furthermore, using the consumption results, we can analyse how vegetation structure affects the diet of the predator. Vegetation structure does not appear to have an influence on the diet of the predator (fig. 6.), confirmed by a Wilcoxon rank sum test comparing the means of each order between each group, demonstrating no significant changes to consumption rate for any order ($p>0.05$).

Discussion

The effectiveness in taking a MSFR approach, as opposed to single-species, is demonstrated in the feasibility of the resulting parameter values produced by each model. Therefore, the results support previous studies demonstrating that single-species approaches result in misleading conclusions on a predator's functional response (Asseburg et al., 2006; Lindstrom et al., 2009; Smout et al., 2010; Yodzis, 1994). Moreover, using the MSFR, this study demonstrates a high degree of prey switching by the generalist predator prey, with the predator exhibiting a type III functional response to three of the five orders. Our analysis suggests that to increase the number of orders and achieve a more detailed understanding of the interactions between predators and their prey, an increased number of study sites is required.

Comparing the results of the single and multi-species functional response models, the importance of taking all possible prey into account is clear and has a large impact on the conclusions drawn from the model. Limiting analysis to a single prey species also resulted in parameter values that were not feasible (Table 1). For example, the handling time of Coleopterans predicted by the single species functional response model was unusually high, relative to the MSFR model. Furthermore, the switching parameters for Dipterans and 'others' were consistently outside of the feasible bounds ($m=1-3$), which indicates that the data supplied to the model for these orders may not have been appropriate for the model to produce sensible values. This may be due to disparities between the abundance and consumption data being too large for the model to cope with and produce credible results. The parameter priors for these orders were adjusted to attempt to receive sensible estimates from the model, however all estimates came out higher than expected ($m>3$). Additionally,

the single species model predicted a very low encounter rate parameter for the 'Other' order. This is unexpected, and therefore unreliable, as the order was present in both the sweep-net availability data and the DNA metabarcoding diet data of the predator. This information suggests that the order would be encountered by the predator at a relatively higher rate for them to be present in their diet. Using these parameters would therefore result in highly misleading conclusions regarding the predator's preference for the given orders. However, once placed together with all other prey, the model could produce sensible estimates for both orders (Table 2).

When examining the results of the MSFR model, the resulting posterior parameter values are sensible, suggesting the MSFR approach is more reliable than single species (Table 2). The model predicts a diet close to that shown by the DNA metabarcoding data (fig. 3.), confirming that the parameter estimates of the MSFR are sensible and do not produce misleading conclusions about the predator's diet. Furthermore, the model indicates that prey switching is prevalent within the system ($m > 1$ for all orders). The posterior parameter means (Table 2) suggest that *R. alcyone* encounters Lepidopterans at the highest rate, and therefore the switching parameter is low, indicating that they have a high preference for this order when it is available at even low abundances. Using a selection of posterior parameter values to illustrate the relationship between consumption rates and prey abundances, the predator shows a type I response to Lepidopterans (fig. 4D). However, the large handling time ($t > 0$) combined with the low switching parameter would indicate a very weak sigmoidal response, which is not demonstrated by the functional response graph. The standard deviation of these values is very large, indicating that the consumption rates, and therefore functional response, may not be reliable. This may be the result of the order being highly represented in the diet data, but not in the sweep-net abundance data. Therefore, more accurate sampling of

the abundance of the order may need to be carried out to provide an accurate representation of the predator's functional response. The low handling time and comparatively high encounter rate of Dipterans also led to the order making up a large proportion of the predator's diet under the model predictions, with the predator showing a type II functional response to changing availability of the order, due to the very low handling time parameter of the order, and m being above 1. On the other hand, Hemipterans are prevalent in the sweep-net data, but did not make up a large proportion of the diet according to the DNA metabarcoding results. Regardless of the orders high abundance, the model accurately predicted that they would not make up a large proportion of the predator's diet, which is the result of the large handling time and low encounter rate parameters (Table 2, fig. 3). Furthermore, the predator exhibits a type III response to this order due to the large switching parameter, although, similarly to lepidopterans the standard errors of the consumption rates are very large (fig. 4C). This is also likely due to a large disparity in the orders representation in the sweep-net and metabarcoding diet data. Additionally, a type III response between the predator, Coleopterans and 'Others' was illustrated (fig. 4A and E). The 'kink' at low densities in the functional response for each of the orders demonstrates where the predator would switch their preferences to other orders whilst feeding. However, there is not a levelling off point for either of these orders, which indicates that sampling them at higher abundances would be necessary to fully illustrate the predator's functional responses. Therefore, the results of the MSFR demonstrate that prey switching is common within the system, with strong evidence for a type III response by the predator to changing abundances of three orders. Although the large standard deviations of the consumption rates for several orders indicates that the results may not be reliable.

Although the results did not provide evidence for changes in diet composition due to vegetation structure (fig. 6), a full exploration of the effect of plantation type on the functional response of the predator is not within the scope of this project. Assessment of the consumption rates showed no significant changes due to vegetation structure. This may be due to structural differences between the three groups not being large enough to cause the availability of orders to change drastically enough to see a change in the predator's diet. Expanding the model to investigate the effects of changing habitat on predator preference and prey switching would require PAI, and farm as a random factor, to be included. Currently, incorporating these variables into the model is not possible.

Model limitations

It is unlikely that the arthropod abundance data precisely represented the proportions of arthropods available within the plantations. For example, Lepidopterans, which were highly represented in the bat diet analysis, were rarely encountered in the arthropod abundance data. The disparity between the two may have made it difficult for the model to land on appropriate posterior distributions. Future studies should therefore conduct a more thorough analysis of arthropod abundance, using techniques that are designed to capture the arthropods known to feature in the predator's diet. Moreover, when collecting arthropod abundance data, individuals were identified through morphology as opposed to DNA metabarcoding. Although care was taken to identify individuals correctly, this could have led to slightly inaccurate results with species being identified to incorrect orders. Finally, increasing the number of plantations sampled will allow a more detailed analysis of diet. Currently the model is restricted to five orders to avoid over-parameterisation, due to three parameters being associated with each order. Increasing the number of plantations sampled will allow

more orders to be incorporated, or the diet to be analysed to a species level. This may prove particularly important when developing models for assessing the consumption of pest species, such as brown capsids.

The model assumes that the rank order of arthropod consumption is preserved in the metabarcoding data, which has been shown in previous studies (Deagle et al., 2014; Srivathsan et al., 2016; Thomas et al., 2013). Although this information is useful, relating the metabarcoding results to abundance or biomass of orders eaten would produce more reliable results, particularly when extending the model to include habitat effects. Therefore, carrying out captive feeding trials on the predators in question, and determining whether consumption or prey body mass is correlated with an increased number of sequencing reads in the metabarcoding results, would improve the accuracy of the study. Using this information, the model could be extended to account for the actual proportion of their diet that will be represented by the signal in the metabarcoding data, as opposed to relying on the rank order of orders eaten.

Focussing solely on a predator's functional response can potentially result in misleading conclusions when monitoring ecosystems, as the functional response largely determines the dynamic stability between a predator and their prey (Abrams & Ginzburg, 2000). Predators have an aggregative response to their prey, and using a functional response model that does not take spatial distributions of predators and prey into account may generate biased consumption rates (Nachman, 2006). The cacao plantation system represents a patchy foraging habitat, which likely results in predators aggregating where preferred arthropod abundances are highest. For example, where plantations harbour greater levels of biodiversity, or preferred orders, predators may aggregate and forage in larger numbers. This

would increase their impact on prey populations, and greater competition may also influence a predator's functional response, leading them to switch to alternative prey species within the plantations. Therefore, expanding the model to determine whether the predator has an aggregative response to particular prey may give insight to the spatial distribution of prey, as they may switch to a patchy distribution as predator density increases (Nachman, 2006). Furthermore, the numerical responses of predators can significantly impact the populations of their prey, and acts over a larger timescale than functional and aggregative responses (Asseburg et al., 2006; Lindstrom et al., 2009; Sinclair A. R. E. et al., 2008; Smout et al., 2010). This response includes the predator populations growth, reproduction and mortality, all of which are linked with the availability of their prey, and would require a function to determine the energy consumption of the predator (Asseburg et al., 2006). Without taking the numerical response into account, our model assumes that the predator population remains constant, however their populations are known to vary as a function of prey density (Gascoigne & Lipcius, 2004). Therefore, should generalist predators be used in long-term monitoring of an ecosystem, their aggregative and numerical responses need to be considered. Finally, the model is unable to directly take habitat context into account. This information may be useful when developing ecosystem management strategies, especially due to increasing concerns on the effect of habitat conversion on the populations of both predators and prey. Furthermore, there is the potential for this information to be used as a proxy for arthropod abundance where the information is not available. This would enable our MSFR to become increasingly effective when investigating the influence of habitat composition on a species functional response, and the availability of prey.

Future applications

Ecosystem-based management strategies are becoming increasingly recognised as a necessary approach for monitoring exploited resources by nations and governmental organisations, particularly through the monitoring of higher predator populations as a proxy of their prey. However, these predators are often generalists, and their population dynamics are linked to a wide range of prey (Asseburg et al., 2006). Consequently, they have previously not been viable proxies due to the difficulty in ascertaining the link between their abundance and that of all their prey. Therefore, this MSFR approach may prove an important step forward in ecosystem-based management of lower trophic levels using generalist predators as a proxy for other processes within an ecosystem. Additionally, extending this model through the incorporation of aggregative and numerical predator responses can increase the accuracy of predicting predator-prey relationships. This model could then be applied to a wide variety of ecosystems using relatively simple field data. Furthermore, this study demonstrates that it is possible to gain an understanding of a predator's functional response to their prey where direct predation observations cannot be made.

Cocoa pests are an increasing problem within cacao plantations, reducing yields and resulting in an increasing reliance on pesticides, resulting in wide ranging ecological impacts (Sonwa et al., 2008). Therefore, developing methods of biological pest control is becoming increasingly important to reduce the environmental impact of cacao farming, whilst maintaining yields. Insectivorous bats feeding in these plantations are thought to consume brown capsids (family: *Miridae*), a known cacao pest. Therefore, collecting accurate abundance data on the pest, identifying them in the predator's diet and expanding the model to include environmental variables, could identify the conditions under which predators

switch their preference to the pest. However, our dietary analysis was unable to detect capsids in the diet of *R.alcyone*, which may have been due to the ZBJ primer, which was designed for lepidopterans but works well for most arthropods (Zeale et al., 2010). Therefore, studies wishing to investigate the relationship between the predator and capsids should identify more appropriate primers.

Moreover, disease control through biological means is of increasing interest. DNA metabarcoding analysis shows a high presence of *Anopheles* genus mosquitoes (order Diptera), which are known vectors of malaria (Neafsey et al., 2015), in the diet of *R.alcyone*. Therefore, a similar approach to that mentioned above could be used to determine the conditions under which the predator preferentially attacks disease transmitting insects.

Finally, expanding the model to include all predators, prey and vegetation, future studies can incorporate dynamic consumption by adding the parametrised MSFR to a generalised Lotka-Volterra model (GLVE) (Beisner, Haydon, & Cuddington, 2003). The resulting food web model can then be initialised under different conditions to investigate the potential stable states of the ecosystem. Developing these methods may prove essential when using generalist predators to monitor the health of ecosystems (Asseburg et al., 2006). There is mounting pressure to reduce the negative impacts of agriculture on biodiversity and using these models, it is possible investigate the trade-offs between biodiversity conservation and productivity in agroecosystems. This could result in management techniques that both benefit farmers, through increasing crop yields and decreasing pest species, and biodiversity conservation.

Conclusions

This study highlights the importance of examining generalist predator diets within the context of all available prey. Comparing the posterior parameter estimates of the MSFR to those generated by a traditional single species approach demonstrates that outwith the context of all prey, parameter estimates can vary widely and are often unfeasible. Consequently, results of single species predator-prey models will lead to misleading conclusions and inappropriate management strategies. Therefore, MSFR approaches should be used when investigating the relationship between a generalist predator and their prey. Furthermore, the Bayesian approach is effective in modelling MSFRs as it allows the inclusion of prior biological knowledge to the model in the form of parameter priors, which is particularly useful where real data supplied to the model may not be accurate. Should the approach be used in long term studies, more accurate parameter priors can be used, which will result in increasingly reliable posterior estimates.

The MSFR model provides promising results for predicting the predator's diet, even where there is disparity between the prey availability data and the true diet of the predator, with our predicted diet being close to that of the true consumption (fig. 3). Additionally, the analysis demonstrates the presence of prey switching within the system, with the predator exhibiting a type III functional response to three orders of its prey (fig. 4). Improving the availability data for orders prevalent in the predator's diet will improve the accuracy of the predator-prey relationship. Lepidopterans make up a large proportion of the predator's diet, however they were seldom counted in the sweep net availability data. This results in a large degree of uncertainty in the resulting consumption rates and predator-prey functional response (fig. 4D), improving our understanding of their availability to the predator may reduce this. Finally, the MSFR approach can be used to investigate the response of the predator to

changing prey fields and vegetation structure. However, under these circumstances there was no evidence to suggest that differences in vegetation structures influences the predators diet (fig. 6).

This study demonstrates that an understanding of the predator's functional response to its prey can be achieved with relatively simple field data. However, to increase the accuracy of prey availability data more care needs to be taken when collecting arthropod abundant data, to ensure that those orders abundant in the diet of the predator are sampled adequately. Arthropod identification using DNA analysis will increase the accuracy of the arthropod availability data, and reduce error that could be introduced through morphological identification. Additionally, carrying out captive feeding trials on the predator will allow the relationship between prey abundance/ biomass and the number of sequence reads generated through metabarcoding to be greater understood. Should a link be established, the model can be extended to include a function accounting for the abundance of prey represented by the sequencing reads. The analysis demonstrates the effectiveness in using DNA metabarcoding analysis to supply data to consumption models. This contrasts with previous approaches to diet analysis, which would require direct consumption observations, or intrusive stomach content analysis (Burgar et al., 2014). Therefore, this DNA analysis of faecal samples may be extended to other ecosystems where traditional observations of generalist predator-prey interactions are not possible. These can include other nocturnal mammals, birds and deep-diving marine mammals. Therefore, this approach will make ecosystem monitoring and management through MSFRs possible for those where traditional diet analysis is not appropriate.

This MSFR method can also provide a link between single species and ecosystem models (Smout et al., 2010). However, several limitations of the model need to be addressed before it could be used in the context of ecosystem management. Although the functional response of a predator does impact the dynamics of the prey populations, focussing solely on this response possibly results in misleading conclusions. For example, the model would need to be extended to include both the numerical and aggregative response of the predator to their prey. Currently the model assumes that the density of the predator population remains constant, whereas they vary alongside of their prey's populations (Gascoigne & Lipcius, 2004).

Therefore, this model provides promising groundwork for investigating the relationship between a generalist predator and multiple prey species using simple prey abundance data and DNA metabarcoding consumption data. This approach has the potential to shed a light on the relationship between a predator and key pest species, which can inform biological control management strategies. However, for the consumption predictions to be reliable, more work needs to be done to extend the model to incorporate the numerical and aggregative response of the predator, as well as the behaviour of prey. Finally, should these limitations be addressed, the model posterior parameter estimates produced by the model may be used to inform further studies using similar approaches to investigate the stable states of the ecosystem.

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Appendix I

The resulting posterior parameter estimates for the simulated (fig. 1) and final model (fig.2).

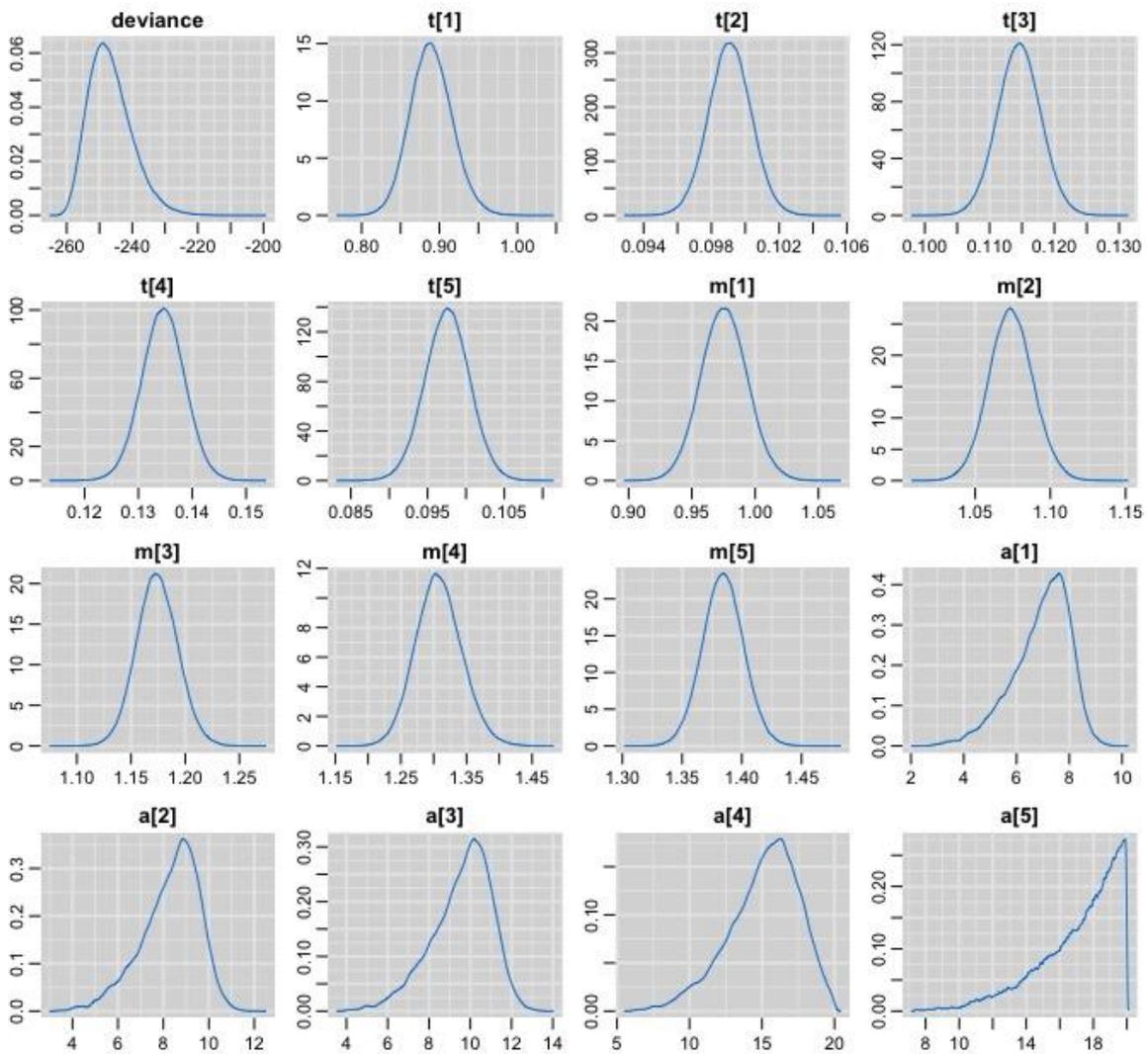


Figure 1. The resulting posterior distributions for each of the parameters using simulated data. 1=Coleopterans, 2=Dipterans, 3=Hemipterans, 4=Lepidopterans and 5='others'. Gelman-Rubin <1.02 for each parameter

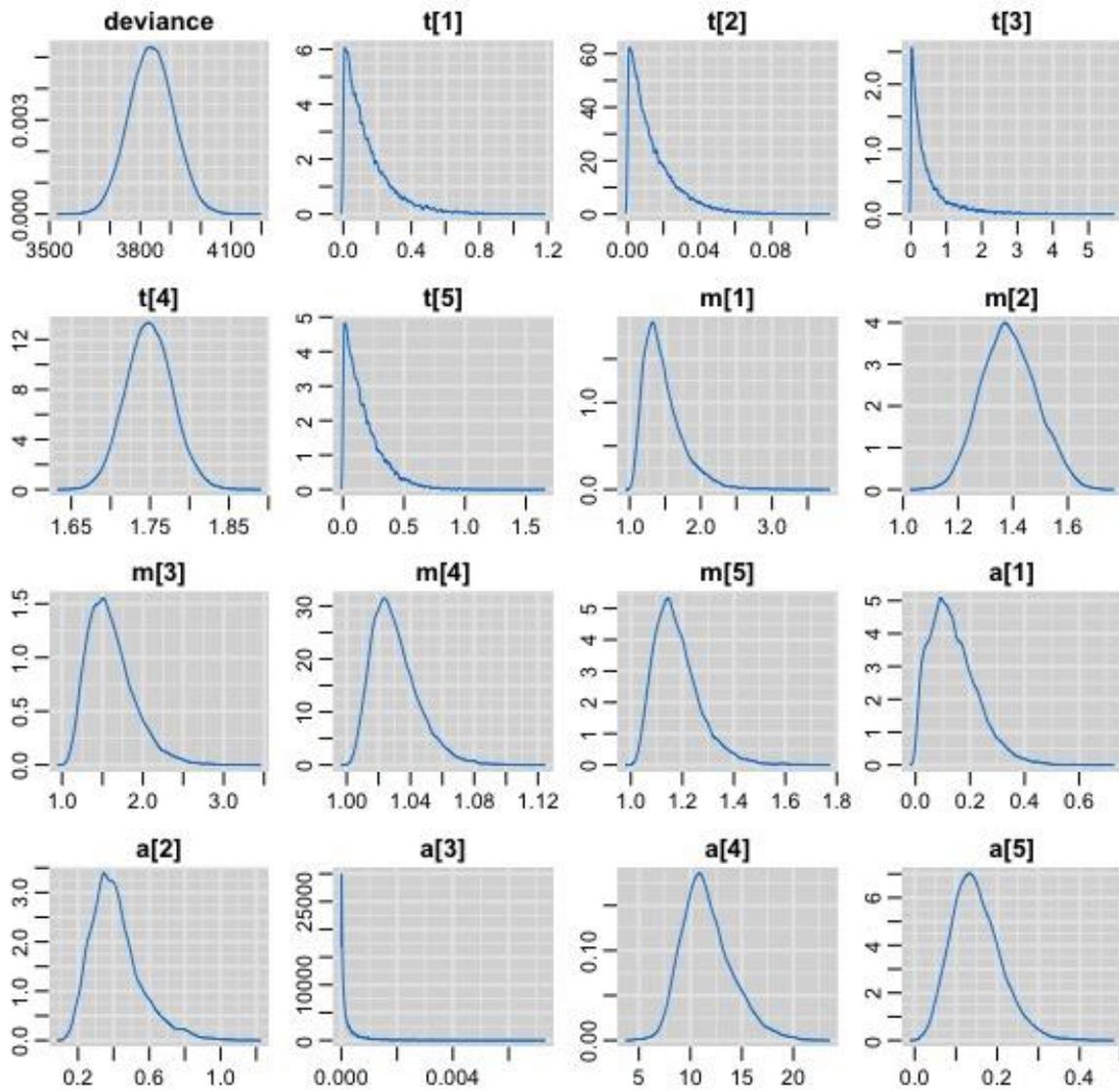


Figure 2. The resulting posterior distributions for each of the parameters using the true data. 1=Coleopterans, 2=Dipterans, 3=Hemipterans, 4=Lepidopterans and 5='others'

Appendix II

See attached R script 'EXAMPLE CODE' for code used to produce MSFR, single species models and plotting the functional response of the predator using data from the MSFR model.