
HOW MUCH PREDATOR GUTS ARE REQUIRED TO PREDICT TROPHIC INTERACTIONS?

A PREPRINT

Anubhav Gupta *

Department of Evolutionary Biology and Environmental Studies
University of Zurich
8057 Zurich, Switzerland
anubhav.gupta@ieu.uzh.ch

Eoin O' Gorman

School of Life Sciences
University of Essex
CO4 3SQ Colchester, UK
e.ogorman@essex.ac.uk

Guy Woodward

Georgina Mace Centre for the Living Planet, Department of Life Sciences
Imperial College London
Ascot, Berkshire SL5 7PY, UK
guy.woodward@imperial.ac.uk

Other authors

XXX XXX
XXX XXX
XXX XXX
XXX XXX

Owen L. Petchey

Department of Evolutionary Biology and Environmental Studies
University of Zurich
8057 Zurich, Switzerland
owen.petchey@ieu.uzh.ch

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Abstract

1) One of the biggest obstacles in food web ecology is the time and effort required to adequately describe the structure of a food web using individual predator guts. Food web models such as the allometric diet breadth model (ADBMs) can be used to circumvent this problem by predicting the interactions based on easily measured characteristics, such as the size of organisms. However, presence-absence data such as predator guts is required to parameterise these food web models, and collecting and analysing these

*Corresponding author

data from the field is an expensive and time-consuming task. Therefore, it is crucial to know how much predator guts is required to parameterise food web models with high accuracy and high precision.

- 2) Here, we explore seven exceptionally well-characterised food webs in the literature and determine the minimum predator guts that would be needed to accurately predict their structure using the ADBM. We use Bayesian computation to parameterise the ADBM, and true skill statistics to measure the goodness of fit, and do so while varying the amount of predator guts used in the parameterisation to test the effect of sampling effort.
- 3) We found that incomplete predator guts can be used to parameterise the ADBM, with the lowest amount of predator guts being 28% of the available predator guts.
- 4) These results suggest that one need not collect such a large quantity of predator guts to predict the structure of a food web, thereby reducing sampling effort considerably, while having little effect on precision or accuracy of predictions.

Keywords predator guts · ADBM · food web accuracy · food web prediction

1 Introduction

Knowledge about the trophic interactions in a food web is crucial in ecology for purposes ranging from identifying keystone species (Jord'an 2009) to quantifying robustness of a food web to species extinctions (Dunne, Williams, and Martinez 2002). This has led to the development of numerous food web models and associated theory (Allesina, Alonso, and Pascual 2008; Cohen, Newman, and Steele 1985; Gravel et al. 2013; Petchey et al. 2008; Tamaddoni-Nezhad et al. 2013). Along with inferring missing links in an observed food web, such food web models are also increasingly used for ecological forecasting (Hattab et al. 2016; Lindegren et al. 2010) and for understanding the underlying mechanism governing trophic interactions in the wild (O’Gorman et al. 2019).

Although food web models are constructed using prior theory about the factors that determine trophic interactions, empirical data about interactions are required to parameterise a model. For example, Petchey et al. (2008) and Gupta, Furrer, and Petchey (2022) used presence-absence information about trophic interactions to parameterise the allometric diet breadth model and thereby predict species interactions. Such empirical information about interactions can come from diverse set of methods such as gut content analysis (Peralta-Maraver, Lopez-Rodriguez, and de Figueroa 2017), stable isotope ratio analysis of tissues (Layman et al. 2007), experimentation (Warren 1989), DNA metabarcoding of gut contents or faeces (Roslin and Majaneva 2016) and literature research (Gray et al. 2015b; Cohen and Mulder 2014a; Goldwasser and Roughgarden 1993a) but each of these sources of information about trophic interactions has serious shortcomings, hindering

the advancement of the field. For example: stable isotope ratio analysis of the organism’s tissue does not give direct taxonomically resolved information of the diet of that organism, but rather it provides approximate trophic position of that species in the food web (Wada, Mizutani, and Minagawa 1991; Jennings and van der Molen 2015) and although mixing models can be used to determine what prey items are most likely fed upon by a predator, this results in uncertainty in the estimates (Kadoya, Osada, and Takimoto 2012; Crawford, McDonald, and Bearhop 2008). Similarly, more recent approaches using DNA metabarcoding may give much higher taxonomic resolution but present other challenges, such as an inability to resolve secondary predation or cannibalism (Pompanon et al. 2012; Nielsen et al. 2018) which are common in nature and also being prone to environmental contamination (e.g. DNA in the water swallowed along with DNA from an aquatic consumer’s prey cannot be differentiated from actual prey) (Kelly et al. 2014). Furthermore, construction of food webs via literature review, which is one of the most common practices in food web research, can lead to false positives—links included when in reality no link would occur because it makes an assumption that the species interactions inferred from a system will occur in another system as well (Gray et al. 2015b; Cohen and Mulder 2014b; Goldwasser and Roughgarden 1993b). It is unsurprising given the limitations of these proxy or inferential approaches that authors such as Nielsen et al. (2018) have shown that gut content analysis method has a better match with real diet when compared to other methods.

Although gut content analysis is viewed as the “gold standard”, acquiring such food web data from direct gut content analysis is extremely time consuming and expensive (Gray et al. 2015b) and it also requires high skill levels in taxonomic identification, often involving dissection and microscopy techniques (Hyslop 1980). The perception that this is unavoidably laborious and costly is also in part due to the assumption that many gut contents must be collected and analysed in order to be confident that the majority of possible trophic links among species have been observed. Most studies fail to quantify the effort needed, with yield-effort curves being the exception rather than the rule and those that have been done often point to the apparent need for hundreds or thousands of guts to be analysed to fully capture a food web’s structure. Hence, it is of huge importance to know the minimum number of predator guts required to parameterise a food web model with high accuracy and high precision: this would enable researchers to allocate resources more effectively a priori, and even having a rough rule of thumb as to when is a good point to stop collecting any further empirical data on the food web is far better than the current common practice of simply taking a fixed set of samples with on yield-effort analyses being undertaken.

Therefore, the key question we are interested in answering is how much presence-absence information, in the form of predator guts, is required to infer food web structure from a food web model with high accuracy and high precision? In other words, how many samples of predator guts should one collect from the field to parameterise a food web model? To answer this question, we use different amount of predator guts to parameterise the allometric diet breadth model (ADBM) thereby predicting trophic interactions in seven different food webs using rejection approximate Bayesian computation, and calculate the minimum number

of predator guts to infer food web structure. Our study provides a guideline on how many predator guts are required to predict food web structure using a food web model.

2 Materials and Methods

We present the empirical food webs, the allometric diet breadth model (ADBM), and the predator guts used to infer the trophic interactions. We also give a detailed account of using partial predator guts to parameterise the ADBM using rejection approximate Bayesian computation (ABC). We assessed model predictions using the true skill statistic for comparison across the food webs.

2.1 The Empirical Food Webs

In our study, we used food webs for which predator guts are available at an individual level and data that is or that we could make FAIR (Findable Accessible Interoperable Reusable; Wilkinson et al. (2016)). In our study, first, we consider food webs where nodes are size classes i.e. individuals are aggregated into these size classes based on their body size. A feeding link occurs between two size classes if at least one prey item within a size class was found in the gut of another size class of predator, irrespective of the taxonomy of the individuals. We used this approach because of several reasons such as to take account the ontogenetic shift in the diet of a predator (Woodward et al. 2010), individual-based interaction based on body size which would not been considered if nodes were aggregated based on taxonomy as a taxonomic node can have a large variation in the body size. Food webs aggregated using size can be used to model the impacts of commercial exploitation on marine ecosystems (Jennings and Brander 2010). Second, we also consider food webs where nodes are aggregated based on the taxonomy of the individuals as this is the most common way of constructing food webs in food web ecology.

Our study food webs are freshwater food webs except the Celtic Sea food web which belongs to a marine ecosystem. Most of the food webs are dominated by invertebrates except Celtic Sea which is dominated by fishes and Tadnoll Brook which is dominated by fishes as well as invertebrates. The food webs vary in the number of nodes, trophic links, connectance and body sizes (Table 1).

Invertebrates in freshwater food webs were collected using Hess or Surber sampler, whereas fishes were caught with electrofisher, and anaesthetised using 2-phenoxyethanol in freshwater food webs. In case of the Celtic Sea, trawling was used to catch fishes.

The foreguts of the collected invertebrate predators were dissected and examined under the microscope. Regression equations were used to convert predator and prey lengths to the respective body masses. In case if the prey items were too highly digested for body lengths to be measured reliably, previously established regressions based on head capsule width were used as an alternative linear dimension. More detailed description of these food webs is present in Gilljam et al. (2011).

Table 1: Information about the empirical food webs. AG: Some information will be updated.

Common food web name (Original Publication)	Location	Predation matrix source	Body size source	General ecosystem	Number of nodes	Number of links	Connectance	Body size range (mg) (approximate)
Broadstone Stream (Woodward et al. 2010)	England, UK 51°05'N 0°03'E	Guy Woodward 2021	Guy Woodward 2021	Freshwater	29	185	0.24	10^{-7} to 10^2
Celtic Sea (Barnes et al. 2016)	British Isles and French coastal shelf 50°50'N 08°00'W	Barnes et al. 2016	Barnes et al. 2016	Marine	48	386	0.17	10^{-2} to 10^4
Tadnoll Brook	England, UK 50°41'N 02°19'W	NA	NA	Freshwater	59	485	0.14	10^{-6} to 10^5
Afon Hirnant (Woodward et al. 2010)	Wales, UK, 50°52'N 03°34'E	David H. Figueora 2022a	David H. Figueora 2022a	Freshwater	33	221	0.20	10^{-6} to 10^2
Coilaco (Figueora 2007)	Chile 39°17'S 71°44'W	David H. Figueora 2022b	David H. Figueora 2022b	Freshwater	45	123	0.06	10^{-6} to 10^2
Guampoe (Figueora 2007)	Chile 39°23'S 71°41'W	David H. Figueora 2022b	David H. Figueora 2022b	Freshwater	44	139	0.07	10^{-6} to 10^3
Trancura (Figueora 2007)	Chile 39°26'S 71°32'W	David H. Figueora 2022b	David H. Figueora 2022b	Freshwater	35	78	0.06	10^{-6} to 10^1

2.2 Allometric Diet Breadth Model (ADBM)

The allometric diet breadth model (ADBM) is based on optimal foraging theory, specifically the contingency foraging model (MacArthur and Pianka 1966). We chose this model because it can predict species interactions based on an easily measurable trait body size. The ADBM predicts the set of prey types (e.g. species or sizes classes) a consumer should feed upon to maximise its rate of energy intake (Petchey et al. 2008). The foraging variables in the model are: energy content of the resources, handling times of the prey, space clearance rate, and prey densities. These are allometrically scaled to the body sizes of the species. Further details on the foraging rules defined in the ADBM and ADBM’s predictive power across different food webs can be found in Petchey et al. (2008).

2.3 Assessment of prediction

The accuracy of the predicted diet of the predators was measured using a widely used accuracy measure in food web ecology namely true skill statistic (TSS) (Gray et al. 2015b; Gravel et al. 2013; Gupta, Furrer, and Petchey 2022). We chose this metric because it takes into account the true and false predictions of both the presence and absence of links defined as:

$$TSS = \frac{ad - bc}{(a + c)(b + d)}$$

where a is the number of observed links that are predicted by the model (true positives), d is the number of observed absences of links that are correctly predicted (true negatives), b is the number of false positives, and c is the number of false negatives. The TSS ranges from -1 to 1 , where $+1$ indicates a perfect prediction. A TSS value of zero or less indicates a performance no better than random (Allouche, Tsoar, and Kadmon 2006).

2.4 Inferring food web using partial predator guts

From an empirical dataset of predator guts, we take a random sample of gut contents of specific size (see below) to create a partial predator guts dataset. We then fit the ADBM to this partial dataset.

To fit the ADBM to partial predator guts dataset, we used the rejection approximate Bayesian computation method we previously developed in Gupta, Furrer, and Petchey (2022) to accept a

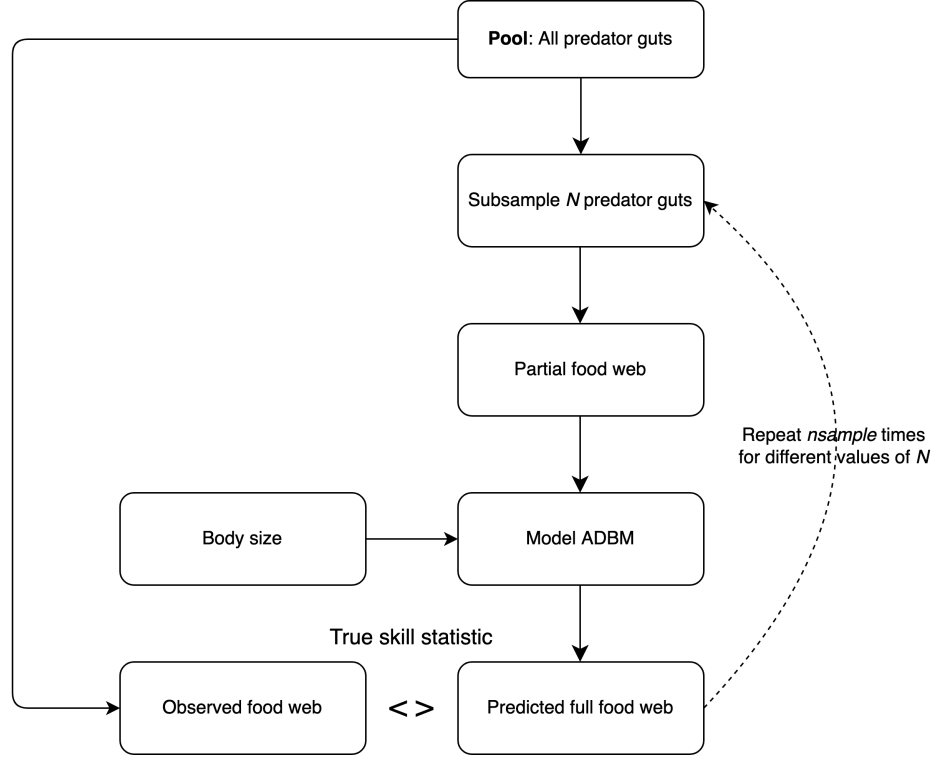


Figure 1: Flowchart of the subsampling method implemented to predict the full food web from the food web model using the predator guts.

parameter value from a prior distribution which would have resulted in the minimum distance, where distance = 1 - TSS. The true skill statistic was computed between the diets predicted from the ADBM, and those observed in the sampled predator guts. We repeated this process n ($= 100$) times for every i number of guts, where i lies between 1 and total number of predator guts in the pool.

Input:

- Predators $P : P = \{p_1, p_2, \dots, p_k\}$
- A pool of predator guts $G : G = \{g_1, g_2, \dots, g_n\}$, where g_n is the observed diet matrix containing ones and zeros.
- A model prediction $model(\theta) : ADBM(\theta) = \{d_{p_1}, d_{p_1}, \dots, d_{p_k}\}$, where d_{p_k} is the predicted diet matrix of predator k containing ones and zeros.

- 142 • A summary statistic $s(x) : s(x) \subseteq model(\theta)$, where $s(x)$ is the diet of some or all of the
143 predators.
- 144 • A distance function $d(x_i, y) : d(x_i, y) = 1 - TSS(x_i, y)$, which quantifies how close the
145 observed diet is to the predicted diet of some or all of the predators.
- 146 • An observed food web $Y : Y = \{d'_{p_1}, d'_{p_1}, \dots, d'_{p_k}\}$, where d'_{p_k} is the observed diet matrix of
147 predator k containing ones and zeros.

148 *Sampling:*

149 for $i = 1, \dots, tgut$ where $tgut$ is the total number of predator guts in the pool G

- 150 • for $j = 1, \dots, nsample$ where $nsample$ is the number of independent samples to be drawn
 - 151 – Subsample a set of predator guts $y = \{g_1, g_2, \dots, g_i\}$ from the pool of predator guts G
 - 152 – for $k = 1, \dots, npar$ where $npar$ is the number of parameter values to be sampled
 - 153 * Draw a set of parameter values θ_k from the prior distribution $\pi(\theta)$
 - 154 * Compute the model result $x_k = model(\theta_k)$
 - 155 * Compute $s(x_k)$ and $d(s(x_k), y)$
 - 156 – Accept θ_j , which results in the $min_k\{d(s(x_k), y)\}$
 - 157 • Compute $TSS_i(x, Y) = \{TSS(x_i, Y) : x_i = ADBM(\theta_j), \theta_j \text{ computed from previous step}\}$
158 using the accepted $\theta_1, \dots, \theta_{nsample}$

159 *Output:*

160 The TSS between observed and predicted food webs, and the posterior parameter distributions
161 for every i number of predator guts drawn from the pool of predator guts.

162 2.5 Computing the minimum number of predator guts

163 Using TSS of the model predicted food webs for different number of predator guts, we computed the
164 number of predator guts that results in the mean TSS equal to the 95% of the mean TSS achieved
165 by the model using all the predator guts available in the pool for a food web. We call this number
166 of predator guts as the minimum number of predator guts.

2.6 Standardising sampling level of the food webs

Since the seven food webs have different levels of sampling effort, with Broadstone Stream being the most sampled among all, and every other food web being undersampled when compared to the Broadstone Stream food web (SI Fig. S2), we used the R *vegan* package to account for the undersampling with respect to the Broadstone Stream food web. We fitted the link accumulation curves using the `fitspecaccum` function to a set of nonlinear regression models suggested in Dengler (2009) and used the AIC criteria for model selection. We then extrapolated the link accumulation curves for all the food webs except the Broadstone Stream and computed the corrected number of predator guts that would have resulted in the gradient of the link accumulation curve equal to the gradient of that of the Broadstone Stream when all the predator guts were used. We also calculated the corrected number of trophic links corresponding to that corrected number of predator guts. For the food webs, we calculated the undersampling factor which is equal to the ratio of corrected number of predator guts to the number of predator guts in the pool. Using the undersampling factor, we further calculated the corrected minimum number of predator guts which is equal to the product of the undersampling factor and the minimum number of predator guts.

3 Results

We first present how the accuracy of the food web model in predicting trophic interactions varies with increasing amount of predator guts provided to the food web model. We investigate how the minimum number of predator guts varied with number of trophic links and number of species.

The true skill statistics of the food webs predicted by the ADBM using incomplete predator guts improved quickly for lower number of predator guts (Fig. 2). Furthermore, the width of the prediction interval of the true skill statistics decreased with increasing number of predator guts with the mean TSS asymptoting to the maximum mean TSS achieved by the ADBM when all the predator guts was used. Although the maximum TSS varied among the food webs, the qualitative increase in the TSS was the same.

For Broadstone Stream food web, with only 381 predator guts, which is 38% of the total predator guts, the ADBM predicted the food web with the mean TSS of 0.74. This was equivalent to 95% of the mean TSS (0.78) achieved using complete predator guts (Fig. 2(a)): i.e. the main

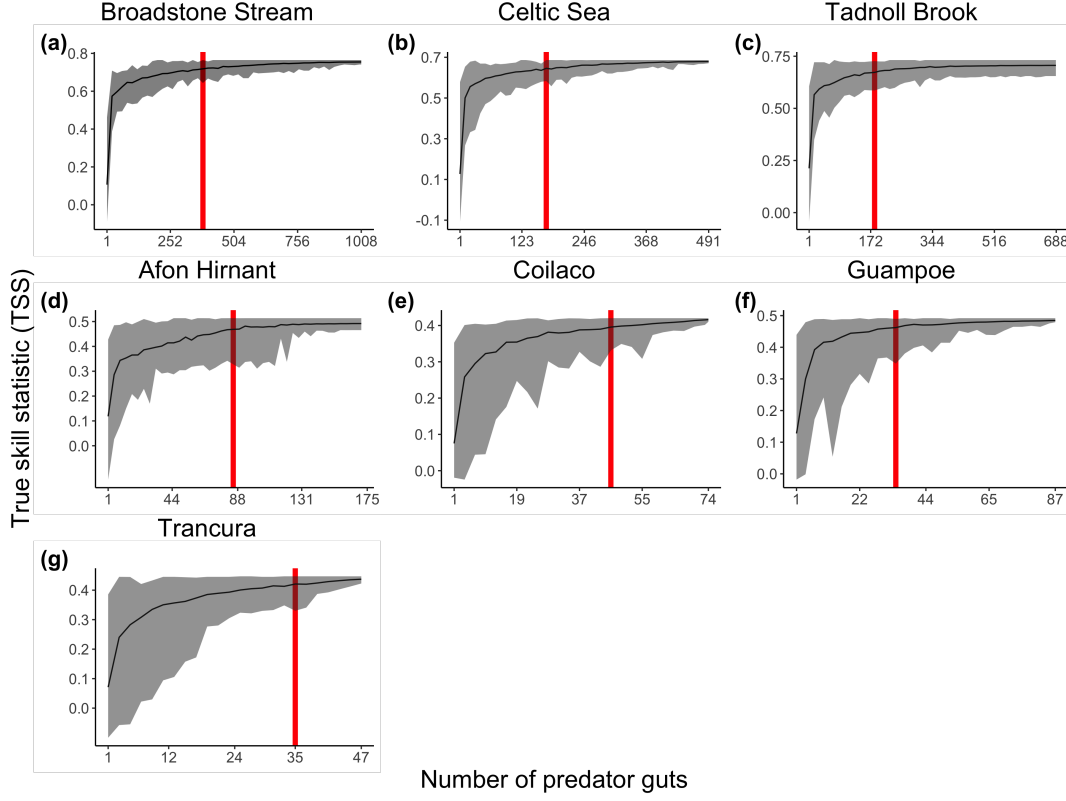


Figure 2: Accuracy of the predicted food web measured using the true skill statistic, predicted by the ADBM parameterised using predator guts. Line and shaded grey region represents the mean and the prediction interval corresponding to 100 independent samples respectively. Red line represents the number of predator guts required to achieve a TSS of 95% of the maximum TSS.

characteristics of the food web could be captured with about 1/3 of the effort used in the original study. In case of the Celtic Sea food web, only 171 predator guts which is 35% of the total predator guts was required by the ADBM to predict food web with TSS equal to 95% of the mean TSS (0.68) achieved using complete predator guts (Fig. 2(b)).

The minimum number of predator guts was not significantly related to number of trophic links (Fig. 3 (a)) and the number of species (Fig. 3 (b)). Similarly, the corrected minimum number of predator guts was not significantly related to corrected connectance, corrected number of trophic links and number of species respectively (Fig. 3 (c, d)). Correcting for the undersampling in the food webs improved the fit between the minimum number of predator guts and the number of trophic links from $R^2 = 0.13$ (Fig. 3 (a)) to $R^2 = 0.43$ (Fig. 3 (c)).

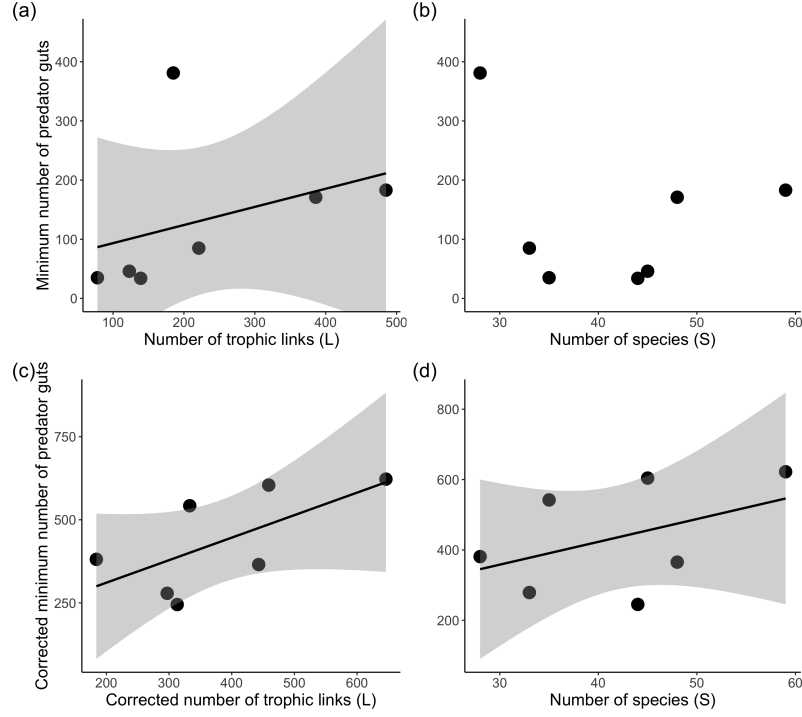


Figure 3: (a, b) Minimum number of predator guts (i.e the amount of predator guts used in order to ensure 95% of the maximum TSS) plotted against number of trophic links (L) and number of species respectively. (c, d) Corrected minimum number of predator guts (i.e. the minimum number of predator guts which takes into account the undersampling level of the food webs) plotted against corrected number of trophic links and number of species (S) respectively. Solid lines are linear regression ((a) $t = 0.876$, $df = 5$, $P = 0.421$; (c) $t = 1.923$, $df = 5$, $P = 0.113$; (d) $t = 1.099$, $df = 5$, $P = 0.322$) and grey region represents 95% confidence intervals.

4 Discussion

We have demonstrated how a food web model can be used to predict the full structure of a food web when incomplete data about trophic interactions is available, which is true in most of the real food webs. This can help inform how much predator guts to actually collect when we are using a food web model to infer trophic interactions for an ecosystem with a given number of species. A future development could be to make the same assessment using other food web models, and to also use food web data other than predator guts to parameterise those models.

Our study provides a ballpark figure of the minimum number of predator guts that need to be sampled to predict the structure of a food web using a food web model for an ecosystem with a

214 given number of species. For instance, Fig. 3 (d) can be used as a rough estimate of how many
 215 predator guts needs to be collected to predict food web structure using a food web model for a given
 216 number of species. This would lead to a reduction in the hundreds of predator guts that would have
 217 to be collected in the first place (Ings et al. 2009), thereby saving considerable time and resources.

218 In our study, we have implemented the approach only with the ADBM, which is a model based
 219 on size rules. Therefore, we suspect to get a similar result (i.e. minimum number of predator guts
 220 for a food web) for a different food web model based on size rules such as the niche model by Gravel
 221 et al. (2013). For a given food web, some food web models might do better job at predicting its
 222 structure as compared to other food web models, so we suggest to extend our approach to other food
 223 web models such as niche model (Williams and Martinez 2000; Gravel et al. 2013; Allesina, Alonso,
 224 and Pascual 2008) and nested hierarchical model (Cattin et al. 2004). A future prospect could be
 225 to study how well different food web models' prediction accuracy vary with different amount of
 226 predator guts. This can also help in making decision as to which food web model to chose from for
 227 a given a set of predator guts. We suspect the relationship (i.e shape of the curve) between the
 228 TSS of the predicted food web and the number of predator guts might vary within food web models
 229 because of the difference on the set of rules used to define those models and how well those rules
 230 explain the food web structure. For example: a food web model based on body size trait would
 231 require less amount of data to predict a size structured food web as compared to a food web model
 232 based on trait other than body size.

233 Some studies have presented how the accuracy of food web prediction change when the amount
 234 of food web data is varied (Gray et al. 2015b). For example Desjardins-Proulx et al. (2017) has
 235 used predictive machine learning models and Caron et al. (2022) has used predictive traits-based
 236 models on partial knowledge of interactions to reconstruct a food web accurately, in contrast to our
 237 study where we used a mechanistic food web model.

238 In all of the seven food webs, the ADBM was able to infer the trophic interactions using
 239 incomplete predator guts because the presence absence information from the predator guts was still
 240 sufficient to constrain the possible model parameter values of the ADBM that best explained the
 241 predators' diets. Although in theory the ADBM can predict trophic interactions using only body
 242 sizes of organisms as it is based on set of foraging rules, it still requires some presence absence data

243 to constrain the posterior parameter space thereby making more accurate predictions (Petchey et al.
244 2008).

245 To characterise trophic interactions which are rare in the nature one would require more
246 predator guts to observe those interactions as compared to characterising trophic interactions which
247 are more frequent in the nature. The model is perhaps able to infer these rare interactions using a
248 relatively lower number of predator guts which one might have inferred directly from the predator
249 guts only after collecting a large number of gut content samples.

250 Like any other food web models, the food web model used (the ADBM) cannot explain all
251 the interactions in any observed food web that it has been fit to. The foraging rules it encodes are
252 based on the body size and have particular structure and assumptions; not all of these are met by
253 all observed interactions (Petchey et al. 2008). For example, the ADBM can only predict diets that
254 are contiguous with respect to the size of prey. I.e. it cannot predict that a predator will consume
255 organism of size 1 and 3, and not organism of size 2. Hence, if the observed diets are not contiguous
256 when prey are ordered by their size, the estimation process could lead to a lower value of the TSS
257 (Gupta, Furrer, and Petchey 2022).

258 Furthermore, the observed data may be missing links, e.g. links that rarely occur. Some of
259 these food webs are undersampled (SI Fig. S2) suggesting those food webs might be missing these
260 rare trophic links, and the false positives from a model might be a correctly predicted link. A future
261 prospect could be to incorporate other sources of presence-absence data such as stable isotope ratio
262 (Layman et al. 2007), DNA metabarcoding (Roslin and Majaneva 2016), literature review (Gray et
263 al. 2015b; Cohen and Mulder 2014a; Goldwasser and Roughgarden 1993a) and experimentation
264 (Warren 1989) to complement any trophic links that were missed by the gut content method.

265 We expected a positive relationship between the minimum number of predator guts and the
266 number of trophic links and number of species respectively. However, we did not find such relation
267 (Fig. 3 (a, b)). We suspect this is due to the possibility that the food webs are sampled at different
268 level (SI Fig. S2), with Broadstone Stream being the most sampled among all the food webs. Taking
269 into account the undersampling factor resulted in a better fit between the corrected minimum
270 number of predator guts and corrected number of trophic links and number of species respectively
271 (Fig. 3 (c, d)), however did not result in a relationship. This could be due to heterogeneity in the

272 predator guts across food webs and heterogeneity among food webs. First, if less number of prey
 273 items are present in a predator gut then more number of predator guts would need to be collected
 274 on an average to quantify the diet of that predator. Second, a food web which has a high proportion
 275 of generalist species would require a high number of predator guts on average to characterise the
 276 food web structure as compared to characterising the structure of a food web which has a high
 277 proportion of specialist species.

278 In our study, we have not considered uncertainty which is involved in analysing the predator
 279 guts (Baker, Buckland, and Sheaves 2014). For example, there are sometimes loose tissues that are
 280 not identifiable and cannot be assigned to a specific prey item with certainty. There are factors
 281 such as sample size of consumers, mechanical prey handling, differential digestion and evacuation
 282 rates of different prey types and volumes, and the ingestion order that in combination result in an
 283 unquantifiable error which is difficult to interpret in the predator diet (Hyslop 1980; Rindorf and
 284 Lewy 2004; Baker, Buckland, and Sheaves 2014). Therefore, the next step could be to incorporate
 285 these different factors of uncertainty in parameterising the model and to understand how these affect
 286 the accuracy of the predicted food webs.

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291 6 Author contributions

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