OIKOS

Research article

Prey nutrient content is associated with the trophic interactions of spiders and their prey selection under field conditions

Jordan P. Cuff[1,2,3], Maximillian P. T. G. Tercel[1,4], Ian P. Vaughan[1], Lorna E. Drake[1], Shawn M. Wilder[5], James R. Bell[2], Carsten T. Müller[1], Pablo Orozco-terWengel[1] and William O. C. Symondson[1]

[1]School of Biosciences, Cardiff University, Museum Avenue, Cardiff, UK
[2]Rothamsted Insect Survey, Rothamsted Research, West Common, Harpenden, Hertfordshire, UK
[3]School of Natural and Environmental Sciences, Newcastle University, Newcastle-upon-Tyne, UK
[4]Durrell Wildlife Conservation Trust, Les Augrès Manor, La Profonde Rue, Trinity, Jersey, Channel Islands
[5]Department of Integrative Biology, 501 Life Sciences West, Oklahoma State University, Stillwater, OK, USA

Correspondence: Jordan P. Cuff (jordancuff@gmail.com)

Oikos
2024: e10712
doi: 10.1111/oik.10712

Subject Editor: James D. Roth
Editor-in-Chief: Pedro Peres-Neto
Accepted 23 September 2024

Consumers are thought to select food resources based on their nutritional content. While laboratory experiments have explored this, the nutritional dynamics of invertebrate predators have been scarcely studied in the field given various methodological constraints. The intersection of these nutritional dynamics with predator traits is also poorly characterised, leading to many gaps in our understanding of how different predators forage and feed in natural systems. Here, we integrate dietary metabarcoding with prey macronutrient (protein, lipid and carbohydrate) content and abundance to assess how nutrients and predator traits (sex, life stage and taxonomy) interactively drive prey preferences in the field, using spider–prey interactions as a model system. Different spider genera, sexes and life stages had nutritionally distinct diets. Our analyses demonstrated disproportionate foraging (selection and avoidance) for prey rich in different macronutrients, with the nature of these relationships differing between spider taxa, life stages and sexes. This may be explained by niche differentiation among spider groups, driven by biases toward prey rich in different nutrients, or nutrient-specific foraging in which individual spiders vary their nutritional preferences to redress deficits, although further evidence is required to confirm this. This insight into the nutritional dynamics of generalist invertebrate predators extends our understanding beyond lab-based behavioural assays and provides a novel framework for other complex real-world systems.

Keywords: DNA metabarcoding, ecological network, food web, nutrient-specific foraging, prey choice, trophic ecology

Introduction

The dietary choices made by individual predators are an important determinant of their fitness, as well as food web structure and function (Toft 1999, Harwood et al. 2004,

Davey et al. 2013, Cuff et al. 2022). Theory suggests that prey choice is driven, or at least affected, by the need to redress or avoid nutritional deficits to maximize fitness, termed nutrient-specific foraging (Greenstone 1979, Mayntz et al. 2005, Schmidt et al. 2012, Rho and Lee 2015, Rendon et al. 2019). This could be achieved either by maintaining a consistently balanced intake of nutrients (e.g. by specialist foragers), or by selecting resources to redress imbalances (e.g. by generalist foragers; Despland and Noseworthy, 2006, Pompozzi et al. 2019, Rendon et al. 2019). Most generalist foragers need to feed on a variety of resources since no individual resource is likely to be nutritionally optimal and solely fulfil the needs of that forager.

Nutrient-specific foraging is conceptually consistent with optimal foraging theory, particularly in the assumptions that fitness drives foraging, and is determined by heritable components, adapting rapidly to a changing environment (Pyke 1984, Simpson et al. 2004, Jensen et al. 2012). While nutrient-specific foraging can occur at any stage of predation, from the selection of specific prey to the extraction of certain nutrients from specific tissues (Pekár et al. 2010, Kohl et al. 2015), evidence identifies selection of specific prey as the primary means (Mayntz et al. 2005). The nutritional dynamics of vertebrate predators have been studied in wild populations (Kohl et al. 2015), but invertebrate studies have often been restricted to controlled laboratory feeding trials (Mayntz et al. 2005, Fanson et al. 2017, Rendon et al. 2019), in part because of the technical challenges of studying invertebrate diets in nature (Cuff et al. 2023a). The disparity in results between lab and field studies of invertebrate nutrition confounds comparison of these data and the application of lab-based findings to natural systems (Wiggins et al. 2018).

Characterisation of nutritional dynamics in invertebrates under field conditions would strengthen our understanding of prey choice in natural systems and provide greater connectivity between the behaviour of individuals and its consequences for trophic network structure and function. Progress in studying these dietary dynamics in nature has been hindered because trophic links become more complex, unpredictable and difficult to measure under field conditions. As such, the nutritional dynamics of invertebrates under field conditions and their influence on invertebrate trophic networks are poorly understood. We have overcome this impasse by relating dietary data generated by high-throughput sequencing of consumer gut content DNA (Pompanon et al. 2012) to prey nutrient contents determined by micro-scale macronutrient analysis (Cuff et al. 2021b), and in-field prey abundances (Cuff et al. 2024b). Using prey choice null network models (Vaughan et al. 2018) and multivariate modelling (Wang et al. 2012), we assessed the nutritional dynamics of spiders in the field. This integrative approach helps connect individual foraging behaviour with the complexity of trophic interactions in nature. We specifically tested the following hypotheses:

1) The prey consumed by different demographic (i.e. sex), ontogenic (i.e. life stage) and phylogenetic (i.e. taxonomic) groups of spiders vary in their macronutrient contents.
2) Prey macronutrient contents explain differences in diet composition between spider groups, suggesting long-term interspecific differences in nutrient requirements.
3) The average macronutrient content of prey consumed is not simply a reflection of the prey available (i.e. spiders are consuming prey of different nutritional proportions than would be expected if they were to forage randomly) and deviation from random foraging differs in nutrient-bias and magnitude between spider groups.
4) Differences in the nutritional niche of spider groups align with their prey selectivity, indicative of nutrients driving foraging ecology.

Material and methods

Fieldwork

Money spiders (Araneae: Linyphiidae) and wolf spiders (Araneae: Lycosidae), the two most abundant spider groups in this study, were visually located along transects in two adjacent barley fields at Burdons Farm, Wenvoe in south Wales (51°26′24.8″N, 03°16′17.9″W) and collected from occupied webs and the ground in daylight hours between April and September 2018. Each belt transect was adjacent to a randomly selected crop tramline and were distributed across the entire field and ran its length. The areas searched were 4-m^2 quadrats at least 10 m apart and all observed linyphiids and lycosids were collected. The 300 spiders taken forward for molecular dietary analysis in this study were taken from 64 randomly selected locations along the aforementioned transects. Following collection of spiders, 4 m^2 of ground and crop stems was suction sampled in each of these 64 sampling locations for approximately 30 s, with the collected material emptied into a bag and any organisms immediately killed with ethyl-acetate. Suction sampling used a 'G-vac' modified garden leaf-blower. All material was later frozen at −20°C for storage before sorting in the lab. Sticky traps were also collected, but were not used in this study as suction sampling was found to represent the interactions of spiders more closely (Cuff et al. 2024b). These invertebrates were collected for background population densities and macronutrient analysis, not for molecular dietary analysis.

All invertebrates were identified to family level using morphological keys: Araneae (Roberts 1993), Diptera (Ball 2008), Coleoptera (Duff 2012), Hymenoptera (Goulet and Huber 1993), Hemiptera (Unwin, 2001), Collembola (Dallimore and Shaw 2013) and Chilopoda (Barber 2008). Further identifications were not carried out due to the inability to identify some of the invertebrate groups beyond family level via the associated metabarcoding-derived dietary data (e.g. Sciaridae), and the difficulty associated with finer taxonomic resolution of many damaged or immature specimens. The only taxa not identified to family level were springtails of the superfamily Sminthuroidea (Sminthuridae and Bourletiellidae, which were often indistinguishable following

suction sampling and preservation due to destruction of the fine features necessary to differentiate them) which were left at super-family, mites (many of which were immature or in poor condition, or lacked appropriate taxonomic keys) which were identified to order level and wasps of the superfamily Ichneumonoidea (which were identified no further due to obscurity of wing venation following damage during collection and storage); in these cases, these taxonomic assignments were used alongside the family-level assignments of other taxa for later analyses.

Extraction, amplification and sequencing of DNA from the individually collected spiders, and its bioinformatic analysis are described by Cuff et al. (2022) and Drake et al. (2022) and are also detailed in the Supporting information. In short, dietary metabarcoding was carried out using two primer pairs, one excluding spider DNA and the other amplifying it, to overcome the problem of overamplification of predator DNA whilst still including spider-spider interactions (Cuff et al. 2023a). Amplified DNA was sequenced on an Illumina MiSeq V3 2x300 cartridge, and resultant data screened for false positives following bioinformatic processing via minimum sequence copy thresholds applied according to read counts in controls and control DNA counts present in samples (Drake et al. 2022).

Macronutrient determination

Specimens were taken for macronutrient analysis from the same suction samples collected for invertebrate community identification. Representatives were taken from each family found in the community samples for which specimens were intact, in visually good condition and relatively clean of soil and other potential contaminants. If specimens were from a relatively uncommon family but unclean, soil and other surface contaminants were physically removed, and the specimen then momentarily dipped in water to remove remaining surface contaminants without greatly dislodging surface lipids. Digestible macronutrient contents were determined following the MEDI protocol (Cuff et al. 2021b, Cuff and Wilder 2021) with minor alterations to account for the small size of most of the invertebrates processed (Cuff 2021) and with the omission of exoskeletal measurement. During extraction, half volumes (i.e. 500 µl) of solvents were used. For the lipid assays, 15 µl of sulfuric acid was added for a 15 min incubation, followed by only 200 µl of vanillin reagent to increase the concentration and development of analyte for more accurate readings from smaller invertebrates. Lipid and protein standard series were diluted to 50% of the concentration specified in the original protocol (i.e. 0–1 mg ml^{-1}). Carbohydrate assays used 140 µl of reagent with 30 min incubation at 92°C followed by a further 30 min at room temperature. Carbohydrate standard series were diluted to 1% of the concentrations specified in the original protocol (i.e. 0–0.02 mg ml^{-1}) to ensure signals overcame the higher limit of detection relative to typical invertebrate carbohydrate content. Mean macronutrient contents were calculated for each taxon and converted into proportions of the total macronutrient mass detected for each taxon (i.e. macronutrient values are given as % total macronutrient mass). Macronutrient data were allocated to each prey taxon. Where macronutrient data were not available for a family (due to no or very few individuals being present in vacuum samples), average data for that order were used.

Statistical analysis

We have assessed nutritional dynamics through a combination of multivariate models and network-based null modelling. All analyses were conducted in R ver.4.0.3 (www.r-project.org).

To compare the nutritional balance of prey consumed by different spider groups, the mean nutrient contents of all prey consumed by each spider were calculated and compared using a multivariate linear model (MLM) via the 'manylm' command in 'mvabund' (Wang et al. 2012). Differences were visualised using ternary plots via 'ggtern' (Hamilton and Ferry 2018) and 'ggplot2' (Wickham 2016). How spider diets differ between spider groups (genera, sexes and life stages) and how this is related to the nutrient contents of those prey was assessed using a fourth corner analysis (FCA). Fourth corner analyses assess how the relationship between the presence of species (or consumed resources in a dietary context) and environmental (or consumer) traits relates to species traits (or prey traits; Brown et al. 2014). First, overall relationships between dietary composition and spider traits were assessed using a multivariate generalized linear model (MGLM) via the *manyglm* command in the 'mvabund' package (Wang et al. 2012) with a binomial error family. These relationships were identified via likelihood ratio test using the *anova.manyglm* command. A fourth corner analysis was performed using the *trait.glm* command in 'mvabund' with the 'R', 'Q' and 'L' matrices representing dietary detections of prey families in each spider, spider trait data (genus (a proxy for many unmeasured traits such as morphology), sex and life stage) and prey proportional macronutrient contents, respectively, with a binomial error family. Log-likelihood ratio tests were carried out using the *anova.traitglm* command with 999 bootstrap iterations and Monte-Carlo resampling. The model was repeated with the least absolute shrinkage and selection operator (LASSO) applied, which is a method of penalised likelihood that reduces model terms to zero if they lack predictive power (i.e. do not reduce the Bayesian information criterion), thereby selecting models with greater predictive accuracy (Brown et al. 2014).

To assess whether the proportions of mean prey nutrient contents deviated from those expected based on random foraging, null diets were simulated using network-based null models in 'econullnetr' (Vaughan et al. 2018) with the 'generate_null_net' command. The *generate_null_net_indiv* function (Cuff et al. 2023b) was used to generate null diets for each individual spider based on local prey communities determined via suction sampling. The mean prey macronutrient contents of spider diets were compared between expected and observed diets using a MLM in 'mvabund', and significant

differences visually represented through a ternary plot using 'ggtern'. To ascertain how differences between spider groups factor into any deviations from random nutrient intake, the difference in macronutrient proportions between expected and observed spider diets was also compared between spider genera, life stages and sexes in a MLM.

To relate prey preferences of different spider groups to different prey and their macronutrient contents, observed interactions were compared against null models based on prey abundances using the *generate_null_net* command in 'econullnetr' (as above) for each of the spider groups and, separately, for individual spiders. Ternary plots representing preference effect sizes for prey of varying macronutrient contents were generated using the group-specific data via 'ggtern'. The observed interactions of individual spiders were divided by the interactions expected in the null model; infinite values (i.e. zero interactions expected and more than zero observed) and NAs (e.g. no interactions expected nor observed) were converted to zero. These observed/expected values were compared between spider groups via permutational multivariate analysis of variance (PerMANOVA). These results were visualised by plotting mean standardised effect sizes for each spider genus, sex and life stage from the prey choice null models via 'ggplot2'.

Results

Demographic, ontogenic and phylogenetic differences in spider prey nutrient contents

The balance of nutrients across all prey consumed by each individual spider varied greatly around the overall mean of each spider group, indicating the stochastic nature of short-term nutrient selectivity compared to longer-term averages (Fig. 1, Supporting information). Mean spider prey nutrient content, irrespective of prey identities, varied between genera (MLM: $F_{4,233}=19.637$, $p=0.002$; Fig. 1, Supporting information) and sexes (MLM: $F_{2,238}=14.804$, $p=0.004$; Fig. 1, Supporting information) but not life stages (MLM: $F_{2,237}=2.595$, $p=0.421$; Fig. 1, Supporting information). Specifically, different genera consumed prey of different proportions of carbohydrate (MLM: $F_{4,233}=7.459$, $p=0.002$), lipid (MLM: $F_{4,233}=6.691$, $p=0.002$) and protein (MLM: $F_{4,233}=5.487$, $p=0.002$). The diets of lycosids (*Pardosa*

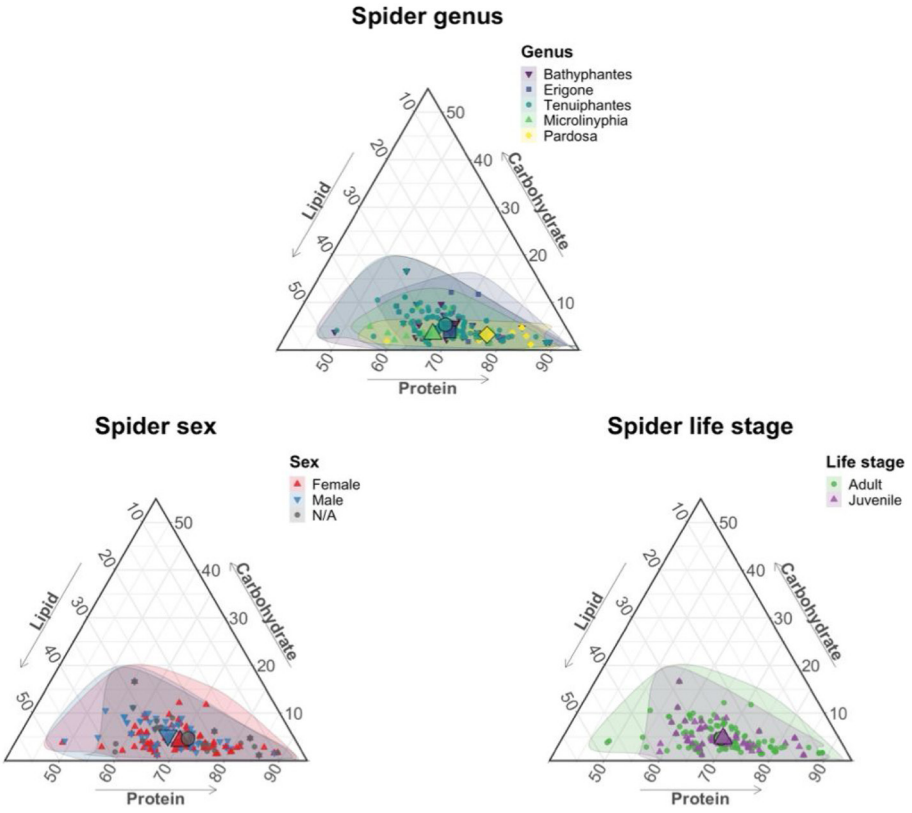

Figure 1. Comparison of observed mean spider prey macronutrient balance between genera, sexes and life stages. Axes represent % total macronutrient mass. Each point denotes the mean macronutrient content of a particular spider's prey. Shaded shapes represent arbitrary delimitations of the areas occupied by points from each of the spider groups. Large, bordered points represent the centroids (i.e. mean prey macronutrient contents) for each category. Genus: indigo upturned triangles, violet squares, teal circles, green triangles and yellow diamonds denote *Bathyphantes*, *Erigone*, *Tenuiphantes*, *Microlinyphia* and *Pardosa*, respectively. Sex: red triangles, blue upturned triangles and grey circles denote female, male and unsexed (immature) spiders, respectively. Life stage: green circles and purple triangles denote adult and juvenile spiders, respectively. The Supporting information provides alternative bar plot representations.

spp.), for example, included prey that were, on average, less carbohydrate-rich than those of the linyphiids. Different sexes consumed prey of different proportions of protein (MLM: $F_{2,238}=5.267$, $p=0.009$), carbohydrate (MLM: $F_{2,238}=5.524$, $p=0.014$) and lipids (MLM: $F_{2,238}=4.013$, $p=0.030$); specifically, the diets of male spiders included prey that were more carbohydrate-rich on average, while the diets of females included more protein-rich prey.

Differences in diet composition between spider groups related to nutrients

Spider diets significantly differed between spider genera (MGLM: Dev = 355.3, df = 239, $p=0.001$), life stages (MGLM: Dev = 75.7, df = 238, $p=0.001$) and sexes (MGLM: Dev = 89.4, df = 236, $p=0.002$). The precise nature of these relationships is described for species-level data by Cuff et al. (2022). The relationship between dietary composition and spider groupings significantly related to prey macronutrient contents (FCA: Dev = 22.79, df = 6783, $p=0.003$). Many of the nutrient-based differences in prey consumption between genera related to protein. The linyphiid genera consumed more carbohydrate-rich prey (i.e. their dietary composition positively related to prey carbohydrate content), unlike *Pardosa*. *Pardosa* and *Microlinyphia* consumed more lipid-rich prey (Fig. 2; although *Pardosa*'s mean prey lipid content was relatively low overall; Fig. 1). Female spiders consumed more carbohydrate-rich prey (Fig. 2; again, despite having lower average prey carbohydrate content). Adult spiders consumed more carbohydrate-rich and lipid-rich prey, converse to juvenile spiders, which consumed slightly more protein-rich prey (Fig. 2).

Mean prey nutrient contents compared to null foraging

The nutritional profiles of spider diets did not significantly differ to the null model nutritional profiles calculated assuming predators consumed prey species according to their relative abundance in the field (MLM: $F_{1,480}=1.883$, $p=0.524$; Fig. 3, Supporting information), although individual spider diets deviated from null model expected prey nutrient balance in all dimensions (i.e. the nutrients that diets were richer in than expected differed between individuals). The difference between each spider's prey nutrient contents and the nutrient profile of their expected diet, determined by null models, was, however, significant between genera (MLM: $F_{4,236}=9.059$, $p=0.005$) and life stages (MLM: $F_{1,235}=17.211$, $p=0.006$), but not sexes (MLM: $F_{2,233}=1.996$, $p=0.666$). Different nutrients drove the differences in deviation from null models, with different genera consuming lipid (MLM: $F_{4,236}=4.744$, $p=0.007$) and protein (MLM: $F_{4,236}=3.181$, $p=0.025$) with varying degrees of dissimilarity to expected random foraging, and different life stages consuming carbohydrate with varying degrees of dissimilarity to expected random foraging (MLM: $F_{1,235}=9.888$, $p=0.008$).

Nutrients as a consequence of prey selection

Significant deviations from random foraging were identified across all spider groups. The taxa for which foraging significantly deviated from null models differed between spider groups and the nutritional profiles of these prey were variable. The observed/expected values significantly differed between genera (PerMANOVA: $F_4=2.434$, $R^2=0.039$, $p=0.001$; Fig. 4, Supporting information) and life stages (PerMANOVA: $F_1=2.074$, $R^2=0.008$, $p=0.015$; Fig. 5, Supporting information), but not sexes (PerMANOVA: $F_2=1.052$, $R^2=0.008$, $p=0.376$; Fig. 5, Supporting information).

Discussion

This study demonstrates that nutrition is linked to spider foraging under field conditions, likely as a driver of prey choice. Specifically, the nutrient contents of prey relate to the frequency of their predation by spiders, and the deviation of the balance of nutrients consumed from random foraging differs between spider groups. The macronutrient content of the prey consumed by spiders differed between spider genera and sexes, often coinciding with differences in their prey selectivity as determined by null network models. The large variation in the average dietary macronutrient contents of individual spiders paired with fairly consistent average intake across spider groups could be consistent with reactive nutrient-specific foraging, influenced by the prey previously encountered by the spiders, but repeated data points representing a sequence of feeding for individuals would be required to

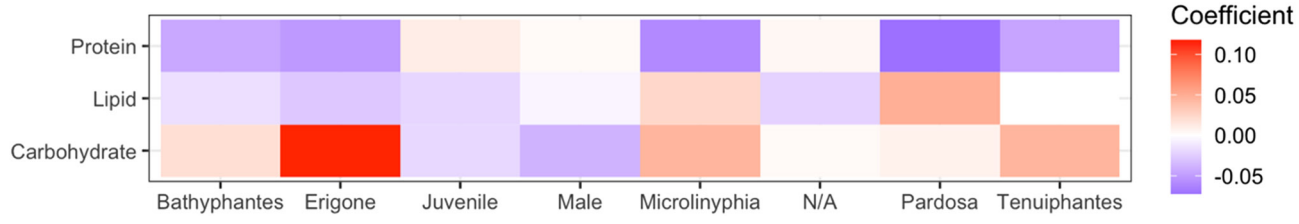

Figure 2. Relationships between spider traits and prey macronutrients in determining dietary composition determined by LASSO-penalised fourth corner analysis. Colours represent standardised coefficients with red, white and blue denoting positive, neutral and negative relationships, respectively, and colour intensity scaled by strength of association. 'N/A' refers to spiders that could not be reliably sexed (e.g. immature spiders).

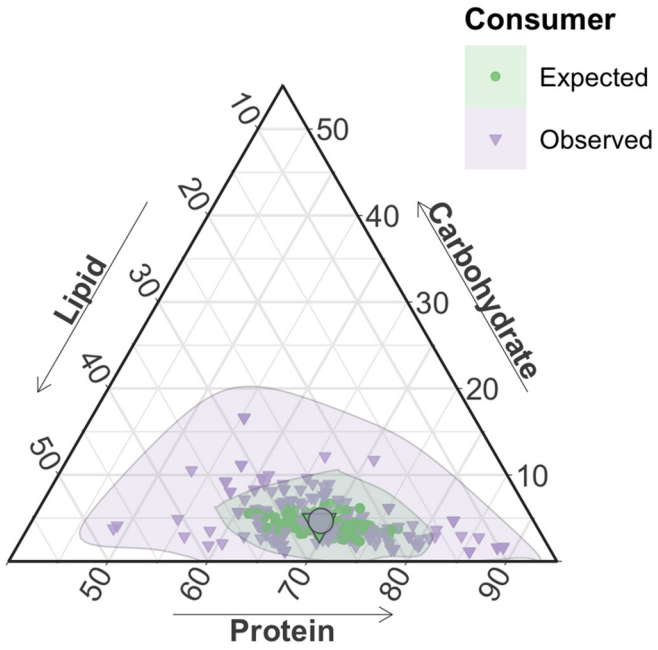

Figure 3. Expected versus observed spider prey macronutrients. Axes represent % total macronutrient mass. Each green circle denotes the null-model-based expected mean macronutrient content of repeated simulations of a particular spider's diet based on local prey abundance, whereas each purple inverted triangle denotes the observed mean macronutrient content of the spider's prey detected via metabarcoding. Shaded shapes represent arbitrary delimitations of the areas occupied by points from the two categories. Large, bordered points represent the centroids (i.e. mean prey macronutrient contents) for each category. The Supporting information provides an alternative bar plot representation.

confirm this. Nevertheless, these results suggest that spiders selectively forage for prey rich in all three macronutrients, but the balance between these shifts depending on the taxon, life stage and sex of the spider, likely to fit the predator's specific needs. Diet regulation by spiders is thought to be adaptive and many previous studies have shown significant effects of dietary nutrient content on spider growth, reproduction and survival (reviewed by Wilder 2011).

Previous work has shown that spiders balance their diet by consuming specific prey or parts of prey with particular nutrient contents (Greenstone 1979, Mayntz et al. 2005). The deviation of mean prey macronutrient contents from random foraging observed in this study suggests that the spiders were engaging in prey choice in a way that affected their macronutrient intake, whether actively or passively. Divergence from expected nutrient intake was large, with individual spiders foraging for all three nutrients in different proportions than expected. The average nutrient intake across spider groups, however, resembled a balanced intake of the nutrients available. This is indicative of individual spiders reactively foraging to redress dynamic nutritional needs as opposed to consistently seeking the same nutrients (i.e. different individuals effectively representing different stages within a sequence of foraging) but could also reflect stochastic foraging in highly heterogeneous prey populations. Differences in nutrient intake between spider genera likely relate to their distinct ecologies and morphologies, but the sex-based difference may indicate a variable need for energy or protein depending on oogenesis, mate-seeking activity and sexual dimorphism (Wilder 2011). For example, male spiders typically show much higher levels of itinerance and locomotive activity than females (Foelix 2011), presumably with concomitant energy requirements.

Without accounting for the nutrients available to each individual spider in the community in which they foraged, the above differences in nutrient intake do not necessarily represent differences in foraging behaviour. By analysing the difference between observed and expected spider-obtained nutrients, we saw that the disparity between individual spider dietary nutrients and the nutrient profile of their expected diet was significantly different between genera and life stages, but not sexes. This implies that nutritional dynamics are likely to be predominantly phylogenetically and developmentlly driven in these spiders, rather than sex-dependent, but this could differ between populations. These relationships may also change over time, although separate analyses with these interaction data highlight that these relationships appear to be largely driven by available prey diversity (Cuff et al. 2023b, 2024), accounted for here by the prey choice analyses.

The deviations of spider diets from null models within each spider group have consequences for the macronutrients that they then obtain from prey. Prey that were richer in carbohydrates, for example, were consumed regularly by adult spiders, reflected by some significant preferences by adult spiders for relatively carbohydrate-rich prey which were not selected beyond expected frequencies by juvenile spiders. Significant preferences for protein-rich prey do not markedly differ between female and male spiders despite the average protein content of their prey differing. The alignment of prey preferences with nutrient intake is indicative either of prey density driving these nutritional dynamics (implying that predators may be co-locating with prey rich in specific macronutrients) or of density-independent prey choice doing so (implying predators are seeking these nutrients in mixed prey communities). From this study, there is an argument for both cases in the same populations, suggesting that nutritional dynamics are simultaneously regulated by multiple behavioural drivers.

Previous studies have cited a lipid bias in predators (Margalida 2008, Salomon et al. 2008, Wilder et al. 2013, 2016, Wiggins and Wilder 2018, Al Shareefi and Cotter 2019) and others have suggested that the balance of protein and lipid is of particular importance in resource choice and nutrient assimilation during foraging (Prabhu and Taylor 2008, Mayntz et al. 2009, Schmidt et al. 2012, Vaudo et al. 2016, Denuncio et al. 2017, Toft et al. 2019, Diaz Gomez et al. 2020). Despite high protein intake having negative fitness consequences (Anderson et al. 2020), some animals will over-feed on protein to obtain sufficient lipid provision (Jensen et al. 2011). This perceived tradeoff between lipid and protein, alongside increasing lipid limitation at higher

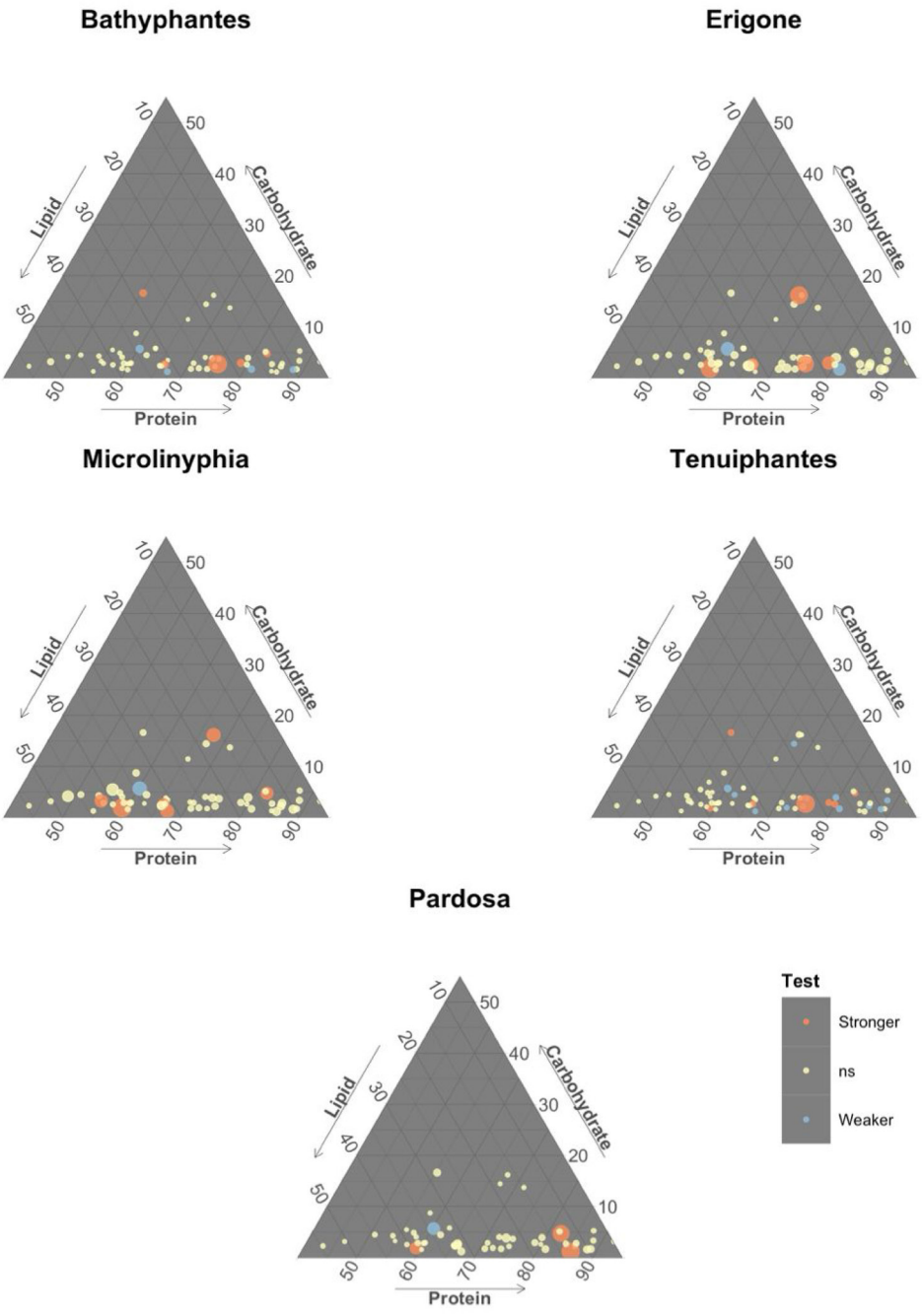

Figure 4. Ternary plots of preference for different prey taxa by macronutrient content for each spider genus. Axes represent % total macronutrient mass. Each point represents a different prey taxon. The size of each point denotes the relative effect size. The position of each point relates to the relative macronutrient content of that taxon (i.e. proximity to a corner of the triangle denotes higher relative content of that macronutrient). Red, white and blue points denote strong (i.e. significantly positive), non-significant and weak (i.e. significantly negative) preference for that taxon, respectively. The Supporting information provides alternative bar plot representations. Standardised effect sizes are also displayed in the Supporting information.

trophic levels (Wilder et al. 2013), has led some studies of predator nutritional ecology to neglect carbohydrate, while others have identified its importance. This study has similarly identified that the nutritional dynamics of predators in the field relate to all three macronutrients and that carbohydrate is important particularly in differentiating between life stages, despite being much scarcer than protein and lipid. Other recent studies demonstrate the importance of carbohydrate in invertebrate foraging (Christensen et al. 2020, Hawley et al. 2016, Nielsen et al. 2022, Wiggins and Wilder, 2022, Wilder et al. 2016); for example, carbohydrates complement high-protein diets in invertebrate predators and

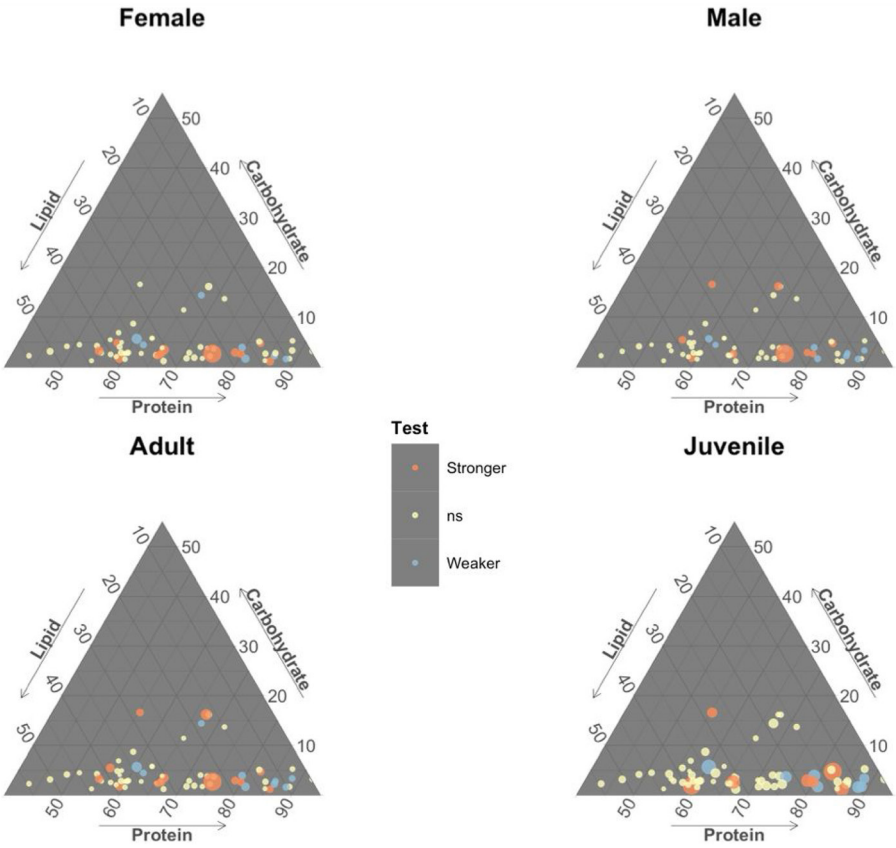

Figure 5. Ternary plots of preference for different prey taxa by macronutrient content for each spider sex and life stage. Axes represent % total macronutrient mass. Each point represents a different prey taxon. The size of each point denotes the relative effect size. The position of each point relates to the relative macronutrient content of that taxon (i.e. proximity to a corner of the triangle denotes higher relative content of that macronutrient). Red, white and blue points denote strong (i.e. significantly positive), non-significant and weak (i.e. significantly negative) preference for that taxon, respectively. The Supporting information provide alternative bar plot representations. Standardised effect sizes are also displayed in the Supporting information.

affect spider growth (Wiggins and Wilder 2022), and including substantial carbohydrate in their diet allows flesh flies to maximize their fitness (Hawley et al. 2016). This three-dimensional approach to nutritional ecology has highlighted several key relationships in these nutritional dynamics while also enhancing our understanding of the ecological implications of nutrient-specific foraging.

Whilst the evidence provided by this study is multi-faceted and identifies relationships previously supported by lab studies, the methodology used presents several constraints which must be considered. The primary limitation is that of metabarcoding, which presents a temporally discrete snapshot of the diet of each spider (Cuff et al. 2023a). Whilst impossible to derive from this study, individual spiders may be targeting prey with nutrient content that is complementary to their past diet. The 'snapshot view' provided by gut content metabarcoding only reveals the diet of individual spiders at discrete points in time without the possibility of comparing individual diets over time. Theories related to these findings, such as nutrient-specific foraging, are based on sequential foraging for nutritionally distinct resources, but the prey detected by metabarcoding cannot be confidently ascribed to a sequence of feeding due to the quantitative biases of the technique. By exploring in tandem the expected individual variation in nutrient intake and average intakes across populations, our data could be interpreted as representing different time scales, but further research is required.

Our investigation of nutritional dynamics is restricted to a single stage of prey choice: that of prey consumption. Nutrient-specific foraging can occur at other stages of predation, such as the extraction of specific nutrients or feeding on specific tissues of prey, which have been observed in controlled lab-based experiments with some spiders (Kohl et al. 2015, Mayntz et al. 2005, Pekár et al. 2010). Other spiders, however, have been shown to redress nutritional deficiencies by consuming different amounts of prey depending on their nutritional contents, and do not enact differential nutrient extraction (Greenstone 1979, Mayntz et al. 2005, Hawley et al. 2014). Indeed, many animals balance their nutrient intake by overfeeding on a particular nutrient and redressing this imbalance by foraging for another, with overall nutrient balancing occurring over the course of several meals (Simpson and Raubenheimer 2012). Ultimately, spiders are thought to exist in a constant state of sub-optimal nutritional

deficit in the field (Symondson et al. 2002), thus wasteful discard of prey nutrients would be surprising given the energy expended in subduing prey. This approach of selective differential nutrient extraction would thus only be beneficial in cases of the prey being too large to consume at once. The sub-optimal nutritional state of predators in the field could also reduce their selectivity (Symondson et al. 2002), creating noisier signals in studies such as this, but this study nevertheless suggests that nutrients are a strong driver of trophic interactions. Spiders can, however, also physiologically adapt to limited nutritional intake by reducing their metabolic rates, increasing nutrient extraction efficiency and surviving long periods of starvation (Wilder and Rypstra 2008, Barnes et al. 2019).

The inclusion of prey abundance data, determined by suction sampling, in the null models treats this as a measure of prey availability, but the disparity between availability and abundance can be insidious (Cuff et al. 2024b). Each prey sampling method can introduce taxonomic biases, such as disproportionate representation of thrips, flies, spiders, true bugs and wasps by suction sampling (Doxon et al. 2011, Zentane et al. 2016), although Cuff et al. (2024b) demonstrate that this method is slightly more representative of spider interactions than alternatives like sticky trapping. Abundant organisms may also be less available to predators based on camouflage (Endler 1978), defences (Provost et al. 2006), escape capability (Lang and Gsodl 2001, Provost et al. 2006), size (Bence and Murdoch 1986, Downes 2002, Turesson et al. 2002) and a myriad of other factors. To account for these differences in an accurate manner would, however, involve a body of work focused on these constraints, undoubtedly magnitudes larger and more complex than this. Our study provides a simplified, but not simplistic, representation of availability and, regardless of the potential auxiliary hypotheses underlying this, we have highlighted in-field nutritional dynamics previously evidenced in lab studies which would be highly unlikely by chance or if these abundances were a highly inaccurate measure of prey availability in this system.

The macronutrient assays conducted according to the MEDI protocol (Cuff et al. 2021a, b) in this study are subject to several important considerations. Firstly, exoskeleton measurement was excluded from the protocol given the size of many of the smaller taxa in this study (e.g. parasitoid wasps, springtails) for which suitably sensitive weighing scales were not available. Exoskeletal chitin is indigestible to most consumers and is therefore not usually assimilated in the way that digestible nutrients are. It is, nonetheless, an important consideration regarding the availability of accessible nutrients within prey (Cuff et al. 2021a, b). The carbohydrate values determined in this study were also sometimes larger than those typically reported for invertebrate body content. These may differ from those reported previously for similar taxa with the MEDI protocol (Cuff et al. 2021a, b) because these populations were all taken from the field, whereas some of those in the original MEDI study were lab-reared, which can have marked effects on invertebrate nutrition (Wiggins et al. 2018). It could also relate to the micro-scaled protocol used to detect macronutrients from smaller specimens, the accuracy of which is likely to be lower than the original protocol given the reduced detectability of the analyte (Cuff 2021). This study regardless presents a unique dataset and framework through which to explore some poorly resolved outstanding ecological questions with many prospects for extension through future research.

Speculations

Given the lack of sequential feeding data, it is impossible with certainty to claim this as evidence for nutrient-specific foraging. The individual variation in consumed prey nutrients, alongside the mean consumed prey nutrients aligning with null models, is, however, consistent with what one might expect from a population engaged in nutrient-specific foraging. Individuals would likely be redressing nutritional deficiencies through imbalanced intake, while the overall population would achieve balanced nutrition consistent with nutritional optima. Optimal nutrition is also, however, unknown, but could be speculated upon from the population-level intake given its relative stability across groups.

Field-based evidence for nutrient-specific foraging remains an unmet keystone in our understanding of complex ecological systems. To address this requires resolution of the sequence of feeding or the nutritional state of predators, prescribing methodological advancement. New analytical frameworks may elucidate the dynamic influence of nutrients on foraging (Cuff et al. 2024a) and molecular innovations such as delineation of prey at different stages of degradation via the combined analysis of DNA and RNA (Neidel et al. 2022) could resolve the temporal sequence of consumption. Even these prospects fall short of a complete solution though, with consumed prey biomass and individual-level nutritional data currently impossible to obtain reliably with these methods.

Conclusions

This study highlights the complex nutritional dynamics of generalist predators in the field and the influence of predator traits on nutritionally-motivated prey preferences consistent with theories such as nutrient-specific foraging. We have provided this evidence through the synergistic application of molecular ecology, ecological chemistry, null modelling and multivariate statistics, ultimately elucidating the highly complex nutritional dynamics governing trophic interactions between spiders and their prey. Spider dietary composition related to prey macronutrient contents, and spiders exhibited density-independent prey choice, with their prey significantly differing in macronutrient contents from the proportions predicted by null models. Spider nutritional preference varied across populations, suggesting individual spiders reactively forage to redress nutritional deficits, diversifying their functional response to prey to enact this preference. This elucidation of in-field nutritional dynamics is centred around the balanced intake of all three macronutrients by spider

populations. This could be regulated through redressive foraging by individual spiders, in turn enacted by variations in prey selection, although further evidence is required to demonstrate this. Contextual information such as this can be used to inform increasingly complex studies of nutritional dynamics from individual to network scales (Cuff et al. 2024a). An improved understanding of nutritional dynamics may be applied for the benefit of ecology, agriculture and conservation. Prey preferences can be exploited by modulating the abundance of available prey through manipulation of field conditions and habitat structure to encourage predation of pests by providing nutritionally complementary prey (Agustí et al. 2003, Bell et al. 2008, Michalko et al. 2017). Ultimately, enhancing and expanding our understanding of nutritional dynamics may facilitate a greater contextual understanding of trophic interactions across the breadth of ecology and evolution.

Acknowledgements – Thanks to Robert Reader for use of Burdons Farm, Wenvoe for fieldwork. Thanks to Professor Eshwar Mahenthiralingam for use of the Tecan plate reader. William O. C. Symondson died during the preparation of this manuscript.
Funding – JPC was funded by the Biotechnology and Biological Sciences Research Council through the South West Biosciences Doctoral Training Partnership (grant BB/M009122/1). SMW was supported by a US National Science Foundation Grant (DEB1838988). JRB was funded by BBSRC's Core Capability Grant (BBS/E/C/000J0200). MPTGT was funded by the Natural Environment Research Council (NE/L002434/1) and Durrell Wildlife Conservation Trust (MR/S502455/1).

Author contributions

Jordan P. Cuff: Conceptualization (equal), Data curation (lead), Formal analysis (lead), Funding acquisition (equal), Investigation (lead), Methodology (lead), Project administration (lead), Visualization (lead), Writing - original draft (lead), Writing - review and editing (lead). **Maximillian P.T.G. Tercel:** Formal analysis (supporting), Investigation (equal), Methodology (equal), Writing - review and editing (equal). **Ian P. Vaughan:** Conceptualization (equal), Formal analysis (equal), Funding acquisition (equal), Investigation (equal), Methodology (equal), Project administration (supporting), Software (lead), Supervision (equal), Validation (equal), Visualization (equal), Writing - review and editing (equal). **Lorna E. Drake:** Data curation (supporting), Formal analysis (supporting). **Shawn M. Wilder:** Formal analysis (supporting), Investigation (equal), Methodology (equal), Writing - review and editing (equal). **James R. Bell:** Conceptualization (equal), Funding acquisition (equal), Investigation (equal), Methodology (equal), Project administration (supporting), Supervision (equal), Writing - review and editing (equal). **Carsten T. Müller:** Conceptualization (equal), Funding acquisition (equal), Investigation (equal), Methodology (equal), Project administration (supporting), Supervision (equal), Writing - review and editing (equal). **Pablo Orozco-terwengel:** Conceptualization (equal), Funding acquisition (equal), Investigation (equal), Project administration (supporting), Supervision (equal), Writing - review and editing (equal). **William O. C. Symondson**: Conceptualization (lead), Funding acquisition (equal), Investigation (equal), Methodology (equal), Project administration (equal), Supervision (lead), Writing - review and editing (equal).

Data availability statement

Data are available from Zenodo: https://doi.org/10.5281/zenodo.13556291 (Cuff et al. 2024c).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Agustí, N., Shayler, S. P., Harwood, J. D., Vaughan, I. P., Sunderland, K. D. and Symondson, W. O. C. 2003. Collembola as alternative prey sustaining spiders in arable ecosystems: prey detection within predators using molecular markers. – Mol. Ecol. 12: 3467–3475.

Al Shareefi, E. and Cotter, S. C. 2019. The nutritional ecology of maturation in a carnivorous insect. – Behav. Ecol. 30: 256–266.

Anderson, T. R., Raubenheimer, D., Hessen, D. O., Jensen, K., Gentleman, W. C., Mayor, D. J. and Anderson, T. R. 2020. Geometric stoichiometry: unifying concepts of animal nutrition to understand how protein-rich diets can be "too much of a good thing." – Front. Ecol. Evol. 8: 196.

Ball, S. 2008. Introduction to the families of British diptera part 2: key to families. – Dipterists Forum.

Barber, A. D. 2008. Key to the identification of British centipedes. – FSC Publications.

Barnes, C. L., Hawlena, D., McCue, M. D. and Wilder, S. M. 2019. Consequences of prey exoskeleton content for predator feeding and digestion: black widow predation on larval versus adult mealworm beetles. – Oecologia 190: 1–9.

Bell, J. R., Traugott, M., Sunderland, K. D., Skirvin, D. J., Mead, A., Kravar-Garde, L., Reynolds, K., Fenlon, J. S. and Symondson, W. O. C. 2008. Beneficial links for the control of aphids: the effects of compost applications on predators and prey. – J. Appl. Ecol. 45: 1266–1273.

Bence, J. R. and Murdoch, W. W. 1986. Prey size selection by the mosquitofish – relation to optimal diet theory. – Ecology 67: 324–336.

Brown, A. M., Warton, D. I., Andrew, N. R., Binns, M., Cassis, G. and Gibb, H. 2014. The fourth-corner solution – using predictive models to understand how species traits interact with the environment. – Methods Ecol. Evol. 5: 344–352.

Christensen, J., Nielsen, S. M. B. and Toft, S. 2020. The three-dimensional macronutrient niche of an invasive generalist predator. – Ecol. Entomol. 45: 644–651.

Cuff, J. P. 2021. Further micro-scaled MEDI (macronutrient extraction and determination from invertebrates). – Protocols.io.

Cuff, J. P. and Wilder, S. M. 2021. MEDI: macronutrient extraction and determination from invertebrates. – Protocols.io, p. 49505.

Cuff, J. P., Wilder, S. M., Tercel, M. P. T. G., Hunt, R., Oluwaseun, S., Morley, P. S., Badell-Grau, R. A., Vaughan, I. P., Bell, J. R., Orozco-terWengel, P., Symondson, W. O. C. and Müller, C. T. 2021b. MEDI: macronutrient extraction and determination from invertebrates, a rapid, cheap and streamlined protocol. – Methods Ecol. Evol. 2021: 593–601.

Cuff, J. P., Tercel, M. P. T. G., Drake, L. E., Vaughan, I. P., Bell, J. R., Orozco-terWengel, P., Müller, C. T. and Symondson, W. O. C. 2022. Density-independent prey choice, taxonomy, life history and web characteristics determine the diet and biocontrol potential of spiders (Linyphiidae and Lycosidae) in cereal crops. – Environ. DNA 4: 549–564.

Cuff, J. P., Kitson, J. J. N., Hemprich-Bennett, D., Tercel, M. P. T. G., Browett, S. S. and Evans, D. M. 2023a. The predator problem and PCR primers in molecular dietary analysis: swamped or silenced; depth or breadth? – Mol. Ecol. Resour. 23: 41–51.

Cuff, J. P., Windsor, F. M., Tercel, M. P. T. G., Bell, J. R., Symondson, W. O. C. and Vaughan, I. P. 2023b. Temporal variation in spider trophic interactions is explained by the influence of weather on prey communities, web building and prey choice. – Ecography 2023: e06737.

Cuff, J. P., Evans, D. M., Vaughan, I. P., Wilder, S. M., Tercel, M. P. T. G. and Windsor, F. M. 2024a. Networking nutrients: how nutrition determines the structure of ecological networks. – J. Anim. Ecol. 93: 974–988.

Cuff, J. P., Tercel, M. P. T. G., Windsor, F. M., Hawthorne, B. S. J., Hambäck, P. A., Bell, J. R., Symondson, W. O. C. and Vaughan, I. P. 2024b. Sources of prey availability data alter interpretation of outputs from prey choice null networks. – Ecol. Entomol. 49: 418–432.

Cuff, J. P., Tercel, M. P. T. G., Vaughan, I. P., Drake, L. E., Wilder, S. M., Bell, J. R., Müller, C. T., Orozco-terWengel, P. and Symondson, W. O. C. 2024c. Prey nutrient content is associated with the trophic interactions of spiders and their prey selection under field conditions [Dataset]. – Zenodo , https://doi.org/10.5281/zenodo.13556291.

Dallimore, T. and Shaw, P. 2013. Illustrated key to the families of British springtails (Collembola). – FSC Publications.

Davey, J. S., Vaughan, I. P., Andrew King, R., Bell, J. R., Bohan, D. A., Bruford, M. W., Holland, J. M. and Symondson, W. O. C. 2013. Intraguild predation in winter wheat: prey choice by a common epigeal carabid consuming spiders. – J. Appl. Ecol. 50: 271–279.

Denuncio, P., Paso, M. N., Machovsky-capuska, G. E., Raubenheimer, D., Blasina, G., Machado, R., Polizzi, P., Gerpe, M., Cappozzo, H. L. and Rodriguez, D. H. 2017. Population variance in prey, diets and their macronutrient composition in an endangered marine predator, the Franciscana dolphin. – J. Sea Res. 129: 70–79.

Despland, E. and Noseworthy, M. 2006. How well do specialist feeders regulate nutrient intake? Evidence from a gregarious tree-feeding caterpillar. – J. Exp. Biol. 209: 1301–1309.

Downes, S. J. 2002. Size-dependent predation by snakes: selective foraging or differential prey vulnerability? – Behav. Ecol. 13: 551–560.

Doxon, E. D., Davis, C. A. and Fuhlendorf, S. D. 2011. Comparison of two methods for sampling invertebrates: vacuum and sweep-net sampling: methods of sampling invertebrates. – J. Field Ornithol. 82: 60–67.

Drake, L. E., Cuff, J. P., Young, R. E., Marchbank, A., Chadwick, E. A. and Symondson, W. O. C. 2022. An assessment of minimum sequence copy thresholds for identifying and reducing the prevalence of artefacts in dietary metabarcoding data. – Methods Ecol. Evol. 13: 694–710.

Duff, A. G. 2012. Beetles of Britain and Ireland volume 1: Sphaeriusidae to Silphidae. – A.G. Duff Publishing.

Endler, J. A. 1978. A predator's view of animal colour patterns. – Evol. Biol. 11: 319–364.

Fanson, B. G., Weldon, C. W., Pérez-Staples, D., Simpson, S. J. and Taylor, P. W. 2017. Nutrients, not caloric restriction, extend lifespan in Queensland fruit flies (*Bactrocera tryoni*). – Aging Cell 8: 514–523.

Foelix, R. F. 2011. Biology of spiders, 3rd edn. – Oxford Univ. Press.

Diaz Gomez, M., Rosen, D. A. S., Forster, I. P. and Trites, A. W. 2020. Prey composition impacts lipid and protein digestibility in northern fur seals (*Callorhinus ursinus*). – Can. J. Zool. 98: 681–689.

Goulet, H. and Huber, J. T. 1993. Hymenoptera of the world: an indentification guide to families. – Agriculture Canada.

Greenstone, M. H. 1979. Spider feeding behavior optimizes dietary essential amino-acid composition. – Nature 282: 501–503.

Hamilton, N. E. and Ferry, M. 2018. ggtern: ternary diagrams using ggplot2. – J. Stat. Softw. 87: 3.

Harwood, J. D., Sunderland, K. D. and Symondson, W. O. C. 2004. Prey selection by linyphiid spiders: molecular tracking of the effects of alternative prey on rates of aphid consumption in the field. – Mol. Ecol. 13: 3549–3560.

Hawley, J., Simpson, S. J. and Wilder, S. M. 2014. Effects of prey macronutrient content on body composition and nutrient intake in a web-building spider. – PLoS One 9: e99165.

Hawley, J., Simpson, S. J. and Wilder, S. M. 2016. Flesh flies regulate the consumption of 3 macronutrients to maximize lifespan and egg production. – Behav. Ecol. 27: 245–251.

Jensen, K., Mayntz, D., Toft, S., Raubenheimer, D. and Simpson, S. J. 2011. Nutrient regulation in a predator, the wolf spider *Pardosa prativaga*. – Anim. Behav. 81: 993–999.

Jensen, K., Mayntz, D., Toft, S., Clissold, F. J., Hunt, J., Raubenheimer, D. and Simpson, S. J. 2012. Optimal foraging for specific nutrients in predatory beetles. – Proc. R. Soc. B 279: 2212–2218.

Kohl, K. D., Coogan, S. C. P. and Raubenheimer, D. 2015. Do wild carnivores forage for prey or for nutrients? Evidence for nutrient-specific foraging in vertebrate predators. – BioEssays 37: 701–709.

Lang, A. and Gsodl, S. 2001. Prey vulnerability and active predator choice as determinants of prey selection: a carabid beetle and its aphid prey. – J. Appl. Entomol. 125: 53–61.

Margalida, A. 2008. Bearded vultures (*Gypaetus barbatus*) prefer fatty bones. – Behav. Ecol. Sociobiol. 63: 187–193.

Mayntz, D., Raubenheimer, D., Salomon, M., Toft, S. and Simpson, S. J. 2005. Nutrient-specific foraging in invertebrate predators. – Science 307: 111–113.

Mayntz, D., Nielsen, V. H., Sørensen, A., Toft, S., Raubenheimer, D., Hejlesen, C. and Simpson, S. J. 2009. Balancing of protein and lipid intake by a mammalian carnivore, the mink, *Mustela vison*. – Anim. Behav. 77: 349–355.

Michalko, R., Petráková, L., Sentenská, L. and Pekár, S. 2017. The effect of increased habitat complexity and density-dependent non-consumptive interference on pest suppression by winter-active spiders. – Agric. Ecosyst. Environ. 242: 26–33.

Neidel, V., Sint, D., Wallinger, C. and Traugott, M. 2022. RNA allows identifying the consumption of carrion prey. - Mol. Ecol.

Resour. 22: 2662–2671. https://doi.org/10.1111/1755-0998.1365
Nielsen, S. M. B., Bilde, T. and Toft, S. 2022. Macronutrient niches and field limitation in a woodland assemblage of harvestmen. – J. Anim. Ecol. 91: 593–603.
Pekár, S., Mayntz, D., Ribeiro, T. and Herberstein, M. E. 2010. Specialist ant-eating spiders selectively feed on different body parts to balance nutrient intake. – Anim. Behav. 79: 1301–1306.
Pompanon, F., Deagle, B. E., Symondson, W. O. C., Brown, D. S., Jarman, S. N. and Taberlet, P. 2012. Who is eating what: diet assessment using next generation sequencing. – Mol. Ecol. 21: 1931–1950.
Pompozzi, G., García, L. F., Petráková, L. and Pekár, S. 2019. Distinct feeding strategies of generalist and specialist spiders. – Ecol. Entomol. 44: 129–139.
Prabhu, V., and Taylor, P. W. 2008. Protein:carbohydrate ratios promoting sexual activity and longevity of male Queensland fruit flies. – J. Appl. Entomol. 132: 575–582.
Provost, C., Lucas, É. and Coderre, D. 2006. Prey preference of *Hyaliodes vitripennis* as an intraguild predator: active predator choice or passive selection? – Biol. Control 37: 148–154.
Pyke, G. H. 1984. Optimal foraging theory: a critical review. – Annu. Rev. Ecol. Syst. 15: 523–575.
Rendon, D., Taylor, P. W., Wilder, S. M. and Whitehouse, M. E. A. 2019. Does prey encounter and nutrient content affect prey selection in wolf spiders inhabiting Bt Cotton fields? – PLoS One 14: e0210296.
Rho, M. S. and Pum LEE, K. P. 2015. Nutrient-specific food selection buffers the effect of nutritional imbalance in the mealworm beetle, *Tenebrio molitor* (Coleoptera: Tenebrionidae). – Eur. J. Entomol. 112: 251–258.
Roberts, M. J. 1993 The spiders of Great Britain and Ireland (compact edition), 3rd edn. – Harley Books.
Salomon, M., Mayntz, D. and Lubin, Y. 2008. Colony nutrition skews reproduction in a social spider. – Behav. Ecol. 19: 605–611.
Schmidt, J. M., Sebastian, P., Wilder, S. M. and Rypstra, A. L. 2012. The nutritional content of prey affects the foraging of a generalist arthropod predator. – PLoS One 7: e49223.
Simpson, S. J. and Raubenheimer, D. 2012. The nature of nutrition: a unifying framework from animal adaptation to human obesity. – Princeton Univ. Press.
Simpson, S. J., Sibly, R. M., Lee, K. P., Behmer, S. T. and Raubenheimer, D. 2004. Optimal foraging when regulating intake of multiple nutrients. – Anim. Behav. 68: 1299–1311.
Symondson, W. O. C., Sunderland, K. D. and Greenstone, M. H. 2002. Can generalist predators be effective biocontrol agents? – Annu. Rev. Entomol. 47: 561–594.
Toft, S. 1999. Prey choice and spider fitness. – J. Arachnol. 27: 301–307.
Toft, S., Cuende, E., Olesen, A. L., Mathiesen, A., Meisner Larsen, M. M. and Jensen, K. 2019. Food and specific macronutrient limitation in an assemblage of predatory beetles. – Oikos 128: 1467–1477.
Turesson, H., Persson, A. and Brönmark, C. 2002. Prey size selection in piscivorous pikeperch (*Stizostedion lucioperca*) includes active prey choice. – Ecol. Freshwater Fish 11: 223–233.
Unwin, D. 2001. A key to the families of British bugs (Insecta, Hemiptera). – FSC Publications.
Vaudo, A. D., Stabler, D., Patch, H. M., Tooker, J. F., Grozinger, C. M. and Wright, G. A. 2016. Bumble bees regulate their intake of essential protein and lipid pollen macronutrients. – J. Exp. Biol. 219: 3962–3970.
Vaughan, I. P., Gotelli, N. J., Memmott, J., Pearson, C. E., Woodward, G. and Symondson, W. O. C. 2018. econullnetr: an R package using null models to analyse the structure of ecological networks and identify resource selection. – Methods Ecol. Evol. 9: 728–733.
Wang, Y., Naumann, U., Wright, S. T. and Warton, D. I. 2012. Mvabund – an R package for model-based analysis of multivariate abundance data. – Methods Ecol. Evol. 3: 471–474.
Wickham, H. 2016. ggplot2: elegant graphics for data analysis (3.3.0). – Springer-Verlag.
Wiggins, W. D. and Wilder, S. M. 2018. Mismatch between dietary requirements for lipid by a predator and availability of lipid in prey. – Oikos 127: 1024–1032.
Wiggins, W. D. and Wilder, S. M. 2022. Carbohydrates complement high-protein diets to maximize the growth of an actively hunting predator. – Ecol. Evol. 12: e9150.
Wiggins, W. D., Bounds, S. and Wilder, S. M. 2018. Laboratory-reared and field-collected predators respond differently to same experimental treatments. – Behav. Ecol. Sociobiol. 72: 19.
Wilder, S. M. 2011. Spider nutrition: an integrative perspective. – Adv. Insect Physiol. 40: 87–136.
Wilder, S. M. and Rypstra, A. L. 2008. Diet quality affects mating behaviour and egg production in a wolf spider. – Anim. Behav. 76: 439–445.
Wilder, S. M., Norris, M., Lee, R. W., Raubenheimer, D. and Simpson, S. J. 2013. Arthropod food webs become increasingly lipid-limited at higher trophic levels. – Ecol. Lett. 16: 895–902.
Wilder, S. M., Yuan, L., Roumilhac, C., LeGal, A., Raubenheimer, D., Simpson, S. J. and McAllan, B. M. 2016. Three-dimensional diet regulation and the consequences of choice for weight and activity level of a marsupial carnivore. – J. Mammal. 97: 1645–1651.
Zentane, E., Quenu, H., Graham, R. I. and Cherrill, A. 2016. Suction samplers for grassland invertebrates: comparison of numbers caught using Vortis™ and G-vac devices. – Insect Conserv. Divers. 9: 470–474.