Title: Predator body size and species identity determine predator-prey interactions in diet DNA metabarcoding data

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ProcB: 6 MS pages, 850 words = 1 page and 2-4 small figures = 1 page (this is already currently too long…)

**Abstract (200 words)**

**Keywords (3-6 words)**

**Introduction**

Baby: The field of food web ecology has spent nearly a century observing and predicting patterns in complex communities of multiple species and their interactions (reviewed in Layman et al. 2015). Through multiple evolutions in the thinking in the field, especially on the understanding of how ecologically complex ecosystems maintain stability (e.g. May 1971 to Polis 1991 to McCann 2001), it has been clear that while there are patterns specific to food webs in different contexts (e.g. environmental; Brose et al. 2006), there seem to be general relationships between the role of consumers in a food web and basic species characteristics, in particular, body size (Woodward 2002, more lit here). Body size is a fundamental trait that predicts feeding behaviors, including how much an individual eats, and for predators, which prey are available to those predator species based on relative body size differences and optimal foraging theory (e.g. Stouffer 2015). In this way, body size has been used to define the niches of consumers, in particular predators, in many of the food web models that best predict observed patterns in nature (e.g. Gravel et al. 2015, Pomeranz et al. 2019).

Baby 2: One of the food web models best able to predict observed patterns of species interactions (measured as a binary presence-absence of interactions) is the niche model (Williams and Martinez 2000), which has been extended to incorporate predator and prey sizes to build species niches (Gravel et al. 2015, Gravel et al. 2013). The niche model with body sizes defines a predator’s diet based on its body size, the allometric relationship between its size and the size of its prey (Cohen et al. 2003; Brose et al, 2006; Riede et al. 2010), and the range of prey items around that central relationship, with larger predators having a wider range of potential prey sizes but with a lower bound based on optimal foraging (e.g. Nakazawa, SI Figure 1). While the body size niche model predicts empirical feeding interactions with high accuracy (Gravel et al. citations), it is improved even more when feeding interactions are constrained by limiting interactions even more to empirically-observed interactions from phylogenetically-similar species of both predators and prey (Grey et al., Pomeranz et al. 2019, check that this is true). Whether it be species, functional grouping (beyond body size, e.g. locomotion, metabolism), or phylogenetic similarity, incorporating aspects of predator characteristics beyond body size is important (Rudolf et al. 2014 OTHERS, Brose 2019 and 2006).

Werewolf: Both a body size and a body size and species identity approach is promising for describing patterns of predator-prey interactions across consumer groups and environmental contexts. However, for some predators, in particular small-bodied invertebrate predators for which empirical diet methods (e.g. gut dissections) are impossible or often unfeasible (CITE From methods paper set of papers, McLaughlin et al. 2010), we have a dearth of observed interaction data with which to validate extrapolated body size or phylogenetic methods of predicting food web structure. For these consumers, species interactions are often inferred from literature reports of observed interactions from phylogenetically-related species (e.g. ) or based on body size feeding constraints (e.g. Hines et al. 2019). Because these are the very two patterns we are aiming to observe in these datasets, then, without empirical data it is unclear whether any patterns in these consumers related to body size or species identity or general patterns or artefacts of the non-empirical diet assignment methods used to compile them. While body body size and species identity have been observed to be empirically important in some invertebrate food webs through empirical observation (e.g. aquatic invertebrate food webs, Woodward and Hildrew 2002, Rudolf et al. 2014), the biology of many terrestrial invertebrate predators suggests that assuming these patterns will hold may be invalid. For example, many terrestrial invertebrate predators use webs or venom to subdue and catch prey (Nakazawa et al.), thus loosening restrictive body-size based interaction assignments. Furthermore, because, unlike other invertebrate systems, in terrestrial food webs, predators are not necessarily bigger than other organisms in the food web (e.g. Sechi et al. 2015), the numerical majority of prey items may be larger than individual predators, thus necessitating variations by some species in predator-prey body size relationships or prey selection criteria.

Werewolf 2: Small-bodied terrestrial invertebrates, including insects and spiders, comprise 50% of the earth’s animal biomass (Bar-On et al. 2018) and the majority of global animal species diversity (Mora et al. 2011 Costello et al. 2013), so understanding their trophic interactions is not only important for finding general food web patterns, but could be crucial for understanding the ecology of the world’s most dominant group of consumers shaping biomass and nutrient cycling dynamics (e.g. Bar-On et al. 2018). Specifically, we have a lack of empirical predator-prey interaction data with which to understand whether body size and species identity shape food web patterns, and thus, we are limited in our ability to build predictive models for this group of consumers based on observed interactions (Polis 1991).

Silver Bullet: In this study, we employ novel diet DNA metabarcoding data from 182 individuals of nine terrestrial invertebrate predator species to document predator-prey interactions between these predators and their prey in natural field conditions. Combined with an extensive dataset of body sizes for both predator individuals and the prey groups identified in their diets, we examine the predator-prey body size relationships for these predators across and within predator species. To understand how predator size and species identity drive empirical predator-prey interactions, we asked: 1) do larger individuals eat larger prey and is this mediated by predator species identity? 2) is prey selection dependent on predator size, species, or both? We then compared the predator-prey body size relationship we observed in this dataset to the predator-prey body size scaling reported from four terrestrial invertebrate food webs (from Brose et al. 2019, CITE OTHERS) to ask: 3) How does the predator-prey body size scaling relationship in empirical DNA-based diet data compare to the predator-prey body size scaling relationship across multiple studies in which a combination of primarily literature with some empirical (observational) methods were used to assign interactions? Using empirical interaction data to understand how body size and species identity shape terrestrial invertebrate food webs will be key to building predictive food web models built on these parameters (Gravel et al. 2015, Pompanez et al. 2018). In addition, this diet DNA metabarcoding dataset provides an opportunity to strengthen our understanding of predator-prey interactions for small-bodied organisms while examining these patterns at the level (individuals) at which predator-prey interactions occur, thus bridging the gap between species-level food webs and individual-level interactions (e.g. Nakazawa 2017, Stouffer 2010).

**Methods:**

*Field site and collections*

We conducted this work on Palmyra Atoll National Wildlife Refuge, Northern Line Islands (5º53’ N, 162º05’W). Palmyra Atoll has a well-characterized species list, and like many atolls, is relatively species poor, allowing for characterization of potential diet items (Handler et al., 2007). Predator individuals were collected across habitat types representing likely loosely-connected compartments in the atoll metaweb (CITE), including different forest types and microhabitats, including understory vegetation, canopy vegetation, and soil habitats. For each of these habitats, we used a combination of methods, including individual collection during visual surveys for understory and soil collections and canopy fogging with insecticide (cite) onto collection sheets for canopy individuals. All individuals were collected individually with sterilized implements (ethanol-burned forceps) in sterilized collection containers containing 95% EtOH to avoid contamination (Greenstone et al., 2011). All individuals were stored in 95% EtOH a -20ºC before DNA extraction.

We identified all predators to morphospecies in a laboratory environment and later validated unique species by DNA metabarcoding sequence data. The predator species used in this study represent the most common predator species found in each food web compartment (habitat location) and span a body size range of 0.2 – 928 mg (wet mass, SI Table 2). These predators included five arachnid species (*Oonopidae* sp., *Neoscona theisi*, *Heteropoda venatoria*, *Smeringopus pallidus*, and *Scytodes longipes*), one dragonfly (*Pantala flavescens*), one predatory katydid (*Phisis holdhausi*), one earwig (*Euborellia annulipes*), and one soil-dwelling centipede species (*Geophilomorpha* sp.). These predators employ various hunting tools, including webs, venom, and grasping forearms and employ several different hunting strategies, including web-building, sit-and-wait, and active hunting. (DO I need a table?)

*DNA extraction, PCR amplification, library preparation, sequencing, and denoising*

Our full DNA extraction, PCR amplification, library preparation, sequencing, and denoising methods can be found in the Supplementary Information, though we provide an abridged version here.

We individually measured the length of each predator (mm) and separated the thorax, opisthosoma, or trunk (depending on predator species, Krehenwinkel, Macias Herndandez) for DNA extraction following a modified CTAB extraction protocol (Fulton et al., 1995). We followed methods in Krehenwinkel et al. (2017) for extracting diet DNA from terrestrial invertebrate predators, using PCR primers (mlCOIintf/Fol-degen-rev; Krehenwinkel et al. 2017, Leray et al. 2013, Yu et al. 2012) targeting the CO1 gene, which is well-represented in online databases (Porter and Hajibabaei 2018). Following amplification of the CO1 gene, we attached Illumina index primers (Nextera XT Index Kit v2) following the standard protocol for these primers (Illumina). To achieve ample sequencing depth (SI Figure 2), we ran samples across four separate sequencing runs (SI Table 1). All individuals within a predator species were sequenced on the same run and each run contained one to five predator species. We ran 19 samples of one predator species (*H. venatoria*) across all runs to quantify run-to-run variation in sequencing (SI Figure 3). We submitted multiplexed samples for sequencing at the University of California, Santa Barbara Biological Nanostructures Laboratory Genetics Core. Samples were run on an Illumina MiSeq platform (v2 chemistry, 500 cycles, paired-end reads) with a 15% spike-in of PhiX. Following sequencing, samples were demultiplexed using Illumina’s bcl2fastq conversion software (v2.20) at the Core facility. We merged, filtered, and denoised our sequences around amplicon sequence variants (ASVs) using the DADA2 algorithm in R (dada2 package version 1.1.14.0; Callahan et al., 2016). We removed samples from analysis that had not been sequenced to sufficient depth using iNEXT (CITE) and a lower quantile cutoff (SI Figures 6 & 7). We rarefied remaining samples (McKnight et al., 2019) based on the sample with the lowest sequencing depth which had been sequenced with 95%+ sampling completeness based on iNEXT (version 2.0.20) interpolation and extrapolation methods (Hsieh & Chao, 2017). We rarefied using the rrarefy() function in the vegan (version 2.5.6) package in R to 15,954 reads per sample.

*ASV taxonomic assignment with BLAST and BOLD*

We performed taxonomic assignment using BLAST and the blastn command (version 2.7.1) and using sequences in the GenBank and BOLD sequence databases (GenBank accessed: November 20, 2019 and BOLD accessed: May 21, 2020). BLAST analyses were run using the computing cluster at UC Santa Barbara. We exported taxonomic assignments using MEGAN Community Edition (version 6.18.0, Huson et al., 2016), using default settings and selecting the subtree with all possible diet items for this species (Kingdom: Animalia, Clade: Bilateria). We chose to combine prey taxonomies at the family level, similar to diet resolution in both metabarcoding and histological methods in this field (e.g. Brose et al. 2019, Kartzinel – find other metabarcoding ones) by summing the cumulative read abundances across the ASVs that corresponded to each diet family in each sample. All DNA matching any predator family present on an individual sequencing run was also removed as a conservative method to account for potential sequence jumping within sequencing runs which could alter prey identity or diversity in favor of predator species on a shared run (CITE SEQUENCE JUMPING).

*Predator and prey size determination*

We converted predator lengths to wet mass using mass-length scaling relationships for each predator species using existing datasets from the literature and the field site (Soehlstrom et al, Su et al. Yaninek et al. 1993, Miller-ter Kuile *unpublished data*, McLaughlin et al. *unpublished data*). Prey masses were taken as the average mass for individuals across species within each family (Supplementary Information).

*Is prey size determined by predator size, species, or both?*

To determine whether individual predator size, species, or both predicted prey size, we used model selection based on AICc to compare a set of nested linear models with the response variable of prey size. The full model included the interaction between log10 predator mass (in mg) and species identity, with a random effect of predator individual. We log10 transformed the response variable (log10 prey mass in wet mg). To perform model selection, we used the dredge() function in the MuMIn package in R (Versions, citations) to compare all nested models and chose the model with the lowest AICc value. We verified model assumptions for best-fitting models using the DHARMa package in R (versions).

*Is prey identity determined by predator size, species, or both?*

To determine whether predator individuals partition prey items based on body size, species identity, or both, we ran a Canonical Correspondence Analysis (CCA) of 73 predator individuals of four species (*P. holdhausi, N. theisi, H. venatoria,* and *E. annulipes*) collected in the same compartment of the food web. We selected one compartment (canopy of the tree species *Pisonia grandis*) because we wanted to examine how individuals partition resources across body sizes and species given one shared potential prey pool. The CCA analysis included the matrix of feeding interactions for the food web compartment (canopy of *P. grandis*) and the variables of species identity and body size (log10 predator mass in mg) as predictors. We determined the likelihood of the model based on an ANOVA comparing the full CCA to a null model. We then extracted the marginal effects of predictor variables if the ANOVA showed a significant difference between the full CCA and a null model (p-value < 0.05).

*One trait examined: does the use of webs relax prey size constraints?*

To explore how predator traits may influence predator-prey size ratios, we divided predators based on whether or not the predator species uses webs to either capture or subdue prey (n = 5 predator species, 101 individuals that build webs; n = 4 predator species, 81 individuals that do not build webs). We determined the ratio of predator to prey size for each of these interactions (raw predator mass/prey mass) and then built a linear mixed model of this ratio (log transformed for data normality) as the response variable, web-building (binary) as a predictor, and predator individual as a random effect. We then compared this model to a model without the web-building term using AICc and confirmed model assumptions in DHARMA.

*How does predator-prey body size scaling compare to literature scaling value?*

Finally, in order to compare our results to those from the literature, we extracted data from four invertebrate terrestrial food webs (compiled in Brose et al. 2019) on predator-prey body size relationships (not within species, so we could not examine the same species effects) to determine how the general scaling of predator-prey body size in our dataset compared to the relationship from previous food webs in which predator-prey interactions are built with a combination of literature documentation, phylogenetic relatedness, body size constraints, and some observation (Cattin Blandenier (2004), Digel et al. (2014), McLaughlin et al. (2010), Piechnik et al. (2008), Simberloff and Wilson (1969)). For this model, we created a full model of log10 prey mass predicted by the interaction between log10 predator mass and web type (DNA versus literature) with a random effect of food web identity, since data were drawn from a collection of food webs. Because our question was whether the scaling relationship was the same or different between our web and that from the literature webs (ANCOVA), we compared a model with and without the interaction between fixed effects (log10 predator mass and web type) to one without the interaction using AICc values to determine whether the scaling relationship we observed was similar to or different from that observed in these literature webs. We verified model assumptions for best-fitting models using the DHARMa package in R (versions). All figures were created in ggplot2 with color palettes from the calecopal package (CITE).

**Results**

*DNA extraction, PCR amplification, library preparation, sequencing, denoising, and ASV taxonomy*

Complete results and QC for each step of the DNA sequencing protocol can be found in the Supplementary Information.

Our final analyses were performed on a total of 182 predator individuals of nine species. Each predator had consumed 1 – 7 (average 1.86 ± 1.21 SD) prey families. Thirty percent (n = 524 of 1,738 total ASVs) of the total ASVs found in samples received taxonomic assignments from GenBank and BOLD corresponding to prey items at the family level or lower and so were used in analyses. These corresponded to 57 prey families (SUPP table?).

*Is prey size determined by predator size, species, or both?*

The best model predicting prey size included the terms of predator mass and predator species identity, but not the interaction between these two terms. (log10(prey mass) = 0.41\*log10(predator mass), R2m = 0.30, R2c = 0.35, with significant variation in by-species intercepts, Figure 1, SI Table 3)

*Is prey identity determined by predator size, species, or both?*

The predictors of predator species identity and body size explained 15.1% of the total variance in prey composition for the 73 predators collected in the same food web compartment (*P. grandis* canopy; R2 = 0.15, adjusted R2 = 0.10). The best CCA model included both species identity and body size (p-value < 0.001), with a significant marginal effect of species identity (marginal p-value < 0.001) and a non-significant effect of predator size (marginal p-value = 0.07).

*One trait examined: does the use of webs relax prey size constraints?*

Though we did not collect our dataset in order to elucidate what traits might drive patterns in terrestrial invertebrate food webs, we did observe that those species that use webs either to capture or subdue prey (five arachnid species) had a greater proportion of prey items closer to them in size than did predators without web-use traits. (p-value = 0.05, β = 1.25, FIGURE).

*How does predator-prey body size scaling compare to literature scaling value?*

The predator-prey mass scaling relationship for our dataset was significantly shallower than the relationship compiled for four terrestrial invertebrate food webs from the literature (log10(prey mass) = 0.26\*log10(predator mass) for our food web versus log10(prey mass) = 0.64\*log10(predator mass) for the four published food webs (ANCOVA p-value < 0.001).

**Discussion**

The diet DNA metabarcoding data in this study add crucial empirical observation data to the field of food web ecology. For terrestrial invertebrate predators like the ones in our study, comprehensive diet analyses have been nearly impossible or time-prohibitive (e.g. Polis 1991) without genetic methods. Understanding how body size and species identity shape feeding interactions for this set of consumers will be key to generalizing food web patterns and extrapolating to describe terrestrial invertebrate feeding interactions across the globe. We found that both predator mass and predator species identity are important drivers of prey selection. Specifically, 1) we found that larger predator individuals do eat larger prey, however, individuals of some predator species eat proportionally smaller or larger prey than would be expected by one general cross-species relationship. Furthermore, 2) in a food web compartment where predator individuals have access to the same prey pool, predator species identity drives prey species composition, while predator size serves a non-significant role. Finally, 3) when we compared the general predator-prey body size scaling relationship in our dataset to the patterns gathered from four literature food webs for similar consumers, we observed that our DNA diet metabarcoding data scaling relationship is significantly shallower than the relationship found in four food webs in the literature (CITE), suggesting that this general cross-food web relationship would overestimate the size of prey for larger individuals in our dataset and underestimate the size of prey for smaller individuals in our dataset. These results highlight that many food web patterns in small, terrestrial, invertebrate predator-prey interactions can be explained by a combination of body size and predator species identity, lending empirical evidence to the approaches used in the field. Furthermore, while our data suggest either methodological or context-specific variation in general patterns between this and other food webs, [something about the Brose vs. us].

[predator-prey size relationships]

There is continued recognition in the field that food web patterns are likely the result of a combination of body size and species- or taxon-specific traits (Raffaieli 2007, Rudolf et al. 2014, Rall et al. 2011). Our results strengthen the need for combining body size with species identity for explaining and predicting food web patterns. For example, in our results, predators that may be more gape-limited (e.g. *Pantala flavescens* and *Geophilomorpha* sp.) have smaller prey items on average compared to predators of similar, or even, smaller size of other species that may not be as gape limited due to “tools” such as webs (e.g. Oonopidae sp). Some traits that limit prey size selection may be phylogenetically conserved (e.g. mandible morphology), suggesting that approaching these food webs similarly to e.g. Grey at al. (DATE) with phylogenetic filters could explain variation not explained by the trait of body size alone. The fact that predators in one food web compartment in our dataset (CCA analysis of *P. grandis* canopy) select prey primarily based on predator identity rather than size lends additional evidence to the importance of including species identity in food web models.

Conversely, it may be that approaching food web construction more generally than phylogeny, and rather using broad traits in addition to body size might be key to observed food web patterns (e.g. Laigle et al. 2017, Brose et al. 2019). For example, Brose et al. (2019) find that traits such as locomotion strategy or metabolism can explain variation in body size scaling patterns. In our study, we found that predator individuals of five arachnid species that use webs to either catch or subdue prey had significantly larger prey proportional to predator individual body size. This idea has already earned attention in terrestrial invertebrate communities (Laigle et al. 2017) and could be further explored by the use of diet DNA metabarcoding datasets to validate and add feeding interactions. While web-using seems to alter predator-prey size relationships, one predator, the centipede Geophilomorpha sp., which uses venom to subdue prey, consumed proportionally smaller prey (GET AVG SIZE HERE), suggesting that not all hunting tools relax body size constraints. Conversely, one predator which likely uses neither of these tools, the dermaptera *E. annulipes,* fed on proportionally very large prey compared to predator body size (GIVE AVG SIZE HERE), either suggesting some other tool use in this predator or a reliance on scavenging (CITE scavenging). These patterns are promising for further studies on the traits that extend within and across groups of terrestrial invertebrate consumers and the use of combined genetic tools (e.g. RNA sequencing) to determine whether prey items detected in predator diets were consumed live or scavenged (CITE THAT PAPER).

[Literature vs. empirical]

[WHAT WERE LITERATURE DIET METHODS to think about why ours are different]. Is this methodological or is it relative food web to food web? All of these food webs have a lot of spiders.

[1] "Cattin Blandenier (2004)" – literature with some niche processes and body size

[2] "Digel et al. (2014)" - observed in feeding trials and/or single-group molecular, phylogenetic relatedness, body size ratios

[3] "McLaughlin et al. (2010)" – dissected 250 individuals but in no case could prey items be identified. Literature diet observations from other studies

[4] "Piechnik et al. (2008), Simberloff and Wilson (1969)" – literature. To order. Body size ratios.

[downsides/pluses/next directions]

New benefits: within-species data demonstrates cross-species differences in scaling (Nakazawa and other “food webs need individual observations” papers)

These and other datasets that describe feeding interactions at the individual level (e.g. Woodward and Hildrew 2002) for small-bodied invertebrates will link patterns that emerge at the food web level with the mechanisms that drive predator-prey interactions at the individual level (Stouffer 2005, Ings et al. 2009).

[Somewhere in here contextualize Eitzinger et al. 2018 paper which is super cool about prey selection vs. prey availability using DNA metabarcoding]

Downsides: prey body size data aggregated at same level as in the past. Better data in databases online could refine these analyses in the future, suggesting they will just get better.

P: Concluding: not body size only, not species only, individuals acting on interactions at the individual level. A promising validation and refinement of what we already know: body size and species identity are important.

**Acknowledgements**

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**Literature Cited**

**Figures**

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Figure 1: Predator size distributions across the nine predator species. The x-axis scale depicts absolute values but has been log10 transformed. Predator individuals span from 2x10-1 to 9.3x102 mg in wet weight and the facets in this figure have been ordered by increasing predator species mean size.



Figure 2: Prey size distribution. Prey family average size spans between 3.8x10-4 to 3.1x 102.



Figure 3: Larger predators eat larger prey based on a log10-log10 transformed relationship (panel (a), log10 prey size = 0.41\*log10 predator size), though the effect is mediated by species identity (b). Continuous axis labels represent absolute values but the scale between them has been log10 transformed. In panel (b), “+” and “-“ icons indicate species that either have higher (“+”) or lower (“-“) prey sizes relative to predator body size and the general predator-prey body size patterns. The dashed line in panel (a) represents the 1:1 relationship between predator and prey size.



Figure 4: CCA bi-plot depicting the loadings on CCA1 and CCA2 driven by species identity for four predator species collected in the same food web compartment and so which share a common potential prey pool. Predator identity significantly contributes to prey composition (marginal p-value < 0.001) while predator size does not significantly contribute to prey identity/compostion (marginal p-value = 0.07).



Figure: Web-using traits increase the relative size of prey compared to predators (smaller ratios equate larger prey). Predators with web-using traits can relax traits related to gape limitation to access larger prey (p-value = 0.05, β = 1.25). The y-axis is presented with absolute values but displayed on a log10-transformed scale to demonstrate spread in the data. The dashed line indicates the 1:1 ratio where predators and prey are the same size.



Figure 5: comparison of our predator-prey size relationship to that from four food webs compiled from the literature. Our predator prey body size relationship had a significantly shallower slope than that of food webs in the literature (log10(prey mass) = 0.26\*log10(predator mass) vs. log10(prey mass) = 0.71\*log10(predator mass), p-value < 0.001).

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