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ARTICLE

Predator–prey interactions of terrestrial invertebrates are determined by predator body size and species identity

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Abstract

Predator–prey interactions shape ecosystems and can help maintain biodiversity. However, for many of the earth's most biodiverse and abundant organisms, including terrestrial arthropods, these interactions are difficult or impossible to observe directly with traditional approaches. Based on previous theory, it is likely that predator–prey interactions for these organisms are shaped by a combination of predator traits, including body size and species-specific hunting strategies. In this study, we combined diet DNA metabarcoding data of 173 individual invertebrate predators from nine species (a total of 305 individual predator–prey interactions) with an extensive community body size data set of a well-described invertebrate community to explore how predator traits and identity shape interactions. We found that (1) mean size of prey families in the field usually scaled with predator size, with species-specific variation to a general size-scaling relationship (exceptions likely indicating scavenging or feeding on smaller life stages). We also found that (2) although predator hunting traits, including web and venom use, are thought to shape predator–prey interaction outcomes, predator identity more strongly influenced our indirect measure of the relative size of predators and prey (predator:prey size ratios) than either of these hunting traits. Our findings indicate that predator body size and species identity are important in shaping trophic interactions in invertebrate food webs and could help predict how anthropogenic biodiversity change will influence terrestrial invertebrates, the earth's most diverse animal taxonomic group.

KEYWORDS
allometry, arthropod, centipede, DNA metabarcoding, hunting strategy, insect, spider

INTRODUCTION

Predator–prey interactions shape the structure and function of ecosystems and their responses to external influences, including anthropogenic global change (Brodie et al., 2014; McCann, 2000). Species interactions are at risk of extinction following or even preceding species loss, meaning losses of interactions that shape ecosystem structure and function (Borrvall & Ebenman, 2006; Donohue et al., 2017; Valiente-Banuet et al., 2015). Given these challenges, being able to understand what shapes predator–prey interactions may help us to understand the consequences of species loss and may help in predicting and preventing the loss of interactions and species (Brodie et al., 2014; Brose et al., 2017).

However, we have little observed interaction data for small-bodied invertebrate predator species for which empirical diet methods (e.g., gut dissections) are impossible or unfeasible to conduct (Gravel et al., 2013; McLaughlin et al., 2010; Sheppard & Harwood, 2005). The lack of empirical interaction data for small-bodied invertebrate taxa is not inconsequential; these taxa represent over 50% of the earth's animal biomass (including terrestrial and marine systems) and most animal species diversity (Bar-On et al., 2018; Costello et al., 2013; Mora et al., 2011; Stork, 2018). Without these data, we cannot validate extrapolated approaches to predicting interactions based on general rules. For these consumers, species interactions are often inferred from literature reports of observed interactions from phylogenetically related species (Laigle et al., 2018; Piechnik et al., 2008; Simberloff & Wilson, 1969), based on body size feeding constraints (Digel et al., 2014; Hines et al., 2019; Laigle et al., 2018), or derived from mesocosms, feeding trials, or molecular diet analyses that include only pre-defined predator–prey identity pairs (Digel et al., 2014; Guzman & Srivastava, 2019; Kalinkat et al., 2013; Rall et al., 2011; Rudolf et al., 2014). In one of the most recent synthetic studies of these and other food webs across environmental contexts (Brose et al., 2019), of 131,025 invertebrate predatory interactions, a total of 13% of interactions were collected via direct observation (2%) or a combination of observation and inference (11%; inference including interactions using literature searches of similar species and body size rules; Appendix S1: Figure S12). Thus, because these interactions are not empirically observed in natural environments, we do not know whether patterns that emerge for these interactions are real broad ecological patterns or artifacts of the rule-based diet assignment methods used to compile them.

Adding empirical data to understand how predator–prey interactions of invertebrate consumers are shaped will help to understand what general rules can predict these interactions. Traditionally, predator–prey interactions have been approached from a species-specific framework; specifically, emphasis is placed on how species identity or phylogenetic relatedness shape feeding interactions (Ings et al., 2009). However, more generalizable predictions of feeding interactions can be made using non-specific traits. Body size, for example, is a key trait that determines feeding interactions between predators and prey across ecosystems (Woodward et al., 2005). Because body size is integral to feeding interactions, dictating both the rate and range of prey a predator can consume, it is one of the primary metrics used for predicting the structure of feeding interactions for biological communities, or food webs (Gravel et al., 2013; Mack, 2000; Nakazawa, 2017; Potapov et al., 2019; Stouffer et al., 2005; Woodward et al., 2005). Whereas body size alone predicts general patterns across food webs in multiple contexts, combining body size with more species-specific characteristics, including species identity, and more broadly, species traits such as locomotion or metabolic group, creates food-web models that look even more similar to empirically observed patterns (Brose et al., 2019; Gray et al., 2015; Pomeranz et al., 2019; Potapov et al., 2019; Rudolf et al., 2014). Using general traits to describe food-web patterns across ecosystems is not only important for the development of generalizable rules describing patterns in biological communities but could also be integral to predicting and mitigating species extinctions given the rate of anthropogenic species loss (Valiente-Banuet et al., 2015).

In this study, we employ novel diet DNA metabarcoding data from 173 samples of nine terrestrial invertebrate predator species to document predator–prey interactions between these predators and their prey in field conditions, which included 305 unique predator–prey interactions. We matched these data to observed data on predator body size and average body sizes of prey families from an extensive data set of observed body sizes for the prey groups identified in predator diets. To understand how predator size, species identity, and hunting traits may drive empirical predator–prey interactions, we asked (1) Do larger predator individuals eat prey species in families with larger body sizes and does this vary by predator species identity? And (2) do predator species traits related to hunting strategy explain variations in prey size selection, or is prey size selection based on predator phylogeny?

MATERIALS AND METHODS

Field site and collections

We conducted this work on Palmyra Atoll National Wildlife Refuge, Northern Line Islands (5°53′ N, 162°05′ W).

Palmyra Atoll has a well-characterized species list, and like many atolls, is relatively species poor, allowing for detailed characterization of potential diet items (Handler et al., 2007). Predator individuals were collected across habitat types, including different forest types and microhabitats (e.g., understory vegetation, canopy vegetation, and soil types). For each of these habitat types, we used several methods, including individual collection during visual surveys for understory- and soil-dwelling predator individuals and canopy fogging with insecticide onto collection sheets for canopy individuals. Palmyra Atoll is a tropical system with relatively low seasonality, but because predator diets can shift with season (Shimazaki & Miyashita, 2005), we collected all samples in summer months between July and August. Most samples were collected in 1 year (2017), with a few samples of one species (*Heteropoda venatoria*) being collected in 2015 ($n = 23$). 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, Miller-ter Kuile et al., 2021a). All individuals were stored in 95% EtOH at −20°C before DNA extraction.

We identified all predators to morphospecies using a species list for Palmyra Atoll (Handler et al., 2007) and later validated unique species by DNA metabarcoding data. The predators sampled represent the most common predator species found in each habitat location and span a body size range of 0.2–998 mg (wet mass, Figure 1, Appendix S1: Figure S13). These predators included five arachnid species (*Opopaea* 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 (*Mecistocephalus* sp.). These predators use various

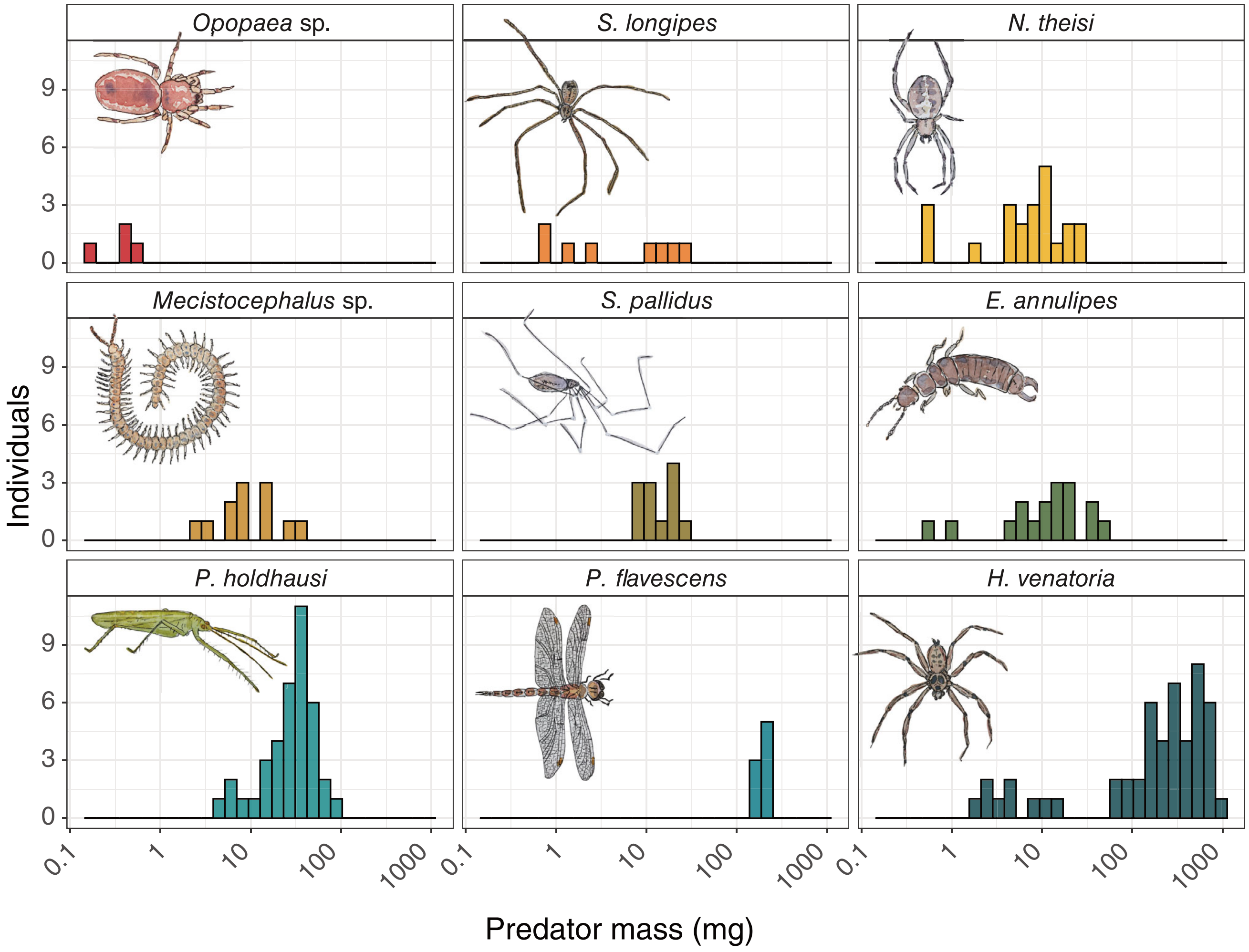

FIGURE 1 Size distributions of predator individuals across the nine predator species. The x-axis scale depicts absolute values but has been $\log_{10}$-transformed. Predator individuals span from 2×10^{-1} mg (*Opopaea* sp.) to 9.9×10^{2} mg (*H. venatoria*) in wet mass. The facets in this figure have been ordered by increasing predator species mean size (art by A. Miller-ter Kuile)

hunting tools, including webs and venom, and employ several different hunting strategies, including active hunting and non-active hunting (e.g., sit-and-wait or ambush, Appendix S1: Table S2).

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 Appendix S1. Here we provide an abridged version.

To determine the identity of prey DNA in predator diets, we extracted and sequenced DNA from samples consisting of one or several predator individuals using high throughput sequencing methods. Multiple predator individuals were combined due to small body size (thus, inability to extract ample DNA) based on shared size (mean length difference ± 0.5 mm), species, and sampling period (70%, or 121/173 samples consisted of one predator individual, and 52/173 consisted of two or more individuals, Appendix S1: Methods and Figures S6 and S7). We extracted DNA from predator samples using a modified CTAB protocol (Miller-ter Kuile et al., 2021a) and following methods outlined in (Krehenwinkel et al., 2017). We amplified the CO1 gene with general metazoan primers (mlCOIintf/Fol-degen-rev; Krehenwinkel et al., 2017, Leray et al., 2013, Yu et al., 2012), multiplexed using Illumina index primers (Nextera XT Index Kit v2; Illumina, San Diego, CA, USA), and sequenced samples on the Illumina MiSeq platform with 250 paired-end reads. We merged, filtered, and denoised our sequences to amplicon sequence variants (ASVs) using the *DADA2* package in R (v1.1.14.0; Callahan et al., 2016; Appendix S1: Figures S2 & S3). We removed samples from analysis with incomplete sequencing depth using interpolation and extrapolation methods (Hsieh & Chao, 2017) and then rarefied all sequencing depths to the lowest sequencing depth of remaining samples (15,954 reads). We performed these steps in R (version 4.0.2; R Core Team, 2020) with the *iNEXT* (version 2.0.20; Hsieh et al., 2016) and *vegan* (version 2.5.6; Oksanen et al., 2020) packages.

ASV taxonomic assignment

To determine the identity of the sequenced DNA, we compared sequencing data to the GenBank and BOLD taxonomic databases (Clark et al., 2016; Hebert & Ratnasingham, 2007). GenBank searches were run using the computing cluster at UC Santa Barbara. We chose to combine prey taxonomies at the family level, similar to diet resolution in both metabarcoding and histological methods in this field (Brose et al., 2019; Eitzinger et al., 2019; Kartzinel et al., 2015) summing the cumulative rarefied read abundances across the ASVs that corresponded to each diet family in each sample. Family-level data provides information comparable to previous studies; additionally, on Palmyra, each family corresponds to an average of 1.9 ± 0.1 (mean ± SE) species, so a family-level taxonomic assignment may closely mirror species-level assignments. We corrected for potential sequence jumping (i.e., "cross-talk") across samples by removing all reads across samples that emerged in negative controls (Oono et al., 2020) and all DNA matching a predator family present on an individual sequencing run was removed across samples on that run as a conservative method to account for potential sequence jumping (van der Valk et al., 2020). We verified ASV specificity based on positive control samples (Appendix S1: Figure S8).

Predator and prey size determination

We measured the length of each predator individual from the front of the head to the end of the abdomen prior to DNA extraction. We converted predator lengths to wet mass using mass–length scaling relationships for each predator species from existing data sets ((Sohlström et al., 2018, Su et al., 2020, Yaninek & Gnanvossou, 1993). Prey species masses were taken as the average mass for individuals across species within each family (Appendix S1: Figures S10 & S11). Averaging prey size by family and using average prey masses in predator–prey mass scaling studies is a common method in the field (Appendix S1: Figure S12), and though not being able to assign prey mass is a limitation of diet DNA metabarcoding data, compiling data in this way allows for comparisons with recent synthetic studies (Brose et al., 2019). In other words, here, we do not report the size of prey individuals that were eaten; rather, for the prey families that were eaten, we report their average body sizes observed in the field.

Data analyses

To determine whether individual predator size, species, or both predicted prey size, we fit a linear mixed effects model with the response variable of $\log_{10}$(prey mass) (in mg) and predictor variables of $\log_{10}$(predator mass) (in mg), species identity, and their interaction, with random intercepts by predator individual to account for dependence among multiple prey species observations within each individual predator. Then, to explore whether predator hunting traits or predator phylogenetic relatedness influences predator–prey size ratios, we divided predator–prey interactions based on whether or not the predator species uses webs to capture prey or uses venom to subdue prey. We determined the ratio of predator to prey size for each of these interactions (raw predator mass/prey mass) and then built a set of linear mixed models using this ratio (log-transformed for data normality) as the response variable, with each type of predator trait as a predictor variable (one model with web-building and one with venom use). We compared these to two predator species relatedness models, choosing to compare the ratio of predator to prey size based on predator species and predator class, with the aim to determine whether, if hunting traits did not influence size selection, individuals within shared taxonomic groups had conserved size ratios. In each of these models, we used a nested random intercept term of predator individual within species. The species model was the "null" model of the other models (no fixed effects and the random effect structure of the other models, i.e., including predator individual and predator species).

Statistical model selection

For the linear mixed-effects models examining how predator size and species identity shape prey size, we performed model selection using the dredge function in the *MuMIn* package in R (package version 1.43.17; Barton, 2020) to compare nested models ($n = 5$ models) and chose the model with the lowest AIC_c value. To compare the predator trait and phylogeny models, we performed model selection by comparing AIC_c values for these models (along with a null model with no predictor variables; $n = 5$ total models). For all models, we verified model assumptions using the *DHARMa* package in R (version 0.3.3.0; Hartig, 2020). The color palette in our figures is from the *calecopal* package (version 0.1.0; Bui et al., 2020).

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 Appendix S1. Raw data are available on GenBank (BioProject: PRJNA715709) and subsequent processed data and code are on Dryad and Zenodo (doi:10.25349/D9M038).

Our final analyses were performed on a total of 173 predator samples of nine species. Each predator sample contained 1–7 (1.76 ± 1.08 [mean ± SD]) prey families. Thirty percent ($n = 524$ of 1738 total ASVs) of the total ASVs found in samples received taxonomic assignments from GenBank and BOLD (Clark et al., 2016; Hebert & Ratnasingham, 2007), corresponding to prey items at the family level or lower ($n = 48$ prey families, 14 orders; Figure 3, Appendix S1: Table S3). Although the predators used in this study represent species at the larger end of the community size spectrum (Figure 1), prey item size distribution resembled the community-wide size distribution (Figure 2). Of the families of prey consumed by predators, 25 (52%) represented families with only one species present on Palmyra Atoll; on average, each family constituted 2.4 ± 0.31 (mean ± SE) species, with a maximum of 11 species in one family (Order: Coleoptera, Family: Curculionidae; Appendix S1: Figure S11).

Predator diet items varied by predator species with the widest diversity of prey items in the order Diptera and the most frequently consumed prey items in the orders Hymenoptera, Lepidoptera, and Orthoptera (Figure 3). Some predator species (including *Mecistocephalus* sp., *E. annulipes*, *S. pallidus*) had common diet items across most individuals; for example, most *Mecistocephalus* sp. (a centipede) individuals ate collembola (Family: Isotomidae) and most *E. annulipes* (an earwig) individuals ate katydids (Family: Tettigoniidae). Conversely, some predator species (including *Opopaea* sp., *N. theisi*, *P. flavescens*, and *S. longipes*) had more diet diversity with fewer shared diet items across individuals. Diet families by

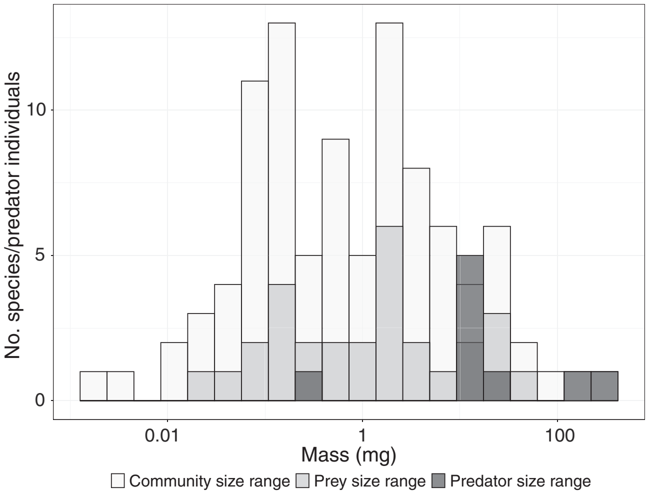

FIGURE 2 While the predator species in this study skew toward the larger side of the size spectrum of the Palmyra community (dark gray, predator individuals; light gray, community species), the prey families detected in DNA data (medium gray) represent much of the range of the community size spectrum

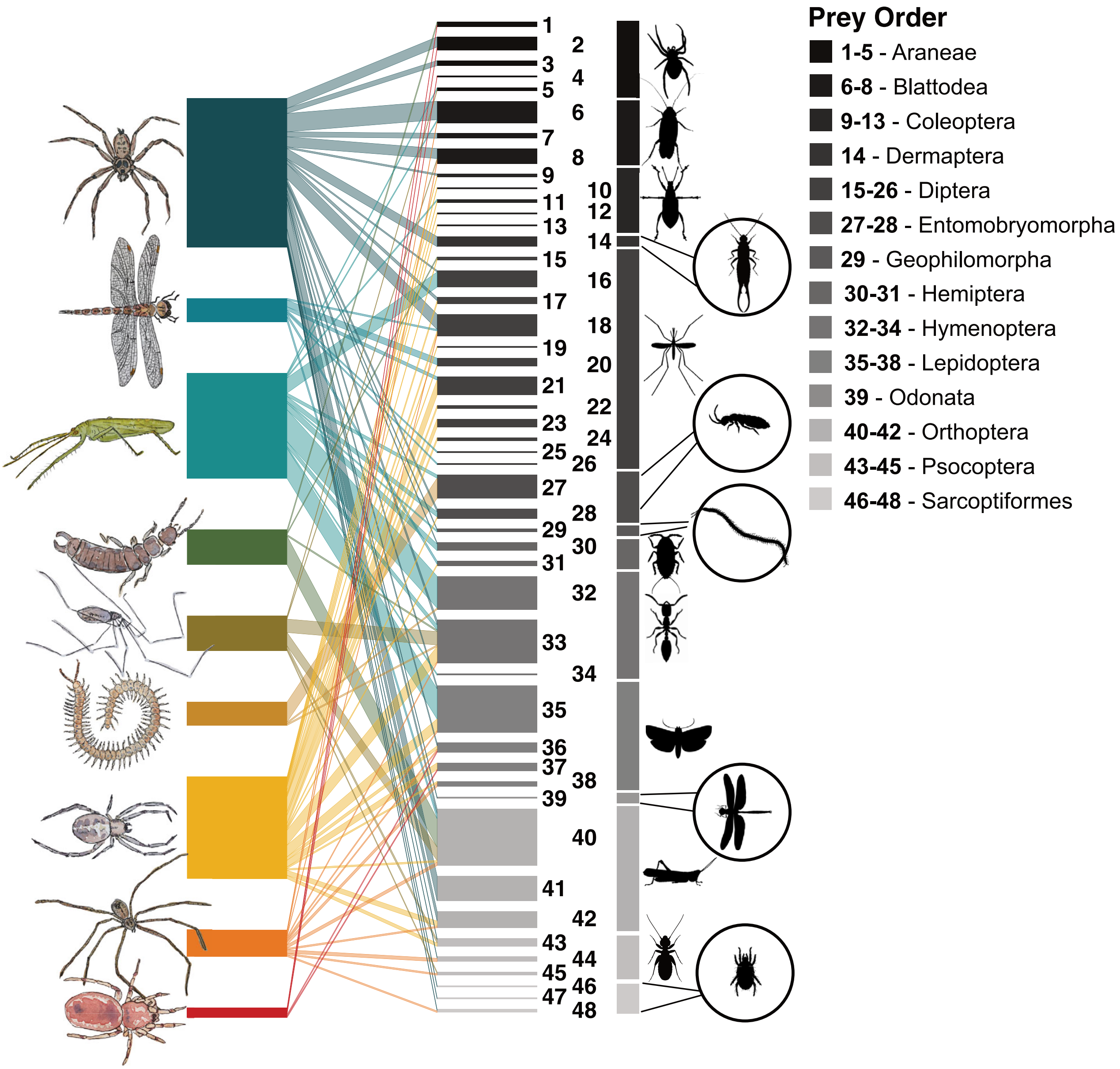

FIGURE 3 Prey families (right bars) detected in the DNA of predator samples (left bars). The width of the predator bars vary due to sample size, the width of the line (interaction) connecting each predator to each prey represents the frequency of that prey family in that predator species sample, and the width of the prey bar corresponds to the number of times that prey family occurs in any predator's diet. Prey families correspond to 48 families (numbered in the plot) of 14 orders of arthropods, including arachnids, collembola, and insects

species are visualized in Figure 3 and summarized in Appendix S1: Table S4.

Prey size and predator:Prey ratio predictors and predation strategy

The best performing model of prey size included the terms of predator mass and predator species identity, but not their interaction, with variation in by-species intercepts (Figure 4, Appendix S1: Table S6; $\beta = 0.32$, $p = 0.001$). The predator trait or species relatedness model that most explained variation in predator:prey size ratio was the model that included predator class as a predictor, followed by the predator species model. In the predator class model, there were statistically significant post-hoc differences between Arachnida and Chilopoda predators and no others (Figure 5, Appendix S1: Table S7).

DISCUSSION

For terrestrial invertebrate predators like the ones in our study, comprehensive field-based diet analyses have been

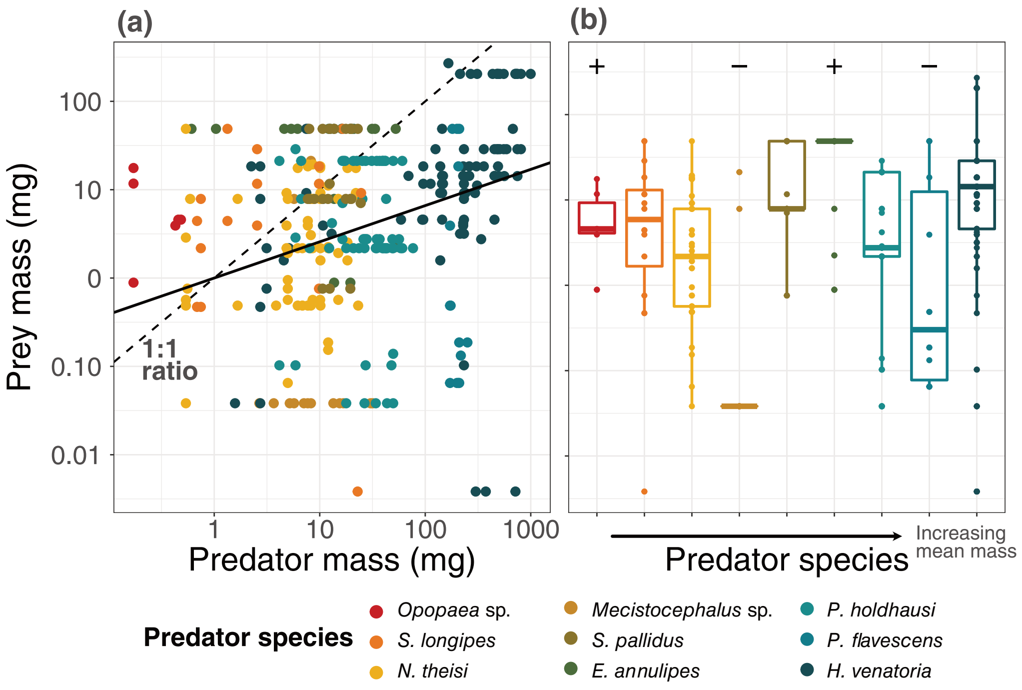

FIGURE 4 A log$_{10}$-log$_{10}$ transformed relationship shows that larger predators eat larger prey families (panel [a], solid line; slope = 0.32), though the effect is mediated by predator species identity (b). The dashed line in panel a represents the 1:1 relationship between predator and prey size. Continuous axis labels represent absolute values but the scale between them has been log$_{10}$ transformed. In panel b, "+" and "−" symbols indicate species that either have significantly higher (+) or lower (−) prey family sizes relative to predator body size and the general predator–prey body size patterns (center line represents median value, with box extent at the 25th and 75th percentile and whiskers 1.5× the interquartile range)

nearly impossible or time-prohibitive without genetic methods (McLaughlin et al., 2010; Polis, 1991). By combining diet DNA metabarcoding data with a well-documented species list and body size data, our study addresses such limitation and provides important empirical examination of interaction patterns for these consumers. We found that predator size and species identity are important drivers of prey size selection and resulting interaction patterns. Specifically, we (1) found that larger predator individuals do eat prey families with larger body sizes, however, individuals of some predator species eat proportionally smaller or larger prey families than would be expected by one general cross-species relationship. Then, we (2) demonstrate that predator species is a strong driver of predator:prey size ratios; no hunting strategies related to hunting tools (e.g., webs and venom) consistently relaxed size constraints across species that possessed those traits. The cross-species predator–prey size scaling relationship in our study is consistent with the combined body size and metabolic group scaling relationship from a recent synthetic study (Brose et al., 2019), though adds important empirical data to a relationship that has previously been built off inferred data for this predator group (Appendix S1: Figure S12). Furthermore, our data suggest that phylogenetic similarity is important for determining predator–prey interaction outcomes. These results highlight that food web patterns in small, terrestrial invertebrate predator–prey interactions may be explained by a combination of predator species characteristics and that not one predator attribute alone predicts all interactions (Pomeranz et al., 2019).

Our results highlight the need for combining multiple predator attributes, including body size and species identity, for explaining and predicting food web patterns (Raffaelli, 2007; Rall et al., 2011; Rudolf et al., 2014). In our results, predator individuals of species that may be more limited in prey sizes they can attack or handle (e.g., *Pantala flavescens* and *Mecistocephalus* sp.) ate prey from families with smaller mean body sizes compared to predators of similar or even smaller size that may be able to attack or handle larger prey (e.g., the spider predators, order Araneae). Whereas both sets of feeding interactions are still constrained by individual predator and prey size, these constraints vary depending on predator identity. Although we did not see evidence that prey family body size was specifically related to tools such as webs or venom, determining what allows predators to relax size constraints is a fruitful area of future study.

Almost one-quarter (24% or 72/305) of the interactions in our data set involved predators that were smaller

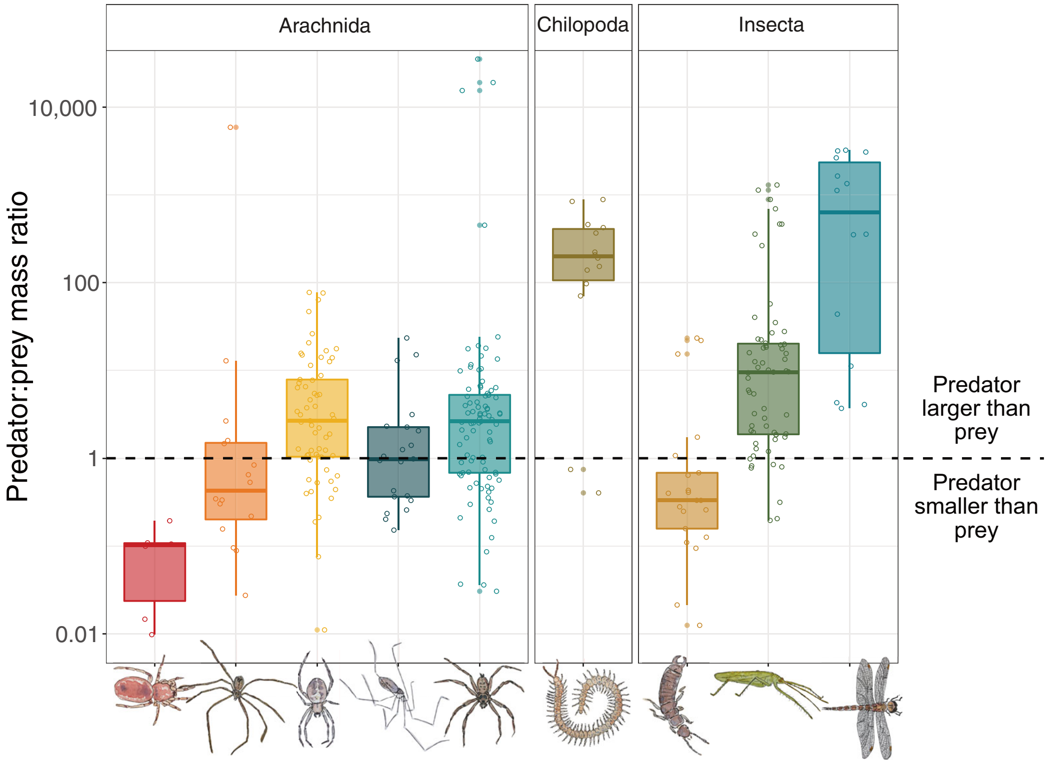

FIGURE 5 Predator class identity was a stronger predictor of predator:prey size ratios than specific hunting traits (e.g., web or venom use). In this figure, the dashed line indicates interactions where predators are the same size as prey families they consumed. The *y*-axis is presented with absolute values but displayed on a $\log_{10}$-transformed scale to demonstrate the spread in the data. Twenty-four percent (72/305) of the interactions in our data set corresponded to predators eating prey families with average sizes larger than themselves (interactions below the dashed line), contrary to assumptions about size-based predation interactions (center line represents median value, with box extent at the 25th and 75th percentile and whiskers 1.5× the interquartile range)

than the mean size of prey families they consumed, seemingly violating assumptions that predators generally eat prey smaller than themselves (Huseynov, 2006a, b; Nakazawa et al., 2013). Some of these interactions may, indeed, suggest that invertebrate predators possess traits that allow them to relax size-based feeding constraints (e.g., extraoral digestion in spiders; Nyffeler et al., 1994). Conversely, it is important to note that these DNA diet data represent mean values for prey families as opposed to the prey individual consumed. This might explain why the earwig in our data set (*E. annulipes*) fed on relatively large prey families (mean ± SE of predator–prey mass ratio = 4.35 ± 1.99:1). A predator like an earwig might not be able to eat a large cricket but might easily eat its eggs or scavenge adult carcasses (Rudolf & Lafferty, 2011; Wilson & Wolkovich, 2011). Thus, while average prey size data may misrepresent the size of prey individuals consumed, these data revealed interaction pairs that would be deemed unlikely or impossible if using body size ratio “rules” based on average prey sizes. Thus, DNA diet data reveals predator–prey interactions that would not be included in food-web models based on mean prey size and predator traits.

Predator hunting strategies, such as web and venom use, have gained attention as important drivers of interactions in invertebrate food webs (Laigle et al., 2018; Schmitz, 2008, 2009) and are often a primary way in which interactions are inferred (Digel et al., 2014; Hines et al., 2019). In our data set, individual species deviated from a general predator–prey body-size scaling relationship, and the traits that have previously gained traction for increasing relative prey size (e.g., venom or web use) did not consistently seem to do so across species; this suggests an evaluation of what other traits (or limitations of traits such as venom and web use) predator species may possess that shape the size constraints of predation interactions. For example, centipedes, which use venom to catch prey, are observed to selectively predate smaller, easier to handle prey to conserve costly venom resources (Dugon & Arthur, 2012). Adult earwigs can use their forceps to subdue large prey, which may explain the relatively large prey of earwigs in our study (da Silva Nunes et al., 2018). Although predatory katydids possess a similar tool in the form of leg spines, which they use to snare prey (Marshall & Hill, 2009), in our data set this species ate relatively small prey, suggesting constraints on prey size for some tools. Even when predators have the ability to consume prey of various sizes, they may select prey based on handling efficiency (e.g., dragonflies selecting smaller Diptera prey; Duong et al., 2017) or nutritional needs (e.g., spiders; Wilder, 2011). There is growing evidence that many invertebrate predators, including those in this study, rely on scavenged food, which is an alternative explanation for the consumption of large prey in some species (Nyffeler et al., 1994; Wilson & Wolkovich, 2011). Conversely to this predator-centric view, it may be that these interactions are more dictated by prey as opposed to predator traits (e.g., predator–prey matching; Gravel et al., 2013; Pomeranz et al., 2019) or prey community availability across microhabitats (similar to seasonal shifts in Shimazaki & Miyashita, 2005). Phylogenetically similar spider species may have distinct ecological niches, especially on islands (Kennedy et al., 2019), and it may be that general patterns of predator–prey interactions may be as much about relative sizes as matching of other predator–prey traits (Gray et al., 2015; Pomeranz et al., 2019).

Diet DNA metabarcoding will continue to be an important tool in understanding the biology of small-bodied invertebrate consumers because it allows the examination of invertebrate diets at the individual level, with the same resolution as that of the diets of larger-bodied species (Baker et al., 2014; Duffy & Jackson, 1986; Hyslop, 1980). As DNA sequence databases continue to grow (Porter & Hajibabaei, 2018), these analyses will likely get more specific and potentially surpass the resolution of other methods (e.g., gut dissection) even for non-invertebrate consumers (McElroy et al., 2020). For example, rather than being confined to family-level taxonomic assignments, future studies, or re-evaluations of past data could reveal a greater depth of species-level data. Although individual body size data had high resolution for the predators included in this study, we are still limited in knowing the abundance or realized size of prey items consumed by these predators because read abundance may not accurately correspond to prey biomass (Elbrecht et al., 2017; Elbrecht & Leese, 2015). Data from DNA can indicate the prey families a predator eats, whereas experimental feeding trials could help to identify constraints on individual prey sizes or determine preferences for live versus dead prey (Rall et al., 2011; Wilson & Wolkovich, 2011). This combination of methods is a promising next step in the field that may reveal important stage structure in invertebrate feeding interactions and even stage specialists (e.g., egg specialists) in apparent general diet assemblages based on DNA metabarcoding alone (Rudolf et al., 2014; Rudolf & Lafferty, 2011). Concurrently, combining multiple genetic methods, such as the use of age-based biomarkers in RNA and DNA sequencing to determine diet age, or amino acid racemization to determine time since prey death, could help determine the age or size of prey and the degree to which predators rely on scavenged food sources, though these methods remain untested in predation interactions (Jarman et al., 2015; Macías-Hernández et al., 2018; Nielsen et al., 2018). Building on existing and emerging methods will allow a clearer picture of the patterns of predator–prey interactions, including those in this study relating to predator traits, but which could also include the examination of environmental and temporal dynamics in predator–prey interactions (e.g., Eitzinger et al., 2019).

Small-bodied invertebrate predators (both terrestrial and marine) are the most diverse and abundant predators on earth (Bar-On et al., 2018; Costello et al., 2013; Mora et al., 2011) and until now, the predation interactions of these consumers in the wild have been largely based on inference and limited observation (e.g., invertebrate food webs in Brose et al. [2019]). Like other predators in multiple other ecosystem contexts (Brose et al., 2019), the predation interactions of small-bodied predators are driven by a combination of measurable and generalizable predator attributes, including body size and species identity. Using empirical data sets, such as those built by diet DNA metabarcoding data, will be key to determining which traits shape and mediate species interactions. Not only will this information build a deeper understanding of the generality of feeding interactions and food webs across environmental contexts and consumer groups, but could be key to predicting and mitigating ongoing biodiversity loss (Borrvall & Ebenman, 2006; Donohue et al., 2017; Valiente-Banuet et al., 2015). Given the growing evidence of global terrestrial invertebrate declines (Desquilbet et al., 2020; van Klink et al., 2020) and the importance of these organisms to broader ecosystem functions, empirical information such as that provided in the present study is critical to develop models and generalizable rules that will aid in understanding and predicting the effects of global change on Earth's ecosystems.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Ana Miller-ter Kuile, Austen Apigo, and Hillary Young conceived the ideas of this study. Ana Miller-ter Kuile, An Bui, Elizabeth S. Forbes, Devyn Orr, Michelle Lee, Taylor Bogar, Jasmine Childress, Rodolfo Dirzo, Maggie Klope, Kevin D. Lafferty, John McLaughlin, Carina Motta, Kevin Park, and David Weber conducted field work for this study. Ana Miller-ter Kuile, Austen Apigo, An Bui, Rachel Behm, Taylor Bogar, Maggie Klope, Michelle Lee, Marisa Morse, John McLaughlin, Kevin Park, and Ronny Young conducted laboratory work for this study. Ana Miller-ter Kuile led the writing of this manuscript with conceptual contributions from Austen Apigo, An Bui, Bartholomew DiFiore, Elizabeth S. Forbes, Michelle Lee, Devyn Orr, Daniel L. Preston, Rodolfo Dirzo, Kevin D. Lafferty, and Hillary Young and all authors provided editorial and intellectual feedback on aspects of the manuscript. All authors have read and agree to the content of this manuscript.

DATA AVAILABILITY STATEMENT

Raw data are available on GenBank under BioProject PRJNA715709 at https://www.ncbi.nlm.nih.gov/bioproject/PRJNA715709. Processed data (Miller-ter Kuile et al., 2021b) are available on Dryad: https://doi.org/10.25349/D9M038. Code (Miller-ter Kuile et al., 2021c) is available on Zenodo: https://doi.org/10.5281/zenodo.5576593.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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