Arthropods as vertebrate predators: A review of global patterns

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Abstract
Aim: Arthropods as vertebrate predators is a generally overlooked aspect in ecology due to the cryptic nature of these events, the relatively small size of arthropods and the difficulty in finding published data. This study represents the largest global assessment of arthropods preying on vertebrates to provide a conceptual framework, identify global patterns and provide a searchable database.

Location: Global.

Time period: Present.

Major taxa studied: Arthropods and vertebrates.

Methods: A systematic literature review was conducted.

Results: Over 1,300 recorded observations were collated from 89 countries. Arthropod predators were from 6 classes and 83 families. Vertebrate prey were from 5 classes and 163 families. Spiders represented over half of all predatory events and were the main predator for all vertebrates except birds, which were mostly preyed upon by praying mantises. Forty percent of all prey were amphibians, specifically frogs. Depredated reptiles were nearly all lizards, half of mammal prey were bats, nearly a third of fish were Cypriniformes and half of bird prey were passerines. Predation by spiders was mainly documented from the U.S., Brazil and Australia, and biased mostly everywhere except the U.S.; insect predatory events were mainly documented from Europe, Australia and the Americas, and biased toward North America; amphibian events were mainly documented from Europe, Australia and the Americas, and biased toward North America; amphibian events were mainly from the Americas and strongly biased everywhere, except for the U.S. and Australia; reptile events were recorded mostly from the Americas and Australia, and biased towards the U.S. and Australia; predation on birds were mainly from the Americas, Australia and Europe, and biased towards Central America and Europe; and mammal events were mostly reported from North and Central America, Australia, and Asia, and strongly biased everywhere except Brazil.

Main conclusions: This study demonstrates that arthropods are underestimated predators of vertebrates. Recognizing and quantifying these predator-prey interactions is vital for identifying patterns and the potential impact of these relationships on shaping vertebrate populations and communities.


1 | INTRODUCTION

Predator–prey interactions are a main driver of natural selection, population dynamics, food web structure, community assemblages and ecosystem function (Darwin, 1859; Gross, 1978; Portailer, Fussmann, Loreau, & Cherif, 2019). As top–down regulators, predators shape ecological communities, having far-reaching effects on environmental processes, ecosystem resilience, and biodiversity (Estes et al., 2011; Sergio, Newton, Marchesi, & Pedrini, 2006; Terborgh & Estes, 2013). This has been demonstrated with the re-introduction of large apex vertebrate predators into their former habitats, which is well known to have substantial effects on ecosystem recovery and restoration of both plants and animals (Beschta & Ripple, 2009; Ripple & Beschta, 2012; Sergio, Newton, & Marchesi, 2005; Sergio et al., 2006). Even relatively small predators can have a top–down control within the food webs of many ecosystems (Moran & Hurd, 1997; Moran, Rooney, & Hurd, 1996), with arthropod predators commonly used as biological control of pests in agriculture and forestry (Kenis, Hurley, Hajek, & Cock, 2017). Arthropod predators can also have a relatively large ecological impact, with spiders alone estimated to consume up to 400–800 million metric tons of insect prey annually (Nyffeler & Birkhofer, 2017), in addition to the vertebrates that they readily prey upon (Baba, Watari, Nishi, & Sasaki, 2019; Butler & Main, 1959; McKeown, 1943; Nyffeler, Edwards, & Krysko, 2017). Despite other arthropods being known to consume vertebrates, vertebrate predation by arthropods remains relatively understudied in ecology compared to other taxonomic groups (Nordberg, Edwards, & Schwarzkopf, 2018).

Recognizing the predator–prey interactions that exist between arthropods and their vertebrate prey is vital for understanding how arthropods can shape vertebrate populations and communities. This could be especially important for threatened vertebrate populations, with recent evidence demonstrating that arthropod predators have the potential to negatively impact conservation efforts of vertebrates, such as fish (Feher, 2019). While some studies have shown arthropods may have a large impact on vertebrates in experimental settings (Kopp, Wachlevski, & Eterovick, 2006; Nordberg et al., 2018; Pearman, 1995; Wizen & Gasith, 2011), very few studies have examined arthropod predation under natural conditions, resulting in these predation events being considered rare in nature. Although there are millions of online videos, photos, and newspaper accounts of arthropods preying on vertebrates, these events are only occasionally documented in scientific literature, with most published articles scattered as single individual observations and appearing in the literature as natural history notes. Despite literature searches becoming much easier with the internet, these articles are still difficult to find, resulting in studies incorrectly stating there are only a few cases recorded (Bastos, Oliveira, & Pombal, 1994; Bernarde, Souza, & Kokubum, 1999) or that they are the first published accounts of such predatory events (Hibbitts, 1992). The complications in finding these published accounts will only be further compounded as natural history science continues to decline (Tewksbury et al., 2014). Furthermore, as this information remains scattered throughout the literature it reiterates the presumed rarity of arthropod predation on vertebrates and makes it increasingly difficult to identify patterns and the potential impact of these trophic relationships.

Recent literature reviews have attempted to recognize and document the importance of arthropod predators on vertebrates. These include reviews of vertebrates such as anurans (Toledo, 2005), geckos (Bauer, 1990), salamanders (Jobe, Montaña, & Schalk, 2019) and squamates (Schalk & Cove, 2018) as vertebrate prey, birds as prey of praying mantises (Nyffeler, Maxwell, & Remsen, 2017), and the prey of giant water bugs (Obha, 2019). However, most reviews are focused exclusively on spiders and their relationships with particular prey, most notably the work by Nyffeler et al., which includes spiders as predators of bats (Nyffeler & Knörrnschild, 2013) and other mammals (Nyffeler & Vetter, 2018), and fish (Nyffeler & Pusey, 2014), as well as the vertebrate prey of jumping spiders (Nyffeler, Edwards, et al., 2017). Other notable reviews include spiders preying on squamates (O’Shea & Kelly, 2017) and on birds (Brooks, 2012). Most of these studies are filtered even further by focusing exclusively within specific regions, such as spiders as predators of amphibians in the Neotropics (Menin, de Jesus Rodrigues, & Menezes, 2017) and Asia (Walther, 2016). Although these major reviews provide a great overview for a specific subset of arthropod predators, they do not provide a comprehensive overview of these relationships, global patterns, or an easily searchable database. The only comprehensive global review of arthropod predation was conducted four decades ago by McCormick and Polis (1982), where they identified arthropods as an important and overlooked predator of vertebrates. In their major review, they detailed a lack of quantitative data and emphasized the importance of studying arthropod predation in future ecological research. However, their recommendation has since been mostly ignored with very little progress having been made and the importance of these trophic relationships remaining largely unclear.

For this study, a global analysis of arthropods preying on vertebrates was undertaken on the available published scientific literature. This systemic literature review was conducted to provide a conceptual framework, identify global patterns and create a searchable database of arthropod predators and their vertebrate prey.

2 | METHODS

An extensive literature search of vertebrate predation by arthropods was undertaken between November 2019 and June 2020. Scientific articles, reviews, bulletins, newsletters, books, theses,
dissertations, government reports and conference proceedings were searched using Google Scholar, BioOne and Web of Science. The literature search was conducted using key search terms (e.g., arthropod, spider, insect, predation, prey, vertebrate, fish, bird, amphibian, etc.), synonyms (e.g., lizard, squamata, reptile), and Boolean language (AND, OR). Literature was found indirectly by reviewing relevant articles cited within the original article. Google Scholar was also used to examine literature that cited the original as well as those recommended by the database using the "cited by" and "related articles" links, respectively. Many secondary citations were from *Herpetological Review*, for which although indexed by Web of Science, abstracts and full text are not archived or searchable. Therefore, their archive from 1967 to 2019 was downloaded and a comprehensive search of their pdf archives was undertaken. Twitter and ResearchGate were also used to enquire about and obtain further citations.

Predatory events were included only if they met the following conditions: (a) an arthropod predator was directly observed attacking and then consuming or attempting to consume a vertebrate; (b) if the prey was not alive it was assumed by the authors to have been caused by the predation event; (c) the event occurred in the field or a natural (not laboratory) experiment (laboratory experiments were thus removed from previous reviews); and (d) the prey was post-hatching (larvae, juveniles, adults). The class, order and family of the prey and predator, as well as the country where the event occurred, were recorded, if available.

A review of all journals referenced was also undertaken on Web of Science to determine what proportion of scientific journals were indexed in a scientific database. An additional literature search was conducted using BioOne to determine the respective bias in the number of published articles between predator and prey groups. All articles between 1965 and 2020 were searched using key search terms, synonyms, and Boolean language; for example, (lizard OR gecko OR snake OR Serpentes OR Squamata OR squamata OR tetrapods OR turtle) was used to search for the number of scientific articles on Squamata. All search terms also included “AND (conservation OR biodiversity OR ecology)” to filter for ecological journals. The data set is openly available from the Dryad Digital Repository (https://doi.org/10.5061/dryad.9p8cz8wd6). A list of the data sources is also found in Supporting Information Appendix S1.

### 2.1 Statistical analysis

A chi-square test was used to compare whether the number of predation events within predator and prey groups was independent of their total number of scientific publications. A post-hoc analysis was conducted using a Bonferroni test to determine any significant differences within the groups (Beasley & Schumacker, 1995).

Since sampling efforts are inherently biased with certain taxa better represented in particular countries than others, stabilized inverse probability weights were calculated to compensate for the imbalance between groups and regions. Inverse probability weights reduce selection bias by adding larger weights to underrepresented observations and lower weights to those overrepresented (Austin & Stuart, 2015; Hernán & Robins, 2020). Stabilized inverse probability weights are calculated by taking the conditional probability of being selected given a set of observed confounding variables and dividing by the marginal probability of the confounding variable. Thus, the stabilized inverse probability weight for each country within a predator or prey class \(W_i\) can be calculated with the formula:

\[
W_i = \frac{P(C = c_i)}{P(C = c_i | X = x_i)}
\]

where \(P(C = c_i | X = x_i)\) is the probability of a predation event in the \(i\)th country within the \(i\)th predator or prey class, and \(P(C = c_i)\) is the observed probability of the \(i\)th country within the study irrespective of predator or prey class. Weights equal to or close to 1 indicate that the conditional probability is equal to its marginal probability and is thus unbiased, weights lower than 1 indicate the observation is overrepresented based on its marginal probability, while weights greater than 1 indicate the observation is underrepresented.

### 3 RESULTS

A total of 1,309 arthropod predation events were found from 737 references (data available from Dryad at https://doi.org/10.5061/dryad.9p8cz8wd6). References included books, theses and conference proceedings, with over 90% comprised of articles from peer-reviewed journals, bulletins, and newsletters (Table 1). Published articles came from a total of 235 different journals with 161 of
them (68.51%) indexed in the Web of Science. Nearly a third of all reported events were obtained from *Herpetological Review*, followed by *Herpetological Notes* with just over 5% (Table 1). However, only ten publication titles recorded over five predation events, with most containing just one or two documented events. Over 7% of articles were obtained from non-English publications (Table 1). Previous reviews contributed 53.89% of all documented predatory events, with the largest contributor of references being McCormick and Polis (1982) (194, 14.82%), followed by Nyffeler and Pusey (2014) (92, 7.02%), Nyffeler, Maxwell, et al. (2017) (65, 4.97%), Toledo (2005) (63, 4.81%), Nyffeler and Knörnschild (2013) (52, 3.97%), with 13 other reviews contributing a combined total of 234 (17.88%) predation events.

Arthropod predators documented in the literature were from 6 classes, 22 orders and 83 families (Figure S2.1 in Supporting Information Appendix S2). The most common class of predators were arachnids (Arachnida), accounting for 56.99% of all observed predation events, followed by insects (Insecta) with 32.54%. Nearly all arachnid observations (93.16%) were spiders (Araneae); insects were made up of mostly true bugs (Hemiptera; 30.75%), mantises (Mantodea; 22.3%), and beetles (Coleoptera; 20.42%); while Malacostraca crustaceans were nearly all decapods (Decapoda; 96.74%) (Figure S2.1 in Supporting Information Appendix S2). The most diverse orders of predators containing the most families were spiders and decapods (Figure S2.1 in Supporting Information Appendix S2). The proportions of spiders, centipedes, mantids, Hemiptera and Malacostraca were significantly higher than would be expected compared to their number of scientific publications, with Coleoptera, Ostracoda and all other insects significantly lower than expected (Figure 1a).

Vertebrate prey were observed from 5 classes, 40 orders and 163 families (Figure S2.2 in Supporting Information Appendix S2). The most common vertebrate class was amphibians (Amphibia) with 40.34% of all observations, followed by reptiles (Reptilia) with 21.85%. For amphibians, 94.70% of observations were frogs (Anura), mainly those in the Hylidae and Leopodactylidae families (Figure S2.2 in Supporting Information Appendix S2). The most commonly preyed upon reptiles (Reptilia) were lizards (Squamata; 89.16%), nearly half of birds (Aves) were passerines (Passeriformes; 47.06%), half of mammals were bats (Chiroptera; 51.59%), while nearly a third of fish (Actinopterygii) were from the Cypriniformes order (28.48%) (Figure S2.2 in Supporting Information Appendix S2). Frogs contained the most prey families, followed by passerines and lizards (Figure S2.2 in Supporting Information Appendix S2). When compared to their respective number of scientific publications, the number of recorded events were significantly greater in amphibians and reptiles and lower in mammals, fish and birds (Figure 1b).

Arachnids, particularly spiders, were by far the main predator for all vertebrates (Figures S3.3, S3.5–3.7 in Supporting Information Appendix S3), except for birds, which were preyed upon by insects.
mainly praying mantises and ants (Figure S3.4 in Supporting Information Appendix S3). Arachnid orders differed in their prey with Amblypygi and Thelyphonida preying mostly on amphibians, and Solifugae mostly on scorpions on reptiles (Figure 2). Although the prey of spiders were somewhat equally distributed (Figure 2), their prey were varied between spider families, with Ctenidae preying mostly on frogs, Theridiidae preying on lizards and rodents (Rodentia), Pisauridae mostly on amphibians and fish, and Araneidae on birds and bats (Figure S3.8 in Supporting Information Appendix S3). For insects, the Hemiptera and Coleoptera orders preyed mostly on amphibians, mantises mostly on birds, and Odonata on amphibians and fish (Figure 2). Decapod predators were observed preying equally on reptiles, birds and amphibians, with centipedes (Chilopoda) preying mainly on reptiles and mammals (Figure 2).

Predatory events were found from 89 countries (see Supporting Information Appendix S1). The United States represented nearly a quarter of all documented events (22.99%), followed by Brazil (16.65%) and Australia (10.62%), with no other country more than 4%. Arachnids were recorded mostly in the United States, Brazil and Australia and were well represented throughout the Americas, Asia (except central Asia), southern and eastern Africa, as well as southern and western Europe (Figure 3a). Arachnid events were biased...
FIGURE 3  Documented arthropod predation events on vertebrates around the world by the inverse probability weights of predator class by country. Size represents total proportion of the taxa and colour represents weights. Weights equal to 1 indicate the number of observations is unbiased, a weight of 0.1 indicates the number of observations is biased towards the country by a multiple of 10 and a weight of 5 indicates the observations is underrepresented by a multiple of 5. Data visualization created with Tableau Public 2020.1 (Tableau Software, Seattle, WA)
towards most regions except in the United States and south Asia (Figure 3a). Insect predation events were mainly from the Americas, particularly the United States and Brazil, southern and eastern Asia, central Europe and southern Africa (Figure 3b). These recorded events were biased towards North America, and underrepresented in Central America, Brazil, and Australia (Figure 3b). Malacostraca were documented most from Brazil, the United States, where they were underrepresented, as well as Central America and the Caribbean where they were overrepresented (Figure 3c). Other arthropods were more sparsely documented, but mainly from the Americas, Australia and Europe, with strong selection bias towards all countries except the United States and Brazil (Figure 3d).

Amphibians were documented throughout the Americas, south and eastern Asia, and west and eastern Africa, with most in Brazil and the United States (Figure 4a). Amphibians were overrepresented in all regions except in North America and Australia (Figure 4a). Birds were documented from the United States, Australia, Europe, South America, and west and southern Africa; and were generally biased towards all regions except for Australia, and North and South America (Figure 4b). Fish events were mostly documented and biased towards North America, especially the United States, as well as southern Asia; and less than expected in Central America, Australia and South Africa (Figure 4c). Mammals were mainly documented from the United States, Australia, Central and northern South America, and southern and eastern Asia; recorded events were underrepresented in Brazil, Peru and Mexico (Figure 4d). Reptile prey were reported mainly from the United States, Australia, Brazil and throughout southern Asia, South America and southern Africa; and generally biased towards most countries, except in Brazil and other South American countries (Figure 4e).
This study represents the largest global assessment of arthropod predation on vertebrate prey, with 1,309 predation events found in the scientific literature. Observations were recorded from 89 countries and every continent where predatory arthropods exist. The largest number of observations were recorded from the United States, Brazil and Australia, which is as expected since ecological studies are heavily skewed toward these regions (Cronin et al., 2014). Although arthropods are more diverse than vertebrates, there are nearly twice as many vertebrate orders and vertebrate families as arthropods. This may be due to ecological research being heavily biased towards vertebrates (Cronin et al., 2014), especially in this study where many of the documented observations were from specialized herpetological and ornithological journals. Furthermore, arthropods are also generally more cryptic due to their smaller size and difficult-to-observe predatory behaviours, which typically occur at night, within forests, or underwater, also likely biasing the results more toward vertebrate prey.

The largest predator group was arachnids, specifically spiders, with nearly half of all documented events, and they were the main predator for all vertebrates except birds. Spiders were mainly reported in the United States, Brazil and Australia and well represented throughout the Americas, Asia and south-western Europe. Studies were biased towards most regions except the United States and south Asia. Despite the large number of observations, the results were significantly much higher than would be expected based on the total number of published arachnid articles. This is unsurprising since the total standing biomass of the global spider community is nearly 25 million metric tons, preying on a similar order of magnitude of prey as all the whales in the world’s oceans (Nyffeler & Birkhofer, 2017). However, these results may also be simply due to spiders being the subject of many review articles (Babangenge et al., 2019; Blondheim & Werner, 1989; Butler & Main, 1959; Maffei, Ubaid, & Jim, 2010; Menin et al., 2005; Morris, 1963; Neill, 1948; Nyffeler, Edwards, et al., 2017; Nyffeler & Knörschild, 2013; Nyffeler & Pusey, 2014; Nyffeler & Vetter, 2018; Steenhouder, 1992). Nevertheless, spiders possess strong fangs capable of piercing vertebrate skin and injecting them with neurotoxins, many specific to the nervous system of vertebrates (Garb & Hayashi, 2013; Gregio, Heleno, Von Eckstedt, & Fontana, 1999). They also have a diversity of tactics such as active hunting, sit-and-wait ambush, and for many, the production of webs that can entangle many small animals. These webs are so strong that birds are often found entangled in them, with many reviews published regarding this phenomenon (Abbott, 1931; Brooks, 2012; Kasambe, Thosar, Rathore, Shivkar, & Sasi, 2010). Another major difference between spiders and other arthropods is that spiders can grow much larger than most arthropods, including very large species such as the goliath bird eater (Theraphosa blondi) in the Theraphosidae family. Their size and the ease of discovering prey caught on their spider webs also make it much easier to observe predation events compared to other arthropods.

Spiders were found to differentiate among their target prey based on the different predatory strategies of their families. Wandering spiders (Ctenidae) are nocturnal, venomous, ambush hunters that preyed mostly on frogs, which are easy targets for these spiders due to their similar nocturnal behaviours and sedentary lifestyle (Valenzuela-Rojas et al., 2019). Tangle-web spiders (Theridiidae) are known for their web building and venomous bite, including those from black widows (Latrodectus) (Nyffeler & Vetter, 2018). This group of spiders are the most common arthropod found in human dwellings, which may explain why the most common prey were lizards and rodents, other common house inhabitants (Leong et al., 2017). Nursery web spiders (Pisauridae), which include fishing spiders, unsurprisingly preyed most on the aquatic animal groups of amphibians and fish, in accordance with previous studies (Baba et al., 2019; Bleckmann & Lotz, 1987; Nyffeler & Pusey, 2014). Lastly, orb-weaver spiders (Araneidae) often feed on birds and bats, which they would be expected to commonly encounter due to their occurrence in gardens, fields and forests. Orb-weavers are known for their strong and very large webs (including the largest web and longest bridge line ever recorded), which makes them well suited to capture these large flying prey (Kuntner & Agranarson, 2010). Nonetheless, these results are also likely due to the differences between the groups and their chance of being observed. Spiders that build webs are generally more conspicuous and visible to humans, who will notice and recognize the captured prey, especially since prey items typically remain stuck in the web for a period of time. Observers will remember where they saw webs and may therefore consciously or subconsciously look for other prey items within these webs. This contrasts with non-web weaving spiders, in which an observer must be in the right place at the right time to be lucky enough to see a predation event.

Other common predators were insects, with different orders also preying on different vertebrate groups. Insects were mainly from North and South America, south-eastern Asia, central Europe and southern Africa. They were biased towards North and South America and underrepresented in Central America and Australia. The largest number of events was from the Hemiptera order, mostly giant water bugs in the Belastomidae family and recorded more than would be expected based on their number of scientific articles. These large, aquatic predators are known to be able to consume everything from turtles to fish due to their large mandibles. In this study, they mostly preyed on aquatic vertebrates such as amphibians and fish. Odonata larvae are another group of large aquatic predators that were found to mostly consume amphibians and fish. Praying mantises as vertebrate predators were reported more than would be expected and were mostly observed preying on birds. Mantises not only eat fledglings but are also well known to capture small birds, especially hummingbirds as they hover in mid-air (Fisher, 1994; Hildebrand, 1949; Lorenz, 2007; Murray, 1958), and are the only known insect to impale their prey with its legs (Rivera & Callohuari, 2019). Malacostraca were also documented more than expected and were documented mainly from Brazil and the United States, where they were underrepresented,
with a bias towards Central America and the Caribbean. Decapod crustaceans, which mostly consisted of crabs, did not exhibit any preference and were found to prey equally on reptiles, amphibians and birds, which may have to do with their wide range of terrestrial, arboreal and aquatic lifestyles (Andrade, Júnior, Júnior, & Leite, 2012; Wehrtmann, Hernández-Díaz, & Cumberledge, 2019). Scorpions were another common predator, being arachnids with a large venomous stinger on their tails and an aggressive hunting strategy, and mainly consumed reptiles and mammals, which are also found in forest environments (Jestrzemski & Schütz, 2016).

The largest group of vertebrate prey were amphibians, representing over 40% of all prey and consisting nearly exclusively of frogs. They were mainly documented throughout the Americas, south-eastern Asia, and western and eastern Africa, with reports strongly biased towards most countries, except for the United States and Brazil. Despite representing such a large proportion of prey, they were documented significantly more than would be expected based on their total number of articles within the scientific literature. Nevertheless, just like with spiders, this bias may also be due to the number of reviews dedicated to amphibians (Babangenge et al., 2019; Costa-Pereira, Martins, Sczesny-Moraes, & Brescovit, 2010; Jobe et al., 2019; Menin et al., 2005; Toledo, Ribeiro, & Haddad, 2007), and because nearly a third of all observations were obtained from Herpetological Review. Nevertheless, frogs are well known to be preyed upon by a wide range of predators, including carnivorous plants, and it has been stated that “practically anything will eat an amphibian” (Duellman & Trueb, 1994). This may be because while many frogs have excellent escape mechanisms (e.g., quick and powerful jumping abilities, production of skin toxins, gliding with large webbed toes, etc.), they are especially vulnerable due to their soft, easily penetrable skin. Compounding this vulnerability, many frogs typically require both aquatic larval and terrestrial adult life stages, with many species also arboreal. This requirement of multi-life stages increases their exposure to the large variety of predators that are present across these habitats. These various predators include diving beetles that are known to feast on tadpoles (Gould, Valdez, Clulow, & Clulow, 2019), water bugs that feast on metamorphs and juveniles (Fadel et al., 2019), and spiders, which may be the most important arthropod predator of adult frogs (Toledo, 2005). The Hylidae group of tree frogs have all these qualities, which may explain why they were the largest order preyed upon. This tendency for frogs to get eaten explains their typical r-selected strategy, with very large clutch sizes compared to other vertebrate groups, which can sometimes number in the tens of thousands (Lever, 2001).

Another large prey group was reptiles, which, compared to their number of scientific articles, were recorded more than would be expected. Reptiles were found throughout the United States, Australia, Brazil, as well as the regions of southern Asia, South America and southern Africa. Observations were biased towards most regions, except for Central and South America. The largest families were geckos, skinks and snakes, which were preyed upon by a diverse group of predators. Although they have various defence mechanisms, groups such as geckos are easy targets due to their relatively small size, compared to larger lizards with stronger teeth and claws. Although snakes are better equipped at protecting themselves given their speed, venoms and fangs, they may still be subdued by the neurotoxins of many of these arthropods, especially scorpions where up to 10% of their diet is snakes (Greene, 1997). Moreover, juveniles and hatchlings are especially vulnerable due to their smaller sizes. The third-largest prey group was birds, which were reported less than would have been expected. Birds were mostly documented from the United States, Australia, Europe, South America and southern Africa, with studies biased towards most regions, except for the United States, South America and Australia. Birds were mostly passerines and hummingbirds, which are small bird species that are more easily caught and consumed by arthropod predators. Hummingbirds include the smallest bird species and were mostly preyed upon by mantises, while spiders had an affinity for passerine birds. Fish were documented less than expected and were preyed upon mostly in North America, Australia, southern Asia and northern South America, and biased towards all regions except Australia and South America. For fish, Cyprinidae was the most common family preyed upon, which is unsurprising as they are not only the most diverse fish family but the most diverse vertebrate family in the world (Froese & Pauly, 2019). Lastly, mammals were also documented less than expected and mainly from the United States, Australia, northern South America, and southern and eastern Asia. Observations were biased towards all regions except Brazil. The most common mammals were bats and rodents, both of which were preyed upon mainly by spiders and centipedes. Although bats can fly, they are easy targets as they roost, particularly their vulnerable young. Juvenile rodents such as rats and mice are also completely helpless as young, requiring extensive parental care, which makes them particularly vulnerable to predation if separated from their parents. However, adults can also easily be taken down by large spiders and centipedes once they have been incapacitated after being injected with venom (Gregio et al., 1999; Ménez, Zimmerman, Zimmerman Ms, & Heatwole, 1990).

Although this study is a systematic review of arthropods preying on vertebrates, it only represents the most common predatory events reported in the scientific literature, which may be more diverse in nature and less biased towards certain groups. Caution is advised when interpreting these results since the frequency or patterns recorded in the literature may not be representative of what occurs in nature, especially since some arthropod predators and predatory events may be more cryptic and much harder to observe than others, making such interactions underrepresented. Nevertheless, these findings provide a good basis for future research to recognize where possible gaps remain. Despite the large number of observations, the results indicate that these predatory events are almost certainly still underestimated. A simple Google search results in hundreds (if not thousands) of accounts on a wide range of arthropod predation on vertebrates, demonstrating how common these predator–prey interactions really are. The difficulty of finding these events is exacerbated due to a large percent of references being in journals that are not indexed.
in a database, in different languages, or in very obscure and specialized bulletins or newsletters. Furthermore, the impact of arthropod predators on vertebrate populations is also much greater than reported here, since this study did not include egg predation, the most vulnerable life stage for all egg-laying vertebrates. Studies have found beetles (Burbano-Yandi, Loaiza-Piedrahita, & Arena-Clavijo, 2018), wasps (Safarek et al., 2010) and spiders (Poo, Erickson, Mason, & Nissen, 2017) consume amphibian eggs, with other studies demonstrating the severe threat of ant predation on turtle nests (Buhlmann & Coffman, 2001; Erickson & Baccaro, 2016; Holbrook, Mahas, Ondhic, & Andrews, 2019; Parris, Lamont, & Carthy, 2002) and bird clutches (Menezes & Marini, 2017). This study also did not include situations where animals were not consumed but were caught in spider webs and subsequently died simply due to being entrapped (Brooks, 2012; Duca & Modesto, 2016; Holbrook, Mahas, Ondhic, & Andrews, 2019; Parris, Lamont, & Carthy, 2002) and bird clutches (Menezes & Marini, 2017). This study also did not include situations where animals were not consumed but were caught in spider webs and subsequently died simply due to being entrapped (Brooks, 2012; Duca & Modesto, 2016; Holbrook, Mahas, Ondhic, & Andrews, 2019; Parris, Lamont, & Carthy, 2002). Both situations would likely remove a considerable number of individuals from a population.

This study demonstrates and further repeats the original assumption of McCormick and Polis (1982) nearly half a century ago, that arthropod predation remains underestimated and quantitative data assessing its impact on vertebrate communities are a necessary link between field and theoretical ecology. Recognizing and understanding arthropod predation and its impact on vertebrate communities have become even more vital in recent years, especially for vulnerable groups with small populations. Evidence from conservation management projects has already demonstrated that arthropod predators can have an impact on the success of conservation efforts (Feher, 2019; Valdez, 2019). However, studies on food webs have been in significant decline during the last four decades (McCa llen et al., 2019), with very few ecological studies on predation or food webs (Carmel et al., 2013). It has, therefore, become more imperative to investigate and quantify the effects of arthropod predators on vertebrate communities within habitats and ecosystems. Although a small number of studies have quantified possible effects, they have occurred under small laboratory settings (Cabrera-Guzmán, Crossland, & Shine, 2012; Pearman, 1995) or involved clay models (Nordberg et al., 2018). However, new methodologies and technological advances can help quantify arthropod predation, such as camera traps (Hobbs & Brehme, 2017), sentinel prey (Lövei & Ferrante, 2017), prey baits and gut analyses (Birkhofer et al., 2017). Recognizing and quantifying these interactions will fill the gap of knowledge remaining in our ecological understanding. This will help to not only understand the role arthropod predators play in shaping vertebrate communities, but also improve the success of conservation efforts by accounting for predators that may currently be overlooked in threat abatement plans.

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DATA AVAILABILITY STATEMENT

The global database is openly available from the Dryad Digital Repository at https://doi.org/10.5061/dryad.9p8c8w6d6

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REFERENCES


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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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