PLOS ONE

Fish Predation by Semi-Aquatic Spiders: A Global Pattern

Martin Nyffeler[1]*, **Bradley J. Pusey**[2]

1 Section of Conservation Biology, Department of Environmental Sciences, University of Basel, Basel, Switzerland, 2 Centre for Excellence in Natural Resource Management, The University of Western Australia, Albany, Australia

Abstract

More than 80 incidences of fish predation by semi-aquatic spiders – observed at the fringes of shallow freshwater streams, rivers, lakes, ponds, swamps, and fens – are reviewed. We provide evidence that fish predation by semi-aquatic spiders is geographically widespread, occurring on all continents except Antarctica. Fish predation by spiders appears to be more common in warmer areas between 40° S and 40° N. The fish captured by spiders, usually ranging from 2–6 cm in length, are among the most common fish taxa occurring in their respective geographic area (e.g., mosquitofish [*Gambusia* spp.] in the southeastern USA, fish of the order Characiformes in the Neotropics, killifish [*Aphyosemion* spp.] in Central and West Africa, as well as Australian native fish of the genera *Galaxias*, *Melanotaenia*, and *Pseudomugil*). Naturally occurring fish predation has been witnessed in more than a dozen spider species from the superfamily Lycosoidea (families Pisauridae, Trechaleidae, and Lycosidae), in two species of the superfamily Ctenoidea (family Ctenidae), and in one species of the superfamily Corinnoidea (family Liocranidae). The majority of reports on fish predation by spiders referred to pisaurid spiders of the genera *Dolomedes* and *Nilus* (>75% of observed incidences). There is laboratory evidence that spiders from several more families (e.g., the water spider *Argyroneta aquatica* [Cybaeidae], the intertidal spider *Desis marina* [Desidae], and the 'swimming' huntsman spider *Heteropoda natans* [Sparassidae]) predate fish as well. Our finding of such a large diversity of spider families being engaged in fish predation is novel. Semi-aquatic spiders captured fish whose body length exceeded the spiders' body length (the captured fish being, on average, 2.2 times as long as the spiders). Evidence suggests that fish prey might be an occasional prey item of substantial nutritional importance.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: martin.nyffeler@unibas.ch

Introduction

A diverse array of predators feed on fish, including piscivorous fish, birds (e.g., egrets, herons, cormorants, gulls, osprey, kites, eagles), fish-eating bats, otters, bears, snakes, certain turtles, etc. [1–5]. Predation by a few large arthropods, that spend all, or at least part, of their life cycle in the aquatic environment and are generally well-adapted at catching aquatic prey such as small fish, tadpoles, frogs, etc., has also been documented [6–7]. For example, water scorpions (Nepidae), giant water-bugs (Belostomatidae), backswimmers (Notonectidae), and water boatmen (Corixidae) are known to kill and eat small fish [7]. A caddisfly species, *Plectrocnemia conspersa* (Polycentropodidae), has been observed preying on fish fry [6], and nymphs of the dragonfly *Cordulegaster dorsalis* (Cordulegastridae) have been reported to kill fish of > 2.5 cm in length [7]. Furthermore, diving beetles (Dytiscidae) and scavenger water beetles (Hydrophilidae) often predate small fish [7], highlighting the plethora of predatory arthropods with trophic interactions with freshwater fish.

Another group of predaceous arthropods known to catch and eat small fish is spiders, particularly large, semi-aquatic pisaurid spiders of the genera *Dolomedes* and *Nilus* ('fishing spiders'). The notion of fish-catching spiders is rather peculiar if we consider that spiders, as a whole, are traditionally viewed as the classic example of a predator that feeds on insects, yet some spiders are well-adapted for life near, or on, the water surface [8]. Despite the widespread assumption of spiders primarily being insectivores,

piscivory is not altogether surprising considering that a number of spiders (e.g., Araneidae, Nephilidae, Pisauridae, Sparassidae, Theraphosidae, and Theridiidae) occasionally supplement their arthropod diet with small vertebrates including frogs, toads, salamanders, lizards, snakes, mice, rats, bats, and birds [7,9–10] and many spiders may be found at the land-water interface. Photographic evidence supporting the existence of fish-catching by 'fishing spiders' has been published [11–13] but published accounts of open-field assessment of fish predation are often anecdotal, from very old literature sources and originate from only few locations [14–19]. Additionally, the majority of published photographic sources depict spiders preying upon fish in captivity [11–13]. More recently, evidence of the extent of fish predation by spiders in laboratory [20–24] and field experiments [25], suggests it is more widespread than traditionally thought. However, the propensity for spiders to feed on fish and the importance of this trophic relationship under natural conditions remains unclear. We conducted a global analysis of all available literature on fish predation by spiders and unpublished information from biologists and naturalists (arachnologists, ichthyologists, aquatic ecologists, photographers, etc.) to provide a broad, conceptual framework for this trophic relationship placed within the context of spider behavior and nutritional ecology.

Table 1. Reports of fish predation by spiders under natural conditions in the field, based upon published literature and unpublished data (File S1 provides detailed documentation of all predation events).

Predator (spider taxon)		Prey (fish taxon)		Estimated total length of fish (cm)	Estimated fish length/spider length ratio	Type of evidence	Country	Source	report #
Species	Family	Species	Family						
Agroeca lusatica	Liocranidae	'Trout' (fry)	Salmonidae	2	2.8	Direct observation	France	[165]	86
Ancylometes bogotensis	Ctenidae	Unidentified	Poeciliidae	N/A	N/A	Photo	Costa Rica	[166]	47
Ancylometes rufus	Ctenidae	Unidentified	Unidentified	N/A	N/A	Direct observation	Brazil	[35]	58
Ancylometes sp.	Ctenidae	Cyphocharax sp.	Curimatidae (Characiformes)	6	2.4	Photo	Ecuador	Ed Germain, pers. comm.	52
Ancylometes sp.	Ctenidae	Unidentified	Characiformes	N/A	N/A	Photo	Ecuador	Tim Wohlberg, pers. comm. http://zufalladventures.com/	53
Ancylometes sp.	Ctenidae	Unidentified	Characiformes	N/A	N/A	Photo	Ecuador	Cleatus Cobb, flickr website	54
Ancylometes sp.	Ctenidae	Unidentified	Characiformes	N/A	N/A	Photo	Ecuador	http://alexlisasouthamerica.blogspot.ch	55
Ancylometes sp.?	Ctenidae	Unidentified	Unidentified	N/A	N/A	Direction observation	Ecuador	http://www.tripadvisor.de	56
Ancylometes sp.	Ctenidae	Unidentified	Characiformes	~7–8	2.7	Photo	Peru	http://thinkjungle.com/amazon-rainforest-life/amazon-rainforest-carnivores/	60
Dolomedes facetus	Pisauridae	Carassius auratus	Cyprinidae	9	3.7	Photo	Australia (Sydney)	[19]	64
Dolomedes facetus	Pisauridae	Xiphophorus sp.	Poeciliidae	5.5	2.2	Photo	Australia (Brisbane area)	Peter Liley, pers. comm.	67
Dolomedes facetus	Pisauridae	Unidentified	Unidentified	N/A	N/A	Direct observation	Australia (Audley, NSW)	[19]	63
Dolomedes facetus	Pisauridae	Unidentified	Unidentified	N/A	N/A	Photo	Australia	Jean-Paul Ferrero, ardeaprints.com	70
Dolomedes mizhoanus	Pisauridae	Unidentified	Unidentified	N/A	N/A	Direct observation	China	[105]	77
Dolomedes okefinokensis	Pisauridae	Gambusia holbrooki	Poeciliidae	4	1.8	Photo	USA (Florida, Big Cypress National Preserve)	Misti Little, pers. comm.	28
Dolomedes okefinokensis	Pisauridae	Gambusia affinis	Poeciliidae	2.5	1.0	Direct observation	USA (Florida, near Lake Washington)/Incidence 1	[121] (ID of spider changed by Carico [29])	21
Dolomedes okefinokensis	Pisauridae	Gambusia affinis	Poeciliidae	2.5	1.0	Direct observation	USA (Florida/near Lake Washington)/Incidence 2	[121] (ID of spider changed by Carico [29])	22
Dolomedes okefinokensis	Pisauridae	Gambusia affinis	Poeciliidae	2.5	1.0	Direct observation	USA (Florida/near Lake Washington)/Incidence 3	[121] (ID of spider changed by Carico [29])	23
Dolomedes plantarius	Pisauridae	Gambusia holbrooki	Poeciliidae	N/A	N/A	Direct observation	Italy	Emanuele Biggi, pers. comm.	85
Dolomedes plantarius	Pisauridae	Pungitius laevis	Gasterosteidae	N/A	N/A	Photo	UK/Incidence 1	Helen Smith, pers. comm.	87

Table 1. Cont.

Predator (spider taxon)		Prey (fish taxon)		Estimated total length of fish (cm)	Estimated fish length/spider length ratio	Type of evidence	Country	Source	report #
Species	Family	Species	Family						
Dolomedes plantarius	Pisauridae	Pungitius laevis	Gasterosteidae	N/A	N/A	Direct observation	UK/Incidence 2	Helen Smith, pers. comm.	88
Dolomedes raptor	Pisauridae	Unidentified	Infraclass Teleostei	5.5	2.2	Photo	Taiwan	I-Min To, pers. comm.	74
Dolomedes saganus	Pisauridae	Oryzias curvinotus	Adrianichthyidae	4.3	1.8	Direct observation	Hong Kong	[167]	75
Dolomedes saganus	Pisauridae	Pseudorasbora parva	Cyprinidae	3.3	1.4	Direct observation	Japan	[168]	73
Dolomedes scriptus	Pisauridae	'Darter'	Percidae	N/A	N/A	Direct observation	USA (unspecified location)	[29]	44
Dolomedes scriptus	Pisauridae	Lepomis cyanellus	Centrarchidae	5.5	2.5	Photo	Canada (Ontario)	Lloyd Alter, pers. comm.	46
Dolomedes scriptus	Pisauridae	Unidentified	Infraclass Teleostei	N/A	N/A	Photo	USA (unspecified location)	http://www.flickr.com/photos/44608110@N06/4114197379/	45
Dolomedes scriptus	Pisauridae	'Minnow'	Cyprinidae	N/A	N/A	Photo	USA (Michigan)	[169]	41
Dolomedes tenebrosus?	Pisauridae	Notemigonus crysoleucas	Cyprinidae	N/A	N/A	Photo	USA (Maine)	Jeffrey Hollis, pers. comm.	40
Dolomedes tenebrosus	Pisauridae	Semotilus atromaculatus	Cyprinidae	6.5	3.0	Photo	USA (Kentucky)	Jason Butler, pers. comm.	33
Dolomedes triton	Pisauridae	Carassius auratus	Cyprinidae	5	2.2	Photo	USA (Texas)	Leslie Todd, flickr website	11
Dolomedes triton	Pisauridae	Gambusia holbrooki	Poeciliidae	4.5	2.0	Photo	USA (Florida, Lady Lake)	Machele White, pers. comm.	20
Dolomedes triton	Pisauridae	Gambusia sp.	Poeciliidae	N/A	N/A	Photo	USA (Florida, near Tampa)	Stacy Cyrus, DavesGarden website	24
Dolomedes triton?	Pisauridae	Gambusia affinis	Poeciliidae	N/A	N/A	Photo	USA (Florida, Washington County)	Paul Moler, pers. comm.	17
Dolomedes triton	Pisauridae	Gambusia affinis	Poeciliidae	N/A	N/A	Unknown	USA (Mississippi)	[170]	15
Dolomedes triton	Pisauridae	Gambusia holbrooki	Poeciliidae	5	1.8	Photo	USA (North Carolina)	Patrick Randall, pers. comm.	30
Dolomedes triton	Pisauridae	Gila ditaenia	Cyprinidae	N/A	N/A	Photo	USA (Arizona)	Andreas Kettenburg, pers. comm.	9
Dolomedes triton	Pisauridae	Fundulus chrysotus	Fundulidae	3	1.2	Photo	USA (Texas)	Richard Dashnau, pers. comm.	10
Dolomedes triton	Pisauridae	Heterandria formosa	Poeciliidae	N/A	N/A	Photo	USA (Florida, Tsala Apopka Lake)	Claire Sunquist-Blunden, pers. comm.	19
Dolomedes triton	Pisauridae	Ictalurus punctatus (fingerling)	Ictaluridae	≤6	≤3	Direct observation	USA (Oklahoma)	[131]	12
Dolomedes triton	Pisauridae	Unidentified	Unidentified	N/A	N/A	Direct observation	USA (Florida, Highlands Hammock State Park)	Brian Kenney, pers. comm.	25
Dolomedes triton	Pisauridae	Unidentified	Unidentified	N/A	N/A	Direct observation	USA (Florida, near Bradenton)	Brian Kenney, pers. comm.	26
Dolomedes triton	Pisauridae	Unidentified	Unidentified	N/A	N/A	Direct observation	USA (Florida, near Venice)	Brian Kenney, pers. comm.	27

Table 1. Cont.

Predator (spider taxon) Species	Family	Prey (fish taxon) Species	Family	Estimated total length of fish (cm)	Estimated fish length/spider length ratio	Type of evidence	Country	Source	report #
Dolomedes triton	Pisauridae	Unidentified	Unidentified	2.5	1.3	Direct observation	USA (New York)	[171] (ID by Carico [29])	39
Dolomedes vittatus	Pisauridae	Unidentified	Fundulidae?	5.5	2.5	Photo	USA (unspecified location)	[172]	43
Dolomedes sp.	Pisauridae	Carassius auratus	Cyprinidae	7	3.0	Direct observation	Australia (Adelaide)/ Incidence 1	[19]	61
Dolomedes sp.	Pisauridae	Carassius auratus	Cyprinidae	7.5	3.0	Photo	Australia (Adelaide)/ Incidence 2	[19]	62
Dolomedes sp.	Pisauridae	Carassius auratus	Cyprinidae	2.5	1.0	Direct observation	Australia (Lismore)	[19]	65
Dolomedes sp.	Pisauridae	Elassoma zonatum	Elassomatidae	3.5	1.8	Direct observation	USA (California)/ Incidence 1	[18,173]	1
Dolomedes sp.	Pisauridae	Elassoma zonatum	Elassomatidae	3.5	1.8	Direct observation	USA (California)/ Incidence 2	[18,173]	2
Dolomedes sp.	Pisauridae	Elassoma zonatum	Elassomatidae	3.5	1.8	Direct observation	USA (California)/ Incidence 3	[18,173]	3
Dolomedes sp.	Pisauridae	Elassoma zonatum	Elassomatidae	3.5	1.8	Direct observation	USA (California)/ Incidence 4	[18,173]	4
Dolomedes sp.	Pisauridae	Elassoma zonatum	Elassomatidae	3.5	1.8	Direct observation	USA (California)/ Incidence 5	[18,173]	5
Dolomedes sp.	Pisauridae	Elassoma zonatum	Elassomatidae	3.5	1.8	Direct observation	USA (California)/ Incidence 6	[18,173]	6
Dolomedes sp.	Pisauridae	Elassoma zonatum	Elassomatidae	3.5	1.8	Direct observation	USA (California)/ Incidence 7	[18,173]	7
Dolomedes sp.	Pisauridae	Elassoma zonatum	Elassomatidae	3.5	1.8	Direct observation	USA (California)/ Incidence 8	[18,173]	8
Dolomedes sp. (not facetus)	Pisauridae	Galaxias olidus	Galaxiidae	7.5	3.4	Photo	Australia (Goomburra)	Loren Jarvis, pers. comm.	66
Dolomedes sp.	Pisauridae	Gambusia affinis	Poeciliidae	N/A	N/A	Direct observation	USA (Kentucky)	[156]	35
Dolomedes sp.	Pisauridae	Gambusia affinis	Poeciliidae	N/A	N/A	Direct observation	USA (Kentucky)	Jason Butler, pers. comm.	34
Dolomedes sp.	Pisauridae	Gambusia affinis	Poeciliidae	N/A	N/A	Direct observation	USA (Louisiana)	[131]	13
Dolomedes sp.	Pisauridae	Lepomis macrochirus	Centrarchidae	N/A	N/A	Direct observation	USA (Louisiana)	[131]	14
Dolomedes sp.	Pisauridae	'Minnow'	Cyprinidae	7.6	3.8	Direct observation	USA (Alabama)	[15]	16

Table 1. Cont.

| Predator (spider taxon) | | Prey (fish taxon) | | Estimated total length of fish (cm) | Estimated fish length/spider length ratio | Type of evidence | Country | Source | report # |
Species	Family	Species	Family						
Dolomedes sp.	Pisauridae	'Minnow'	Cyprinidae	3.2	1.6	Photo	USA (Georgia)	[18]	29
Dolomedes sp.	Pisauridae	'Minnow'	Cyprinidae	8.3	4.1	Direct observation	USA (New Jersey)	[15]	36
Dolomedes sp.	Pisauridae	*Oncorhynchus mykiss* (fry)	Salmonidae	N/A	N/A	Direct observation	USA (Tennessee)	[17]	32
Dolomedes sp.	Pisauridae	*Oncorhynchus mykiss* (fingerling)	Salmonidae	5.7	3.0	Direct observation	USA (Tennessee)	[17]	31
Dolomedes sp.	Pisauridae	Unidentified	Centrarchidae	5	2.5	Direct observation	USA (Pennsylvania)/Incidence 1	[15]	37
Dolomedes sp.	Pisauridae	Unidentified	Centrarchidae	5	2.5	Direct observation	USA (Pennsylvania)/Incidence 2	[15]	38
Dolomedes sp.	Pisauridae	Unidentified	Unidentified	N/A	N/A	Direct observation	USA (northern Florida)	Paul Moler, pers. comm.	18
Dolomedes sp.	Pisauridae	*Micropterus dolomieu*	Centrarchidae	4.5	2.0	Photo	USA (Wisconsin)	Tod Lewis, pers. comm.	42
Nilus curtus	Pisauridae	Unidentified	Unidentified	probably >4	2.0	Direct observation	South Africa	Astri Leroy, pers. comm.	79
Nilus massajae	Pisauridae	Unidentified	Unidentified	4	1.7	Photo	Zimbabwe	Marcelo de Freitas, pers. comm.	81
Nilus sp.	Pisauridae	*Aphyosemion* sp.	Nothobranchiidae	4.5	2.2	Photo	Cameroon	Duncan Reid, pers. comm.	82
Nilus sp.	Pisauridae	*Aphyosemion walker*	Nothobranchiidae	3	1.5	Photo	Ivory Coast/Incidence 1	[174]	83
Nilus sp.	Pisauridae	*Aphyosemion walker*	Nothobranchiidae	N/A	N/A	Direct observation	Ivory Coast/other incidences	[174]	84
Nilus sp.	Pisauridae	'Trout' (fry)	Salmonidae	N/A	N/A	Direct observation	South Africa	[14]	80
Pardosa pseudoannulata	Lycosidae	*Elassoma zonatum*	Elassomatidae	1.9	1.9	Direct observation	India	[82]	78
Trechalea sp.	Trechaleidae	Unidentified	Characiformes	N/A	1.8	Photo	Brazil	Jacques Jangoux, pers. comm.	59
Trechalea sp.	Trechaleidae	Unidentified	Characiformes	N/A	1.9	Photo	Colombia	Juan Esteban Arias A., pers. comm.	50
Trechalea sp.	Trechaleidae	Unidentified	Characiformes	N/A	2.2	Photo	Colombia	Solimary Garcia Hernandez, pers. comm.	51
Trechalea sp.	Trechaleidae	Unidentified	Characiformes	N/A	2.2	Photo	Panama	Jessica Stapley, pers. comm.	48
Unidentified	Ctenidae	Unidentified	Siluriformes (most likely Pimelodidae)	N/A	N/A	Photo	Ecuador	Craig Harrison, travel blog/ecuador	57
Unidentified	Trechaleidae?	Unidentified	Characiformes	N/A	N/A	Direct observation	Panama	[17]	49

Table 1. Cont.

Predator (spider taxon)		Prey (fish taxon)		Estimated total length of fish (cm)	Estimated fish length/ spider length ratio	Type of evidence	Country	Source	report #
Family	Species	Family	Species						
Pisauridae	Unidentified	Cyprinidae	*Cyprinus carpio*	2	1.0	Direct observation	Australia (Victoria)	Alison King, pers. comm.	89
Pisauridae	Unidentified	Melanotaeniidae	*Melanotaenia* spp.	N/A	N/A	Direct observation	Australia (Cairns)	Bradley Pusey, pers. comm.	68
Pisauridae	Unidentified	Cyprinidae	*Parazacco spilurus*	2.5	N/A	Direct observation	Hong Kong	David Dudgeon, pers. comm.	76
Pisauridae	Unidentified	Pseudomugilidae	*Pseudomugil* spp.	N/A	N/A	Direct observation	Australia (Cairns)	Bradley Pusey, pers. comm.	69
Pisauridae	Unidentified	Cyprinidae	*Rasbora callliura*	6	3.5	Photo	Borneo	Michael Lo, pers. comm.	72
Pisauridae?	Unidentified	Unidentified	Unidentified	N/A	N/A	Direct observation	Australia	Morsten 1835 (cited by [19])	71

doi:10.1371/journal.pone.0099459.t001

Methods

An extensive bibliographic search was conducted to locate information concerning fish predation by spiders. The search was based largely on the Thomson-Reuters database (Web of Science), Google Scholar, Google Books, and ProQuest Dissertations & Theses. In addition, an internet search for information on this topic was conducted; authors of photographic material and reports on fish predation by spiders were contacted to obtain detailed information on these observations. Furthermore, inquiries among biologists were undertaken for unpublished reports on this topic. A total of 89 incidences of fish predation by spiders was gathered (Table 1). For the most part, only incidences of fish predation by free living spiders are listed in Table 1; however, a few incidences where semi-aquatic spiders killed fish in aquaria after wandering into buildings (not-staged situations; [15,18]) are included. Staged observations of captive spiders predating fish in aquaria, fish tanks, or garden pools are included in Tables 2 and 3. Fourty-four (49%) of the incidences in Table 1 were previously reported in the scientific literature and 44% of observations included photographic documentation of predation.

Unpublished photographs of such events gained during the study were sent to ichthyologists and spider taxonomists for identification (see Acknowledgements for details). The resolution of a small number of the images was reduced sufficiently to result in uncertain identification beyond genus level but in most cases, identification to species level was considered appropriate. This is true for fish and spiders. Nomenclature of spiders follows Platnick [26]. Data on the live weight and size of spiders and fish were taken from the arachnological [11,13,17,19–20,22–25,27–43] and ichthyological [1,44–68] literature. Unless reported in the literature or by the respondents in our survey, the total lengths of the fish prey were estimated based on the photographs (see Table 1). The vast majority of reported spiders were adult pisaurids ~2–2.5 cm in length (cephalothorax plus abdomen; Table 2) and knowing their approximate body length, this was used as a standard (replacing a reference scale) to roughly estimate fish lengths. In cases where spider length remained doubtful (e.g., immature *Trechalea* spp.) no estimates of fish length were made. The estimates obtained in this manner were similar to those reported in the literature where the lengths of predated fish were measured in the laboratory indicating that our estimates are fairly accurate. Report numbers used in the tables refer to the respective detailed report description (see File S1).

Results

Geographic Distribution of Fish Predation by Spiders

Fish capture by spiders has been reported from all continents with the exception of Antarctica, where semi-aquatic spiders are absent ([26]; Fig. 1; Table 1). Approximately 90% of observed fish predation events were from regions of warmer climate between 40° S and 40° N (Fig. 1) and were typically observed at the margin of freshwater streams, rivers, creeks, bayous, lakes, ponds, swamps, and fens (see File S1).

Fish predation by spiders has been most frequently documented in North America, with 45 incidences from the USA (51% of the total; Figs. 2–3; Table 1; report # 1–45) with those concentrated in the east and southeast, particularly in Florida wetlands and neighbouring regions (Fig. 2). Elsewhere in North America, nine incidences of fish predation from the western USA are known to us (eight from California and one from Arizona; report # 1–9), two from the Midwest (one from Michigan and one from Wisconsin; report # 41–42) and a single observation from Canada of a semi-

Table 2. Fresh weight and body length (cephalothorax plus abdomen) of adult spider species reported to catch fish.

Spider species	Spider family	Weight (g)	Body length (cm)	Location of observation	Source	report #
Agroeca lusatica	Liocranidae	N/A	~0.7	Wild	[30,165]	86
Ancylometes bogotensis	Ctenidae	1.4–2.6	2	Wild	[22,35]	47
Ancylometes rufus	Ctenidae	≤7	3–4	Wild	[35,41]	58
Argyroneta aquatica	Cybaeidae	~0.1–0.3	1.2–1.9	Captivity	[23,38,88]	
Desis marina	Desidae	~0.1	1–1.5	Captivity	[19,31–32]	
Dolomedes dondalei	Pisauridae	N/A	2.5	Captivity	[11]	
Dolomedes facetus	Pisauridae	N/A	2	Wild	[19]	63–64, 67, 70
Dolomedes fimbriatus	Pisauridae	~0.5	2	Captivity	[13,23,89,175]	
Dolomedes mizhoanus	Pisauridae	N/A	2.4	Wild	[40]	77
Dolomedes okefinokensis	Pisauridae	~2*	2.5	Wild	[27,29]	21–23, 28
Dolomedes plantarius	Pisauridae	N/A	2–2.5	Wild	[13]	85, 87–88
Dolomedes raptor	Pisauridae	N/A	2.6	Wild	[40]	74
Dolomedes saganus	Pisauridae	N/A	2.4	Wild	[40]	73, 75
Dolomedes scriptus	Pisauridae	N/A	2.4	Wild	[27]	41, 44–46
Dolomedes sulfureus	Pisauridae	N/A	2.6	Captivity	[23]	
Dolomedes tenebrosus	Pisauridae	~2	1.5–2.6	Wild	[27,43]	33, 40
Dolomedes triton	Pisauridae	1–1.5	1.5–2.5	Wild	[20,34,36]	9–12, 15, 17, 19–20, 24–27, 30, 39
Dolomedes vittatus	Pisauridae	N/A	2	Wild	[27]	43
Dolomedes sp. – photographed in Queensland (not *facetus*)	Pisauridae	N/A	N/A	Wild	Loren Jarvis, pers. comm.; Robert Raven, pers. comm.	66
Hemirrhagus pernix	Theraphosidae	N/A	3.5	Field experiment	[25]	
Heteropoda natans	Sparassidae	N/A	2.5	Captivity	[21,93]	
Hysterocrates gigas	Theraphosidae	N/A	4–9	Captivity	[87]	
Nilus spp.	Pisauridae	0.45–0.6	1.5–3	Wild	[17,37,39]	79–84
Pardosa pseudoannulata	Lycosidae	0.1	1	Wild	[28,42,82]	78
Tinus sp.	Pisauridae	N/A	1.4	Field experiment	[25]	
Trechalea spp. (e.g., *Trechalea tirimbina*)	Trechaleidae	~1.5	2	Wild	[33]; Witold Lapinski, pers. comm.	48–51, 59

The genus name *Thalassius* has been changed to *Nilus* [26,176].
* Weight roughly estimated using data for similar-sized adult female *Dolomedes tenebrosus* [43].
doi:10.1371/journal.pone.0099459.t002

aquatic spider feeding on a fish while sitting on the dock wall at Shoe Lake, Ontario (report # 46).

Multiple incidences of fish predation have been reported (14 reports) from the Neotropics of large semi-aquatic spiders with a nocturnal life-style found either on the banks of rivers and streams in tropical forests in Brazil, Colombia, Costa Rica, Panama, and Peru or near shallow puddles and creeks on the lowland tropical forest floor in Ecuador (Figs. 4-5; report # 47–60). A third region where multiple fish predation events have been witnessed is Australia (twelve incidences; report # 61–71, 89), where pond fish were repeatedly caught by spiders in suburban/urban gardens of Adelaide, Brisbane, Lismore and Sydney or native freshwater fish were predated by spiders on the fringes of slow flowing streams in New South Wales and Queensland ([19]; Loren Jarvis, pers. comm.; Bradley Pusey, pers. comm.; Figs. 6A–B). Less common are reports of predation in Asia (seven reports, Figs. 6C–D; report # 72–78), which is surprising given the richness of spider taxa throughout this region [26,42]. Similarly, there is a paucity of information on fish predation by spiders in Africa, with only six documented cases from tropical secondary forests and garden

ponds (Fig. 6E–F; report # 79–84). Interestingly, only four reports originate in Europe, namely from the United Kingdom, Italy, and France (Fig. 7; Table 1; report # 85–88).

Which Spider Species are Engaged in Fish Predation?

The superfamilies Lycosoidea and Ctenoidea are those documented as preying upon fish under open-field conditions and all can be loosely categorized as hunting spiders (i.e., spiders that forage without the use of a catching web). Approximately 80% of reports of fish predation were attributable to Pisauridae (nursery web spiders), with Ctenidae (wandering spiders; 10.3%), Trechaleidae (longlegged water spiders; 4.5%), Lycosidae (wolf spiders; 1.1%) and Liocranidae (spinylegged sac spiders; 1.1%) comprising the remainder (Fig. 8; Table 1).

The most dominant group of fish-catching spiders are in the genus *Dolomedes* (Pisauridae) (Figs. 2–3, 6A–B, D, 7-8). The spiders in this worldwide distributed genus are semi-aquatic predators with a legspan of 6–9 cm and a weight of ~0.5–2 g ([26]; Table 2). Although the various *Dolomedes* spp. appear to differ in their foraging time, some species being diurnal and others nocturnal
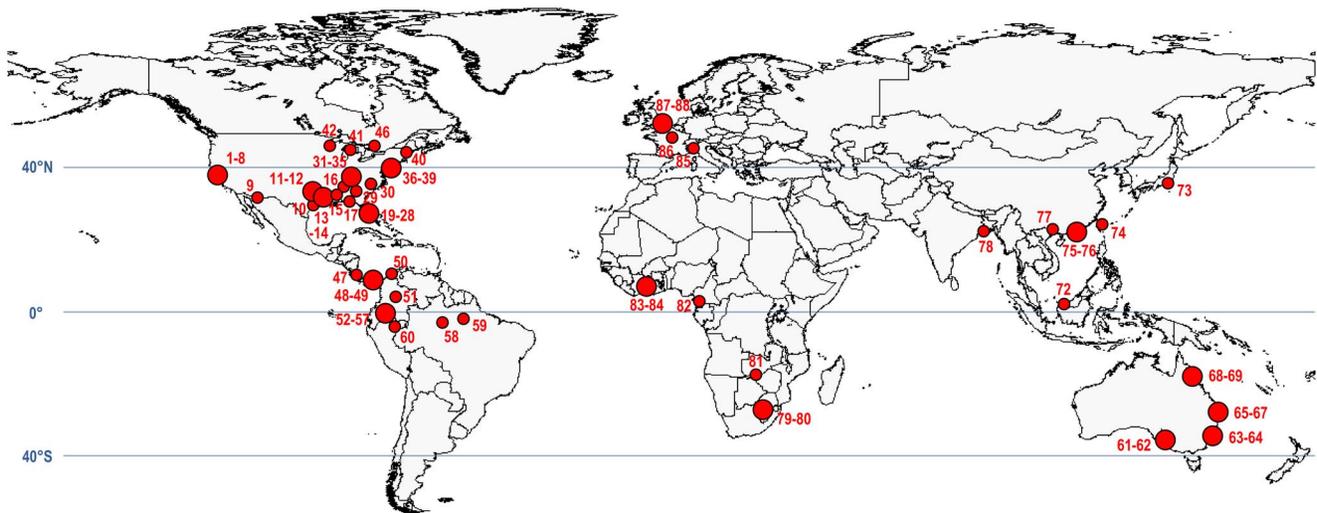
Figure 1. Geographic distribution of fish predation by spiders worldwide. Map depicts locations were spiders were observed predating fish (red dots). Large red dots indicate that several reports originated from same geographic region. Numbers refer to detailed report description (see File S1). GPS coordinates were unavailable for reports #18, 43–45, and 70–71; report # 89 not included.
doi:10.1371/journal.pone.0099459.g001

(File S1; [11]), these spiders share a common foraging trait in that they can swim, dive and walk on the water's surface film [69]. Indeed, the spiders in this genus are voracious predators with broad diets [69–71] and of the more than 90 species in *Dolomedes* (see Platnick [26]), eleven have been recorded catching fish in the wild (Figs. 2–3, 6A–B, D, 7; Tables 1–2). A species particularly adept at catching and eating fish in the wild is the North American *Dolomedes triton* (Figs. 2A–E, 3A; Table 1). Three more species in this genus have been observed catching fish under laboratory conditions (Table 2) suggesting that the real number of fish-catching *Dolomedes* is considerably higher than the number reported in this paper. Some species may, however, be poorly adapted to catching fish. For example, only the largest of New Zealand's three species of *Dolomedes* (*Dolomedes dondalei*) was capable of catching fish in laboratory experiments whereas the two smaller species (*Dolomedes aquaticus* and *Dolomedes minor*) were not [11].

Elsewhere in the Pisauridae, the spiders of the genus *Nilus* (Figs. 6E–F) are also semi-aquatic with similar feeding habits as *Dolomedes* [72]. They have a legspan of ~6 cm and a weight of ~0.5 g (Table 2). This genus is restricted to Africa and Asia [26] and thus far only two species – *Nilus curtus* and *Nilus massajae* – have been reported as engaging in fish predation under natural conditions (Fig. 6; Table 1). Given that other pisaurid spiders have a similar semi-aquatic lifestyle (e.g., *Megadolomedes*, *Thaumasia*, and *Tinus*), it can reasonably be deduced that such species could include fish in their diet as well ([25,73]; Kelly Swing, pers. comm.).

A number of spiders outside the Pisauridae also prey upon fish. Spiders in the genus *Ancylometes* (Ctenidae) (Fig. 4) occur mostly in South America, typically inhabiting moist Neotropical forests where they hunt at night at the edge of water bodies [26,35]. *Ancylometes rufus*, the largest species in this genus, has a leg span of 20 cm and a weight of up to 7 g [35]. *Ancylometes* can dive for up to 20 minutes [35] and at least two species – *Ancylometes bogotensis* and *Ancylometes rufus* – are known to catch fish in the wild (Tables 1–2). In addition to feeding on fish, these spiders also predate a variety of other small vertebrates such as tadpoles, frogs, toads, and lizards [41,74–77].

Members of the Neotropical genus *Trechalea* (Trechaleidae) also engage in fish predation ([17]; Fig. 5). These spiders are also large

(average adult weight of ~1.5 g and a legspan of up to 17 cm) and are typically found near shallow freshwater streams in Central and South America [33,78–79]. Adults are strictly nocturnal whereas immatures frequently hunt both day and night [33,78–79]. The trechaleids depicted in Fig. 5 could not be identified to species and might be immatures given that they were photographed during the daylight hours. Contrary to the pisaurids, the trechaleids do not chase their prey across the water surface and unlike many other fish-catching spiders are not capable of diving [79]. In similar fashion to the ctenids, *Trechalea* spp. feed on a diverse array of other food items, including insects, shrimps, and frogs [78–80].

Aside from the abovementioned spiders, with well documented though poorly understood fish-catching abilities, a number of other spiders have been reported in the literature as occasionally preying upon fish (Table 2). For example, the diurnal *Pardosa pseudoannulata* (pond wolf spider) is limited to parts of Asia and is found in stagnant pools, rice fields and swamps where it rests on aquatic plants [26,81–82]. This semi-aquatic spider, capable of swimming and diving, is one of the smallest spiders observed catching fish and there is only one report of such an event witnessed in the wild from a pond in India [82]. However, the fish-catching capability of *Pardosa pseudoannulata* has further been documented in the laboratory [82]. The capture and consumption of small vertebrates other than fish by lycosids, however, has repeatedly been reported in the literature [7,16,41,76,83–86]. This suggests that many other lycosids could include fish in their diet as well.

There is laboratory evidence that spider species of even more families (e.g., Cybaeidae, Desidae, and Sparassidae) are capable of catching and eating fish [19,21,25,85,87]. A good example is the water spider *Argyroneta aquatica* (Cybaeidae), the only truly aquatic spider (spending its entire life under water) known so far, which has been observed killing and devouring tiny fish of the families Cichlidae, Gasterosteidae, and Poeciliidae when kept in aquaria ([23,38,85,88–90]; Dolores Schütz, pers. comm.). This small spider (~0.1–0.3 g), equipped with very potent venom enabling it to kill tiny fish instantly, constructs a 'diving bell' (i.e., dome-shaped underwater web filled with air) between aquatic plants in which it digests prey, mates, etc. [23,38,90]. Two other examples of spiders reported catching fish in captivity are the semi-marine

Figure 2. Fish caught by spiders – examples from North America. A – *Dolomedes triton* caught mosquitofish (*Gambusia*) in backyard pond near Tampa, Florida (photo by Stacy Cyrus, DavesGarden website; report # 24). **B –** *Dolomedes triton* feeding on fish (probably mosquitofish *Gambusia holbrooki*) in garden pond near Lady Lake, Florida (photo by Machele White, Lady Lake, Florida; report # 20). **C –** *Dolomedes triton* feeding on small fish (presumably least killifish *Heterandria formosa*) on Tsala Apopka Lake, Florida (photo by Claire Sunquist-Blunden, Ocala, Florida; report # 19). **D –** *Dolomedes triton* feeding on fish (probably mosquitofish *Gambusia holbrooki*) in garden pond near Lady Lake, Florida (same incidence as in Fig. 2B; report # 20). **E –** *Dolomedes triton* devouring fish (probably mosquitofish *Gambusia holbrooki*) on edge of small, slow-moving stream near Fayetteville, North Carolina (photo by Patrick Randall, Fort Bragg, North Carolina, USA; report # 30). **F –** *Dolomedes okefinokensis* feeding on small fish (probably mosquitofish *Gambusia holbrooki*) in swamp in Big Cypress National Preserve, Florida (photo by Misti Little, Stagecoach, Texas; report # 28).
doi:10.1371/journal.pone.0099459.g002

species *Desis marina* (Desidae) and the 'swimming' huntsman spider *Heteropoda natans* (Sparassidae) [21,91–93]. There are also reports of tarantulas (Theraphosidae) swimming and diving in the laboratory [87] and there are even a few reports of tarantulas seen swimming in the wild [94]. Captive theraphosids devoured dead freshwater fish which is not surprising given that these spiders are voracious, opportunistic feeders [95–96]. Some researchers assumed that certain theraphosid species in the subfamilies Eumenophorinae and Theraphosinae might be capable of predating fish [25,87]; but there are others who consider this as improbable (Robert Raven, pers. comm.).

How Do Spiders Catch Fish?

The prey capture and feeding behavior of *Dolomedes* and *Nilus* has been well documented [11,16,20,69,72,97–98] and it was widely reported in the past that these semi-aquatic spiders depend largely on vision for prey detection [69]. However, it has since become apparent that vision plays a relatively minor role in prey detection and instead both *Dolomedes* and *Nilus* rely on stimuli perceived by mechanoreception [11,20]. Typically, semi-aquatic pisaurids anchor their hind legs to a stone or plant, with their front legs resting on the surface of the water [11,19,29,72,98], ready to ambush their prey. Carico [29] states: "....they use the surface film

Figure 3. Fish caught by spiders – examples from North America. A – *Dolomedes triton* captured Sonora chub (*Gila ditaenia*) in small stream in Sycamore Canyon, Pajarito Mountains, Arizona (photo by Andreas Kettenburg, Thousand Oaks, California, USA; report # 9). **B –** *Dolomedes tenebrosus* devouring creek chub (*Semotilus atromaculatus*) on bank of Bullskin Creek near Brutus, Kentucky (photo by Jason Butler, Lexington, USA; report # 33). **C, D –** *Dolomedes* sp. caught smallmouth bass, *Micropterus dolomieu*, on shore of Flambeau River near Ladysmith, Wisconsin, USA (photo by Tod Lewis, Austin, Texas; report # 42). **E, F –** *Dolomedes scriptus* feeding on fish (probably green sunfish *Lepomis cyanellus*) fished out of 1.8 m deep water on dock at Shoe Lake near Dorset, Ontario, Canada (photo by Lloyd Alter, Toronto, Canada; report # 46). **G –** *Dolomedes* sp. scuttled out very quickly from underneath dock attempting to attack live bait fish (probably golden shiner *Notemigonus crysoleucas*) after a mis-cast resulted in bait fish landing just off edge of dock near Sebago Lake, Maine, USA (photo by Jeffrey Hollis, East Haddam, Connecticut, USA; report # 40).
doi:10.1371/journal.pone.0099459.g003

as if it were a web, because they sit at the edge of the water and pursue insects that accidentally fall upon the water and are trapped by the surface tension". He continues "….Apparently the ripples caused by an insect provide the stimulus for the predatory response and possibly also provide information as to the location of the prey". While this behavior may be efficient for catching insect prey, it may be less effective at catching fish due to the spiders' rather low response to fish-generated surface waves [20] and only works under calm conditions [11]. In laboratory experiments the majority of successful fish catches occurred after the spiders' attack behavior had been triggered through direct touch, facilitated by the dorsal fin of a fish touching one of the spider's outstretched legs [11,20]. The fish catching behavior of ctenids and trechaleids resembles that of the pisaurids [14,22,33,78–79].

Which Species of Fishes are Captured by Spiders?

All 89 cases of fish predation listed in Table 1 involve small freshwater fish. In 17% of the reported incidences the fish prey remained unidentified. The identifiable prey belonged primarily to the orders Cyprinodontiformes (28% of total identifiable fish prey), Cypriniformes (22%), Perciformes (20%), and Characiformes (14%) but also included the Atheriniformes, Beloniformes, Gasterosteiformes, Osmeriformes, Salmoniformes, and Siluriformes (Table 3). The captured fish usually are among the most common fish occurring in their respective geographic area (e.g., mosquitofish [*Gambusia* spp.] in the southeastern USA, fish of the order Characiformes in the Neotropics, killifish [*Aphyosemion* spp.] in Central and West Africa, as well as Australian fishes of the genera *Galaxias*, *Melanotaenia*, and *Pseudomugil*). Spiders killed small-sized fish predominantly 2–6 cm in length (Table 1; File S1). Prey species included adults of small bodied species, usually weighing

Figure 4. Fish caught by spiders – examples from the Neotropics. A – In marshy area in Cuyabeno Wildlife Reserve, Ecuador, adult *Ancylometes* sp. (probably *Ancylometes rufus*) lifted catfish - most likely family Pimelodidae - out of the water (photo by Craig Harrison, Hertford, UK; report # 57). **B –** Ctenid spider (*Ancylometes* sp.) feeding on characiform in Tahuayo river area de Conservacion Regional Communal Tamshiyacu-Tahuayo Loreto, Peru (photo by Alfredo Dosantos Santillan c/o Amazonia Expeditions, Tampa, USA; report # 60). **C –** Adult male of *Ancylometes* sp. (possibly *Ancylometes rufus*) caught characiform (*Cyphocharax* sp.) near Samona Lodge, Cuyabeno Wildlife Reserve, Ecuador (photo by Ed Germain, Sydney, Australia; report # 52). **D –** Adult *Ancylometes* sp. preying on characiform near Samona Lodge, Cuyabeno Wildlife Reserve, Ecuador (photo by Tim Wohlberg, Kelowna, BC Canada; report # 53).
doi:10.1371/journal.pone.0099459.g004

~0.1–7 g (Table 3; e.g., *Aphyosemion* spp., *Elassoma zonatum*, *Gambusia* spp., *Heterandria formosa*, and *Pungitius laevis*) or the very small immatures of species which achieve larger body size (e.g., *Ictalurus punctatus*, *Lepomis cyanellus*, *Lepomis macrochirus*, *Micropterus dolomieu*, and *Oncorhynchus mykiss*). *Ictalurus punctatus* and *Oncorhynchus mykiss* can reach a body weight of >10 kg once fully grown.

Predator–Prey Size Ratio

In general, spiders feed predominantly on prey items – usually insects – that are smaller than themselves [99]. This is true in spiders from many different families including semi-aquatic pisaurid spiders feeding on insect prey [100–101]. However, results herein show that semi-aquatic spiders from different families captured fish prey whose body length exceeded the spiders' body length (the captured fish being, on average, 2.2 times as long as the spiders [based on data from Table 1]).

Similar departures involve weight; spiders of the genera *Dolomedes* and *Nilus*, with a weight of ~0.5–2 g (Table 2), can catch fish prey up to 4.5 times the spider's weight [15–16,20]. In laboratory experiments, attempts by *Dolomedes triton* to catch goldfish, *Carassius auratus*, weighing 7.5–10.5 times the spiders' weight always failed (Bleckmann & Lotz [20]). Under the assumption that the largest fishing spider, the ctenid *Ancylometes rufus* weighing up to 7 g (Table 2), is as effective in overpowering oversized prey as the smaller-sized pisaurids, fish of up to 30 g might conceivably be killed in the wild. The largest fish reported, however, to have been captured by a pisaurid spider was a *Carassius auratus* ~9 cm in length and presumably weighing >10 g (Table 3); this incidence had been witnessed in a garden pond in Sydney, Australia (report # 64).
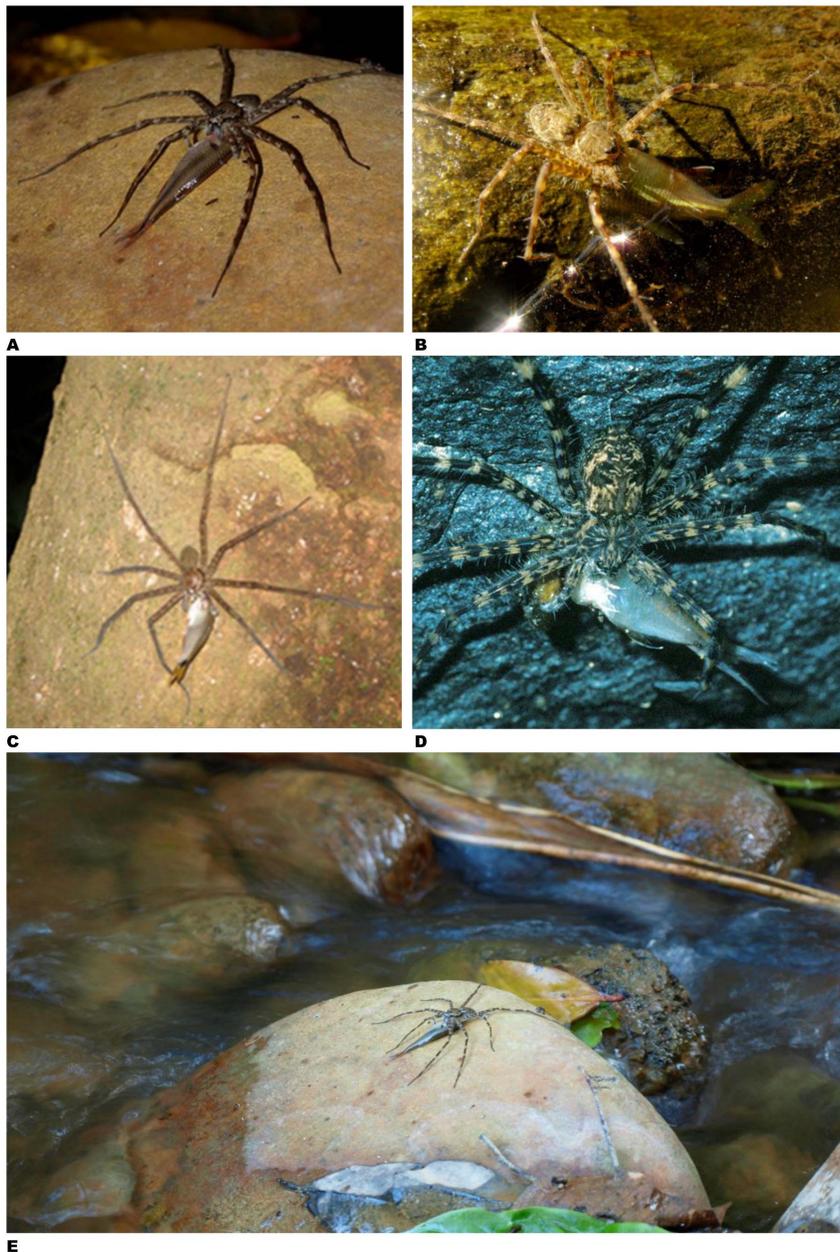
Figure 5. Fish caught by spiders – examples from the Neotropics. A – *Trechalea* sp. eating characiform while sitting on a rock in middle of small river near Paratebueno, Cundinamarca, Colombia (photo by Solimary Garcia Hernandez, Instituto de Biociências, Universidade de São Paulo, Brazil; report # 51). **B** – *Trechalea* sp. pulling characiform on stone on edge of shallow, small stream near Quebrada Valencia, Magdalena, Colombia (photo by Juan Esteban Arias A., Cali, Colombia; report # 50). **C** – *Trechalea* sp. devouring characiform while sitting on tree trunk on edge of Rio Frijoles, Central Panama (photo by Jessica Stapley, University of Sheffield, UK; report # 48). **D** – *Trechalea* sp. eating characiform on bank of Rio Maicuru, Pará State, Brazil (photo by Jacques Jangoux, Belém, Brazil; report # 59). **E** – *Trechalea* sp. eating characiform while sitting on rock in middle of small river near Paratebueno, Cundinamarca, Colombia (photo by Solimary Garcia Hernandez, Instituto de Biociências, Universidade de São Paulo, Brazil; report # 51).

doi:10.1371/journal.pone.0099459.g005

Discussion

Are the Documented Incidences of Fish Consumption Real Predation Events?

It is arguable whether all incidences reported in this paper are real predation events or whether some are just cases of scavenging. Predation requires that a prey item must have been killed and eaten by the predator [102]. Both behavioral traits – killing and consumption – have been witnessed many times by a large number of researchers in the wild and in captivity. These spiders possess large strong chelicerae capable of piercing the skin of vertebrates [23] and are equipped with powerful venoms containing hundreds of different neurotoxins, some of which are specific to vertebrate nervous systems [103–105]. The vast majority of fish (~85%) are bitten by the spiders at the base of the head (Figs. 2–7). How long it takes in a particular case to kill a fish depends on the size and species of the fish in question [23]. Small fish with a thin skin may die within a few seconds to minutes after the bite [13,19–20,23–
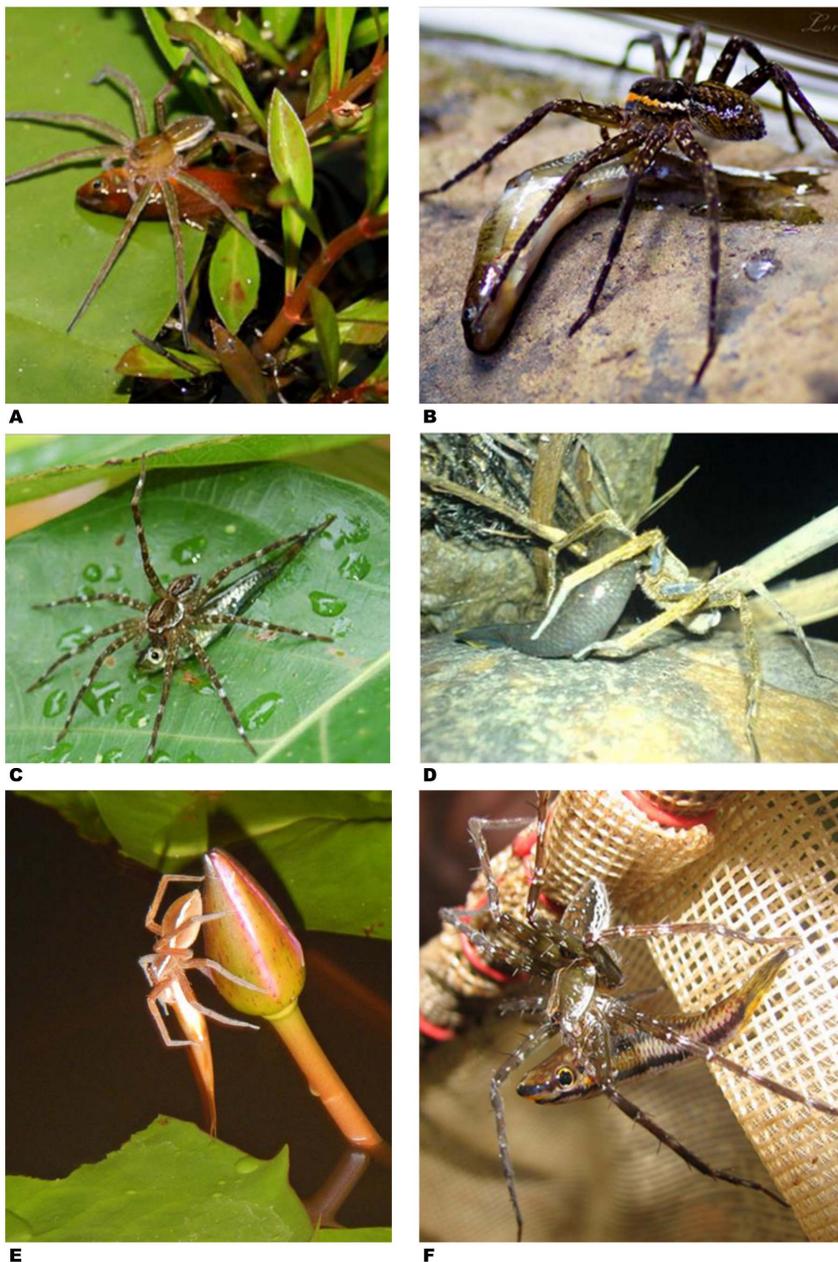
Figure 6. Fish caught by spiders – examples from Australia, Asia, and Africa. A – *Dolomedes facetus* captured pond fish (genus *Xiphophorus*) in garden pond near Brisbane, Queensland, Australia (photo by Peter Liley, Moffat Beach, Queensland; report # 67). **B –** *Dolomedes* sp. preying on mountain galaxias (*Galaxias olidus*) on bank of North Branch Creek near Goomburra, Queensland, Australia (photo by Loren Jarvis, near Brisbane, Queensland; report # 66). **C –** Semi-aquatic pisaurid devouring fish (presumably *Rasbora calliura*) at edge of shallow river flowing through forest in eastern Batang Sadong basin, Borneo (photo by Michael Lo, City of Kuching, Malaysia; report # 72). **D –** Unspecified teleost fish captured by *Dolomedes raptor* on edge of stream near Tung-Shih, Taichung county, Taiwan (photo by Tai-Shen Lin, Tunghai University, Taiwan; report # 74). **E –** Semi-aquatic pisaurid spider (*Nilus* sp.), dangling from lily flower bud, pulled unidentified fish (~4 cm in length) out of water of garden pond in Victoria Falls, Zimbabwe (photo by Marcelo de Freitas, Cresta, South Africa; report # 81). **F –** Pisaurid spider (*Nilus* sp.) in fish net attacked and captured small killifish (*Aphyosemion* sp.) in stream near city of Kribi, Cameroon (photo by Duncan Reid, Yale University, USA; report # 82).
doi:10.1371/journal.pone.0099459.g006

24,69] although burbot fish (*Lota lota*) with an average fresh weight of ~0.4 g required 50 minutes before death [23]. Injecton of the venom of the semi-aquatic spider *Dolomedes sulfureus* into the thorax of zebrafish (*Danio rerio*) in the laboratory caused severe neurological disturbance resulting in disorientation, uncoordinated movement (spinning), lack of buoyancy control and ultimately death within 20 min [24]. Gudger [15] reports two cases, both witnessed

in the wild, where fish bitten by *Dolomedes* spiders exhibited similar spinning behavior prior to dying.

A fish prey must always first be dragged by the spider to a dry place before the feeding process can begin [13]. Such a dry feeding site can be a rock, tree trunk, halfway immersed log, or an aquatic plant emerging from the water (Figs. 2A–B, D–F, 3B–G, 4–7). The behavior of always first moving a fish prey to a dry site prior to

Figure 7. Fish caught by spider – example from Europe. Gravid adult female *Dolomedes plantarius* captured stickleback (*Pungitius laevis*) in turf pond at Redgrave and Lopham Fen National Nature Reserve in East Anglia, UK (photo by Helen Smith, South Lopham, Norfolk, UK; report # 87).
doi:10.1371/journal.pone.0099459.g007

Figure 8. Relative importance of different spider families as fish predators – based on 89 incidences reported in Table 1.
doi:10.1371/journal.pone.0099459.g008

feeding can be explained by the spiders' extraintestinal digestion – first pumping digestive enzimes into the prey and thereafter sucking in the dissolved tissue through the mouth opening [106]; otherwise the digestive enzymes would be diluted in the water and, thus, become ineffective [8]. This type of feeding behavior has been witnessed in spiders from all families engaged in fish-catching. A second reason for this behavior may be that on land the spider has physical superiority over its aquatic prey and its potential for escape is greatly reduced.

In captivity *Dolomedes* spiders accepted dead sticklebacks as food, but this was observed only in hungry adult females during periods of increased food requirements between mating and oviposition [69]. Thus, scavenging may occasionally occur in the wild as well, if the spiders are hungry enough. On the other hand, *Trechalea* spp. did not feed on dead prey if offered in captivity [79,107]. A special case is given when spiders grab fish in fishing nets (Fig. 6F; report # 82) or – as in one case observed in Maine – attack a live bait fish landing on the dock wall after a fishing mis-cast (Fig. 3G; report # 40). We consider such incidences as predation attempts since the spider is grabbing a living fish with the intention to kill and devour it. The fact that fish are attacked even outside the water shows the high propensity for such spiders to feed on fish. A careful consideration of all the evidence available to us, where spiders had been observed/photographed feeding on fish in the wild and in captivity, led to the conclusion that the vast majority of incidences reported in this review refer to fish predation and not scavenging.

How Frequent are Incidences of Fish Predation by Spiders?

The majority of incidences of spider predation upon fishes were reported from the Americas, especially the eastern part of USA, whereas few were reported from Africa, Asia, Australia or Europe. To a large extent, the pattern shown in Fig. 1 may simply reflect the distribution of potential observers and especially those with the capacity or propensity to report observations of spider predation. There is a high concentration of major universities and government agencies with research labs engaged in ecological
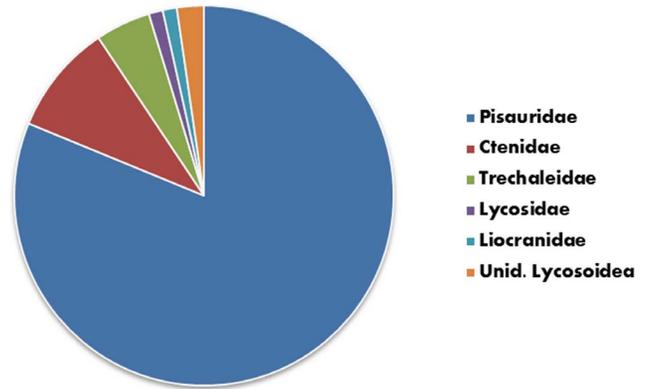
projects in nearby wetland habitats in the eastern part of USA. In addition, this region contains numerous nature enthusiasts that visit the wetlands of the eastern USA for recreation and subsequently post reports and photographs of rare incidences on the world wide web. Such a concentration of researchers and enthusiasts is unlikely elsewhere, with the exception of Europe which plausibly contains as many research institutions, scientists and amateur enthusiasts, and thus may potentially bias our view of geographical patterns of the incidence of spider predation on fish. In the Neotropical region, fish predation was probably strongly underreported due to the fact that the dominant Neotropical semi-aquatic spiders (i.e., *Trechalea* spp. and *Ancylometes* spp.) occur most commonly in remote areas of the tropical rainforest and are strictly nocturnal as adults [22,35,78–79], characteristics that make their observation in the wild difficult.

Semi-aquatic spiders may be more common in some geographic regions than in others and our reported distribution of observations may reflect this difference in abundance and diversity. Semi-aquatic spiders are very common in eastern USA, particularly in the freshwater wetlands of Florida and neighboring regions (6 spp.; [29]). Nine species of *Dolomedes* occur in North America, in contrast to Europe which contains only two species [13,29]. One of the two European species (*Dolomedes plantarius*; Fig. 7), which is associated with open water and which is known to predate upon fish in the wild, has now become so rare that it is considered a threatened species – largely a consequence of the continuous loss of European freshwater wetland habitat [13,108–110]. The second European species (*Dolomedes fimbriatus*) appears to depend on open water to a lesser degree [13,108,111] and has so far never been seen predating fish in the wild (e.g., Heiko Bellmann, pers. comm.; Emanuele Biggi, pers. comm.; Franz Renner, pers. comm.; Jakob Walter, pers. comm.). It must be said that *Dolomedes fimbriatus* often occurs in wetlands such as highly acidic moorlands or seasonally intermittent marshy areas in which fish are naturally absent [101,111]. *Dolomedes fimbriatus* is perhaps less well-adapted to predating fish in the wild. An extensive observational study by Poppe & Holl [101] in moorlands of northwestern Germany revealed that *Dolomedes fimbriatus* very rarely exhibited a behavior of 'fishing' or underwater hunting while foraging for aquatic arthropod prey. Instead this species fed predominantly on terrestrial arthropods captured on plants [101]. Thus, it appears that spiders of the genus *Dolomedes* are less common (or as in the case of *Dolomedes fimbriatus* show less affinity with water inhabited by fish) in Europe than in the eastern part of USA. This may result in a lower likelihood of encountering or observing feeding on fish

Table 3. Fresh weight and total length of fish species reported to be captured by spiders.

Fish species	Fish family	Weight (g)	Total length (cm)	Location of observation	Source	report #
Aphosemion spp.	Nothobranchiidae	0.2–0.7	3.5–4.5	Wild	[54,66]	82–84
Carassius auratus	Cyprinidae	0.5–7	2.5–7.5	Wild	[49,60]	11, 61–62, 65
Carassius auratus	Cyprinidae	~12	9	Wild	[49]	64
Cyphocharax sp.	Curimatidae	N/A	6	Wild	Ed Germain, pers. comm.	52
Cyprinus carpio	Cyprinidae	0.2	2	Wild	Alison King, pers. comm.; Bradley Pusey, pers. comm.	89
Elassoma zonatum	Elassomatidae	0.1–0.5	1.7–3.1	Wild	[61]	1–8, 78
Fundulus chrysotus	Fundulidae	<0.1–7.8	2.3–4.5	Wild	[61]	10
Galaxias olidus	Galaxiidae	4–5.5	7.7	Wild	[53]	66
Gambusia affinis	Poeciliidae	0.5–2	3–4.5	Wild	[56]	13, 15, 17, 21–23, 34–35
Gambusia holbrooki	Poeciliidae	0.2–1.8	2.5–4.5	Wild	[51–52]	20, 28, 30, 85
Gasteropelecus sternicla	Gasteropelecidae	N/A	4–5	Captivity	[20]	
Gasterosteus aculeatus	Gasterosteidae	1.1–2.6	5.1–6.6	Captivity	[55]	
Gila ditaenia	Cyprinidae	4.5	N/A	Wild	[63]	9
Glaniopsis hanitschi	Balitoridae	0.6	~3	Captivity	[21]; http://fishbase.mnhn.fr/PopDyn/	
Gobiomorphus sp.	Eleotridae	N/A	3	Captivity	[11]	
Heterandria formosa	Poeciliidae	<0.1–0.5	0.6–3.2	Wild	[61]	19
Ictalurus punctatus (fingerling)	Ictaluridae	5	6	Wild	[68]	12
Lamprologus pulcher	Cichlidae	N/A	1.5	Captivity	Dolores Schütz, pers. comm.	
Lebistes sp.	Poeciliidae	0.1	N/A	Captivity	[11,44]	
Lepomis cyanellus	Centrarchidae	2	5.3	Wild	[47]	46
Lepomis macrochirus	Centrarchidae	0.2–3	2.7–6	Wild	[61,67]	14
Limia melanogaster	Poeciliidae	N/A	3	Captivity	[22]	
Melanotaenia spp.	Melanotaeniidae	1	5	Wild	[58]; Bradley Pusey, pers. comm.	68
Micropterus dolomieu	Centrarchidae	~1–2	4–5	Wild	http://www.garden-island.com/bass-weight-formula-calculator.htm	42
Notemigonus crysoleucas	Cyprinidae	1.6–2.5	6.5–7.5	Wild	[62]	40
Oncorhynchus mykiss (fry)	Salmonidae	1	3	Wild	[57]	32
Oncorhynchus mykiss (fingerling)	Salmonidae	~3–4	5	Wild	[48]	31
Oryzias curvinotus	Adrianichthyidae	N/A	2–4	Wild	http://www.fishbase.org/summary/Oryzias-curvinotus.html	75
Parazacco spilurus	Cyprinidae	N/A	2.5	Wild	David Dudgeon, pers. comm.	76
Phoxinus phoxinus	Cyprinidae	0.7–2	4–6	Captivity	[1]	
Poecilia mexicana	Poeciliidae	0.7	2–3	Field experiment	[25,46]	
Poecilia reticulata	Poeciliidae	0.5–0.8	3.5–4	Captivity	[50]	
Pseudomugil spp.	Pseudomugilidae	~0.5	3.5	Wild	[58]; Bradley Pusey, pers. comm.	69
Pseudorasbora parva	Cyprinidae	0.7	3.3	Wild	[64]	73
Pungitius laevis	Gasterosteidae	0.3–0.7	3.4–4.8	Wild	[55]	87–88
Rasbora calliura	Cyprinidae	N/A	6–7	Wild	Michael Lo, pers. comm.	72
Semotilus atromaculatus	Cyprinidae	2–3	6	Wild	[45]	33
Xiphophorus helleri	Poeciliidae	1.3	4	Wild	[59]	67
Unknown	Order Characiformes	~1–4	4–6	Wild	[65]	48–55, 59–60
Unknown	Percidae	N/A	N/A	Wild	[29]	44
Unknown	Pimelodidae	N/A	N/A	Wild	Craig Harrison, pers. comm.	57

Table 4. Estimated fresh weight (g/prey item) and caloric value (kJ/g dry weight) of different prey categories used by semi-aquatic spiders.

Prey category	Fresh weight (g/prey item)	Caloric value (kJ/g dry weight)	Source
Freshwater fish (Teleostei)	<1–7	21–24	[177]
Other vertebrates (tadpoles, frogs)	<1–9	21–25	[178–179]
Crustaceans (crayfish, shrimps)	1–6	12–18	[177,180]
Water striders (Gerridae)	~0.03	N/A	[181–182]
Backswimmers (Notonectidae)	~0.01–0.1	24	[183–185]
Water boatmen (Corixidae)	~0.02–0.05	22	[181,186]
Water beetles (Dytiscidae)	<0.01–0.02	22	[181–182]
Water scavenger beetles (Hydrophilidae)	N/A	23	[181]
Caddisflies (Trichoptera)	<0.01–0.04	22–23	[181–182,184]
Mayflies (Ephemeroptera)	<0.01–0.06	22–23	[177,181–182]
Stoneflies (Plecoptera)	<0.01–0.2	21–22	[177,182]
Midges (Chironomidae)	≤0.01	21–23	[181–182,184]
Mosquitoes (Culicidae)	<0.01	22	[181,187]
Dragonflies, Damselflies (Odonata)	0.1–1.5	21–22	[177,181,184,188]

prey by such spiders in Europe. Notably however, *Dolomedes* is particularly species rich in south-east Asia [26], yet we found few verifiable records of fish predation for this region; more likely due to underreporting than the absence of fish predation per se.

Most of the reported incidences of fish predation were from a broad latitudinal band from 40° S to 40° N, with very few reported instances of fish predation by spiders occurring north of 40° N despite the fact that members of *Dolomedes*, at least, occur there [29]. This is true in both North America and Europe. The difference between the frequency of fish predation at high versus low latitude in North America is well illustrated if we compare a study from a northern location (latitude 56° N, Fairview, Canada) with one from a southern location (latitude 27° N, Tampa Bay area, Florida). Spending approximately 400 man-hours conducting some 13,000 field observations while wading slowly at the perimeter of natural ponds near Fairview, Zimmermann & Spence [100] never witnessed incidences of fish predation by *Dolomedes triton* (from a total of 625 predation events). Instead the spiders were seen feeding almost exclusively on arthropods and in one instance on a small frog [100]. The rarity of fish predation in Canada is also evidenced by the fact that according to our knowledge only one such incidence has so far been reported in this country, and this refers to a location in the most southern part of Ontario (latitude 45° N; Lloyd Alter, pers. comm.). In contrast, Brian Kenney (pers. comm.) witnessed at least half a dozen incidences of fish predation by *Dolomedes triton* while spending approximately 300 man-hours as a wildlife photographer in freshwater wetlands in the Tampa Bay area in Florida.

Fish eating spiders are constrained in the size of fish they can capture and a greater reliance on fish as prey may occur in regions inhabited by more small-bodied fish, not withstanding the fact that all large-bodied fish must also be small-bodied while juvenile. Freshwater fish assemblages of North America and Europe do indeed contain fewer small-bodied species at higher latitudes [112–114]. Further support of the hypothesis that the availability of fish of a suitable size increases reliance on this food source (assuming that reliance may be related to the frequency with which instances of fish predating upon fish are observed and reported) is provided by the relative reporting differences for eastern and

western North America shown in Fig. 1. Moyle & Herbold [115] report that the comparatively higher richness observed in eastern North America rivers compared to western North America is mainly due to the highly diversified, small-bodied taxa that occur principally in small streams in the former region.

Reduced oxygen levels lead to higher risk of predation for fish, since the fish tend to rise to the surface to exploit the oxygen-saturated surface layer [116–118]. Depletion of dissolved oxygen is particularly severe in heavily vegetated swamps and stagnant pools such as those that occur in Florida and neighboring regions [119]. Areas located at higher latitudes like Canada or much of Europe are likely characterized by lower temperatures coupled with comparatively higher dissolved oxygen levels [120], potentially resulting in lower risk of predation by *Dolomedes* spp. The same may be true for freshwater wetlands in the northern part of Asia where very few incidences of fish predation have been reported so far (Fig. 1). In Florida and neigboring regions, where fish predation has been particularly frequently witnessed, the captured fish were often mosquitofish (*Gambusia* spp.) (Figs. 2A–B, D–F). These fish, which are morphologically and behaviorally well-adapted for inhabiting oxygen deficient waters [116], are among the most abundant fish in the wetlands of this geographic region [119,121–122] and with a live weight of ~0.1–1.5 g (Table 3) they optimally fit the spiders' prey size range. As 'surface feeders', feeding on insects trapped at the water surface, and as 'surface breathers' these fish are in particular vulnerable to the attack by *Dolomedes* spp. which can walk and run on the water surface [123]. Foraging at the water's surface for terrestrial arthropod prey by both predator and prey (spider and fish, respectively) may also increase the likelihood of interaction for a range of fish species other than *Gambusia*. Australian rainbowfish (*Melanotaenia*) and blue-eyes (*Pseudomugil*) both consume terrestrial insects from the water surface [58] and both have been observed being consumed by spiders (Bradley Pusey, pers. comm.; Table 1). It is striking that the geographic distribution of fish predation by spiders in North America (Fig. 1) overlaps largely with that of mosquitofish [124]. Mosquitofish occur also in streams of southern Europe (i.e., certain regions in Portugal, Spain, southern France, Italy, and Greece; [125]) and one of the four incidences of fish predation witnessed in

Europe involved this species (report # 85). While extensive ecological field studies had been conducted in the more northern parts of Europe, the ecology of spiders in southern Europe is less well-studied and it is possible that fish predation by spiders in that region has been underreported due to the lack of studies conducted in mosquitofish habitats. In large parts of Europe and Palearctic Asia, mosquitofish are absent and *Dolomedes* spiders may have difficulty catching other types of resident small fish, all of which are less likely to venture close to the water surface (e.g., sticklebacks and minnows of the genus *Phoxinus*) (David Dudgeon, pers. comm.). This seems to be in line with the observations of filmmaker Martin Dohrn (Bristol, UK), whereupon several specimens of *Dolomedes fimbriatus* had difficulty capturing stickle-backs (*Gasterosteus aculeatus*) and minnows (*Phoxinus phoxinus*) in a pool (staged situation). In the case of the sticklebacks, their dorsal spines makes it difficult for predators to catch them [126] and for spiders to bite them at the base of their head. Nevertheless, sticklebacks have very rarely been captured by *Dolomedes plantarius* in a turf pond at Redgrave and Lopham Fen National Nature Reserve in East Anglia, UK (Fig. 7; report # 87–88). Other factors may also drive habitat selection by fish and increase their likelihood of encountering a waiting spider. For example, *Gambusia* spp. frequently occur in shallow water or densely vegetated stream margins in order to avoid predation by piscivorous fishes, a behavior common amongst small-bodied stream dwelling fishes [127].

How Important is Fish Predation in Nutritional Ecology of Spiders?

All five spider families reported in this paper as fish predators under natural conditions (Ctenidae, Liocranidae, Lycosidae, Pisauridae, and Trechaleidae) are known from the literature to feed predominantly on arthropods [79,100–101,128–130]. The feeding biology of ctenids, liocranids, lycosids, and trechaleids in the field is still poorly understood and one cannot currently judge whether predating fish is significant from a feeding ecological point of view. However, the one incidence of a spider of the family Liocranidae feeding on a tiny fish is rather surprising. Due to its terrestrial life style and its very small size (measuring <1 cm in length) this liocranid is an unlikely fish predator and the incidence reported here (report # 86) might have been a peculiar chance event.

Fish probably constitute a minor proportion of the diet of semi-aquatic members of the family Pisauridae [8,11,100–101]. Nonetheless, in certain circumstances predation may become highly focussed upon fish. For example, fish predation by semi-aquatic pisaurids has been particularly frequently witnessed in shallow freshwater wetlands at many different locations in Florida (report # 17–28), with multiple incidences of this feeding behavior witnessed at a single location (e.g., [121]). Gudger [17] and Meehan [131] noted that large numbers of small fish were killed and devoured by semi-aquatic pisaurids in hatchery rearing ponds in Oklahoma and Tennessee, respectively (report # 12, 31–32). In one rearing pond in Oklahoma the spiders exhibited a behavior of 'wasteful killing' of fish (i.e., despite apparent satiation the spiders continued killing fish, thereafter consuming each fish prey item only partially; see [131–133]). Semi-aquatic pisaurids are indeed capable of killing several prey in succession [23]. Still another example of piscivorous feeding behavior is reported from the San Francisco, California, area where numerous small fish were killed and devoured within just a few days by a single spider specimen (presumably a *Dolomedes* sp.), that had become established next to an aquarium in the Steinhart Aquarium building ([18]; report # 1–8). Admittedly, these examples are not based on natural

conditions but clearly the spiders involved evidently were temporarily specializing on fish prey (i.e., complete piscivory). This suggests that although *Dolomedes* spp. are predators with broad diets composed of invertebrates and vertebrates [69–71], they are capable of temporarily narrowing their feeding niche by feeding to a large extent on small fish prey when this prey type becomes available in large numbers.

Multiple incidences of fish predation by semi-aquatic spiders have been reported from the Cuyabeno Wildlife Reserve in Ecuador (report # 52–57). In this wildlife reserve, semi-aquatic ctenid spiders (*Ancylometes* spp.) were observed to feed heavily on fish at the edge of forest puddles or creeks. There is substantial observational evidence that subadults and adults of *Ancylometes* spp. feed to a large extent on small aquatic vertebrates [35,41,74–77,134–137], whereas the immatures of these spider species are probably predominantly arthropod eaters ([129]; Thierry Gasnier, pers. comm.). In this case, the relative reward of switching to a diet comprised substantially of fish may have been improved by more efficient foraging due to the shallow nature of the aquatic habitat (i.e., puddles).

It takes semi-aquatic spiders many hours to consume a fish [11,13,69], suggesting that spiders can extract a substantial amount of energy while feeding on such large prey. Indeed, a fish prey has a ~20–200 times higher biomass than average-sized insect prey (e.g., water striders *Gerris* spp. with an average weight of ~0.03 g; Table 4). Typically predators are much larger than their prey. Brose et al. [138] estimate an average $\log_{10}$ predator/prey ratio of 1.62 ± 0.03 (i.e., 42 times larger) and in this respect, the disparity in size of fish catching spiders and their prey is especially noteworthy. It must be added that the caloric value of fish and insect tissue do not differ significantly (~20–24 kJ/g dry weight; Table 4) and that fish and insect prey are both excellent sources of protein [139]. A substantial proportion of the mass of an arthropod is comprised of exoskeleton which is of no nutritional value to a spider. In contrast, the great bulk of the mass of a fish is comprised of muscle tissue. On an individual prey basis, fish are likely a more rewarding meal than an equivalently sized invertebrate, and especially energetically and nutritionally reward-ing given the size of the meal particularly where fish are easily acquired. Fish may, thus, represent a 'big ticket item' in the nutritional budget of semi-aqautic spiders. Feeding on fish may be particularly advantageous during the mating period when the elevated energy and protein requirements of gravid female spiders require increased food intake [13] or at times of limited availability of invertebrate prey when feeding frequency is otherwise depressed and cannibalism elevated [100–101]. Complete piscivory is probably rare and restricted to those occasions when semi-aquatic spiders gain easy access to small fish kept at high density in artificial rearing ponds or aquaria [18,131] or in small shallow waterbodies (see references above pertaining to *Ancylometes*). Additional research will be needed to reveal the extent and nutritional importance of fish in the diet of these spiders.

How Important are Semi-Aquatic Spiders in Aquatic Food Webs?

Riparian zones are widely recognised as ecotones of high productivity, diversity and ecological importance and cross boundary transfer of material from terrestrial and aquatic environments is frequently fundamental to the nature of the food webs of both [140–143]. Spiders do occur in the diet of fish specialising in the consumption of terrestrial invertebrates that inadvertently enter and subsidise food webs of the aquatic environment [58,144–147] and semi-aquatic spiders serve as food for numerous aquatic and semi-aquatic vertebrate predators such

as juvenile crocodilians [148–152], marshsnakes [153], anurans [145], wading birds such as herons [29,154], and passerine birds [155]. Furthermore, semi-aquatic spiders may compete with aquatic predators for insect prey floating on the water surface (e.g., *Dolomedes* spp. versus sunfish *Lepomis* spp. [144,156]). Apart from fish, a variety of aquatic crustaceans (i.e., crayfish, crabs, shrimps, and amphipods) are consumed by these spiders [19,78,157–159] and furthermore the adult stage of many aquatic insects is consumed by semi-aquatic spiders. Adults of aquatic insect species greatly enhance the overall abundance of insects in riparian zones [160] and this subsidy allows spider abundance, biomass and diversity to be significantly elevated (see Sanzone et al. [161]). Semi-aquatic spiders are an important component of freshwater and terrestrial food webs with multiple linkages within and between both [39,100,162].

Concluding Remarks

It has been long-known that semi-aquatic spiders of the family Pisauridae occasionally predate small fish; however, past studies focused on just two genera of a single family (i.e., *Dolomedes* and *Nilus* [8,163–164]). We found that the diversity of spider families engaged in fish predation is much higher than previously thought and encompasses at least eight spider families. Fish predation by spiders is geographically widespread but largely limited to the warmer areas between 40° S and 40° N. Semi-aquatic spiders capture a wide diversity of fish species but are constrained in the size of prey they can capture. The capture and consumption of fish by spiders represents a significant departure from the average dietary patterns and predator-prey size ratios reported in the literature and fish might be an occasional prey item of substantial nutritional importance. A better understanding of the nutritional ecology of the semi-aquatic spiders and their ecosystem role is needed.

Acknowledgments

Supporting Information

File S1 Detailed Reports Description.
(DOC)

Flow Diagram S1 PRISMA 2009 Flow Diagram.
(DOC)

Checklist S1 PRISMA 2009 Checklist.
(DOC)

Author Contributions

References

1. Raven P (1986) The size of minnow prey in the diet of young Kingfishers *Alcedo atthis*. Bird Study 33: 6–11.
2. Aizpurua O, Garin I, Alberdi A, Salsamendi E, Baagøe H, et al. (2013) Fishing long-fingered bats (*Myotis capaccinii*) prey regularly upon exotic fish. PLoS ONE 8: e80163.
3. Madenjian MP, Gabrey SW (1995) Waterbird predation on fish in western Lake Erie: A bioenergetics model application. Condor 97: 141–153.
4. Pitt WC, Conover MR (1996) Predation at intermountain west fish hatcheries. J Wildlife Manage 60: 616–624.
5. Helfman G, Collette BB, Facey DE, Bowen BW (2009) The diversity of fishes: biology, evolution, and ecology. Second edition. Oxford, UK: Wiley-Blackwell. 736 p.
6. Townsend CR, Hildrew AG (1978) Predation strategy and resource utilisation by *Plectrocnemia conspersa* (Curtis) (Trichoptera: Polycentropodidae). In: Crichton MI, editor. Proceedings of the 2nd International Symposium on Trichoptera. The Hague: Junk. pp. 283–291.
7. McCormick S, Polis GA (1982) Arthropods that prey on vertebrates. Biol Rev 57: 29–58.
8. Gertsch WJ (1979) American spiders. Second edition. New York: Van Nostrand Reinhold. 196 p.
9. Brooks DM (2012) Birds caught in spider webs: A synthesis of patterns. Wilson J Ornithol 124: 345–353.
10. Nyffeler M, Knörnschild M (2013) Bat predation by spiders. PLoS ONE 8: e58120.
11. Williams DS (1979) The feeding behaviour of New Zealand *Dolomedes* species (Araneae:. Pisauridae). New Zeal J Zool 6: 95–105.
12. Foelix RF (1992) Biologie der Spinnen. 2. Auflage. Stuttgart: Georg Thieme Verlag. 331 p.
13. Bellmann H (1997) Kosmos-Atlas Spinnentiere Europas. Stuttgart: Franckh-Kosmos-Verlag. 304 p.
14. Pickard-Cambridge FOP (1903) On some new species of spiders belonging to the families Pisauridae and Senoculidae; with characters of a new genus. P Zool Soc Lond 73: 151–168.
15. Gudger WE (1922) Spiders as fishermen. J Am Mus Nat Hist 22: 565–568.
16. Abraham N (1923) Observations on fish and frog-eating spiders of Natal. Ann Natal Mus 5: 89–95.
17. Gudger WE (1925) Spiders as fishermen and hunters. J Am Mus Nat Hist 25: 261–275.
18. Gudger WE (1931) Some more spider fishermen. Nat Hist 31: 58–61.
19. McKeown KC (1943) Vertebrates captured by Australian spiders. Proc R Zool Soc NSW 1942/43: 17–30.
20. Bleckmann H, Lotz T (1987) The vertebrate-catching behaviour of the fishing spider *Dolomedes triton* (Araneae, Pisauridae). Anim Behav 35: 641–651.

21. Airamé S, Sierwald P (2000) Hunting and feeding behavior of one *Heteropoda* species in lowland rainforest on Borneo (Aranae, Sparassidae). J Arachnol 28: 251–253.

22. Brzostowicz F, Greven H (2007) Beobachtungen an der Fischerspinne *Ancylometes bogotensis* Keyserling,1877 (Araneae). Acta Biol Benrodis 14: 39–54.

23. Uzenbaev SD, Lyabzina SN (2009) An experimental study of the effects of spider venom on animals. Entomol Rev 89: 479–486.

24. Wang H, Zhang F, Li D, Xu S, He J, et al. (2013) The venom of the fishing spider *Dolomedes sulfurous* contains various neurotoxins acting on voltage-activated ion channels in rat dorsal root ganglion neurons. Toxicon 65: 68–75.

25. Horstkotte J, Riesch R, Plath M, Jäger P (2010) Predation by three species of spiders on a cave fish in a Mexican sulphur cave. Bull Brit Arachnol Soc 15: 55–58.

26. Platnick NI (2013) The world spider catalog, version 14.0. American Museum of Natural History. Available: http://research.amnh.org/iz/spiders/catalog/. Accessed 2013 October 18.

27. Bishop SC (1924) A revision of the Pisauridae of the United States. B NY St Mus 252: 1–140.

28. Ito Y (1964) Preliminary studies on the respiratory energy loss of a spider *Lycosa pseudoannulata*. Res Popul Ecol 6: 13–21.

29. Carico JE (1973) The Nearctic species of the genus *Dolomedes* (Araneae: Pisauridae). Bull Mus Comp Zool 144: 435–488.

30. Jones D (1983) The country life guide to spiders of Britain and Europe. Feltham, UK: The Hamlyn Publishing Group. 320 p.

31. Mcqueen DJ, Pannell LK, McLay CL (1983) Respiration rates for the intertidal spider *Desis marina* (Hector). New Zeal J Zool 10: 393–399.

32. McLay CL, Hayward TL (1987) Population structure and use of *Durvillaea antarctica* holdfasts by the intertidal spider *Desis marina* (Araneae: Desidae). New Zeal J Zool 14: 29–42.

33. Carico JE (1993) Revision of the genus *Trechalea* Thorell (Araneae, Trechaleidae) with a review of the taxonomy of the Trechaleidae and Pisauridae of the Western Hemisphere. J Arachnol 3: 226–257.

34. Suter RB, Rosenberg O, Loeb S, Wildman H, Long JH (1997) Locomotion on the water surface: propulsive mechanisms of the fisher spider *Dolomedes triton*. J Exp Biol 200: 2523–2538.

35. Höfer H, Brescovit AD (2000) A revision of the neotropical spider genus *Ancylometes* Bertkau (Araneae: Pisauridae). Insect Syst Evol 31: 323–360.

36. Suter RB, Gruenwald J (2000) Spider size and locomotion on the water surface (Araneae, Pisauridae). J Arachnol 28: 300–308.

37. Leroy J, Leroy A (2003) Spiders of Southern Africa. Cape Town: Struik Publishers. 96 p.

38. Schütz D, Taborsky M (2003) Adaptations to an aquatic life may be responsible for the reversed sexual size dimorphism in the water spider, *Argyoneta aquatica*. Evol Ecol Res 5: 105–117.

39. Vonesh JR (2003) Sequential predation in a complex life history: interactions among egg, larval, and post-metamorphic predators of the East African tree frog, *Hyperolius spinigularis*. Ph.D. thesis, University of Florida, Gainesville, Florida, USA.

40. Zhang JX, Zhu MS, Song DX (2004) A review of the Chinese nursery-web spiders (Araneae, Pisauridae). J Arachnol 32: 353–417.

41. Menin M, Rodrigues DJ, Azevedo CS (2005) Predation on amphibians by spiders (Arachnida, Aranae) in the Neotropical region. Phyllomedusa 4: 39–47.

42. Sebastian PA, Peter KV (2009) Spiders of India. First edition. Hyderabad: Universities Press. 734 p.

43. Nicholas AC, Stratton TA, Reed D (2011) Reproductive allocation in female wolf and nursery-web spiders. J Arachnol 39: 22–29.

44. Schuster-Woldan E (1939) Über die individuelle Empfindlichkeit von *Lebistes reticulatus* gegenüber Nikotinlösungen verschiedener Konzentrationen. Naunyn Schmiedebergs Arch Pharmacol 194: 156–164.

45. Moshenko RW (1972) Ecology of the northern creek chub, *Semotilus atromaculatus atromaculatus* (Mitchill), in the Mink River, Manitoba. M.Sc. thesis, University of Manitoba, Winnipeg, Manitoba, Canada.

46. Bryan PG (1980) The efficiency of mollies, *Poecilia mexicana*, as a live bait for pole-and-line skipjack fishing: fishing trials in the tropical Pacific. Mar Fish Rev 42: 15–24.

47. Mannes JC, Jester DB (1980) Age and growth abundance and biomass production of green sunfish, *Lepomis cyanellus* (Centrarchidae), in a eutrophic desert pond. Southwest Nat 25: 297–311.

48. Hughes SG (1984) Effect of excess dietary riboflavin on growth of rainbow trout. J Nutr 114: 1660–1663.

49. Holopainen IJ, Pitkanen AK (1985) Population size and structure of crucian carp (*Carassius carassius* (L.)) in two small, natural ponds in Eastern Finland. Ann Zool Fenn 22: 397–406.

50. Loonen H, Parsons JR, Govers HAJ (1994) Effect of sediment on the bioaccumulation of a complex mixture of polychlorinated dibenzo-p-dioxins (PCDDs) and polychlorinated dibenzofurans (PCDFs) by fish. Chemosphere 28: 1433–1446.

51. Schaefer JF, Heulett ST, Farrell TM (1994) Interactions between two poeciliid fishes (*Gambusia holbrooki* and *Heterandria formosa*) and their prey in a Florida marsh. Copeia 1994: 516–520.

52. Mulvey M, Newman MC, Chazal A, Keklak MM, Heagler MG, et al. (1995) Genetic and demographic responses of mosquitofish (*Gambusia holbrooki* Girard 1859) populations stressed by mercury. Environ Toxicol Chem 14: 1411–1418.

53. Zampatti B, Raadik TA (1997) An assessment of environmental flow requirements for Hoddles Creek, Marine and Freshwater Resources Institute Freshwater Ecology Division, prepared for Melbourne Water Corporation. Available: http://melbournewater.com.au/waterdata/waterwaydiversionstatus/Documents/Hoddles-Creek-stream-flow_management-plan.pdf. Accessed 2013 October 18.

54. King RP (1998) Weight-fecundity relationships of Nigerian fish populations. Naga, The ICLARM Quarterly 21: 33–36.

55. Soleng A, Bakke TA (1998) The susceptibility of three-spined stickleback (*Gasterosteus aculeatus*), nine-spined stickleback (*Pungitius pungitius*) and flounder (*Platichthys flesus*) to experimental infections with the monogenean *Gyrodactylus salaris*. Folia Parasit 45: 270–274.

56. Offill YA, Walton WE (1999) Comparative efficacy of the threespine stickleback (*Gasterosteus aculeatus*) and the mosquitofish (*Gambusia affinis*) for mosquito control. J Am Mosquito Contr 15: 380–390.

57. LaFrentz BR, LaPatra SE, Jones GR, Cain KD (2003) Passive immunization of rainbow trout, *Oncorhynchus mykiss* (Walbaum), against *Flavobacterium psychrophilum*, the causative agent of bacterial coldwater disease and rainbow trout fry syndrome. J Fish Dis 26: 371–84.

58. Pusey BJ, Kennard MJ, Arthington AH (2004). Freshwater fishes of northeastern Australia. Melbourne: CSIRO Publishing. 645 p.

59. James R, Sampath K (2004) Effect of animal and plant protein diets on growth and reproductive performance in an ornamental fish, *Xiphophorus helleri*. Indian J Fish 51: 75–86.

60. Rybczyk A, Szypuła J (2005) Age as well as length and weight growth of crucian carp from the Szczecin lagoon and the Leszczynskie lakeland, EJPAU 8(3):06. Available: http://www.ejpau.media.pl/volume8/issue3/art-06.html. Accessed: 2013 October 18.

61. Tate WB, Walsh SJ (2005) Distribution and ecological requirements of the Okefenokee pygmy sunfish and the blackbanded sunfish in Florida. Final report. Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida, USA. 29 p. Available: http://research.myfwc.com/engine/download_redirection_process.asp?file = 05tate_3836.pdf&objid = 49824&dltype = publication. Accessed 2013 October 18.

62. Leblond C, Reebs SG (2006) Individual leadership and boldness in shoals of golden shiners (*Notemigonus crysoleucas*). Behaviour 143: 1263–1280.

63. Estabrook GF, Smith GR, Dowling TE (2007) Body mass and temperature influence rates of mitochondrial DNA evolution in North American cyprinid fish. Evolution 61: 1176–1187.

64. Kapusta A, Bogacka-Kapusta E, Czarnecki B (2008) The significance of stone moroko, *Pseudorasbora parva* (Temmick and Schlegel), in the small-sized fish assemblages in the littoral zone of the heated Lake Licheńskin. Arch Pol Fish 16: 49–62.

65. Fontoura NF, Jesus AS, Larre GG, Porto JR (2010) Can weight/length relationship predict size at first maturity? A case study with two species of Characidae. Neotrop Ichthyol 8: 835–840.

66. Okorie A, Abiodun O (2010) Laboratory evaluation of the biocontrol potential of *Aphyosemion gulari* against *Anopheles* larvae. J Vector Dis 47: 181–184.

67. Yamamoto Y, Tsukada H, Nakai D (2010) Latitudinal gradient in the body weight of bluegill *Lepomis macrochirus* in Lake Biwa, Japan. Zool Stud 49: 625–631.

68. Arias CR, Cai W, Peatman E, Bullard SA (2012) Catfish hybrid *Ictalurus punctatus × I. furcatus* exhibits higher resistance to columnaris disease than the parental species. Dis Aquat Organ 100: 77–81.

69. Schmidt G (1957) Einige Notizen über *Dolomedes fimbriatus* (CL). Zool Anz 158: 83–97.

70. Nyffeler M, Symondson WOC (2001) Spiders and harvestmen as gastropod predators. Ecol Entomol 26: 617–628.

71. Nyffeler M, Moor H, Foelix RF (2001) Spiders feeding on earthworms. J Arachnol 29: 119–124.

72. Sierwald P (1988) Notes on the behavior of *Thalassius spinosissimus* (Arachnida: Araneae: Pisauridae). Psyche 95: 243–252.

73. Queensland Museum (2013) Spiders. Available: http://www.qm.qld.gov.au/Find+out+about+/Animals+of+Queensland/Spiders/Modern+Spiders+Infraorder+Araneomorphae/Water+Fishing+or+Nursery+Spiders/Giant+Water+Spider. Accessed 2013 October 18.

74. Caldwell JP, de Araújo MC (1998) Cannibalistic interactions resulting from indiscriminate predatory behavior in tadpoles of poison frogs (Anura: Dendrobatidae). Biotropica 30: 92–103.

75. Eterovick PC, Brandao RA (2001) A description of the tadpoles and advertisement calls of members of the *Hyla pseudopseudis* group. J Herpetol 35: 442–450.

76. Maffei F, Ubaid FK, Jim J (2010) Predation of herps by spiders (Araneae) in the Brazilian Cerrado. Herpetol Notes 3: 167–170.

77. Moura MR, Azevedo LP (2011) Observation of predation of the giant fishing spider *Ancylometes rufus* (Walckenaer, 1837)(Araneae, Ctenidae) on *Dendropsophus melanargyreus* Cope, 1877 (Anura, Hylidae). Biota Neotropica 11: 349–351.

78. Berkum FH van (1982) Natural history of a tropical, shrimp-eating spider (Pisauridae). J Arachnol 10: 117–121.

79. Silva ELC, Picanço JB, Lise AA (2005) Notes on the predatory behavior and habitat of *Trechalea biocellata* (Araneae, Lycosoidea, Trechaleidae). Biociências 13: 85–88.

80. Hernández-Cuadrado EE, Bernal MH (2009) *Engystomops pustulosus* (Tungara Frog) and *Hypsiboas crepitans* (Colombian Tree Frog). Predation on anuran embryos. Herpetol Rev 40: 431–432.

81. Koh JKH (1989) A guide to common Singapore spiders. Singapore: Singapore Science Centre. 160 p.

82. Bhattacharjee GC (1931-32) The fish-eating spiders in Bengal and their habits. Transact Bose Res Inst Calcutta 7: 238–249.

83. Corey DT (1988) Comments on a wolf spider feeding on a green anole lizard. J Arachnol 16: 391–392.

84. Rubbo MJ, Townsend VR, Smyers SD, Jaeger RG (2003) An experimental assessment of invertebrate/vertebrate predation: the interaction between wolf spiders (*Gladicosa pulchra*) and terrestrial salamanders (*Ambystoma maculatum*). J Zool 261: 1–5.

85. Hillyard P (2007) The private life of spiders. London: New Holland Publishers. 160 p.

86. Gettmann W (1978) Untersuchungen zum Nahrungsspektrum von Wolfsspinnen (Lycosidae) der Gattung *Pirata*. M Dtsch Gesell Allg Ange Ent 1: 63–66.

87. Marshall SD (2001) Tarantulas and other arachnids. Hauppauge, NY: Barron's Educational Series. 112 p.

88. Sisson RF (1972) The spider that lives under water. Natl Geogr 1972: 694–701.

89. Schmidt G (1980) Spinnen – Alles Wissewerte über Lebensweise, Sammeln, Haltung und Zucht. Minden, Germany: Albrecht Philler Verlag. 176 p.

90. Seymour RS, Hetz SK (2011) The diving bell and the spider: the physical gill of *Argyroneta aquatica*. J Exp Biol 214: 2175–2181.

91. Robson CH (1877) Notes on a marine spider found at Cape Campbell. Transact Proc New Zealand Inst 10: 299–300.

92. Pocock RI (1902) On the marine spiders of the genus *Desis*, with description of a new species. P Zool Soc Lond 72: 98–106.

93. Jäger P (2005) A 'swimming' *Heteropoda* species from Borneo (Araneae, Sparassidae, Heteropodinae). J Arachnol 33: 715–718.

94. Dunlop J (1996) Swimming in tarantulas. Forum Am Tarantula Soc 5: 79–81.

95. Baerg WJ (1938) Tarantula studies. J New York Entomol Soc 46: 31–43.

96. Breene RG Jr. (2006) Quick and Easy Tarantula Care. Neptune City, NJ: TFH Publications. 64 p.

97. Chubb EC (1913) Fish-eating habits of a spider. Nature 91: 136.

98. Bristowe WS (1958) The world of spiders. London: Collins. 304 p.

99. Wise DH (1993) Spiders in ecological webs. Cambridge, UK: Cambridge University Press. 328 p.

100. Zimmermann M, Spence JR (1989) Prey use of the fishing spider *Dolomedes triton* (Pisauridae, Araneae): An important predator of the neuston community. Oecologia 80: 187–194.

101. Poppe S, Holl A (1995) Ernährungsbiologie und Nahrungsspektrum der Gerandeten Jagdspinne *Dolomedes fimbriatus* (Araneae: Pisauridae). Arachnol Mitt 9: 1–11.

102. Begon M, Townsend CR, Harper JL (2005) Ecology: From individuals to ecosystems. Fourth edition. Oxford, UK: Blackwell Publishing. 752 p.

103. McCormick KD, Kobayashi K, Goldin SM, Reddy NL, Meinwald J (1993) Characterization and synthesis of a new calcium-antagonist from the venom of a fishing spider. Tetrahedron 49: 11155–11168.

104. Gregio AMT, Heleno MG, Von Eicksted VR, Fontana MD (1998) The neuromuscular action of *Ancylometes* sp. spider venom in the rat phrenic nervediaphragm preparation. Toxicon 37: 545–550.

105. Jiang L, Liu C, Duan Z, Deng M, Tang X, et al. (2013) Transcriptome analysis of venom glands from a single fishing spider *Dolomedes mizhoanus*. Toxicon 73: 23–32.

106. Foelix RF (2011) Biology of spiders. Third edition. New York: Oxford University Press. 432 p.

107. Carico JE, Adis J, Penny ND (1985) A new species of *Trechalea* (Pisauridae: Araneae) from Central Amazonian inundation forests and notes on its natural history and ecology. Bull Brit Arachnol Soc 6: 289–294.

108. Duffey E (1995) The distribution, status and habitats of *Dolomedes fimbriatus* (Clerk) and *D. plantarius* (Clerk) in Europe. In: Ružicka V, editor. Proceedings of the 15th European Colloquium of Arachnology, Ceské Budejovice. pp. 54–65.

109. Smith H (2000) The status and conservation of the fen raft spider (*Dolomedes plantarius*) at Redgrave and Lopham Fen National Nature Reserve, England. Biol Conserv 95: 153–164.

110. Leroy B, Paschetta M, Canard A, Bakkenes M, Isaia M, et al. (2013) First assessment of effects of global change on threatened spiders: Potential impacts on *Dolomedes plantarius* (Clerck) and its conservation plans. Biol Conserv 162: 155–163.

111. Helsdingen PJ van (1993) Ecology and distribution of *Dolomedes* in Europe (Araneida: Dolomedidae). Boll Acc Gioenia Sci Nat 26: 181–187.

112. McDowall RM (1994) On size and growth in freshwater fish. Ecol Freshw Fish 3: 67–79.

113. Knouft JH (2004) Latitudinal variation in the shape of the species body size distribution: an analysis using freshwater fishes. Oecologia 139: 408–417.

114. Griffiths D (2006) Patterns and process in the ecological biogeography of European freshwater fish. J Anim Ecol 75: 734–751.

115. Moyle PB, Herbold B (1987) Life-history patterns and community structure in stream fishes of western North America: comparisons with eastern North America and Europe. In: Matthews WJ, Heins DC, editors. Community and evolutionary ecology of North American stream fishes. Norman: University of Oklahoma Press. pp 25–32.

116. Lewis WH (1970) Morphological adaptations of cyprinodontoids for inhabiting oxygen deficient waters. Copeia 2: 319–326.

117. Kramer DL (1987) Dissolved oxygen and fish behavior. Environ Biol Fish 18: 81–92.

118. Moore MK, Townsend VR (1998) The interaction of temperature, dissolved oxygen and predation pressure in an aquatic predator-prey system. Oikos 81: 329–336.

119. McKinsey DM, Chapman LJ (1998) Dissolved oxygen and fish distribution in a Florida spring. Environ Biol Fish 53: 211–223.

120. Lewis WM Jr (1996) Tropical lakes: how latitude makes a difference. In: Schiemer F, Boland KT, editors. Perspectives in tropical limnology. Amsterdam: SPB Academic Publishers. pp. 43–64.

121. Barbour T (1921) Spiders feeding on small cyprinodonts. Psyche 28: 131–132.

122. Jordan F, Jelks HL, Kitchens WM (1994) Habitat use by the fishing spider *Dolomedes triton* in a northern everglades wetland. Wetlands 14: 239–242.

123. Bleckmann H (1988) Prey identification and prey localization in surface-feeding fish and fishing spiders. In: Atema J, Fay RR, Popper AN, Tavolga WN, editors. In sensory biology of aquatic animals. New York: Springer-Verlag. pp. 619–641.

124. U.S. Geological Survey (2013) Nonindigenous aquatic species database. Gainesville, Florida. Available: http://nas.er.usgs.gov/queries/FactSheet.aspx?SpeciesID = 849. Accessed 2013 October 18.

125. Vidal O, Garcia-Berthou E, Tedesco PA, Garcia-Marin J (2010) Origin and genetic diversity of mosquitofish (*Gambusia holbrooki*) introduced to Europe. Biol Invasions 12: 841–851.

126. Hoogland R, Morris D, Tinbergen N, (1956-57) The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as means of defence against predators (*Perca* and *Esox*). Behaviour 10: 205–236.

127. Perna CN, Cappo M, Burrows DW, Pusey BJ (2009) Floodplain degradation and restoration in northern Queensland: the response of the alien fish pest *Gambusia holbrooki*. Ecol Manage Restor 10: 241–243.

128. Kiritani K, Kawahara S, Sasaba T, Nakasuji F (1972) Quantitative evaluation of predation by spiders on the green leafhopper *Nephotettix cincticeps* Uhler, by sight count method. Res Popul Ecol 13: 187–200.

129. Gasnier TR, Azevedo CS, Torres-Sanchez MP, Höfer H (2002): Adult size of eight hunting spider species in central Amazonia: temporal variations and sexual dimorphisms. J Arachnol 30: 146–154.

130. Ishijima C, Taguchi A, Takagi M, Motobayashi T, Nakai M, et al. (2006) Observational evidence that the diet of wolf spiders (Araneae: Lycosidae) in paddies temporarily depends on dipterous insects. Appl Entomol Zool 41: 195–200.

131. Meehean OL (1934) Spiders that fish. Nat Hist 34: 538–540.

132. Johnson DM, Akre BG, Crowley PH (1975) Modeling arthropod predation: wasteful killing by damselfly naiads. Ecology 56: 1081–1093.

133. Samu F, Biro Z (1993) Functional response, multiple feeding and wasteful killing in a wolf spider (Araneae: Lycosidae). Eur J Entomol 90: 471–476.

134. Bernarde PS, Souza MB, Kokubum MCN (1999) Predation *Hyla minuta* Peters, 1872 (Anura, Hylidae) by *Ancylometes* spp. (Araneae, Pisauridae). Biociências 7: 199–203.

135. Prado GM, Borgo JH (2003) *Scinax alter* (NCN). Predation. Herpetol Rev 34: 238–39.

136. Pazin VFV (2006) *Dendrophryniscus minutus* (Amazonian tiny tree toad). Predation. Herpetol Rev 37: 336.

137. Rodrigues DJ, Arruda R (2007) *Dendropsophus sarayacuensis* (Shreve's Sarayacu Treefrog). Predation. Herpetol Rev 38: 437.

138. Brose U, Jonsson T, Berlow EL, Warren P, Banasek-Richter C, et al. (2006) Consumer-resource body-size relationships in natural food webs. Ecology 87: 2411–2417.

139. van Huis A, Van Itterbeeck J, Klunder H, Mertens E, Halloran A, et al. (2013) Edible insects –Future prospects for food and feed security. FAO Forestry Paper 171: 1–201.

140. Nakano S, Miyasaka H, Kuhara N (1999) Terrestrail-aquatic linkages: riparian arthropods alter trophic cascades in a stream food web. Ecology 80: 2435–2441.

141. Naiman RJ, Bilby RE, Schindler DE, Heyfield JM (2002) Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5: 399–417.

142. Ballinger A, Lake PS (2006) Energy and nutrient fluxes from rivers and streams to terrestrial food webs. Mar Freshwater Res 57: 15–28.

143. Zeug SC, Winemiller KO (2008) Evidence supporting the importance of terrestrial carbon in a large river food web. Ecology 89: 1733–1743.

144. Figiel CR, Miller GL (1994) Effects of fish on the growth and survival of two fishing spider populations (*Dolomedes triton*; Araneae, Pisauridae). J Arachnol 22: 185–189.

145. Suter RB (2003) Trichobothrial mediation of an aquatic escape response: directional jumps by the fishing spider, *Dolomedes triton*, foil frog attacks. J Insect Sci 3: 1–7.

146. Pusey BJ, Arthington AH (2003) Importance of the riparian zone to the conservation and management of freshwater fishes: a review with special emphasis on tropical Australia. Mar Freshwater Res 54: 1–16.

147. Chan EKW, Zhang Y, Dudgeon D (2008) Arthropod 'rain' into tropical streams: the importance of riparian forest and influence on fish diets. Mar Freshwater Res 59: 653–660.

148. Delany MF, Abercrombie CL (1986) American alligator food habits in northcentral Florida. J Wildlife Manage 50: 348–353.

149. Da Silveira R, Magnusson WE (1999) Diets of spectacled and black caiman in the Anavilhanas Archipelago, Central Amazonia, Brazil. J Herpetol 33: 181–192.

150. Riley J, Huchzermeyer FW (2000) Diet and lung parasites of swamp forest Dwarf Crocodiles (Osteolaemus tetraspis osborni) in the Northern Congo Republic. Copeia 2000: 582–586.

151. Wallace KM (2006) The feeding ecology of yearling, juvenile and sub-adult Nile crocodiles, Crocodylus niloticus, in the Okavango Delta, Botswana. M.Sc. thesis, University of Stellenbosch, Matieland, South Africa.

152. Cupul-Magaña FG, Rubio-Delgado A, Molano-Rendón F, Reyes-Juárez A (2008) Contenido estomacal de neonatos de Crocodylus acutus (Cuvier, 1807) en Boca Negra, Jalisco. Bol Soc Herpetol Mex 16: 41–45.

153. Greene HW (1997) Snakes: The evolution of mystery in nature. Berkeley: University of California Press. 351 p.

154. Niethammer KR, Kaiser MS (1983) Late summer food habits of three heron species in northeastern Louisiana. Colon Waterbird 6: 148–153.

155. Eguchi K (1980) The feeding ecology of the nestling great tit, Parus major minor, in the temperate ever-green broadleaved forest II. With reference to breeding ecology. Res Popul Ecol 22: 284–300.

156. Krupa JJ, Sih A (1998) Fishing spiders, green sunfish, and a stream-dwelling water strider: male-female conflict and prey responses to single versus multiple predator environments. Oecologia 117: 258–265.

157. Bristowe WS (1941) The comity of spiders II. London: Ray Society. 560 p.

158. Whitcomb WH, Exline H, Hunter RC (1963) Spiders of the Arkansas cotton field. Ann Entomol Soc Am 56: 653–660.

159. Kosuge T, Sasaki T (2002) Predation of the freshwater crab Geothelphusa minei, by the spider, Dolomedes raptor. Biol Mag (Okinawa) 40: 51–52.

160. Lynch RJ, Bunn SE, Catterall CP (2002) Adult aquatic insects: potential contribution to riparian foodwebs in australia's wet-dry tropics. Austral Ecol 27: 515–526.

161. Sanzone DM, Meyer JL, Marti E, Gardner EP, Tank JL, et al. (2003) Carbon and nitrogen transfer from a desert stream to riparian predators. Oecologia 134: 238–250.

162. Greenwood M (2007) The population dynamics of a riparian spider: interactive effects of flow-related disturbance on cross-ecosystem subsidies and spider habitat. Ph.D. thesis, University of Canterbury, Christchurch, New Zealand.

163. Turnbull AL (1973) Ecology of the true spiders (Araneomorphae). Annu Rev Entomol 18: 305–348.

164. Dippenaar-Schoeman AS, Jocqué R (1997) African spiders, an identification manual. Pretoria: Plant Protection Research Institute Handbook 9, Agricultural Research Council. 392 p.

165. Berland L, Pellegrin J (1934) Sur une araignée pêcheuse de poissons. B Soc Zool Fr 59: 210–212.

166. Lapinski W, Tschapka M (2013) Habitat use in an assemblage of Central American wandering spiders. J Arachnol 41: 151–159.

167. Dudgeon D (1999) Tropical Asian streams: zoobenthos, ecology and conservation. Hong Kong: Hong Kong University Press. 844 p.

168. Akabane H (1995) A record of predation of fish by Dolomedes pallitarsis. Kishidaia 69: 40–41 (in Japanese).

169. Mohrhardt D (1963) (Photograph of Dolomedes scriptus preying on minnow). Turtox News 41: 197.

170. Suhr JM, Davis JD (1974) The spider Dolomedes sexpunctatus as a predator on mosquitofish, Gambusia affinis, in Mississippi. Ass Southeast Biol Bull 21: 87.

171. Davis WT (1891) A spider fisherman. Entomol News 2: 77.

172. Zahl P (1971) What's so special about spiders? Natl Geogr 140: 190–219.

173. Adams W (1927) Note on a fishing spider. Bull Zool Soc NY 30: 77.

174. Romand R (1980) Die Schutzanpassung von Aphyosemion walkeri im Waldgebiet der Elfenbeinküste. DATZ 33: 262–264.

175. Crome W (1951) Die Wasserspinne. (Die Neue Brehm-Bücherei, Heft 44). Leipzig: Akademische Verlagsgesellschaft. 47 p.

176. Jäger P (2011) Revision of the genera Nilus O. Pickard-Cambridge 1876, Sphedanus Thorell 1877 and Dendrolycosa Doleschall 1859 (Araneae: Pisauridae). Zootaxa 3046: 1–38.

177. Ciancio J, Pascual M (2006) Energy density of freshwater Patagonian organisms. Ecología Austral 16: 91–94.

178. Cummins KW (1967) Calorific equivalents for studies in ecological energetics. Second Edition. Pittsburgh: Pymatuning Laboratory of Ecology, University of Pittsburgh. 52 p.

179. Pandian TJ, Marian MP (1985) Time and energy costs of metamorphosis in the Indian bullfrog Rana tigrina. Copeia 3: 653–662.

180. Comita GW, Schindler DW (1963) Calorific values of microcrustacea. Science140: 1394–1396.

181. Benoy GA, Nudds TD, Dunlop E (2002) Patterns of habitat and invertebrate diet overlap between tiger salamanders and ducks in prairie potholes. Hydrobiologia 481: 47–59.

182. Morante T, García-Arberas L, Antón Á, Rallo A (2012) Macroinvertebrate biomass estimates in Cantabrian streams and relationship with brown trout (Salmo trutta) populations. Limnetica 31: 85–94.

183. Staddon BW (1963) Water balance in the aquatic bugs Notonecta glauca L. and Notonecta marmorea Fabr. (Hemiptera: Heteroptera). J Exp Biol 40: 563–571.

184. Salonen K, Sarvala J, Hakala I, Viljanen ML (1976) The relation of energy and organic carbon in aquatic invertebrates. Limnol Oceanogr 21: 724–730.

185. Matthews PGD, Seymour RS (2011) Oxygen binding properties of back-swimmer (Notonectidae, Anisops) haemoglobin, determined in vivo. J Insect Physiol 57: 1698–1706.

186. Needham KM (1990) Specific and seasonal variation in survival and sodium balance at low pH in five species of waterboatmen (Hemiptera: Corixidae). M.Sc. thesis, University of British Columbia, Vancouver, Canada.

187. Rueda L, Patel K, Axtell R, Stinner R (1990) Temperature-dependent development and survival rates of Culex quinquefasciatus Say and Aedes aegypti (Diptera: Culicidae). J Med Entomol 27: 892–898.

188. Krebs JR, Avery MI (1984) Chick growth and prey quality in the European bee-eater (Merops apiaster). Oecologia 64: 363–368.