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SHORT COMMUNICATION

Oophagy in spiders: consumption of invertebrate and vertebrate eggs

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Abstract. In this paper, we present an update on our knowledge on egg predation (oophagy) by spiders. Based on a survey of 233 reports, ghost spiders (Anyphaenidae), lynx spiders (Oxyopidae), jumping spiders (Salticidae), and yellow sac spiders (Cheiracanthiidae) were the most prominent groups of spiders engaged in oophagy. Around 75% of the reports referred to the consumption of lepidopteran and spider eggs worldwide. Another 10% referred to the consumption of eggs/embryos of anurans – especially predation upon embryos of glass frogs (Centrolenidae) by spiders from the families Anyphaenidae and Trechaleidae in the Neotropics. The remaining 17% included rare instances of feeding on eggs of coleopterans, dermapterans, dipterans, heteropterans, homopterans, hymenopterans, acarids, neuropterans, opilionids, and squamates. Our study demonstrates that oophagy in spiders is much more widespread than previously thought, both geographically and taxonomically. The finding that spiders feed on eggs/embryos from so many different invertebrate and vertebrate taxa is novel.

Keywords: Anyphaenidae, Cheiracanthiidae, Oxyopidae, Salticidae, Egg predation, Invertebrata, Anura, Squamata

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Nyffeler et al. (1990) published an extensive review on spiders as egg predators, which led to the conclusion that spiders frequently feed on lepidopteran and spider eggs and very rarely on coleopteran eggs. This study inspired many other researchers to follow up on this topic (e.g., Ruberson & Greenstone 1998; Miliczky & Calkins 2002; Pfannenstiel 2008; Myers et al. 2020). Three decades later, we conducted an update on this topic, revealing that oophagy in spiders is much more widespread and diverse than previously anticipated (Table 1). The update is based on 233 reports, 130 (56%) of which were not included in the Nyffeler et al. (1990) paper (see Supplemental Table S1, online at https://doi.org/10.1636/JoA-S-21-016.s1). In the following, we report this additional information.

Roughly 75% of the reports referred to the consumption of lepidopteran and spider eggs (Table 1; Figs. 1A-D). Less frequently, instances of feeding on the eggs of coleopterans, dermapterans, dipterans, heteropterans, homopterans, hymenopterans, acarids, neuropterans, and opilionids were reported in the literature (Table 1; Figs. 2A-B). Spider predation on arthropod eggs has been reported from all continents except Antarctica (see Table S1).

Not only do spiders feed on arthropod eggs, the natural diets of various spider groups also include vertebrate eggs (Table 1; Fig. 3). The third most common type of oophagy referred to spiders devouring anuran eggs/embryos (23 in 233 reports). This type of oophagy referred for the most part to predation upon embryos of about a dozen different glass frog species (Centrolenidae) in Central and South America (Figs. 3A-B; Rojas-Morales & Escobar-Lasso 2013; Valencia-Aguilar et al. 2012, 2020, 2021; and others). In addition, feeding on frog eggs/embryos has now been documented from several other anuran families (Table 1) and must be placed in a broader context with anurophagy in spiders (see Nyffeler & Altig 2020). Finally, a report from Sri Lanka documents spider predation on lizard eggs (Squamata; Priyadarshana & Wijewardana 2016). In this latter case, an unidentified huntsman spider, *Heteropoda* Latreille, 1804 (Sparassidae) killed an adult female Common House Gecko (*Hemidactylus frenatus* Duméril & Bibron, 1836) and, after 14 hours, the gecko was totally consumed, along with its eggs (Fig. 3C).

Eggs are singly deposited or laid in clutches (such an egg mass is defined as a group of eggs layed simultaneously in close proximy). There are few records of attacks on single eggs. Such rare attacks on singly deposited eggs had been reported for monarch butterflies, swallowtail butterflies, and lacewings (Suwarno 2010; Hermann et al. 2019; Mezőfi et al. 2020). When attacking egg masses, the spiders usually consumed several eggs in a row (Ron Atkinson, pers. comm.; Suwarno 2010; Ahmed et al. 2018; Marangelo 2019; Cukier 2020; and others). It appears that mostly unguarded egg masses were attacked by spiders (e.g., Pasquet et al. 1997; Buzatto et al. 2007; Jackson et al. 2008; Guayasamin et al. 2019).

As oopghagy in spiders is widespread, the question arises whether specific adaptations for oophagy are known in this predator group. Such adaptations are indeed known as regards the consumption of spider eggs. Firstly, the web-building spider *Amaurobius ferox* (Walckenaer, 1830) (Amaurobiidae) produces "trophic eggs," which means that the mother provides non-developing eggs for its freshly hatched offspring to eat (Kim & Roland 2000). This reproductive strategy markedly increases the survival probability of the offspring of this spider species. Secondly, in some species of the ant-mimicking jumping spiders in the genus *Myrmarachne* MacLeay, 1839, males have strikingly enlarged chelicerae that make them highly efficient in opening other spiders' silken retreats and eating their eggs after invading alien webs (Jackson & Willey 1994). This is likely a case of morphological adaptation for oophagy. Thirdly, Jackson and colleagues have shown in a series of papers that numerous salticid species habitually invade alien webs to steal prey (kleptoparasitism) and eat the resident spider as well as its eggs (Fig. 1A; Jackson & Pollard 1996; Cerveira et al. 2003). In these cases, web invasion followed by eating the resident spiders' eggs is one of the diverse predatory strategies employed by the salticids (Jackson & Pollard 1996). The same behavior of web invasion coupled with kleptoparasitism, araneophagy, and oophagy was also observed in several other spider families (Jackson & Whitehouse 1986; Jarman & Jackson 1986; Cerveira & Jackson 2005). Invasion of alien webs followed by oophagy can be very rewarding, as shown by the example of the salticid *Phyaces comosus* Simon, 1902, which invades the webs of much larger salticids (Jackson 1986). As a case in point, a *P. comosus* invading the web of the salticid *Bavia aericeps* Simon, 1877, is able to

Table 1.—List of egg taxa reported to be consumed by spiders based on a literature survey ($n = 233$ reports; see Supplementary material for a complete list of all reports).

Egg taxon	Number of reports	Egg predator (spider family) [A]	Source
ARACHNIDA:			
Araneae [A]	(86)		
AGE, AMA, ARA, ATR, CHE, CLU DYS, GNA, HER, LYC, PHO, SAL, SCY, SIC, SPA, THE, THO, ULO	86	AGE, AMA, ARA; ATR; CHE, CLU, DYS; GNA, LYC, MIM; PAL; PHO; SAL, SCY, SIC, SPA; THE, THO, ULO	Jackson 1986, 1990; Jackson & Whitehouse 1986; Jarman & Jackson 1986; Nyffeler et al. 1990; Jackson & Willey 1994; Pasquet et al. 1997; Marc et al. 1999; Kim & Roland 2000; Cerveira & Jackson 2005; Donovan & Hill 2017; Banerjee et al. 2019; and others
Opiliones	(5)		
Gonyleptidae	5	ANY, SAL	Buzatto et al. 2007; Requena et al. 2009
Acari	(1)		
Ixodidae	1	N/A	Samish & Rehacek 1999
INSECTA			
Coleoptera	(5)		
Chrysomelidae	3	LIN, N/A	Chang & Snyder 2004
Curculionidae	2	ANY, TRA	Nyffeler et al. 1990
Dermaptera	(2)		
Chelisochidae	2	SAL	Zabka & Kovac 1996
Diptera	(1)		
Calliphoridae	1	N/A	Merfield et al. 2004
Heteroptera	(11)		
Acanthosomatidae	1	N/A	Kudo & Nakahira 1993
Coreidae	3	ANY, SAL	Phillips & Gardiner 2016; Ahmed et al. 2018
Pentatomidae	6	OXY, SAL	Jones-Walters 1993; Ehler 2002; Morrison et al. 2016; Cukier 2020; Tillman et al. 2020
Tessaratomidae	1	SAL	Ron Atkinson, pers. comm.
Homoptera	(1)		
Psyllidae	1	N/A	Catling 1970
Hymenoptera	(9)		
Formicidae	9	LIN, SAL	Guseinov et al. 2004; Nelson & Jackson 2009a; Cushing 2012; Parmentier et al. 2015
Lepidoptera	(85)		
Lycaenidae	1	SAL	Ranasinghe 2016
Lymantriidae	3	SAL, N/A	Nyffeler et al. 1990
Noctuidae	59	ANY, ARA, CHE, CLU, COR, DIC, LIN, LYC, THO, OXY, PIS, SAL, TRA	Ruberson & Greenstone 1998; Pfannenstiel 2008; Pérez-Guerrero et al. 2014; Marangelo 2019; and others
Nymphalidae	3	SAL, THO	Hermann et al. 2019; Myers et al. 2020
Papilionidae	3	OXY, SAL	Suwarno 2010
Pieridae	1	N/A	Hooks et al. 2006
Pyralidae	7	ARA, CLU, LIN, LYC, SAL, THE	Negm & Hensley 1969
Sphingidae	1	OXY	Nyffeler et al. 1990
Tortricidae	5	CHE, CLU, SAL	Miliczky & Calkins 2002
N/A	2	ARA, SAL	Two internet reports
Neuroptera	(3)		
Chrysopidae	3	CHE, SAL, THE	Pérez-Guerrero et al. 2014; Mezőfi et al. 2020; Fig. 2B
ANURA:	(23)		
Centrolenidae	16	ANY, TRE, N/A	McDiarmid 1975; Gibbons et al. 2010; Valencia-Aguilar et al. 2012; Delia et al. 2013; Rojas-Morales & Escobar-Lasso 2013; Valencia & Delia 2016; Rios-Soto et al. 2017; Delia et al. 2019; Guayasamin et al. 2019; Ospina-L et al. 2020; Valencia-Aguilar et al. 2020, 2021
Eleutherodactylidae	1	N/A	Stewart & Woolbright 1996
Hylidae	2	TRE	Hernandez-Cuadrado & Bernal 2009
Leptodactylidae	2	LYC, TRE	Villa et al. 1982; Hernandez-Cuadrado & Bernal 2009
Microhylidae	1	N/A	Simon 1983
Rhacophoridae [B]	1	PIS	Poo et al. 2017
SQUAMATA:	(1)		
Gekkonidae	1	SPA	Priyadarshana & Wijewardana 2016
Total	233		

[A] Spider families: AGE = Agelenidae; AMA = Amaurobiidae; ANY = Anyphaenidae; ARA = Araneidae; ATR = Atracidae; CHE = Cheiracanthiidae; CLU = Clubionidae; COR = Corinnidae; DIC = Dictynidae; DYS = Dysderidae; GNA = Gnaphosidae; HER = Hersiliidae; LIN = Linyphiidae; LYC = Lycosidae; MIM = Mimetidae; OXY = Oxyopidae; PAL = Palpimanidae; PHO = Pholcidae; PIS = Pisauridae; SAL = Salticidae; SCY = Scytodidae; SIC = Sicariidae; SPA = Sparassidae; THE = Theridiidae; THO = Thomisidae; TRA = Trachelidae; TRE = Trechaleidae; ULO = Uloboridae; N/A = ID not available.

[B] This record remains somewhat doubtful because the researchers were unable to provide hard evidence that the spider was actually feeding on the egg clutch.

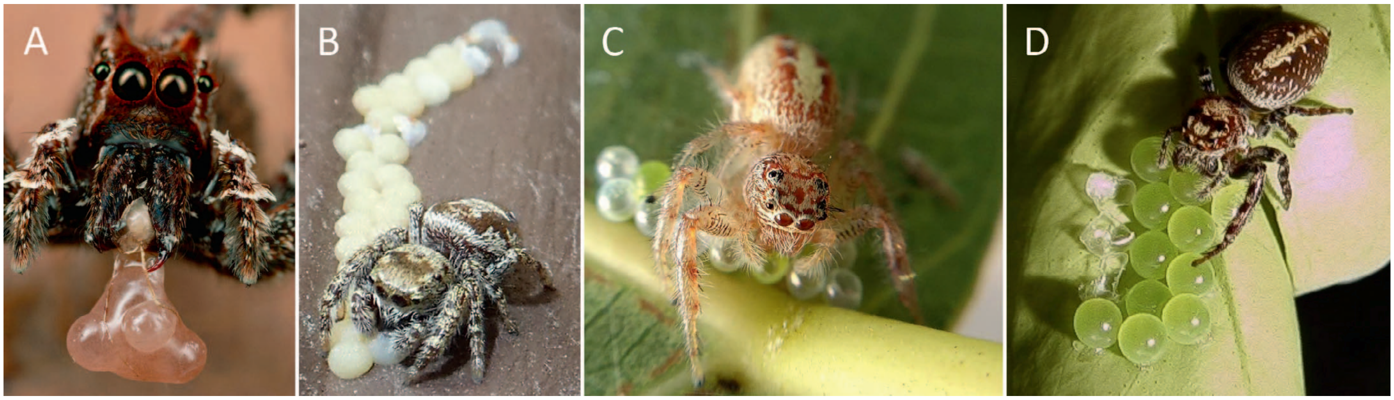

Figure 1.—Salticid spiders consuming arthropod eggs. (A) *Portia fimbriata* (Doleschall, 1859), eating the eggs of a defeated conspecific female in Queensland, Australia (Photo copyright: Mark Moffett). (B) *Pelegrina* cf. *aeneola* (Curtis, 1892) consuming eggs of a noctuid moth (presumably *Xylena cineritia*) in Montana, USA (Photo by Glenn Marangelo). (C) *Thyene coccineovittata* (Simon, 1886) feeding on the egg of a pentatomid bug on a *Ficus* tree in Rio de Janeiro, Brazil (Photo by Laíza Mussap Cukier). In another photo, presented by Cukier (2020), punctured eggs whose internal contents had been sucked out by the spider can be seen. (D) Unidentified jumping spider (*Opisthoncus* L. Koch, 1880) consuming eggs of the Bronze orange bug *Musgraveia sulciventris* (Tessaratomidae) in Queensland, Australia (Photo by Ron Atkinson). On the left side of the picture, three empty eggshells – a clear indication of the feeding activity performed by the jumping spider – can be seen.

eat a single egg almost as large as itself. As Jackson (1986) wrote, "….the egg mass in a single egg sac is a veritable bonanza."

What specific adaptations for oophagy are known by spiders in which consumption of insect eggs is concerned? Several salticid species have been reported to feed on ant eggs after entering the ants' nests (Nelson & Jackson 2009a; Cushing 2012). The fact that the spiders were able to feed on ant eggs unhindered by the ants implies that the spiders in question must be chemically disguised so that the ants could not recognize them as foreign intruders (Nelson & Jackson 2009a; Parmentier et al. 2015). In the case of the salticid *Cosmophasis bitaeniata* (Keyserling, 1882), spiders acquire the ants' odor through the consumption of ant larvae (Elgar & Allan 2004); this would be classified as a case of behavioral adaptation. In many other cases eating insect eggs appears to be largely an occasional, opportunistic occurence (David Hill, pers. comm.). But such cases of opportunistic feeding are limited to a large extent to a group of "active searchers" equipped with the sensory systems needed for the detection and identification of immobile prey such as eggs (see Nelson & Jackson 2009b; Gallagher et al. 2013). In particular, Anyphaenidae, Cheiracanthiidae, Oxyopidae, and Salticidae are known to opportunistically feed on insect eggs (Table 1). These same spider groups are also occasionally seen feeding on other immobile food such as various types of plant matter (Nyffeler et al. 2016).

How does oophagy affect the food supply of spiders? So far very few quantitative assessments of eggs as spider prey exist. In two studies on the natural diets of salticids, insect eggs made up ≈2–4% of

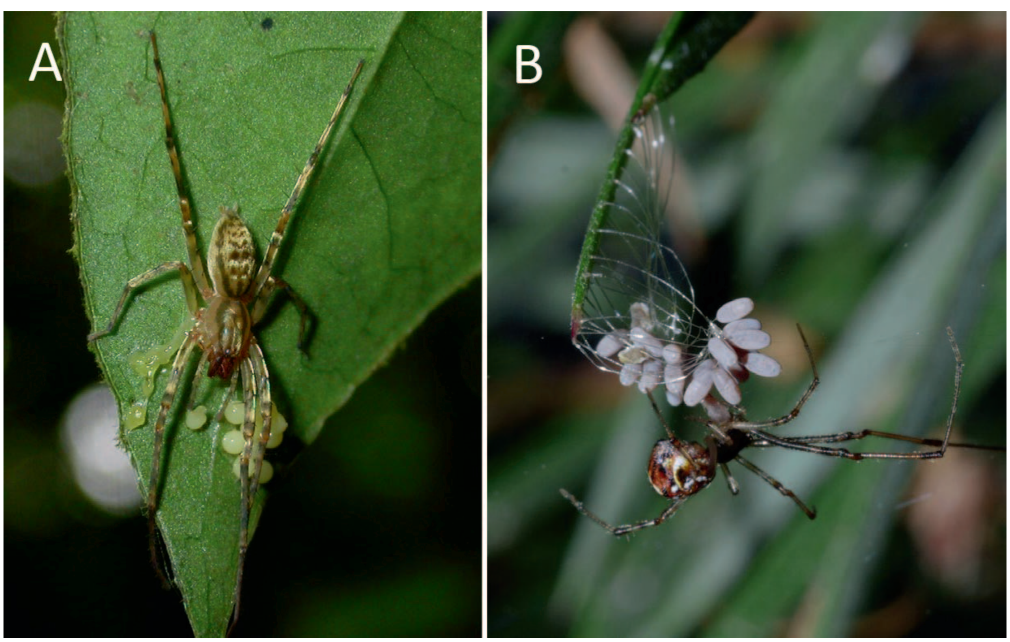

Figure 2.—(A) Juvenile *Osoriella rubella* (Keyserling, 1891) (Anyphaenidae) consuming an egg of the harvestman *Iporangaia pustulosa* (Gonyleptidae) near Sao Paulo, Brazil (Photo by Gustavo S. Requena). (B) *Parasteatoda tepidariorum* spider (Theridiidae) lassoed lacewing eggs (Chrysopidae) with its web and then started eating them as they hatched; picture taken in Airlie Beach, Queensland (Photo Steve & Alison Pearson).

Figure 3.—Spiders consuming vertebrate eggs. (A) Juvenile wandering spider *Cupiennius getazi* Simon, 1891 (Trechaleidae) near an egg clutch of the glass frog *Agalychis callidryas* (Centrolenidae) is consuming one of the embryos. The incident was witnessed in Costa Rica (Photo by Peter van Zandt). (B) Unidentified wandering spider, *Cupiennius* Simon, 1891 (Trechaleidae) devouring eggs of an unidentified glass frog (Centrolenidae) in the Manduriacu Reserve, Ecuador (Photo copyright: Jaime Culebras). (C) Spider *Heteropoda* sp. (Sparassidae) feeding on an immature egg of the gecko *Hemidactylus frenatus* in Sri Lanka (Photo by Tharaka Sudesh Priyadarshana & Ishara Harshajith Wijewardana).

the spiders' total prey (Zabka & Kovac 1996; Guseinov et al. 2004), while in other studies insect eggs seem to have been absent in the diets of salticids (e.g., Jackson 1977; Edwards 1980). Thus, predation on insect eggs appears to contribute rather insignificantly to the annual food supply of jumping spider populations. Nevertheless, if we look at it from the point of view of a single individual, opportunistically feeding on an insect egg mass may be quite rewarding for an individual. In studies on the natural diets of two other cursorial hunters – an unidentified palpimanid (*Palpimanus* Dufour, 1820) and a salticid (*Myrmarachne melanotarsa* Wesołowska & Salm, 2002) – spider eggs composed 13–17% of the total prey (Cerveira & Jackson 2005; Jackson et al. 2008). Feeding on spider eggs therefore appears to be rewarding for araneophagic spiders that habitually invade alien webs.

In conclusion, the significance of oophagy for the food supply of spiders appears to vary considerably depending on the species of spider in question. The use of eggs as a supplementary food source represents an opportunity to enlarge the spiders' food base, which might be of nutritional significance most notably during periods of food scarcity. Oophagy becomes even more meaningful considering that arthropod eggs and vertebrate eggs are high quality prey due to their high protein content (Eubanks & Denno 2000; Neckel-Oliveira & Wachlevski 2004).

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SUPPLEMENTAL MATERIALS

Supplemental Table S1.— Reports of oophagy by spiders. Online at https://doi.org/10.1636/JoA-S-21-016.s1

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