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Intraguild predation on hornets and yellowjackets of vespine wasps by spiders, and vice versa

Daisuke Noguchi [1*] & Kenichi Ikeda [2]
[1] Nagasaki University, Bunkyo–machi 1–14, Nagasaki, 8528521, Japan
[2] Ecological Information, Japan
* Corresponding author e-mail address: a.chemist.noguchi.d@gmail.com

Abstract

Not only spiders (Arachnida: Araneae) but also vespine wasps (Hymenoptera: Vespidae: Vespinae) including hornets (the genus *Vespa*) and yellowjackets (the genera *Vespula* and *Dolichovespula*) belong to top-predator community within arthropod food webs. Thus, between two communities, intraguild predation (IGP) defined as killing and eating among potential competitors is considered to occur. However, the possibility has not investigated enough so far. In the present study by means of bibliographic survey it has been reported that the observations of predation on *Vespa*, *Vespula*, and *Dolichovespula* of vespine wasps by spiders; i.e., large web-building spider *Argiope* spp. (Araneidae) captured *Vespa orientalis*, *A. amoena* and *A. bruennichi* fed on hornets *V. analis*, jumping spiders such as *Phidippus audax* (Salticidae) preyed on yellowjackets (*Vespula germanica*, *Dolichovespula maculate*, and *D. arenaria*), a tunnel web spider *Porrhothele antipodiana* (Mygalomorphae) consumed *Vl. germanica*, orb-weavers *A. aurantia* and *A. florida* captured *Vl. squamosa*, diet of wandering spider *Phoneutria boliviensis* (Ctenidae) contained *Vespula* sp. By contrast, 20 cases were that vespine wasps foraged spiders from 10 publications with certain species names. Accordingly, symmetric IGP between vespine wasps and spiders is suggested. Observations on kleptoparasitism by hornets, an escaping from a spider's web by a vespulid wasp, and a killing between a spider and a yellowjacket each other were also known. Although spiders are both prey and predators of vespine wasps, further studies are required to elucidate quantitatively the interaction of prey-predator relationship as symmetric IGP.

Keywords: Araneae, Diet, Food Chain, IGP, Predator-Prey Relationships, Vespinae.

Introduction

Spiders (Arachnida: Araneae), one of ubiquitous predators in terrestrial ecosystems (Wise, 1993), are constituting a community as a top-predator species among arthropods (e.g., Schmitz & Suttle, 2001). In fact, as quantitatively, an annual prey kill of the global spider community has in the range of 400-800 million metric tons, with insects and collembolans (Nyffeler & Birkhofer, 2017). Meanwhile, as another usual top-predators of a wide variety of arthropod prey like insects, most species of the subfamily Vespinae (Hymenoptera: Vespidae), containing the largest and best-known eusocial wasps of true hornets (the genus *Vespa*), yellowjackets (the genera *Vespula* and *Dolicovespula*) and nocturnal hornets (the genus *Provespa*), inhabiting mainly Eurasia, North Africa, North America and Oceania, have been also recognized (e.g., Richards, 1971; Matsuura & Yamane, 1990; Matsuura, 1991; Richter, 2000). Though in vespine wasps it is revealed that they are consisting of a community as a top-predator species among arthropods (e.g., New, 2016), it seems that the impact of them has not been studied quantitatively enough yet compared with spiders.

Because both spiders and vespine wasps are commonly known as generalist/semi-specialist predator community with some exceptions (e.g., Foelix, 2011; Matsuura, 1991; Wise, 1993), predation with each other occur occasionally in areas where their habits overlap. Matsuura (1984), for example, has described that vespine wasps sometimes feed "Araneae" and Miyashita & Shinkai (1995) have reported that a part of the diet of large orb-web spiders was composed "Hymenoptera". Regrettably, these species of prey-items were characterized by only their order level. If more certain species names of them are available, the relationship between spiders and vespine wasps would be expected to strongly demonstrate as "Intraguild predation (IGP)" in ecosystems based on precise scientific observations in detail.

Intraguild predation (IGP) is defined as killing and eating among potential competitors, appearing to be pervasive within arthropod food webs, with frequencies of 58-87% (e.g., Yasuda, 1996; Arim & Marquet, 2004; Hunter, 2009; Schowalter, 2016). Here, a guild is defined as a group of species that exploit the same class of environmental resources in a similar way (Root, 1967). Generally, asymmetric IGP occurs when one species (A, by convention) has been always the predator on B, whereas symmetric IGP occurs during mutual predation between A and B (Polis *et al.*, 1989). IGP could be important because it reduces predation pressure on vegetative predators, adds redundancy to simple trophic cascades and increases ecosystem stability (Polis & Holt, 1992; Holt & Polis, 1997; Finke & Denno, 2005).

Note that it has been hypothesized that predators deliberately engage in IGP for the nutrients of another predator (Matsumura *et al.*, 2004; Michalko *et al.*, 2021). Within spiders (Hodge, 1999) and Hymenoptera (Feldhaar, 2011) of IGP and a possibility that wasps prey spiders as IGP were studied before (Crowder & Snyder, 2010). The relationship may be nutritionally of significance, even if the amount of predation on each other is small for spiders and vespine wasps. Nevertheless, studies on the prey-predator relationship between spiders and vespine wasps as IGP are few as far. How much is known about the predation on vespine wasps by spiders, and vice versa? One of the authors previously reported exact such cases; i.e., *Argiope amoena* and *A. bruennichi* preyed on *Vespa analis insularis* in Fig. (1) (Noguchi, 2020; 2021), which remained sporadic records. Perhaps, observational cases on vespine wasps prey spiders, and vice versa, were reported independently without summarizing comprehensively.

Fig. 1. Observations of *Argiope amoena* (left) and *Argiope bruennichi* (right) feeding on *Vespa analis* (Noguchi, 2020, 2021).

To the best of our knowledge, there seems to be no comprehensive overview of observed cases of predation on vespine wasps by spiders, and vice versa. Therefore, we searched scientific research articles regarding observational cases of predation among spiders and vespine wasps each other with a viewpoint of symmetric/asymmetric IGP around the world to achieve a fundamental step for convenience.

Material and Methods

Firstly, we have checked books dealing with the biology of vespine wasps such as "The biology of the social wasps (Hymenoptera, Vespidae)" (Richards, 1971), "Wasps: An account of the biology and natural history of social and solitary wasps" (Spradbery, 1973), "Biology and pest status of venomous wasps" (Akre & Davis, 1978), "Social wasps" (Akre, 1982), "Biology of the vespine wasps" (Matsuura & Yamane, 1990), "*Vespa* and *Provespa*" (Matsuura, 1991), "Social wasp (Hymenoptera: Vespidae) foraging behavior" (Richter, 2000), "Wasps" (Schmidt, 2009), "Individual and social foraging in social wasps" (Jeanne & Taylor, 2009), and "Enemies of wasps subverting the sting" (Eaton, 2021). Then, we searched papers on Google Scholar by the keywords like "hornet", "yellowjacket", "vespine wasps" combined with "spider", "Araneae", "predation" and "feed".

Results

An escape of *Vespula germanica*, not a hornet but a yellowjacket, caught in spider webs was reported by Fordham (1961). This finding seems to be the only case of escaping successfully from spider webs by a vespulid documented so far. It has been known that insects have evolved a variety of anti-predator defences in predator-prey relationships (e.g., Sugiura, 2020). Sugiura *et al.* (2019) reported that when mantids were placed in the web of *A. bruennichi*, some mantids could use their mouthparts to escape

from the spider silk wrapped around their forelegs. While, other mantids were fed on by the spiders resulting in the failure to escape. Consequently, it was hypothesized that the escape from spider webs may be also observed in other insects with powerful mouthparts (e.g., hornets) by means of further observations and experiments.

It is summarized in Table (1) that research articles where general remarks, belonged to genera of spiders had not determined, regarding prey-predation interactions between vespine wasps and spiders were described. The prey of *Vespa mandarinia* in the field were mainly large caterpillars and large web-building spiders (Matsuura & Sakagami, 1973). *Vespula flaviceps* foraged on spiders (Iwata, 1971). *Vespula consobrina* captured small spiders (Akre *et al.*, 1982). *Vespa analis* and *Vespa simillima* fed on spiders (Matsuura, 1984). *Vespula pensylvanica* preyed on Araneae (Gambino *et al.*, 1987; Wilson *et al.*, 2009) and Philodromidae (Wilson *et al.*, 2009). *Vespula vulgaris* preyed on Araneae and Salticidae (Broekhuizen & Hordijk, 1968; Harris, 1991; Harris & Oliver, 1993).

Lycosidae, Sparassidae, and Argiopidae [The now suppressed familial name for Araneidae] (Madden, 1981), Araneae and Salticidae (Harris, 1991; Harris & Oliver, 1993; Harris, 1996) and spiders (Sackmann *et al.*, 2000) were preyed on by *Vl. germanica*. Foraging by *Vl. germanica* can cause localized drastic reductions in spiders (Spradbery & Maywald, 1992; Donovan, 1992). Meanwhile, the proportion of spiders in the diet of *Vl. germanica* was small depending on conditions (Kasper *et al.*, 2004). *Agelenopsis aperta* (Agelenidae) may prey on Vespidae (Riechert, 1991).

Table 1. The cases of the predator-prey relationships of vespine wasps and spiders by means of general description.

Predators	Prey	References
V. mandarinia	large web-building spiders	Matsuura & Sakagami, 1973
V. analis	spiders	Matsuura, 1984
V. simillima	spiders	Matsuura, 1984
Vl. vulgaris	Araneae and Salticidae	Broekhuizen & Hordijk, 1968; Harris, 1991; Harris & Oliver, 1993
Vl. flaviceps	spiders	Iwata, 1971
Vl. consobrina	small spiders	Akre *et al.*, 1982
Vl. pensylvanica	Araneae	Gambino *et al.*, 1987; Wilson *et al.*, 2009
	Philodromidae	Wilson *et al.*, 2009
Vl. germanica	Lycosidae Sparassidae Argiopidae (= Araneidae)	Madden, 1981
	Araneae and Salticidae	Harris, 1991; Harris & Oliver, 1993; Harris, 1996
	spiders	Spradbery & Maywald, 1992; Donovan, 1992; Sackmann *et al.*, 2000; Kasper *et al.*, 2004
Ag. aperta	Vespidae (potential prey)	Riechert, 1991

Articles with detailed statements containing scientific names of species and/or genera of both vespine wasps and spiders as predators/prey are as follows: Matsuura & Yamane (1990) summarized several observations of vespine wasps predation on spiders (Table 2); *Vespa mandarinia* preyed on *A. amoena* and *A. bruennichi* (Araneidae,

respectively) (Matsuura, 1984); *Vespula vulgaris* preyed on spiders such as *Philodromus* sp. (Philodromidae) [in the original article, classified as Thomisidae], *Trochosa* sp. (Lycosidae), *Theridion ovatum* (Theridiidae), *Meta segmentata* (Argiopidae) [= *Metellina segmentata* of Tetragnathidae], *Linyphia triangularis* and *Drapetisca socialis* (Linyphiidae) (Broekhuizen & Hordijk, 1968).

Table 2. The cases of the predator-prey relationships of spiders and vespine wasps by means of detailed description with scientific names of species and/or genera.

Predators	Prey	References
V. mandarinia	*A. amoena* *A. bruennichi*	Matsuura, 1984
Vl. vulgaris	*Philodromus* sp. *Trochosa* sp. *Th. ovatum* *M. segmentata* *L. triangularis* *D. socialis*	Broekhuizen & Hordijk, 1968

The followings are reported cases found in literature searches by Google Scholar: *Eriophora pustulosa* (Gibbs, 1980) and *Zygiella x-notata* (Pasquet *et al.*, 2007) (Araneidae) were preyed on by *Vl. germanica*. *Vespa* sp. took *Trichonephila clavata* away (Miyashita, 1994). *Vespula vulgaris* preyed on *Er. pustulosa* (Toft & Rees, 1998; Lester & Beggs, 2019). *Vespula pensylvanica* preyed on Araneae of the genera of *Cheiracanthium* sp. (Cheiracanthiidae), *Vespa affinis* captured *Cyclosa confusa* (Araneidae) (Chou *et al.*, 2005). *Habronattus* (Salticidae), *Achaearanea*, *Theridion* (Theridiidae, respectively) and *Mecaphesa* (Thomisidae) (Wilson *et al.*, 2009). *Vespa crabro* preyed on *A. bruennichi* (Helsdingen, 2011; Bruggisser *et al.*, 2012). These cases of yellowjackets fed on spiders with certain species names from above are in Table (3).

Tunnel web spider *Porrhothele antipodiana* (Mygalomorphae: Porrhothelidae) captured *Vl. germanica* (Laing, 1973). *Vespa orientalis* wasps were captured by *Argiope* spp. (Hendawy, 2004). *Argiope aurantia* and *A. florida* preyed on *Vespula squamosa* (Carrel & Deyrup, 2019). By virtue of one of the authors' observations, *A. amoena* (Noguchi, 2020) and *A. bruennichi* (Noguchi, 2021) preyed on *V. analis*. DNA metabarcoding analysis revealed that *Vespula* sp. was one of the diets of wandering spider *Phoneutria boliviensis* (Ctenidae) (Ramírez *et al.*, 2021). These reported cases are shown in Table (4).

About 100 years ago, several observed cases regarding the prey-predator relationship between vespine wasps and spiders had been reported (Bilsing, 1920). *Vespula germanica*, *Dolichovespula arenaria* and *D. maculata* [in the original article, stated as *Vespa germanica*, *Vespa diabolica* and *Vespa maculata*] were foraged by *Phidippus audax* (Salticidae [in the original article, stated as Attidae]); *D. arenaria* was preyed by *Neoscona domiciliorum* (Araneidae) [in the original article, stated as *Epeira domiciliorum*]; *Vl. germanica* was fed on by *Hogna carolinensis* (Lycosidae) [in the original article, stated as *Lycosa carolinensis*], *Araneus trifolium* [in the original article, stated as *Epeira trifolium*], *Epeira gigas* [= *Araneus bicentenarius*] and *Argiope trifasciata* (Araneidae). These cases, observed in field or cage, are shown in Table (5).

Table 3. Cases of hornets and yellowjackets preyed on spiders with species and/or genera names were shown.

Predators	Prey	References
Vl. germanica	*Er. pustulosa*	Gibbs, 1980
	Z. x-notata	Pasquet *et al.*, 2007
Vespa sp.	*T. clavata*	Miyashita, 1994
Vl. vulgaris	*Er. pustulosa*	Toft & Rees, 1998; Lester & Beggs, 2019
V. affinis	*C. confusa*	Chou *et al.*, 2005
Vl. pensylvanica	*Cheiracanthium* sp. *Habronattus* sp. *Theridion* sp. *Achaearanea* sp. *Mecaphesa* sp.	Wilson *et al.*, 2009
V. crabro	*A. bruennichi*	Helsdingen, 2011; Bruggisser *et al.*, 2012

Table 4. Cases of hornets and yellowjackets preyed by spiders, both species and/or genera names were shown.

Predators	Prey	References
Po. antipodiana	*Vl. germanica*	Laing, 1973
Argiope spp.	*V. orientalis*	Hendawy, 2004
A. aurantia *A. florida*	*Vl. squamosa*	Carrel & Deyrup, 2019
A. amoena	*V. analis*	Noguchi, 2020
A. bruennichi	*V. analis*	Noguchi, 2021
Ph. boliviensis	*Vespula* sp.	Ramírez *et al.*, 2021

In addition, studies on observed cases of kleptoparasites by a vespine wasps caught in spider webs are shown. *Vespula germanica* preyed on a hover-fly that was caught in a spider web (O'Rourke, 1945). Workers of *Vespa mongolica* [now a subspecies of *V. simillima*] have been seen removing workers of *Vespa* spp. from spider webs (Iwata, 1971; Akre, 1982). *Vespa affinis* attacked prey in the web of *C. confusa* (Chou *et al.*, 2005). *Vespa crabro* has been reported to steal and feed on the web prey of the spiders: *Argiope aurantia* (Davis, 2011) and *A. bruennichi* (Helsdingen, 2011).

Interactions of not exact predator-prey relationships such as offence or defence were also reported. Once, a case of killing each other at the same time between *Tegenaria atrica* and *Vl. germanica* was reported (Scott, 1930). A founders of *V. analis* were found to capture and dump a spider approaching her nest (Yamane & Makino, 1977).

Table 5. The Cases of predation on yellowjackets (the genera *Vespula* and *Dolichovespula*) by spiders (Bilsing, 1920).

Predators	Prey	Reference
Ph. audax	*Vl. germanica* *D. arenaria* *D. maculata*	Bilsing, 1920
H. carolinensis *Ar. trifolium* *Ep. gigas* *A. trifasciata*	*D. arenaria*	

Discussion

It is found from the results above that predator-prey relationships between vespine wasps and spiders, and vice versa, have not been studied enough yet quantitatively. Compared with the reported cases of predation on spiders by vespine wasps, there have been fewer cases of predation on vespine wasps by spiders. In spite that predation on spiders by vespine wasps is relatively more common in the observational records characterized within the species and/or the genera level, it may not have been investigated exhaustively in the habitats. The cases of predation on vespine wasps by spiders which could be found are reported by only five references (Bilsing, 1920; Laing, 1973; Hendawy, 2004; Carrel & Deyrup, 2019; Ramírez *et al.*, 2021) excepting for the research articles by one of the authors (Noguchi, 2020; 2021), suggesting that these observations remain very fragmentary with considering their actual interactions in the global ecosystem. As observed by Fordham (1961), predation on vespine wasps by spiders might be prevented by escaping from spider webs using the powerful mouthparts of vespine wasps like mantids did (Sugiura *et al.*, 2019). One possible reason for the records remaining fractional could be supposed that predation on vespine wasps by spiders has not been well documented by wasp's researchers, because they were simply not familiar with spiders, or they overlooked the ecological importance of the predator-prey relationships among them. Besides, it may also be due to the fact that prey of spiders has been difficult to be investigated within the species level.

Otherwise, among the conditions constituting IGP, the cases of "predation on predators by predators" have been found to occur not limited to specific areas at least qualitatively. Spiders have been shown to have different trophic levels among taxa and developmental stages based on the characteristics of $\delta^{15}N$ (Sanders *et al.*, 2015), on the other hand, there may be still a possibility that predation does not occur depending on the levels of species of spiders. It would be possible that asymmetric IGP between spiders and vespine wasps, which differ in relative body sizes each other. And the possibility of symmetric IGP between large-sized spiders and vespine wasps may be suggested by the observations that *V. analis* and *Argiope* spp. feed on each other (Matsuura, 1984; Noguchi, 2020, 2021) and same as *Vl. germanica* and spiders (Tables 1, 3-5). So, "symmetric IGP" may be occurring at least between the hornet *V. analis* and argiopids and the yellowjacket *Vl. germanica* and several spiders. Although symmetric IGP is more common, body-sizes and developmental stages are often important factors (Polis *et al.*, 1989). In fully metamorphosed wasps, body-sizes and developmental stages are not factors in symmetric IGP; for this reason, this may be an unusual case and the frequency of this phenomenon has to be further investigated. Another condition for IGP is "habiting the same place in time and space" (Potter *et al.*, 2018), which spiders and vespine wasps seem to satisfy. But if flying vespine wasps in airborne, ambushing spiders in the web and wandering spiders in the ground are in the same guild, this would be considered a characteristic case.

It will be needed to gather further information on the prey-predatory relationship between vespine wasps and spiders more generally and in detail and be examined whether these relationships are equivalent to IGP. It should be also necessary to study what kind of diet of spiders are for vespine wasps in terms of quantity and quality, and vice versa. From a quantitative point of view, it would be of great importance to conduct a more detailed survey to determine the proportion of each diet items, as in such as Matsuura (1984) and Miyashita & Shinkai (1995). In recent years, DNA analysis of intestinal contents is also performed (e.g., Aebi *et al.*, 2011). For qualitative aspects, it may be required to conduct experiments by limiting the menu of prey items, or to verify ecochemometrics like Matsumura *et al.* (2004). Regrettably, it is not shown in the present

study, it would be also necessary to verify whether food resources are really shared in the same ecosystem between spiders and vespine wasps. Assuming the same ecosystem in Honshu, Japan, the captured prey items overlap well at the order level as the results of Matsuura (1984) and Miyashita & Shinkai (1995). Incidentally, the overlap at the species level is still unclear and should be investigated in more detail.

A total of 67 species of vespine wasps exists in the world (Carpenter & Kojima, 1997). According to the observational cases demonstrated above, predation on spiders by vespine wasps, and vice versa, there are only seven species of hornets of *V. affinis*, *V. analis*, *V. crabro*, *V. mandarinia*, *V. orientalis*, *V. simillima*, *V. velutina*, and eight species of yellowjackets of *Vl. consobrina*, *Vl. flaviceps*, *Vl. germanica*, *Vl. pensylvanica*, *Vl. squamosa*, *Vl. vulgaris*, *D. arenaria*, *D. maculate*. The predator-prey interactions between spiders and the remained 52 species (78%) of vespine wasps have not studied yet. Especially, there are only a few studies reported before about the cases of predation on yellowjackets (Bilsing, 1920; Laing, 1973; Carrel & Deyrup, 2019; Ramírez *et al.*, 2021) and hornets (Hendawy, 2004; Noguchi, 2020; 2021) by spiders having various types of predation; ambushing orb-weavers (Araneidae), jumping spiders (Salticidae), wandering spiders (Ctenidae and Lycosidae) and a tunnel web spider (Mygalomorphae: Porrhothelidae). Over a century, researchers have reported their observations on the prey-predation interaction between vespine wasps and spiders; however, there are only limited scientific articles shown herein to elucidate the whole ecological aspect regarding the symmetric IGP between vespine wasps and spiders. Hence, further research is essential in the future.

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