# Estimate of the daily catch of prey by the wasp spider *Argiope bruennichi* (Scopoli) in the field: Original data and minireview

**Martin Nyffeler**

**ABSTRACT** Contrib. Nat. Hist. 12: 1007–1020.

**Prey capture by the large orb-weaving spider *Argiope bruennichi* (Scopoli) (Araneidae) was investigated in uncut grassland (heavily infested with flowering weeds and shrubs) in the outskirts of Zurich, Switzerland, on three consecutive days in early August (between 09:00 and 18:00 hours). *A. bruennichi* was found to be a predominantly diurnal predator of larger-sized grassland insects (Hymenoptera and Orthoptera composing approx. 90% of the total prey biomass). On average, 38% of the encountered spiders were feeding. It is estimated that adult female *A. bruennichi* captured, on average, approx. 90 mg (fresh weight) prey web$^{-1}$ day$^{-1}$, which is the equivalent of the weight of a worker honey bee. My results were compared with the published estimates of other researchers.**

Keywords: Wasp spider, *Argiope bruennichi*, Araneidae, feeding frequency, prey capture rate, uncut grassland, Zurich, Switzerland.

## Introduction

In recent years, orb-weaving spiders have become popular model systems to address questions in various fields of biology such as evolutionary biology, ecology, ethology, neurobiology, physiology, and even silk and venom chemistry (e.g., Craig 1994; Elgar & al. 2000; Herberstein & al. 2005; Blackledge & Hayashi 2006; Schneider & al. 2005, 2006; Blamires & al. 2007, 2008; Brooks & al. 2008; Foellmer 2008), which makes it necessary to keep/breed these spiders under laboratory conditions (Zschokke & Herberstein 2005). "...Natural prey capture rates may provide helpful starting points when designing feeding regimes in the laboratory..." (Zschokke & Herberstein 2005). Also, natural prey capture rates need to be known in order to evaluate the spiders' potential as biological control agents of insect pests (see Robinson & Robinson 1974; Nyffeler & Benz 1989; Malt 1996a, b). The assessment of the natural prey capture rates is therefore essential from a point of view of basic and applied biological sciences.

A large number of field studies on prey capture of orb-weaving spiders have been published in the past (e.g., Uetz & al. 1978; Horton & Wise 1983; Murakami 1983; Pasquet 1984; Nentwig 1985; Higgins 1987; McReynolds & Polis 1987; Nyffeler & al. 1987; Nyffeler & Benz 1989; Malt 1996a; Ludy 2007). In most of these studies, prey capture was assessed by collecting prey remains from spider webs once per day only. Data obtained in this manner are biased due to the fact that all those prey items that have been discarded by the spiders from the webs prior to the time of web examination are not included in the prey census, resulting in underestimates (see McReynolds & Polis 1987). Discarded carcasses can often be found below the webs (Turnbull 1973; Malt 1996a), unless they have been removed by scavenging ants (Nyffeler unpubl.). In order to get accurate estimates, spider webs should be monitored periodically, at 1–2 hour intervals, all day long. So far few quantitative field studies of this kind exist (e.g., Robinson & Robinson 1970, 1973; Bruce & al. 2004; Ludy 2007). In the following report data on the daily prey capture rate of the orb-weaving spider *Argiope bruennichi* (Scopoli) (Araneidae) in a grassland patch near Zurich, Switzerland, shall be presented.

## Methods

### Study species

*A. bruennichi* is one of Europe's largest and most conspicuous orb-weaver species. The female, characterized by the wasp-like, yellow and black striped colouration of its abdomen (see Bush & al. 2008), has a stenochronous life cycle, reaching adulthood sometime in late July. Females die in October and juveniles hibernate in the egg-sac during winter (Leborgne & Pasquet 2005). The adult female spins nearly vertical (ca 25 cm Ø) orbs, near ground level amongst grass and low herbage (Nyffeler 1982). The webs contain one or two white radial zigzags (stabilimenta), arranged above and below the centre (Prokop & Gryglakova 2005). *A. bruennichi* hangs at the hub head downward waiting for prey to get entangled in the web. Spiders of the genus *Argiope* exhibit a very effective predatory behaviour towards large and dangerous prey (including stinging bees, wasps, and large grasshoppers), disarming them by swiftly wrapping the prey in a shroud of silk thrown from a secure distance and manipulated about the insect by the long hind legs of the spider, followed by a venomous bite (see Eisner & Dean 1976; Olive 1980; Foelix, 1996). Owing to this attack behaviour large prey with a length up to 200% the spiders' body length can be overcome (Nyffeler & al. 1987). *A. bruennichi* has been reported to occur at densities of 0.3–1.0 adult female per $m^2$ (Nyffeler 1982; Szymkowiak & al. 2005; Taraschewski & al. 2005). Local mass occurrences (with densities of >1.0–6.0 adult females per $m^2$), usually followed by a population breakdown in the year thereafter have been reported from time to time (e. g., Malt 1996a; Nyffeler 2000). This species, which disperses mainly by ballooning, continously expanded its geographic range in Europe during the last decades and is found today as far north as Scandinavia (Scharff & Langemark 1997; Jonsson & Wilander 1999; Szymkowiak & al. 2005; Walter & al. 2005; Hickling & al. 2006; Koponen & Fritzen 2007).

## Study site

The studies were conducted on a 0.02 ha plot of uncut grassland located in Zurich-Höngg, Switzerland. At the time of this investigation, the land was heavily infested with flowering weeds (mainly thistle *Cirsium arvense*) and shrubs (blackberry *Rubus* sp.). The study area is located in the transition zone between the Western European oceanic climate and the Eastern European continental climate. Zurich (47.2° northern latitude) has a mean annual temperature of 8.8° C and an annual variation of 17.8°C. In the year of investigation, the mean temperature for the month of August measured by the Weather Station Zurich (Swiss Meteorological Institute) was 15.7°C.

## Sampling technique

*A. bruennichi* is a predominantly diurnal forager which spins its web early in the morning and captures mostly diurnal insects (Pasquet 1984; Baba & Miyashita 2006; Prokop 2006). This spider rebuilds its web daily (Baba & Miyashita 2006). It can be seen feeding at the hub all day long, the maximum activity occurring between 12.00 and 16.00 hours (Tab. 1). After sundown, a certain percentage of the spider population may continue feeding on prey caught earlier. The webs of adult females were monitored periodically, at 1–2 hour intervals, between 09:00 and 18:00 hours, on three consecutive days in early August (covering a period of 27 hours observation time). The number of

| Time of the day | % feeding spiders<br>Mean ± SE |
|---|---|
| 09.00 | 22.2 ± 9.6 |
| 12.00 | 42.6 ± 6.0 |
| 14.00 | 42.0 ± 9.1 |
| 16.00 | 44.6 ± 7.7 |
| 18.00 | 38.5 ± 11.1 |
| Overall mean ± SE | 38.0 ± 4.1 |

**Tab. 1. Feeding frequency (= number of spiders feeding x 100%/number of spiders encountered) of adult female *Argiope bruennichi* feeding at various times of the day in a grassland habitat near Zurich (mean ± SE, three consecutive days in early August).**

examined webs on the different days varied between 10 and 17, depending on availability of undamaged webs. Basically the approach of Robinson & Robinson (1970) was used in this study. According to these authors checking the webs at two-hour intervals is sufficient since all but the smallest prey organisms are fed upon by *Argiope* for more than two hours. During each examination the prey items found in webs were classified (according to taxon and size), counted, and recorded. To be able to convert the number of captured insects to the weight of prey caught per web per day, the average weights of grassland insects need to be known. Insect weights were estimated based on information from the literature (mostly Malt 1996a). In the genus *Argiope* the adult males are dwarfs compared to the adult females (Hormiga & al. 2000; Bush & al. 2008). These dwarf males contribute little to the population energy budget (Becker 1982; Howell & Ellender 1984; Foellmer & Fairbairn 2005; Herberstein & al. 2005) and were therefore neglected in this study.

## Results and Discussion

### Feeding frequency

On average, 38% of *Argiope bruennichi* females encountered during the daylight hours were feeding (overall mean of three days from 09:00–18:00 hours, Tab. 1). This is a fairly high level of feeding activity compared to the values obtained in other orb-weaving spider studies (overall mean for larger-sized orb-weavers: 25.9 ± 6.4%, and for smaller-sized orb-weavers: 7.3 ± 3.2%) (Tab. 2). Also, the feeding frequency of *A. bruennichi* is much higher than that reported for members of non-orb-weaving spider families which are usually

| Spider species | % feeding spiders | Authors |
|---|---|---|
| **Larger-sized orb-weavers:** | | |
| *Argiope bruennichi* | 38.0 [a] | This paper |
| *Aculepeira ceropegia* | 27.7 [a] | Nyffeler (1982) |
| *Araneus diadematus* | 27.8 [a] | Nyffeler (1982) |
| *Larinioides cornutus* | 54.7 [a] | Nyffeler (1982) |
| *Neoscona arabesca* | 17.5 [a] | Culin & Yeargan (1982) |
| *Nephila clavata* | 6.6 | Miyashita (2005) |
| *Nephila maculata* | 9.3 | Miyashita (2005) |
| Overall mean ± SE | 25.9 ± 6.4 | – |
| **Smaller-sized orb-weavers:** | | |
| *Araniella cucurbitina* | 20.7 [a] | Nyffeler (1982) |
| *Cyclosa turbinata* | 1.4 | Nyffeler et al. (1994) |
| *Gea heptagon* | 7.0 | Nyffeler et al. (1994) |
| *Tetragnatha laboriosa* | 1.1 | Culin & Yeargan (1982) |
| *Tetragnatha laboriosa* | 12.0 | LeSar & Unzicker (1978) |
| *Tetragnatha laboriosa* | 1.5 | Nyffeler et al. (1994) |
| Overall mean ± SE | 7.3 ± 3.2 | – |

[a] Mean value for surveys at different times of the day.

**Tab. 2. Feeding frequency (= no. spiders feeding x 100%/no. spiders encountered) of various species of orb-weaving spiders in the field (based on literature data).**

<10% (see reviews by Nyffeler & Breene 1990; Nyffeler & al. 1994; Nyffeler & Sunderland 2003). Evidently, the large orb-webs of *A. bruennichi* function as very effective insect traps (i. e. high foraging success).

## Taxonomic composition of the catch

The overall composition of *A. bruennichi*'s diet observed in this study (Tab. 3) parallels that found by other workers, although diet may vary in detail (see Becker 1982; Pasquet 1984; Malt 1996a; Prokop 2006). Large-sized Hymenoptera and Orthoptera made up the bulk of the spider catch (approx. 90% of total prey biomass)(Tab. 3). Such a predominantly insectivorous foraging pattern is typical for the vast majority of orb-weaving spider species (see Nyffeler 1999), though there are some exceptions (Nyffeler & Symondson 2001). Members of the genus *Argiope* are very cannibalistic and regularly terminate copulations by aggressively attacking the male (Sasaki & Iwahashi 1995; Herberstein & al. 2005; Schneider & al. 2005, 2006). Experiments by Fromhage & al. (2003), however, have shown that the additional food intake due to sexual cannibalism did not significantly increase the fitness of adult female *A. bruennichi*: neither the number of clutches, nor clutch size or hatching success were affected by consumption of males. Araneae composed an insignificant percentage of the total prey biomass of *A. bruennichi* in this study (Tab. 3) and in other studies (Becker 1982; Nentwig 1985; Malt 1996a; Szymkowiak & al. 2005; Ludy 2007).

## Daily catch of prey

The rate of predation upon larger-sized prey (>3 mm in length) on three consecutive days is presented in Tab. 3. The table shows that, on average, 1.09 larger-sized prey web$^{-1}$ day$^{-1}$ was captured. This value is an underestimate due to the fact that only larger-sized insects have been recorded in Tab. 3. Appart from larger-sized prey, some tiny insects (dipterans, aphids and thrips of 1–3 mm lenth), each weighing 1–2 mg, are regularly entangled in the webs. Large orb-weaving spiders tend to ignore such tiny insects as food (which is in agreement with foraging theory) and many researchers came to the conclusion that exclusively the larger-sized insects trapped in the webs should be considered to be prey (e.g., Robinson & Robinson 1970, 1973; Uetz & al. 1978; Murakami 1983). [Some of the tiny insects ignored by the adult female orb-weavers are removed (eaten) by conspecific males that enter female webs during the reproductive periode (Becker 1982; Bradley 1993) and/or by theridiid kleptoparasites that habitually invade large orb-webs in the more southern areas of the globe (e.g., Vollrath 1979; Higgins 1987; Grostal & Walter 1997; Kerr 2005).] According to Nentwig (1985, 1987) the tiny insects belong to the spiders' diet, too. He stated that the tiny insects caught in orb-webs are often too weak to free themselves; they die undetected and remain attached to the web. Orb-weaving spiders such as *A. bruennichi* which rebuild their web daily and eat the old silk in order to recycle the web proteins, also eat these attached small insects (Peakall 1971; Nentwig 1987; Malt 1996a). Though tiny insects were not recorded in my prey census (see above), the capture rate of prey of all sizes can be estimated based on Tab. 3, if the average ratio of the numbers of large-sized to small-sized prey caught in the webs is known. The average ratio of the number of larger-sized to small-sized prey caught by the webs of adult female *A. bruennichi* was approx. 20% : 80% (based on a series of prey collections with a total of >900 prey items), suggesting that the total capture rate (including tiny prey) may have been 5 x 1.01 prey web$^{-1}$ day$^{-1}$ = approx. 5 prey web$^{-1}$ day$^{-1}$. In a most recent German field study, Ludy (2007) monitored adult female *A. bruennichi* webs continuously

| Prey type | Number of prey caught web$^{-1}$ day$^{-1}$ | Weight per prey item (in mg) | Weight of prey caught web$^{-1}$ day$^{-1}$ (in mg) |
|---|---|---|---|
| Apidae | 0.61 ± 0.13 | 100 | 61.3 ± 13.5 |
| Orthoptera | 0.10 ± 0.10 | 145 | 14.5 ± 14.5 |
| Syrphidae | 0.05 ± 0.02 | 10 | 0.5 ± 0.2 |
| Araneae | 0.03 ± 0.03 | 20 | 0.7 ± 0.7 |
| Homoptera | 0.03 ± 0.03 | 4 | 0.1 ± 0.1 |
| Heteroptera | 0.02 ± 0.02 | 15 | 0.3 ± 0.3 |
| Coleoptera | 0.02 ± 0.02 | 10 | 0.2 ± 0.2 |
| Lepidoptera | 0.02 ± 0.02 | 45 | 0.9 ± 0.9 |
| Unidentified | 0.21 ± 0.11 | 10 | 2.1 ± 1.2 |
| Total | 1.09 ± 0.29 | | 80.6 ± 26.2 |

**Tab. 3. Estimate of the average daily catch of larger-sized prey (fresh weight web$^{-1}$ day$^{-1}$) of *Argiope bruennichi* near Zurich (overall mean ± SE, of three consecutive days in early August).**

from 11:00 to 18:00 hours on three days in August, resulting in an overall mean capture rate of 4.87 ± 4.63 prey web$^{-1}$ day$^{-1}$ which is very similar to my own estimate. My estimate and that of Ludy (2007) fall within the range of published estimates for *A. bruennichi* and other *Argiope* species (Tab. 4).

The daily catch of prey (in terms of numbers) has been converted to prey biomass caught web$^{-1}$ day$^{-1}$ (Tab. 3). This yielded an estimated average catch of prey of approx. 80 mg fresh weight web$^{-1}$ day$^{-1}$, considering the larger-sized prey (Tab. 3). Though tiny insects were not recorded in Tab. 3, it is known from other investigations that tiny insects compose, on average, roughly 10% of the total prey biomass of *A. bruennichi* (Nyffeler 1982; Malt 1996a) and of other *Argiope* spiders (Nentwig 1985; Bradley 1993). Taking this into consideration, the weight of prey of all sizes captured by *A. bruennichi* in my study in early August can be estimated at approx. 90 mg web$^{-1}$ day$^{-1}$, which is the equivalent of the weight of a worker honey bee. This estimate relates to adult females only, occurring in August and September, that spin strong, large webs. Of course the prey capture rate is a seasonally changing variable; the immature stages of *A. bruennichi*, occurring between May and mid-July, make smaller webs and capture less food (Malt 1996a; Nyffeler unpubl.).

## Daily catch of prey of *A. bruennichi* compared to other orb-weavers

My estimate of the daily catch of approx. 90 mg prey web$^{-1}$ day$^{-1}$ for *A. bruennichi* is comparable to that of Robinson & Robinson (1970) for the tropical orb-weaver *Argiope argentata* in Panama. These authors estimated that an adult female *A. argentata* caught, on average, 1.63 larger-sized prey web$^{-1}$ day$^{-1}$ which translates to 89 mg (fresh weight) prey web$^{-1}$ day$^{-1}$ (overall mean of a one year census). Robinson & Robinson (1970) may have overlooked some of the smallest insects in their prey census, as they themselves admit. But it is known from other field work in Panama that tiny insects comprise, on average, roughly 10% of the total prey biomass of *A. argentata* (Nentwig 1985). Taking this into account it can be estimated that the average catch of prey biomass of adult female *A. argentata* in Robinson & Robinson's study may have been approx. 100 mg web$^{-1}$ day$^{-1}$, if tiny prey were included.

It can be estimated that the average daily prey catch of 90–100 mg by an adult female *Argiope* equals approx. 20% of the spider's body weight, assuming a spider weight of 400–500 mg (see data on spider weights by Robinson & Robinson 1970; Carrel & Heathcote 1976; Friedel & Nentwig 1989). Kajak (1971), wo surveyed 950 webs in Polish grasslands over a two year period, found that the average daily prey catch of web-building spiders equalled approx. 18% of the spider's body weight. From a prey catch of 90–100 mg web$^{-1}$ day$^{-1}$ an *Argiope* can ingest at least 45–50 mg food spider$^{-1}$ day$^{-1}$, the spiders' energy requirements thereby being fully met, evidenced by high reproductive success (compare Robinson & Robinson 1970; Bradley 1993; Leborgne & Pasquet 2005; Nyffeler unpubl.). A food ingestion rate of 45–50 mg spider$^{-1}$ day$^{-1}$ equals approx. 10% of the spider's body weight which is within the range of energy requirement estimates known for other spider taxa (see Foelix 1996).

The similarity of the daily catch of prey of *A. bruennichi* (this study) and *A. argentata* (study by Robinson & Robinson 1970) obviously reflects the fact that these are two similar-sized orb-weavers (see Hormiga & al. 2000) with similar energy requirements. In several studies it was found that the average prey capture rate of orb-weavers of similar size did not differ significantly if different locations were compared (e.g., Higgins 1987; McNett & Rypstra 1997). This was demonstrated beautifully by Higgins (1987) who compared prey capture of the orb-weaver *Nephila clavipes* in two different habitat types in Texas. Spiders at the two locations differed significantly in the types of prey captured and the contribution of each prey type to the total prey biomass. Despite these differences, the number of prey and the estimated weight of prey captured by the spiders was not different between the two locations

| Spider species | Estimated mean number of prey web$^{-1}$ day$^{-1}$ | Evaluation methode* | Authors |
|---|---|---|---|
| *Argiope bruennichi* | 5 | ADL | This paper |
| *Argiope bruennichi* | 4.9 | ADL | Ludy (2007) |
| *Argiope bruennichi* | 4.3 | OPD | Pasquet (1984) |
| *Argiope bruennichi* | 5.9-6.5 | OPD | Malt (1996a) |
| *Argiope savignyi* | 3.0 | OPD | Nentwig (1985) |
| *Argiope argentata* | 4.2 | OPD | Nentwig (1985) |
| *Argiope argentata* | 1.6** | ADL | Robinson & Robinson (1970) |
| Overall mean ± SE | 4.2 ± 0.6 | | |

* ADL = web examinations all day long
OPD = web examination once per day
** Tiny insects not included in prey census

**Tab. 4. Estimates of prey capture rates for adult female *Argiope* spiders (literature data).**

(Higgins 1987). Hoffmaster (1985) compared orb-weaver guilds (including *Argiope* spiders as prominent guild members) of Texas and Panama grasslands. She found that the orb-weavers in the two areas exhibited very similar foraging patterns, supporting the idea that resources were equally utilized in each area.

The availability of various types of potential prey may differ from year to year (Horton & Wise 1983) and from location to location (Brown 1981; Nyffeler 1982; Higgins 1987; Szymkowiak & al. 2005). But orb-weaving spiders apparently can adjust food consumption to their requirements to a certain degree by altering the size of their web and the frequency of rebuilding it, and/or moving to more profitable web sites (see Witt & al. 1968; Sherman 1994; McNett & Rypstra 1997; Nakata & Ushimaru 1999; Chmiel & al. 2000; Miyashita 2005).

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## References


Baba, Y. & Miyashita, T. (2006): Does individual internal state affect the presence of a barrier web in *Argiope bruennichi* (Araneae: Araneidae)? — Journal of Ethology 24: 75–78.

Becker, H. (1982): Untersuchungen zur Biologie der Wespenspinne (*Argiope bruennichi* Scopoli)(Araneae: Araneidae). — 150 pp., Dissertation, Universität Erlangen-Nürnberg.

Blackledge, T.A. & Hayashi, C.Y. (2006): Silken toolkits: biomechanics of silk fibres spun by the orb web spider *Argiope argentata* (Fabricius). — Journal of Experimental Biology 209: 2452–2461.

Blamires, S.J., Thompson, M.B. & Hochuli, D.F. (2007): Habitat selection and web plasticity by the orb spider *Argiope keyserlingi* (Argiopidae): Do they compromise foraging success for predator avoidance? — Austral Ecology 32: 551–563.

Blamires, S.J., Hochuli, D.F. & Thompson, M.B. (2008): Why cross the web: decoration spectral properties and prey capture in an an orb spider (*Argiope keyserlingi*) web. — Biological Journal of the Linnean Society 94: 221–229.

Bradley, R.A. (1993): The influence of prey availability and habitat on activity patterns and abundance of *Argiope keyserlingi* (Araneae: Araneidae). — Journal of Arachnology 21: 91–106.

Brook, A.E., Stricker, S.M., Joshi, S.B., Kamerzell, T.J., Middaugh, C.R. & Lewis, R.V. (2008): Properties of synthetic spider silk fibers based on *Argiope aurantia* MaSp2. — Biomacromolecules 9: 1506–1510.

Brown, K.M. (1981): Foraging ecology and niche partitioning in orb-weaving spiders. — Oecologia 50: 380–385.

Bruce, M.J., Heiling, A.M. & Herberstein, M.E. (2004): Web decorations and foraging success in *'Araneus eburnus'* (Araneae: Araneidae). — Annales Zoologici Fennici 41: 563–575.

Bush, A.A., Yu, D.W. & Herberstein, M.E. (2008): Function of bright coloration in the wasp spider *Argiope bruennichi* (Araneae: Araneidae). — Proceedings of the Royal Society B-Biological Sciences 275: 1337–1342.

Carrel, J.E. & Heathcote, R.D. (1976): Heart rate in spiders: influence of body size and foraging energetics. — Science 193: 148–150.

Chmiel, K., Herberstein, M.E. & Elgar, M.A. (2000): Web damage and feeding experience influence web site tenacity in the orb-web spider *Argiope keyserlingi* Karsch. — Animal Behaviour 60: 821–826.

Craig, C.L. (1994): Predator foraging behavior in response to perception and learning by its prey - Interactions between orb-spinning spiders and stingless bees. — Behavioral Ecology and Sociobiology 35: 45–52.

Culin, J. D. & Yeargan, K. V. (1982): Feeding behavior and prey of *Neoscona arabesca* (Araneae: Araneidae) and *Tetragnatha laboriosa* (Araneae: Tetragnathidae) in soybean fields. — Entomophaga 27: 417–424.

Eisner, T. & Dean, J. (1976): Ploy and counterploy in predator-prey interactions: orb-weaving spiders versus bombardier beetles. — Proceedings of the National Academy of Sciences 73: 1365–1367.

Elgar, M.A., Schneider, J.M. & Herberstein, M.E. (2000): Female control of paternity in the sexually cannibalistic spider *Argiope keyserlingi*. — Proceedings of the Royal Society of London, Series B-Biological Sciences 267: 2439–2443.

Foelix, R. F. (1996): Biology of spiders (2nd edn.). — 330 pp., Oxford University Press, New York.

Foellmer, M.W. (2008): Broken genitals function as mating plugs and affect sex ratios in the orb-web spider *Argiope aurantia*. — Evolutionary Ecology Research 10: 449–462.

Foellmer, M.W. & Fairbairn, D.J. (2005): Selection on male size, leg length and condition during mate search in a sexually highly dimorphic orb-weaving spider. — Oecologia 142: 653–662.

Friedel, T. & Nentwig, W. (1989): Immobilizing and lethal effects of spider venoms on the cockroach and the common mealbeetle. — Toxicon 27: 305–316.

Fromhage, L., Uhl, G. & Schneider, J.M. (2003): Fitness consequences of sexual cannibalism in female *Argiope bruennichi*. — Behavioral Ecology & Sociobiology 55: 60–64.

Grostal, P. & Walter, D.E. (1997): Kleptoparasites or commensals? Effects of *Argyrodes antipodianus* (Araneae: Theridiidae) on *Nephila plumipes* (Araneae: Tetragnathidae). — Oecologia 111: 570–574.

Herberstein, M.E., Gaskett, A.C., Schneider, J.M., Vella, N.G.F. & Elgar, M.A. (2005): Limits to male copulation frequency: Sexual cannibalism and sterility in St Andrew's Cross spiders (Araneae, Araneidae). — Ethology 111: 1050–1061.

Hickling, R., Roy, D.B., Fox, R. & Thomas, C.D. (2006): The distributions of a wide range of taxonomic groups are expanding polewards. — Global Change Biology 12: 1–6.

Higgins, L.E. (1987): Time budget and prey of *Nephila clavipes* (Linnaeus) (Araneae. Araneidae) in southern Texas. — Journal of Arachnology 15: 401–417.

Hoffmaster, D.K. (1985): Resource breadth in orb-weaving spiders: A tropical-temperate comparison. — Ecology 66: 626–629.

Hormiga, G., Scharff, N. & Coddington, J.A. (2000): The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). — Systematic Biology 49: 435–462.

Horton, C.C. & Wise, D.H. (1983): The experimental analysis of competition between two syntopic species of orb-web spiders (Araneae: Araneidae). — Ecology 64: 929–944.

Howell, F.G. & Ellender, R.D. (1984): Observations on growth and diet of *Argiope aurantia* Lucas (Araneidae) in a successional habitat. — Journal of Arachnology 12: 29–36.

Jonsson, L.J. & Wilander, P. (1999): Is the wasplike spider, *Argiope bruennichi*, established in Sweden? — Entomologisk Tidskrift 120: 17–21.

Kajak, A. (1971): Productivity investigation of two types of meadows in the Vistula Valley. IX. Production and consumption of field layer spiders. — Ekologia Polska 19: 197–211.

Kerr, A.M. (2005): Behavior of web-invading spiders *Argyrodes argentatus* (Theridiidae) in *Argiope appensa* (Araneidae) host webs in Guam. — Journal of Arachnology 33: 1–6.

Koponen, S. & Fritzen, N.R. (2007): Two orb-weavers new to Finland – *Argiope bruennichi* and *Neoscona adianta* (Araneae, Araneidae). — Memoranda Societatis pro Fauna et Flora Fennici 83: 20–21.

Leborgne, R. & Pasquet, A. (2005): Time of oviposition and reproductive success in *Argiope bruennichi* (Araneae: Araneidae). — European Journal of Entomology 102: 169–174.

LeSar, C. D. & Unzicker, J. D. (1978): Life history, habits, and prey preferences of *Tetragnatha laboriosa* (Araneae: Tetragnathidae). — Environmental Entomology 7: 879–884.

Ludy, C. (2007): Prey selection of orb-web spiders (Araneidae) on field margins. — Agriculture, Ecosystems and Environment 119: 368–372.

Malt, S. (1996a): Untersuchungen zur Rolle ausgewählter netzbauender Spinnen (Araneida) im trophischen Beziehungsgefüge von Halbtrockenrasen. — 134 pp., Dissertation, Universität Jena.

Malt, S. (1996b): Untersuchungen zur Rolle ausgewählter netzbauender Spinnen (Araneae) im trophischen Beziehungsgefüge von Halbtrockenrasen. — Arachnologische Mitteilungen 12: 70–74.

McNett, B.J. & Rypstra, A.L. (1997): Effects of prey supplementation on survival and web site tenacity of *Argiope trifasciata* (Araneae, Araneidae): a field experiment. — Journal of Arachnology 25: 352–360.

McReynolds, C.N. & Polis, G.A. (1987): Ecomorphological factors influecing prey use by two sympatric species of orb-web spiders, *Argiope aurantia* and *Argiope trifasciata* (Araneidae). — Journal of Arachnology 15: 371–383.

Miyashita, T. (2005): Contrasting patch residence strategy in two species of sit-and-wait foragers under the same environment: A constraint by life history? — Ethology 111: 159–167.

Murakami, Y. (1983): Factors determining the prey size of the orb-web spider, *Argiope amoena* (L. Koch)(Argiopidae). — Oecologia 57: 72–77.

Nakata, K. & Ushimaru, A. (1999): Feeding experience affects web relocation and investment in web threads in an orb-web spider, *Cyclosa argenteoalba*. — Animal Behaviour 57: 1251–1255.

Nentwig, W. (1985): Prey analysis of four species of tropical orb-weaving spiders (Araneae: Araneidae) and a comparison with araneids of the temperate zone. — Oecologia 66: 580–594.

Nentwig, W. (1987): The prey of spiders. — In: Nentwig, W. (ed.), Ecophysiology of spiders, pp. 249–263, Springer-Verlag, Berlin, New York.

Nyffeler, M. (1982): Field studies on the ecological role of the spiders as predators of insects in agroecosystems. — 174 pp., Ph. D. Dissertation. Swiss Federal Institute of Technology (ETH), Zurich.

Nyffeler, M. (1999): Prey selection of spiders in the field. — Journal of Arachnology 27: 317–324.

Nyffeler, M. (2000): Killing power of the orb-weaving spider *Argiope bruennichi* (Scopoli, 1772) during a mass occurrence. — Newsletter of the British arachnological Society 89: 11–12.

Nyffeler, M. & Benz, G. (1989): Foraging ecology and predatory importance of a guild of orb-weaving spiders in a grassland habitat. — Journal of Applied Entomology 107: 166–184.

Nyffeler, M. & Breene, R.G. (1990): Evidence of low daily food consumption by wolf spiders in meadowland and comparison with other cursorial hunters. — Journal of Applied Entomology 110: 73–81.

Nyffeler, M. & Sunderland, K.D. (2003): Composition, abundance and pest control potential of spider communities in agroecosystems: a comparison of European and U.S. studies. — Agriculture, Ecosystems & Environment 95: 579–612.

Nyffeler, M. & Symondson, W.O.C. (2001): Spiders and harvestmen as gastropod predators. — Ecological Entomology 26: 617–628.

Nyffeler, M., Dean, D.A. & Sterling, W.L. (1987): Feeding ecology of the orb-weaving spider *Argiope aurantia* (Araneae: Araneidae), in a cotton agroecosystem. — Entomophaga 32: 367–375.

Nyffeler, M., Sterling, W. L. & Dean, D. A. (1994): Insectivorous activities of spiders in United States field crops. — Journal of Applied Entomology 118: 113–128.

Olive, C.W. (1980): Foraging specialization in orb-weaving spiders. — Ecology 61: 1133–1144.

Pasquet, A. (1984): Prey and predatory strategies of two orb-weaving spiders: *Argiope bruennichi* and *Araneus marmoreus*. — Entomologia Experimentalis et Applicata 36: 177–184.

Peakall, D.B. (1971): Conservation of web proteins in the spider *Araneus diadematus*. — Journal of Experimental Zoology 176: 257–264.

Prokop, P. (2006): Prey type does not determine web design in two orb-weaving spiders. — Zoological Studies 45: 124–131.

Prokop, P. & Gryglakova, D. (2005): Factors affecting the foraging success of the wasp-like spider *Argiope bruennichi* (Araneae): Role of web design. — Biologia 60: 165–169.

Robinson, M.H. & Robinson, B. (1970): Prey caught by a sample population of the spider *Argiope argentata* (Araneae: Araneidae) in Panama: a year's census data. — Zoological Journal of the Linnean Society 49: 345–358.

Robinson, M.H. & Robinson, B. (1973): Ecology and behaviour of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. — Smithsonian Contributions to Zoology 149: 1–76.

Robinson, M.H. & Robinson, B. (1974): A census of web-building spiders in a coffee plantation at Wau, New Guinea, and an assessment of their insecticidal effect. — Tropical Ecology 15: 95–107.

Sasaki, T. & Iwahashi, O. (1995): Sexual cannibalism in an orb-weaving spider *Argiope aemula*. — Animal Behaviour 49: 1119–1121.

Scharff, N. & Langemark, S. (1997): Hvepseedderkoppen, *Argiope bruennichi* (Scopoli), i Danmark (Araneae; Araneidae). — Entomologiske Meddelser 65: 179–182.

Schneider, J.M., Fromhage, L. & Uhl, G. (2005): Extremely short copulations do not affect hatching success in *Argiope bruennichi* (Araneae, Araneidae). — Journal of Arachnology 33: 663–669.

Schneider, J.M., Gilberg, S., Fromhage, L. & Uhl, G. (2006): Sexual conflict over copulation duration in a cannibalistic spider. — Animal Behaviour 71: 781–788.

Sherman, P.M. (1994): The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. — Animal Behaviour 48: 19–34.

Szymkowiak, P., Tryjanowski, P., Winiecki, A., Grobelny, S. & Szymon, K. (2005): Habitat differences in the food composition of the wasp-like spider *Argiope bruennichi* (Scop.) (Aranei: Araneidae) in Poland. — Belgian Journal of Zoology 135: 33–37.

Taraschewski, C., Sanders, D., Nickel, H. & Platner, C. (2005): Effects of the wasp-spider, *Argiope bruennichi*, on planthoppers and leafhoppers. — Beiträge zur Zikadenkunde 8: 49–58.

Turnbull, A. L. (1973): Ecology of the true spiders (Araneomorphae). — Annual Review of Entomology 18: 305–348.

Uetz, G.W., Johnson, A.D. & Schemske, D.W. (1978): Web placement, web structure, and prey capture in orb-weaving spiders. — Bulletin of the British arachnological Society 4: 141–148.

Vollrath, F. (1979): Vibrations: Their signal function for a spider kleptoparasite. — Science 205: 1149–1151.

Walter, A., Bliss, P. & Moritz, R.F.A. (2005): The wasp spider *Argiope bruennichi* (Arachnida, Araneidae): Ballooning is not an obligate life history phase. — Journal of Arachnology 33: 516–522.

Witt, P. N., Reed, C. F. & Peakall, D. B. (1968): A spider's web. — 107 pp., Springer-Verlag, New York.

Zschokke, S. & Herberstein, M.E. (2005): Laboratory methods for maintaining and studying web-building spiders. — Journal of Arachnology 33: 205–213.

## Address of the author:

PD Dr. Martin Nyffeler
Section Conservation Biology (NLU)
Department of Environmental Sciences
University of Basel
St. Johanns-Vorstadt 10
CH–4056 Basel, Switzerland