Feeding biology of spiders

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Arachnida

- Most groups of Arachnida are mostly true predators
- Opilionida
  - Many are omnivores consuming plants and fungi
  - Some are scavengers (dead plant and animal material, faeces)
- Schizomida documented to consume cyanobacteria
- Acari evolved wide variety of foraging strategies

Foraging strategies of Acari

- Predators
  - Gamasida
  - Biocontrol agents
- Herbivores
  - Tetranychoidea
  - Pests
- Decomposers and fungivores
  - Oribatida
- Parasites
  - Ixodida, Acaridida, Gamasida

Spiders

- Most abundant and diverse group of terrestrial true predators
- Global spider community consumes 400-800M tons of prey annually
- Spiders affect ecosystem functioning including nutrient and biogeochemical cycling
- Important for biological control of pests in agroecosystems and improve crop performance

Coddington & Levi 1991 Annu Rev Ecol Evol Syst; Schmitz 2010 Resolving Ecosystem Complexity; Nyffeler & Birkhofer 2018 Sci Nat; Michalko et al. 2019 Glob Ecol Biogeogr

Prey of spiders


Cukier 2020 Peckhamia

- Spiders capture wide variety of prey taxa
- Spiders catch mostly invertebrates
  - Mainly insects from the groups Diptera, Hemiptera, Hymenoptera, and Coleoptera
  - Sometimes earthworms and Crustacea and Isopoda (woodlice)
- Predation on vertebrates is rare in comparison to invertebrates
  - Fish, amphibians, reptiles, birds, bats, rodents
- Spiders catch mostly living moving prey
- Oophagy
- Rarely scavenging

Sandage 2003 Nature; Rezac at al. 2008 J Zool; Nyffeler & Pusey 2014, PloS One; Michalko & Pekar 2016 Oecologia; Roubinet et al. 2017 Ecol Appl; Cukier 2020 Peckhamia; Nyffeler & Altig 2020 J Arachnol; Nyffeler & Gibbons 2021 J Arachnol;

Herbivory in spiders

- Probably more frequent than previously thought but only as a supplementary food
- Pollen intercepted in spider webs or nectar feeding in cursorial spiders
- Nectar and pollen actively taken by cursorial spiders
- Consumption of pollen and nectar sometimes increase fitness sometimes no effect
- *Bagheera kiplingi* (Salticidae) mostly herbivorous – Beltian food bodies (leaf ends of acacia)

Sanders 2013: Herbivory in spiders. In Ecophysiology of Spiders

Diet breadth of spiders

- Most spider species are generalist utilizing variety of prey taxa
- Whole gradient of niche widths: eury-, oligo-,steno-, monophagy
- Monophagy is very rare
    - *Ammoxenus amphalodes* prey only on one termite species *Hodotermes mossambicus*

Pekar et al. 2012 Evolution; Pekar et al. 2015 Sci Rep



Diet breadth of spiders

Type of specialisations

- Myrmecophagy (50%; e.g. *Zodarion, Euryopis*)
- Araneophagy (18%; e.g., *Portia*, *Ero*, *Palpimanus*)
- Lepidopterophagy (14%, *Mastophora, Scoloderus*)
- Termitophagy (10%; *Ammoxenus*, *Janula*)
- Dipterophagy (7%, juvenile Mastophora)
- Crustaceophagy (3%; e.g., *Dysdera*)

Pekar et al. 2012 Evolution

Diet breadth of spiders

Local specialisation

- Local populations of a generalist species specialise on locally abundant prey

- Portuguese populations of *Oecobius navus* specialize on dipterans while Uruguayans on ants

Liznarova et al. 2013 Zoology

Diet breadth of spiders

Facultative specialisation

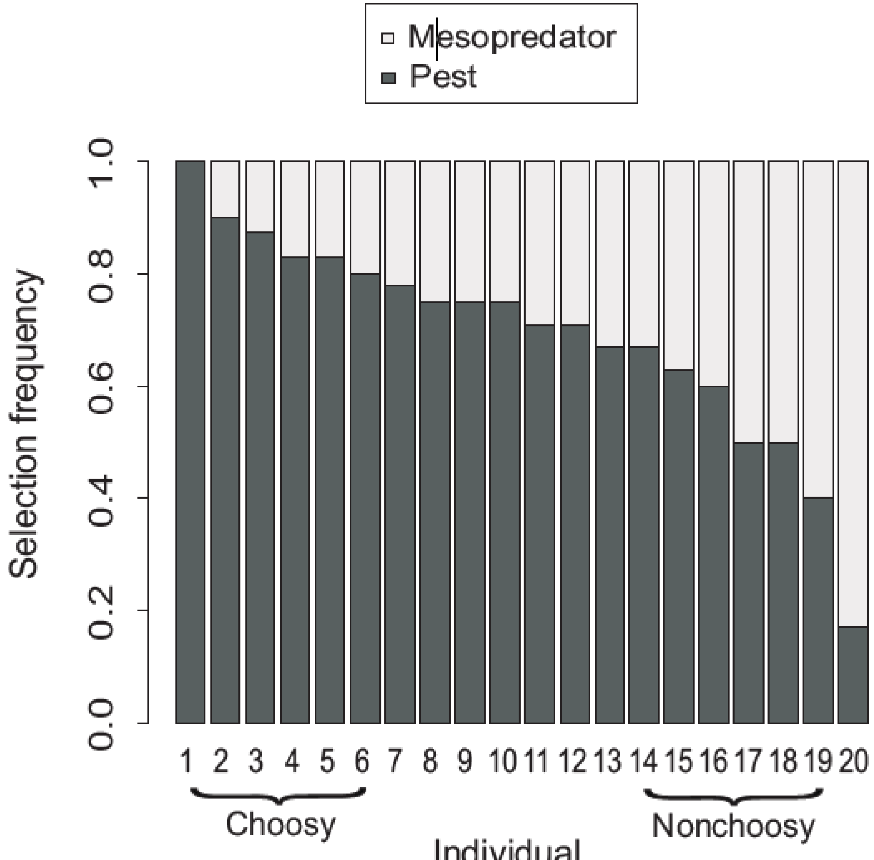
- Spiders have narrow niche because of low diversity of available prey
- *Plexippus paykuli* preyed exclusively on cockroaches that were the only available prey

Nyffeler et al. 1990 Peckhamia

Diet breadth of spiders

Individual specialisation

- Population is generalised but (some) individuals are specialists
- Some individuals of *Philodromus* sp. prey on psylla and spiders other individuals only on psylla

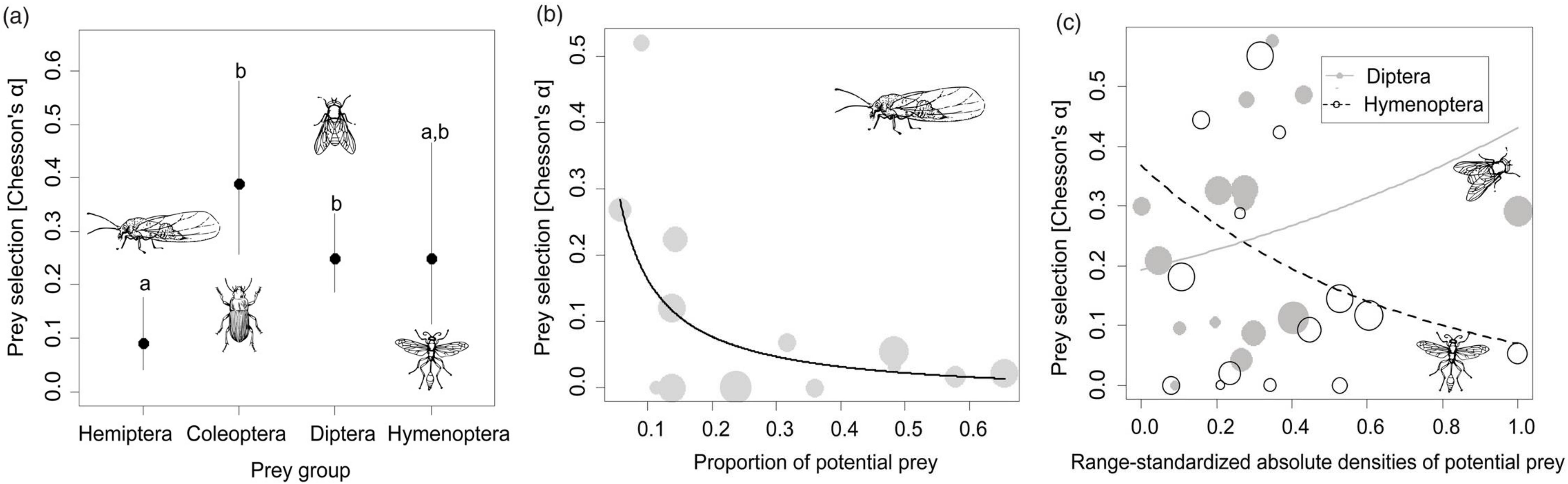


Michalko & Pekar 2017 Am Nat

Prey selection by spiders

Gasteracantha hasselti

- The composition of spider diets is disproportional to composition of available prey community
- Prey selection has constant and dynamic components



Michalko et al. 2020 J Trop Ecol

Prey selection by spiders

- Interaction between passive and active prey selection that are based on internal (connected to the spiders) and external factors (i.e. not connected to the spider)

	Passive selection	Active selection
Internal factors	Hunting strategy, body size, morphological adaptations, life stage, personality etc.	Decision based acceptance or avoidance Preference, aversion, negative and positive switching
External factors	Prey availability, body size, dangerousness, defensiveness, presence of enemies, interaction between prey, etc.	

Hunting strategies of spiders

- Hunting strategy is one of the primary filters degerming prey selection
- Generalist spiders with different hunting strategies capture mostly similar prey types but in different proportions
- Various classifications of hunting strategies that differ in criteria and details
- The main distinction is web building spiders vs. cursorial spiders
- Web-building spiders capture proportionally more mobile prey than cursorial spiders
- Cursorial spiders capture proportionally more other spiders than web-builders

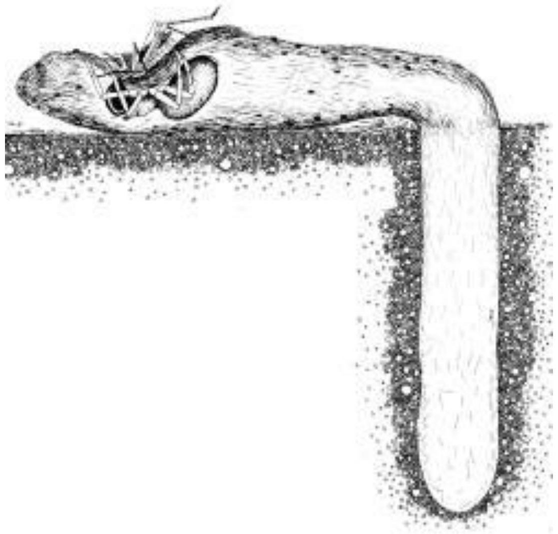
Nyffeler 1999 J Arachnol; Uetz et al. 1999 J Arachnol; Cardoso et al. 2011 Plos One; Birkhofer & Wolters 2012 Glob Ecol Biogeogr; Michalko & Pekar 2016 Oecologia

Web building spiders

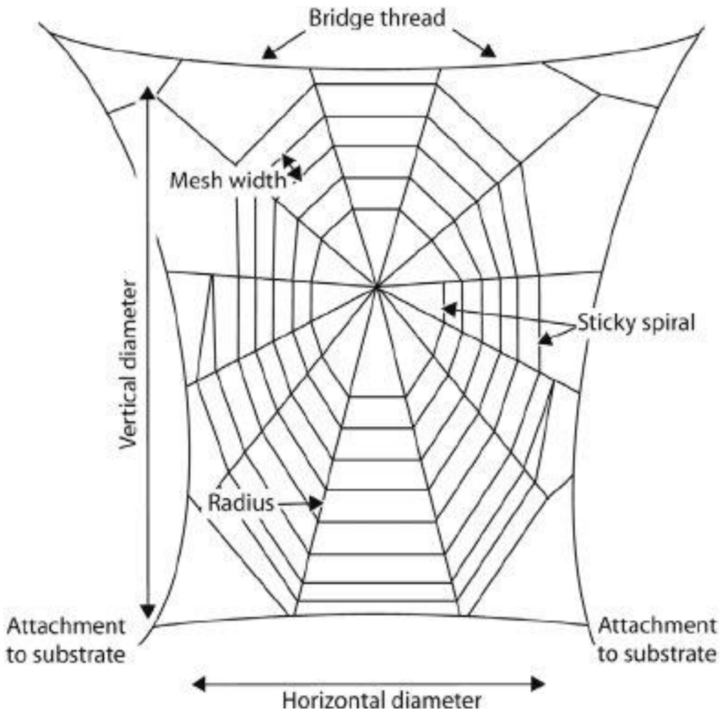
Sensing web

- Spiders are usually hidden in retreats and signal threads are connected to the retreats
- The primary function of their web is to detect prey
- Ground, walls, tree bark
- For example: Liphistiide, Theraphosidae, Atypidae, Segestriidae, Oecobiidae

Cardoso et al. 2011 PloS One; Eberhard 2021 Spider Webs



Web building spiders



Orb web

- 2D planar webs with regular structure
- Vertical as well as horizontal
- Function as a capture device that intercepts mostly flying prey
- Retreat outside web and sometime signal thread from the web to the retreat
- Vegetation
- Main prey groups: Diptera >>> Hemiptera & Hymenoptera
- For example: Araneidae, Tetragnathidae, Nephilidae, Uloboridae

Cardoso et al. 2011 PloS One; Michalko & Pekar 2016; Eberhard 2021 Spider Webs

Web building spiders

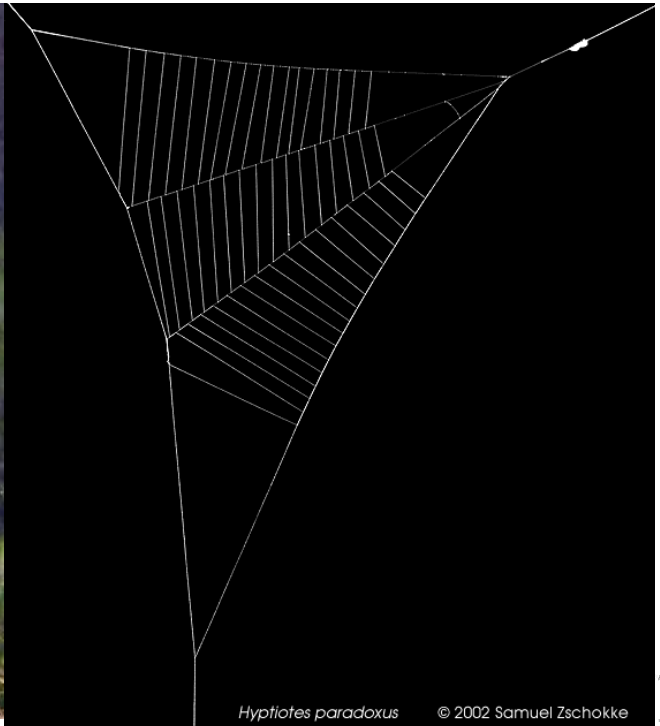
Orb web

- Many modifications

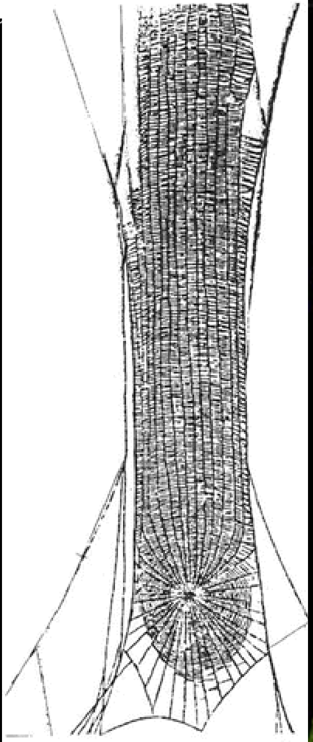
Eberhard 2021 Spider Webs

Cyrtophora

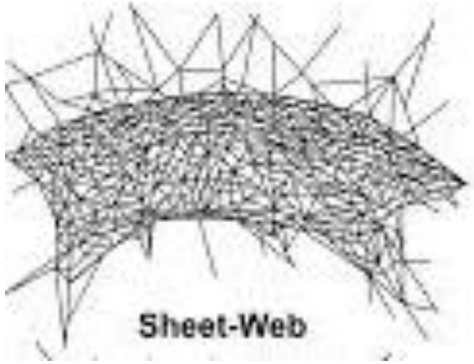
Hyptiotes



Scoloderus



Web building spiders

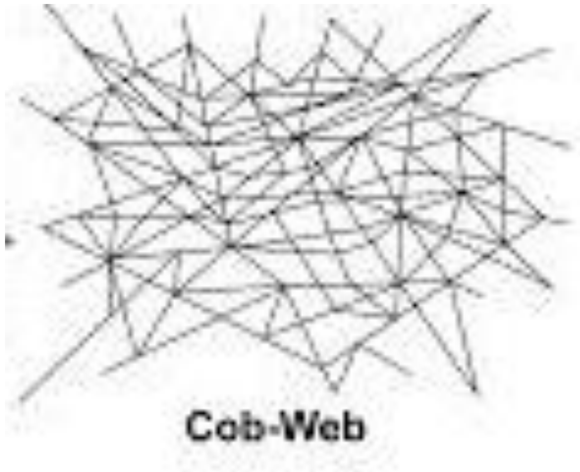


Sheet web

- Silk threads form a dense sheet that serves as a platform where a spider hunts
- Barrier threads that knock flying / crawling prey on the sheet
- Spider can be on or under the sheet
- Retreat usually outside the sheet
- Vegetation or closely above ground
- Main prey groups: Diptera > Hemiptera > Hymenoptera
- For example: Agelenidae, Amaurobiidae, Hahniidae, Linyphiinae,

Cardoso et al. 2011 PloS One; Michalko & Pekar 2016; Eberhard 2021 Spider Webs

Web building spiders



Space web

- 3D mesh of threads
- Function as a capture device as well as a retreat
- Vegetation or closely above ground
- Main prey groups: Coleoptera & Diptera > Hemiptera & Hymenoptera
- For example: Theridiidae, Dictynidae, Pholcidae

Cardoso et al. 2011 PloS One; Michalko & Pekar 2016; Eberhard 2021 Spider Webs

Cursorial spiders

Ambushers

- Wait in one place motionless and ambush their prey
- Mostly vegetation but also ground
- Main prey groups: Hymenoptera > Diptera
- For example: Thomisidae, Sicariidae, Selenopidae

Cardoso et al. 2011 PloS One; Michalko & Pekar 2016

Cursorial spiders

Ground hunters

- Actively search and pursue their prey or frequently change patches and ambush their prey
- Ground
- Main prey groups: Diptera & Araneae > Hemiptera > Collembola
- For example: Lycosidae, Gnaphosidae, Zoridae, Liocranidae

Cardoso et al. 2011 PloS One; Michalko & Pekar 2016

Cursorial spiders

Vegetation hunters

- Actively search and pursue their prey or frequently change patches and ambush their prey
- Vegetation
- Main prey groups: Diptera > Hemiptera > Hymenoptera & Araneae
- For example: Salticidae, Philodromidae, Clubionidae, Oxyopidae

Cardoso et al. 2011 PloS One; Michalko & Pekar 2016

Adaptations for prey capture in specialised spiders

- Adaptations enable specialists to utilize their focal prey more effectively than generalists
- Often just improved function of pre-adaptations occurring in ancestors

Morphological adaptations

- *Dysdera*: flattened chelicerae, *Palpimanus*: thick cuticle, massive forelegs with dense scopulae, *Eriauchenius*: prolonged ‘neck’ region and chelicerae

Rezac et al. 2008 J Zool; Pekar et al. 2012 Sci Nat; Wood et al. 2012 Cladistics; Pekar & Toft 2015 Biol Rev

Adaptations for prey capture in specialised spiders

Behavioural adaptations

- Often include some form of aggressive mimicry
- Adult females of *Mastophora* use a bolas with substance imitating female pheromones of certain moth species; *Portia* pulls threads of web-spiders pretending to be entangled prey and then deliver a surprising attack

Jackson & Whitehouse 1986 J Zool; Haynes et al. 2002 Chemecology; Pekar & Toft 2015 Biol Rev

Adaptations for prey capture in specialised spiders

Venomic adaptations

- Venom of prey specialized contains more prey-specific compounds that make the venom more effective against their focal prey

Pekar et al. 2018 J Anim Ecol.

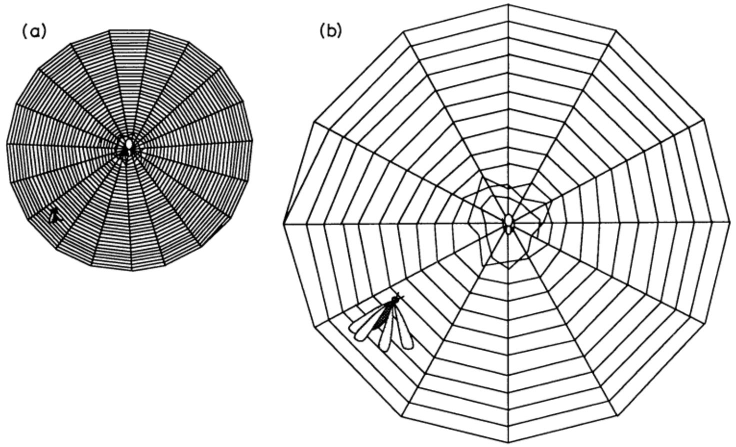
Flexibility and versatility in prey capture

- Spiders encounter various prey types
- Spiders can change capture tactic depending on prey characteristics
- Behavioural versatility (also conditional strategy) is change in behaviour as immediate response to current situation
- Behavioural flexibility is longer but reversible change in behaviour

Flexibility and versatility in prey capture

Flexibility of web-building spiders

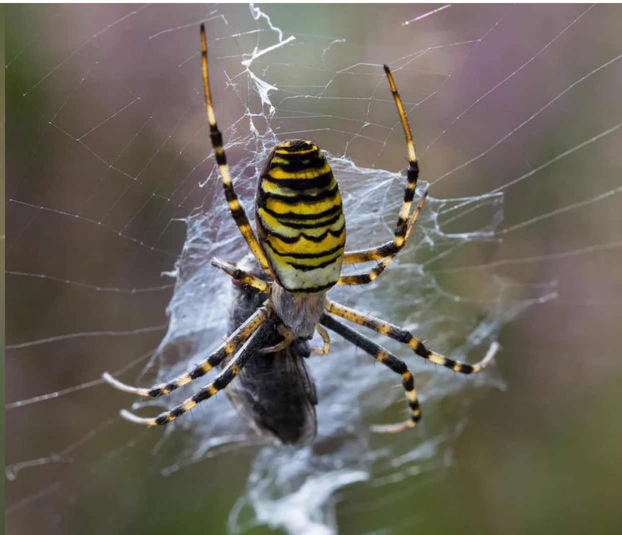
- Spiders can change web properties to increase capture success of certain prey type / size
- Increasing the capture efficiency for one prey type can decrease the efficiency for another
- *Nephila pilipes* produces stiffer webs by producing thicker silk threads and more radii when capturing crickets, prey with high kinetic energy, than flies, prey with low kinetic energy
- *Parawixia bistriata* builds small webs with fine mesh to capture small dipterans but large webs with wide mesh to capture swarming termites



Flexibility and versatility in prey capture

Versatility of web-building spiders

- Web spiders are able to recognize the type of intercepted prey through vibrations in web and then by direct contact
- ‘Pluck-out’ attack: small innocuous prey
- ‘Bite’ attack: larger prey that can quickly escape from web
- ‘Wrap’ attack: dangerous and noxious and large prey



Flexibility and versatility in prey capture

Versatility of cursorial spiders

- Versatility a] in direction and body part of prey in which a spider aims its attack, b] in grasping technique, and c] amount of venom delivery
- Dangerous prey can be approached by a stealth attack from behind or on distant part of its body
- Safe prey is rapidly approached and attacked head on

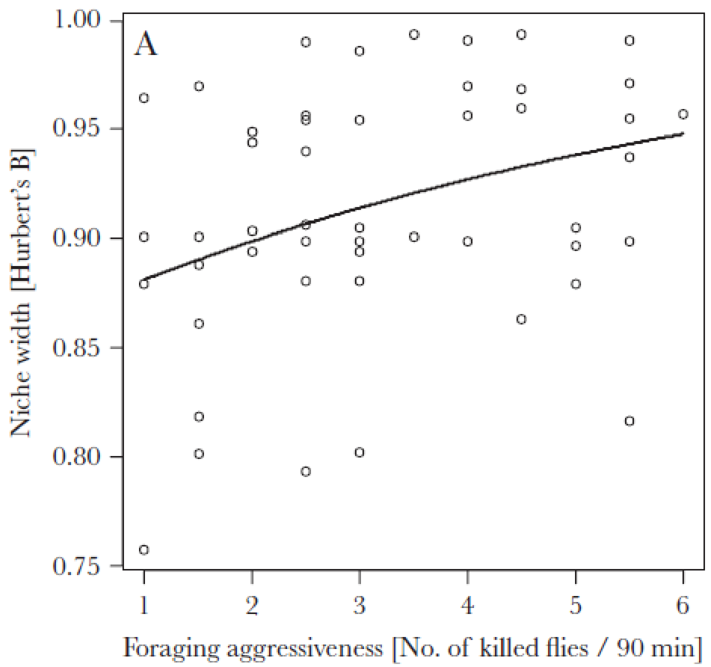
Flexibility and versatility in prey capture

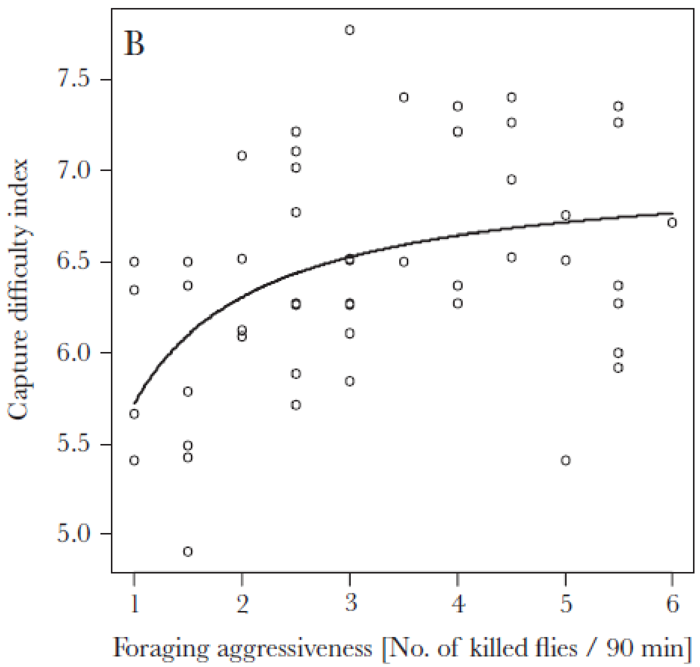
Versatility of cursorial spiders

- Grasping with chelicerae with no venom injection: small innocuous prey
- Catching with forelegs in a ‘basket’ and delivering venomous bite: innocuous prey with good escape abilities
- Bite and hold while keeping legs out of prey reach: dangerous but relatively weak prey
- Bite and release and wait: dangerous prey
- Spiders can inject more venom in dangerous than innocuous prey

Spider behavioural type / personality

- Personality is defined as consistent inter-individual differences in behaviour
- Personality in spiders can be product of phenotypic plasticity as well as genetically fixed
- Aggressive individuals are less selective than non-aggressive individuals and have wider niches as they incorporate more dangerous prey





Michalko et al. 2021 Behav Ecol

Prey and spider body size

- Too small prey is unprofitable or it is outside of sensory spectra
- Too large prey is hard to subdue
- Spiders prey on wider prey size range than any other predators
- Preferred prey size is between 50-80% body size of spiders

Nentwig & Wissel 1986, Oecologia

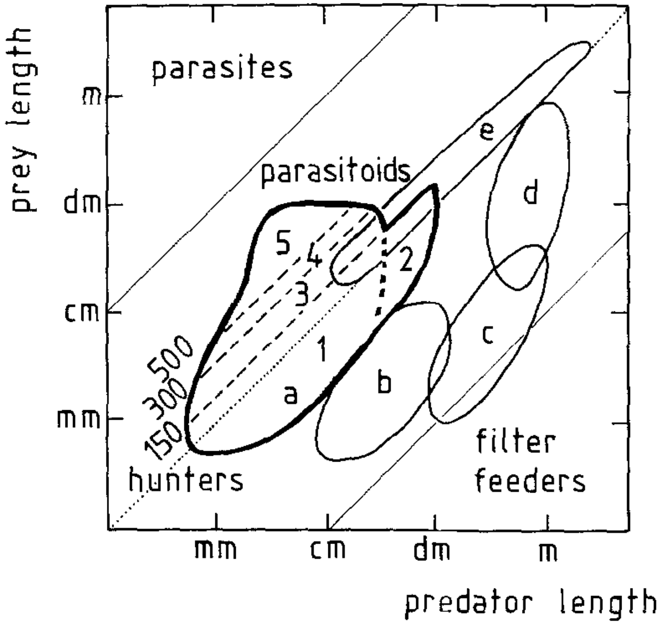


Fig. 5. Generalized pattern of the relative lengths of predator and prey. The surrounded areas indicate size relations for *a* spiders; *b* chewing insects; *c* insectivorous birds; *d* hawks, owls; *e* ants, dogs (pack hunters). Spiders are subdivided to *1* non-webbuilding spiders; *2* large mygalomorph spiders; *3* non-webbuilding spiders specialized on large prey items (e.g. some salticids or thomisids); *4* solitary webbuilding spiders; *5* social webbuilding spiders. The central dotted line indicates equality of size of predator and prey; the peripheral unbroken lines indicate prey (predator) one-hundredth length of predator (prey); the three broken lines indicate prey 150%, 300%, and 500% of the length of the predator (modified after Enders 1975)

Okuyama 2007, Appl. Entomol. Zool.

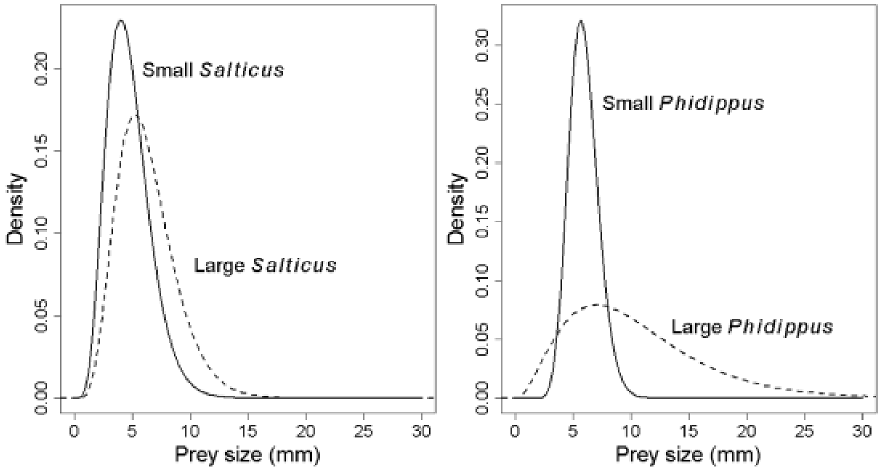
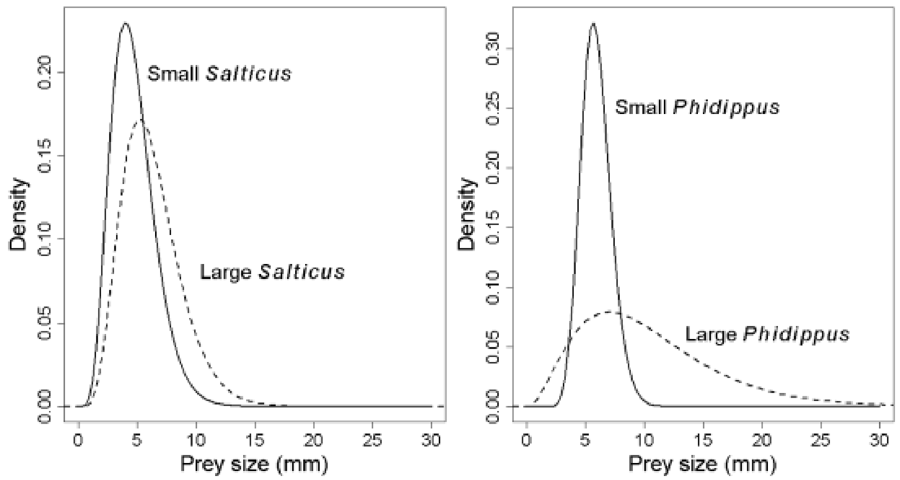


Fig. 2. Estimated gamma distributions describing the density of prey size utilized by small class (solid line) and large class (dashed line) of *Salticus scenicus* (left) and *Phidippus audax* (right). For both species, plotted distributions are based on model 2.

Prey and spider body size

- Prey body size increases with spider body size
- Spider body size can determine selectivity for some prey groups
- Large spiders capture proportionally less collembolan and aphids than small and medium sized spiders



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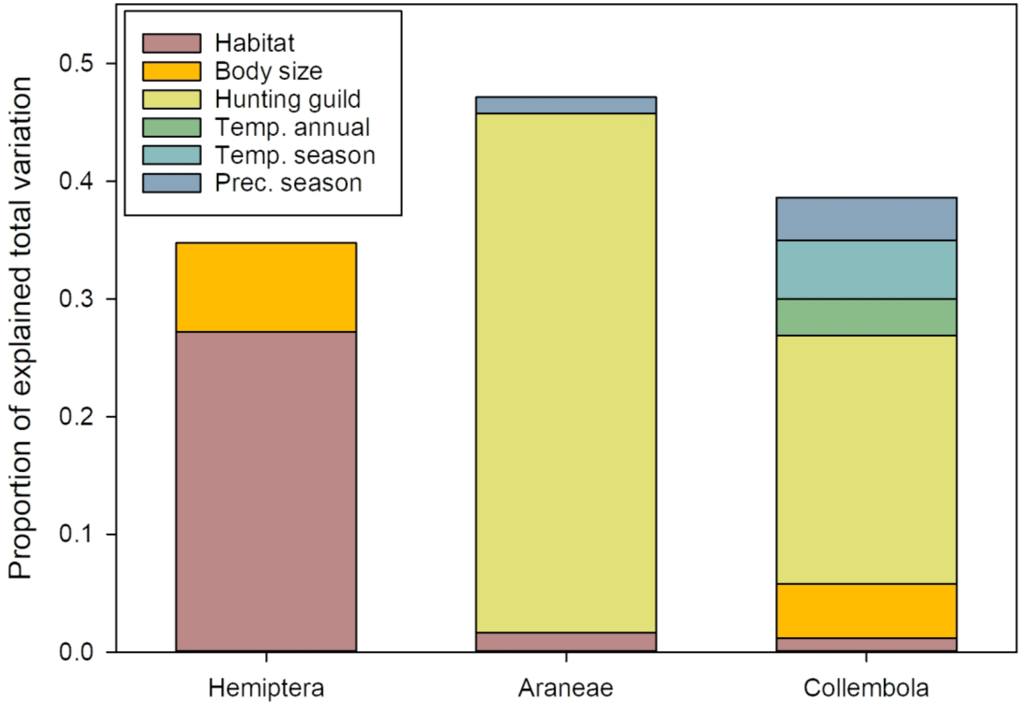
Okuyama 2007, Appl. Entomol. Zool.

Birkhofer et al. under review



Prey defensiveness and dangerousness

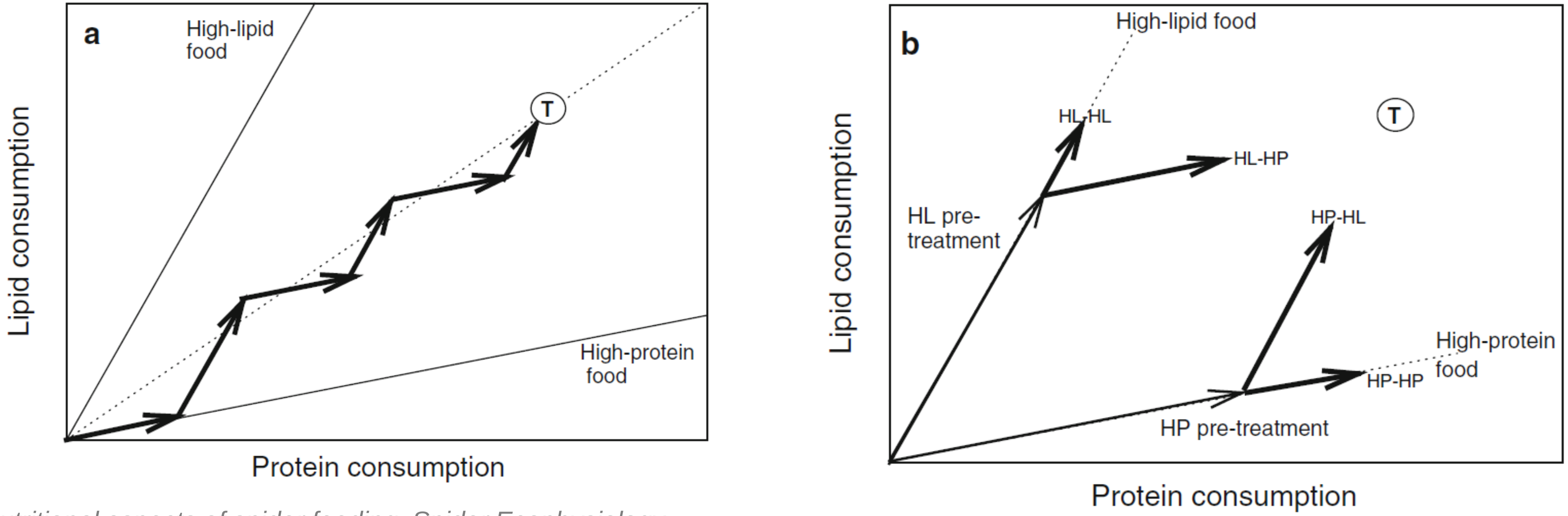
- Heavily sclerotized cuticle of prey (e.g. Coleoptera) is hard to penetrate
  - Strong chelicerae and often toothed (e.g. Araneidae)
  - Thin claws of chelicerae and ability to restrain movement so the spider can find membrane (e.g. Theridiidae)
- Dangerous prey (other predators, large strong jumpers) can injure spiders
  - Structures that restrain from direct contact and movement of prey (e.g. erectile spines, scopula, web, strong venom)

Prey defensiveness and dangerousness

- Excretion of noxious / toxic substances (e.g. some Heteroptera)
  - Wrapping prey or struggling prey in web can wipe out these substances

Nutritional content of prey

- Energetic and nutritional content of prey is important
- Spiders need to optimize nutritional intake and ingest certain composition of nutrition to maximize their fitness (i.e. nutritional target (T)), e.g. certain lipid : protein ratio
- Spiders can prey on a high quality prey or complementary prey types
- Nutritional target can change during ontogeny



Toft 2013. Nutritional aspects of spider feeding. Spider Ecophysiology

Toxic content of prey

- Prey can contain toxins that can show acute toxicity or interfere with prey acceptance or nutrient assimilation (many aphids and some collembolans)
- Prey induced aversion on the given prey that is relatively short-term

Toft 1999 J Arachnol

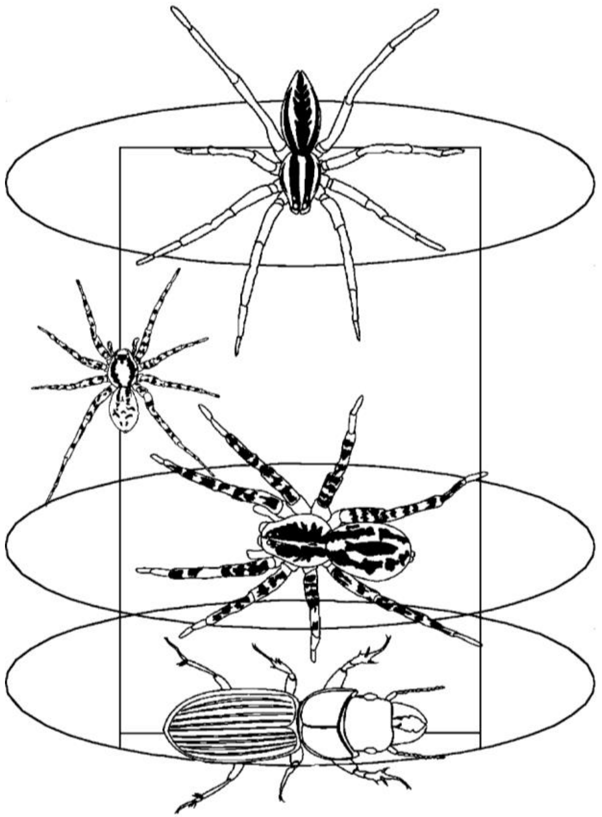
Prey availability

- Spiders are well adapted to long periods of starvation
  - Spiders are able to ingest very large amount of food at once (expandable abdomen with soft cuticle, intestinal diverticula)
  - Slow metabolism in comparison to insects
- Hungry spiders are opportunistic and less choosy than well-fed spiders

Riechert & Harp 1987, Nutritional ecology of spiders.

Presence of enemies

- Spiders reduce their activity or change microhabitat in the presence of their enemies
- Due to reduced activity they capture less prey
- Spiders in new microhabitats encounter different prey types



Sitvarin & Rypstra 2014 Ecology

Riechert & Hedrick 1993 Anim Behav; Rypstra et al. 2007 Oikos; Sitvarin & Rypstra 2014 Ecology;