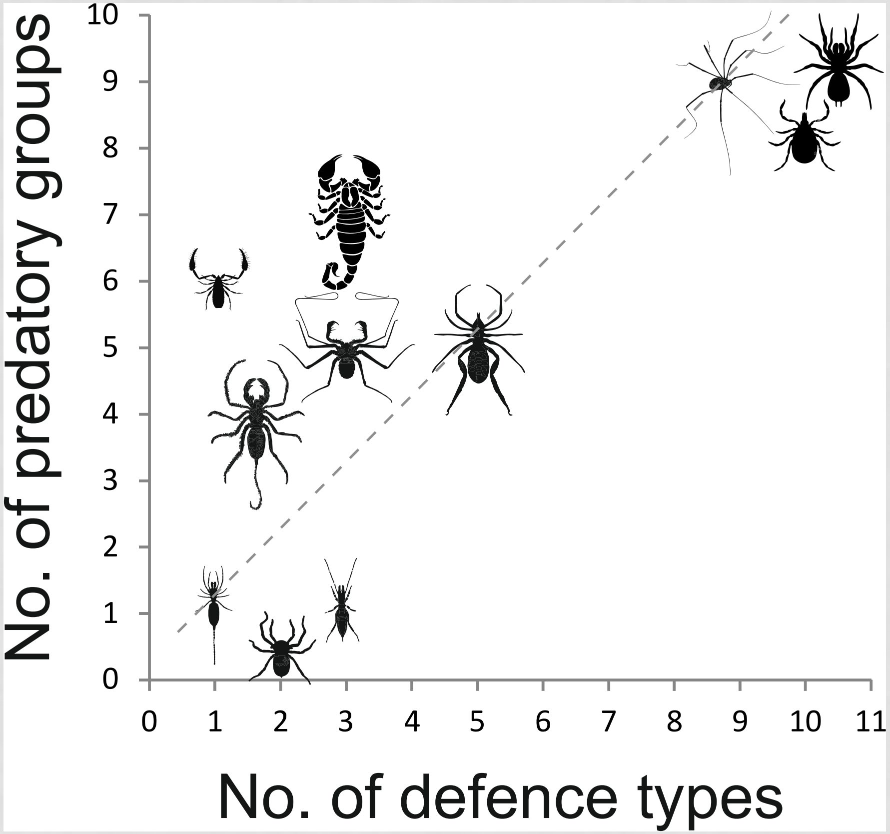
Defensive strategies in arachnids

Arachnology

Stano Pekár

Enemies of spiders

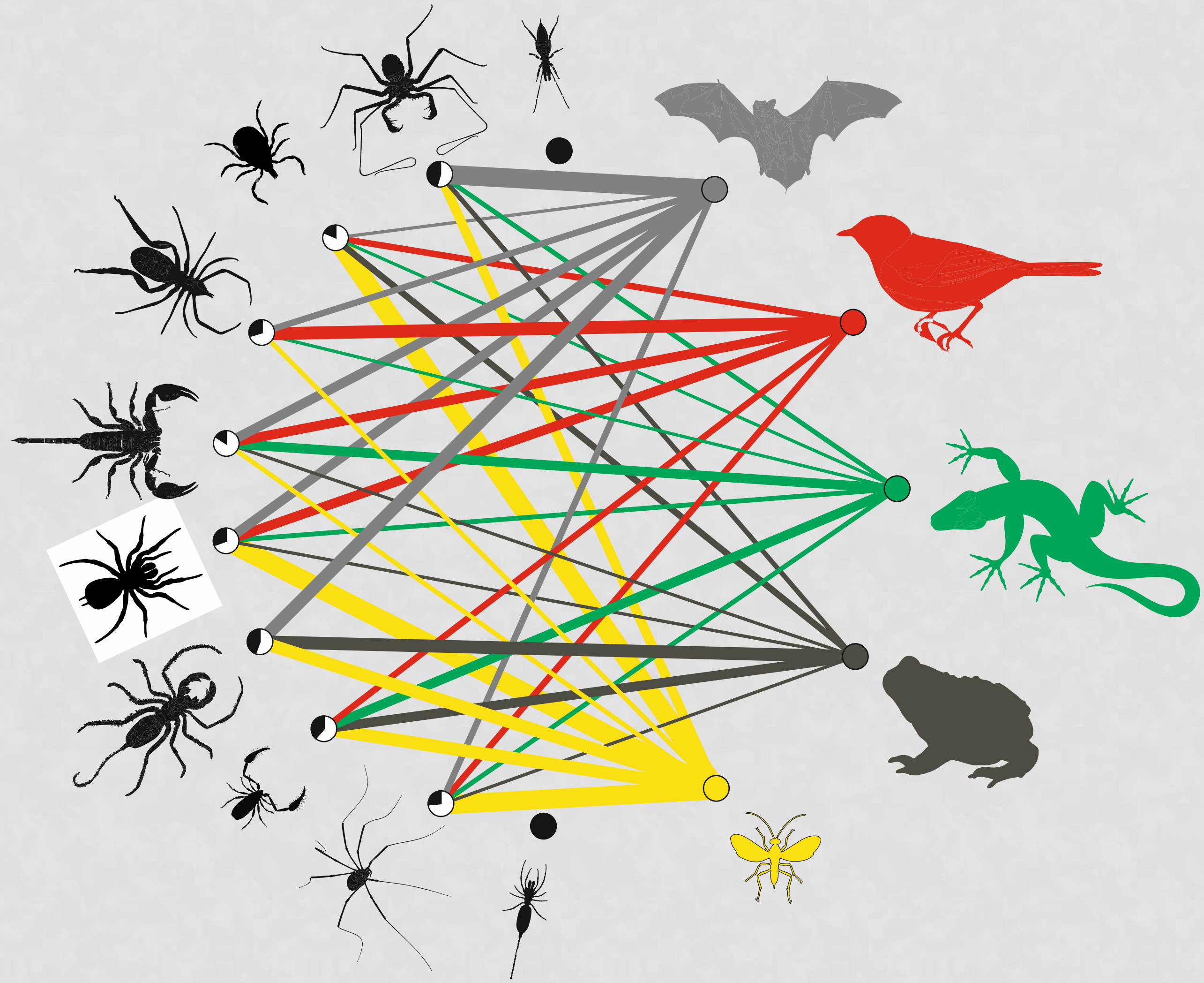
- Insectivorous plants
- Parasites (Nematodes, Acari, Neuroptera)
- Parasitoids (wasps, flies)
- Predators (Arachnida, Insecta, Pisces, Amphibia, Reptilia, Aves, Mammalia)



Pekár & Raspotnig (2022)

Arachnid orders

Predatory groups



Proportion of arachnid enemies

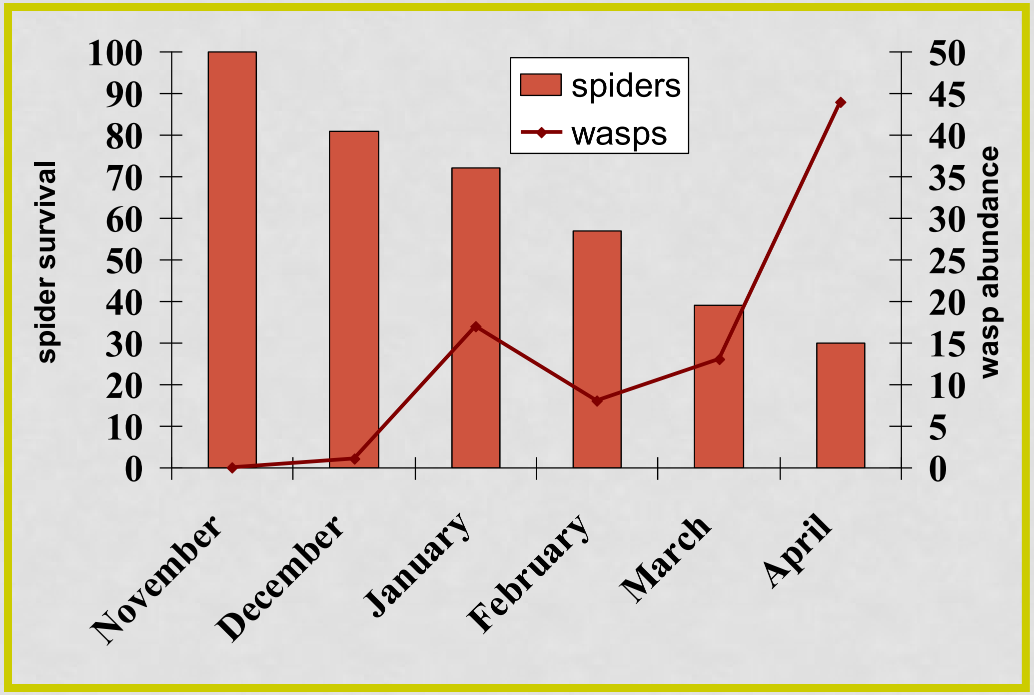
Pekár & Raspotnig (2022)

Eupithecia

Pompilid wasp

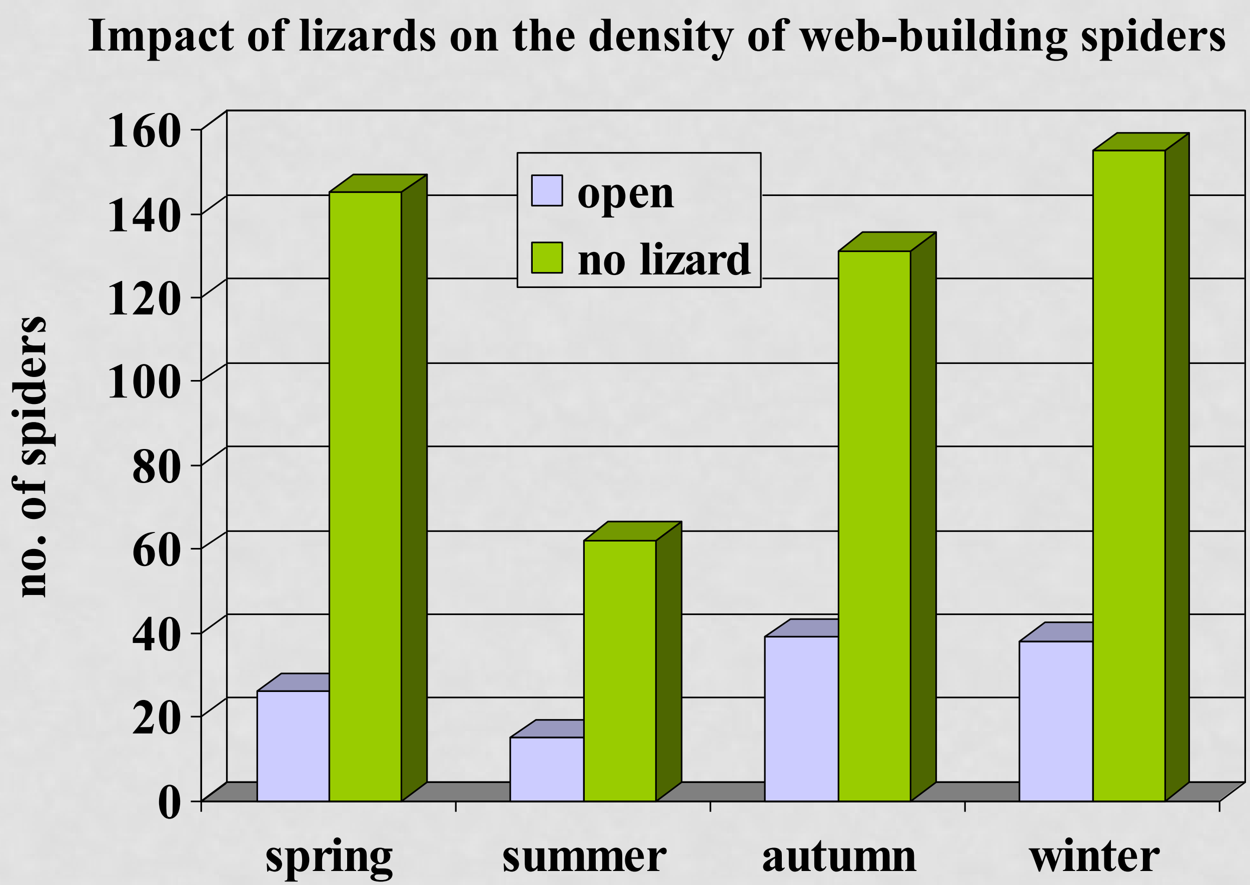
Toft & Rees (1998)

- *Vespula vulgaris* is an important predator of invertebrates in New Zealand
- probability of spiders' (*Eriophora*) survival was negatively correlated with wasp abundance
- more spiders survived in the area with reduced wasp abundance than in the control area



Spiller & Schoener (1988)

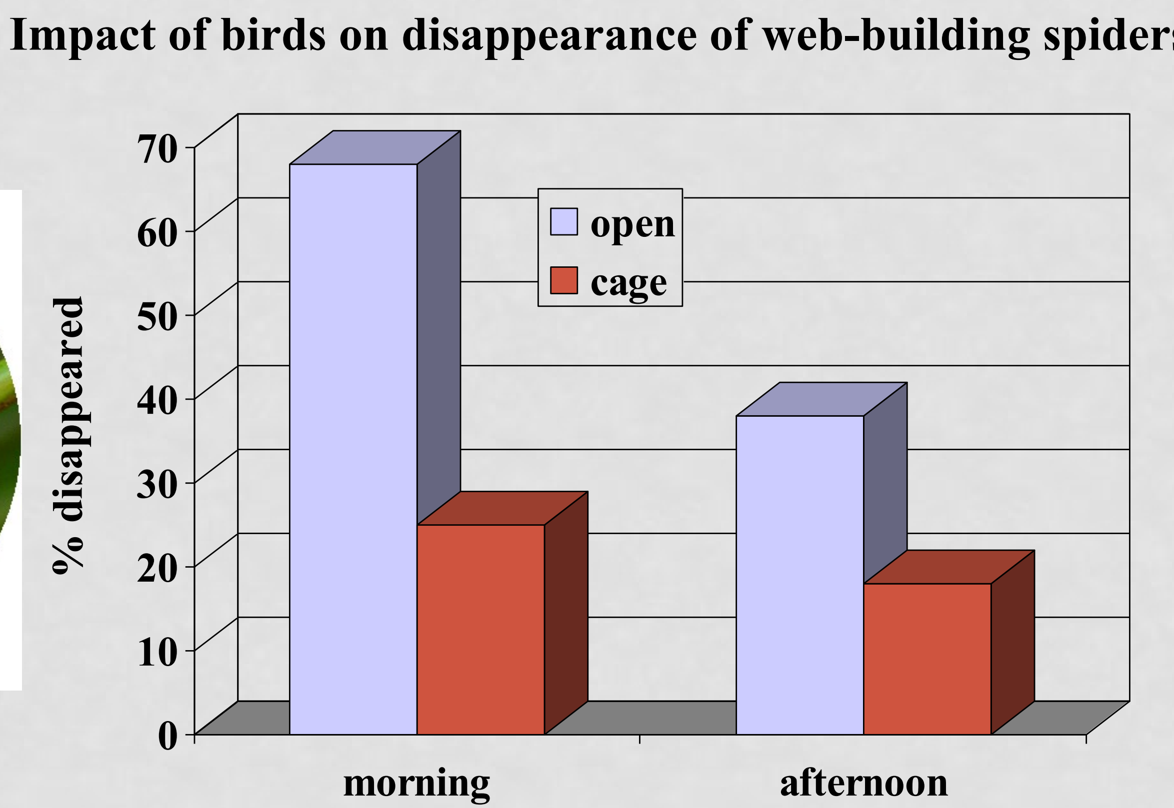
- Bahamian islands without lizards have higher densities of spiders
- removing lizards increased the average number of spiders by three-fold



Anolis

Rypstra (1984)

- survival of spiders in tropical regions was higher when they were protected by cages that excluded vertebrates (birds, primates)
- Cages did not prevent movement of spiders and their prey



Defences

Multiple defences

- Each species evolved suite of defences used

– at different stages of attack by a single predator
– against different predators

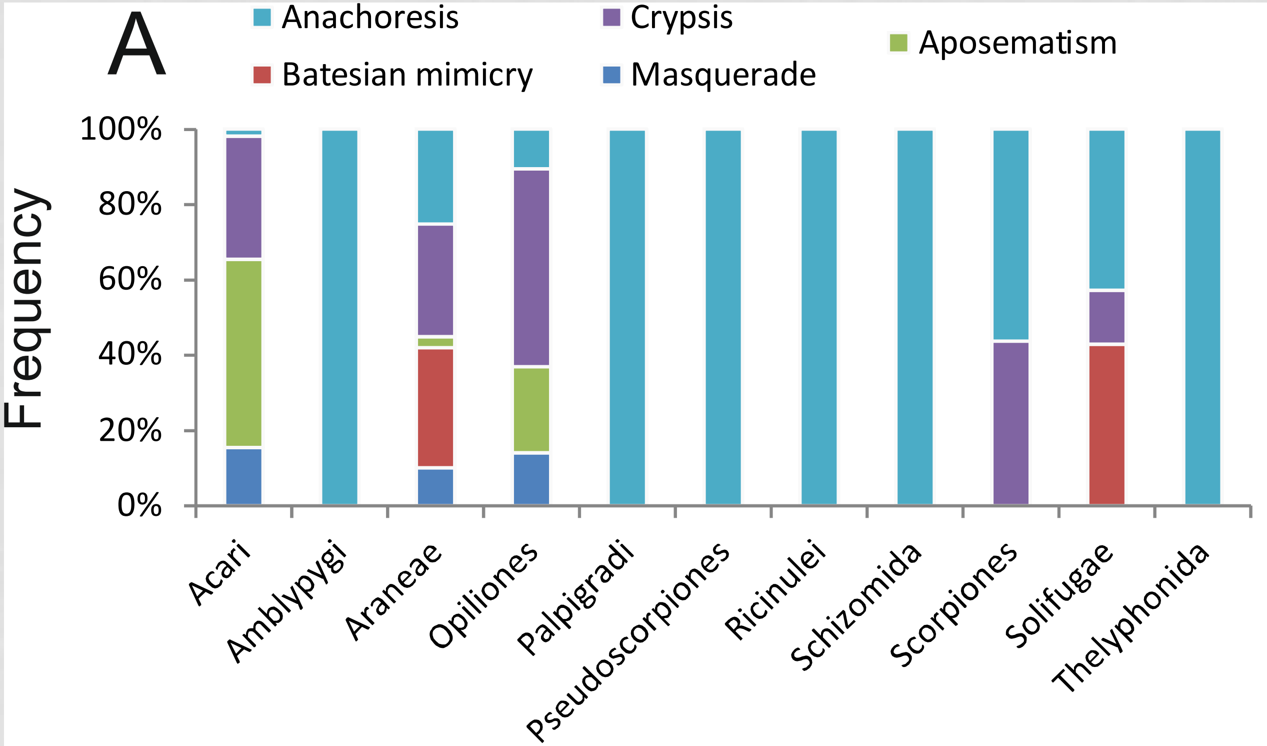
Frequency-dependent selection – the fitness of a phenotype as it depends on the composition in a population

Positive – gives an advantage to common phenotypes
Negative (apostatic) – advantageous for rare forms

Ruxton et al. (2019)

Primary defences

- prevent detection
- operate before a predator initiates prey-catching behaviour
- anachoresis, background matching, disruptive colouration, countershading, transparency



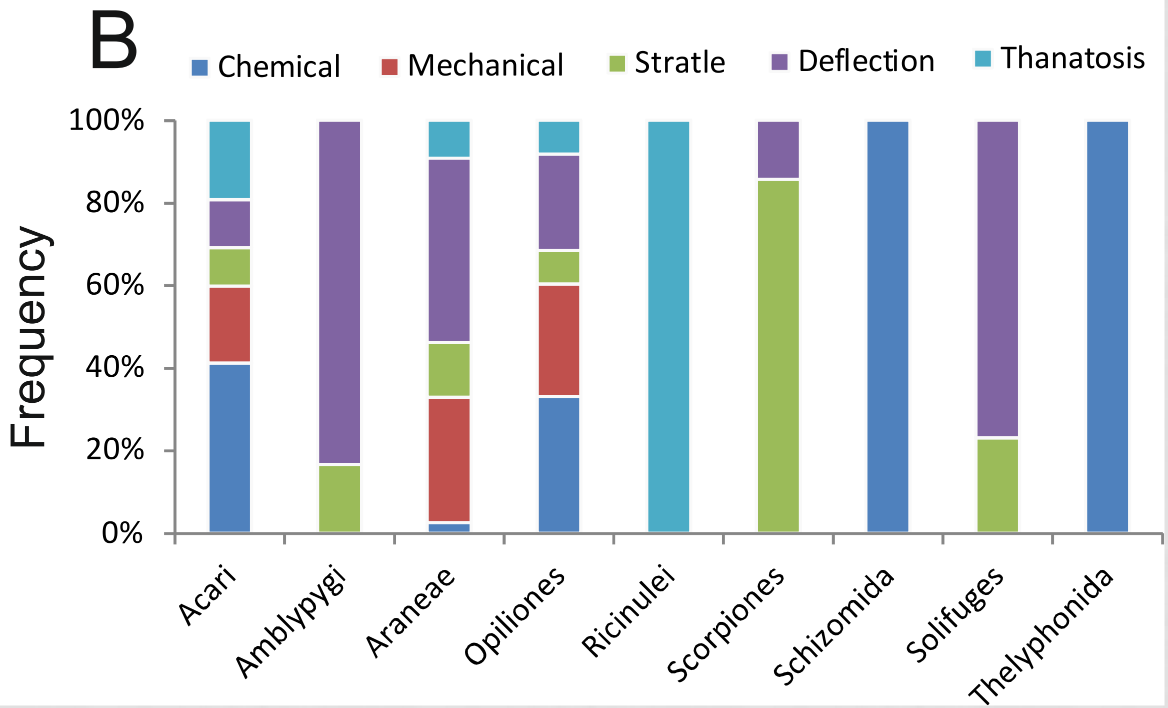
Pekár & Raspotnig (2022)

Secondary defences

- operate after detection to avoid attack - function to reduce probability of capture
- secondary defences, warning displays, Mullerian mimicry

Other defences

- to mislead predators
- Batesian mimicry, camnouflage, startle, deflection, thanatosis




Anachoresis

- to stay out of predator's environment
- hide under bark (Pseudoscorpiones), in caves (Amblypygi), under stones (Ricinulei), in burrows (Scorpiones, Solifugae), in retreats (Araneae)
- hide temporarily or permanently
- used by all orders

Costs:
- loss of many ecological opportunities

Eukoenia

Galeodes

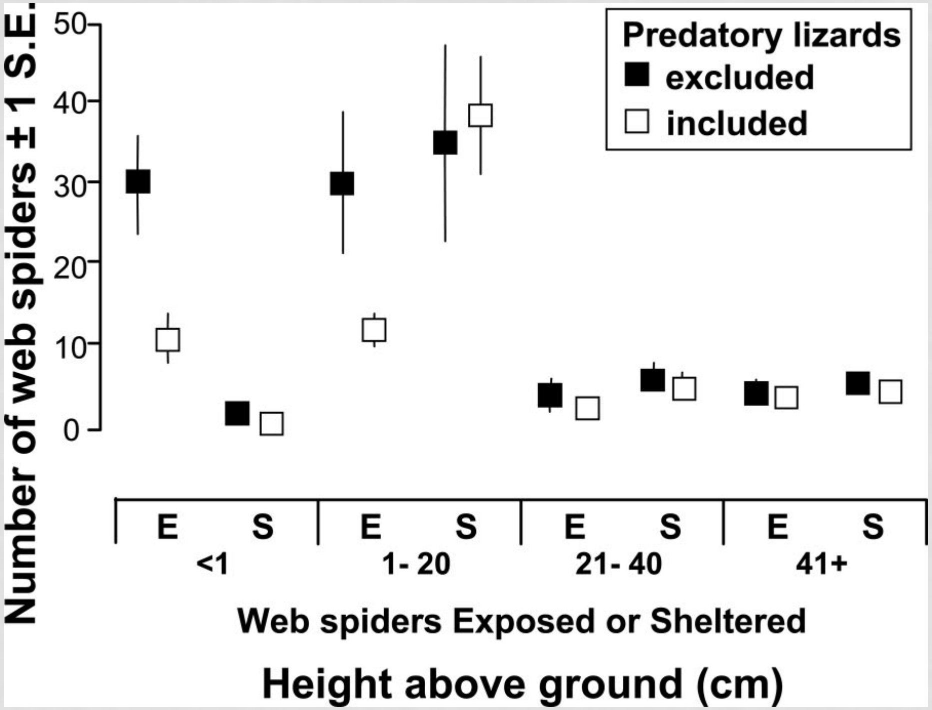
Bothriocyrtum

Manicom et al. (2008)

- manipulative experiment to assess the effectiveness of self-made shelters
- exposed (without shelters) vs. sheltered spiders
- exposed spiders were more negatively affected by lizards than sheltered ones near to the ground

Argiope

Cyrtophora




Background matching

- resembles the colour, pattern, and lightness of background
- used by diurnal species employing sit-and-wait foraging strategy
- species move slowly, stealthily or rapidly
- used by almost all orders

Costs:
- investment into pigmentation
- reduced opportunities in foraging, mating, thermoregulation
- restricts occurrence of spiders to a certain microhabitat

Misumena

Ricinoides

Trogulus

pseudoscorpion

Arctosa

Sitticus

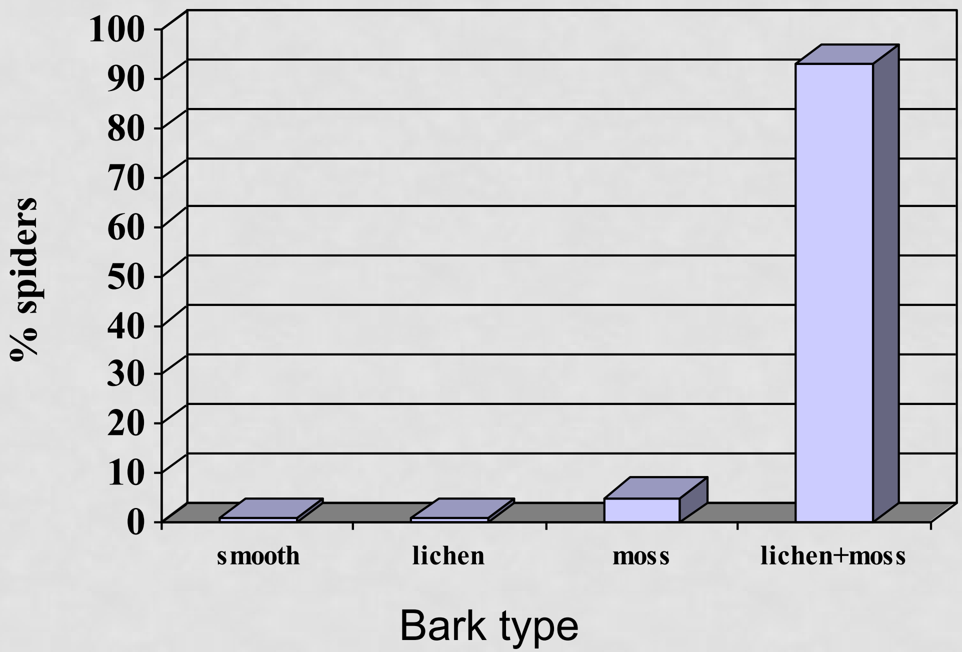
Hygropoda

Pandercetes

Messas et al. (2014)

Background selection

- passive or active selection of a background or change colour
- araneid *Eustala perfida*
- most frequent on trees covered by mosses and lichens
- motionless during day and foraging and web-building during night

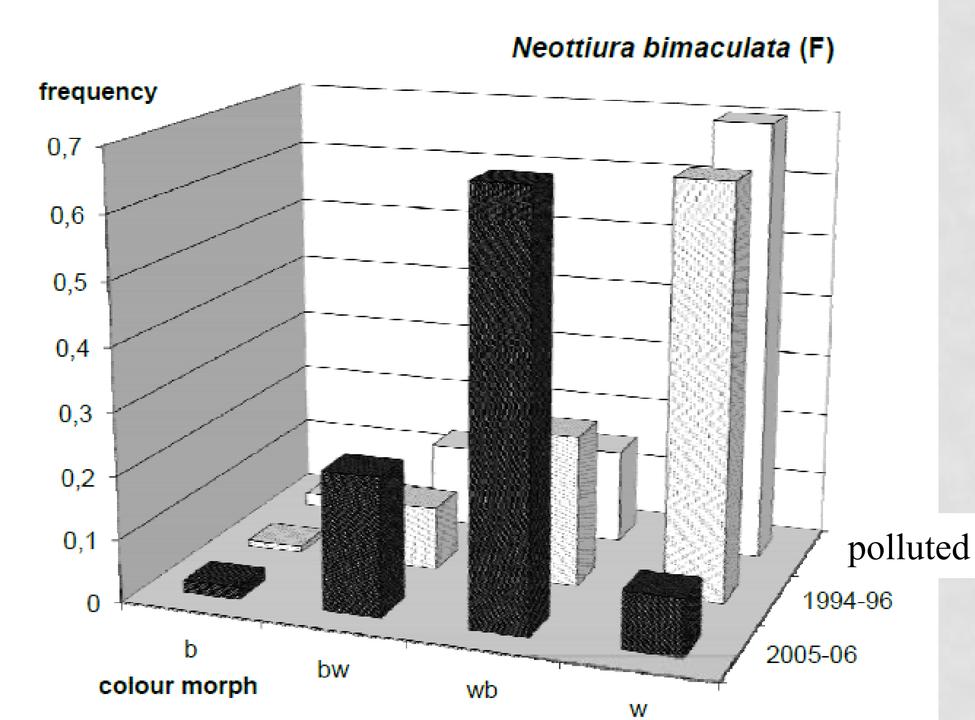


Colour polymorphism

Schaller & Kohler (2008)

- maintained by apostatic selection due to formation of a search image in predator
- melanic forms of *Neottiura* predominated in polluted habitat
- after habitat regeneration darker individuals increased in abundance

Neottiura bimaculata




Disruptive colouration

- colouration creates false boundaries - some body parts are more discernible than others
- can be independent of background
- in ground and vegetation dwelling arachnids
- used by Acari, Araneae, Opiliones, Scorpiones, Solifuges

<u>Costs</u>:

- as in background matching

Phalangium

solifuge

Phlegra

Countershading

- colouration of an arachnid cancels its shadows
- surface exposed to light is darker than the opposite surface
- independent from background, diurnal activity in open habitat
- used probably by Opiliones and Araneae

Costs:
- thermoregulation
- exposure to predators

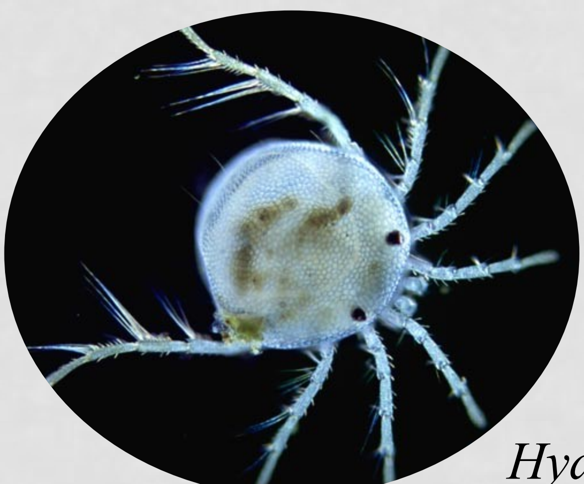
Argyrodes

Frontinella

Transparency

- blends with background - typically in water due to similar light refraction conditions
- whole body (all organs) is transparent
- used by water mites

<u>Costs</u>:
- minimise consumption



Hydrachne

Theridion


Secondary defences
JSCross 2019

- deployed during/before contact with predator – reduce probability of capture
- chemical, mechanical, behavioural

Benefits:
- predators learns more quickly

Costs:
- reallocation energy to produce defences

Evolutionary models
- Kin selection – aggregated defended individuals, killing few individuals will prevent attack on kins
- Individual selection – an individual will survive attack, provide protection for itself (thick cuticle)

Chemical defences

- production of toxins, irritating repellents (volatile compounds)
- venom glands – Araneae, Scorpiones, Pseudoscorpiones
- exocrine glands – Opiliones, Acari, Thelyphonida, Schizomida

Irritant/repellent chemicals

- hydrocarbons, terpenes, aromatics – Astigmatid mites
- quinones, phenolics, acyclic ketones – Opiliones
- carboxylic acids – Thylephonida, Schizomida

Poisons

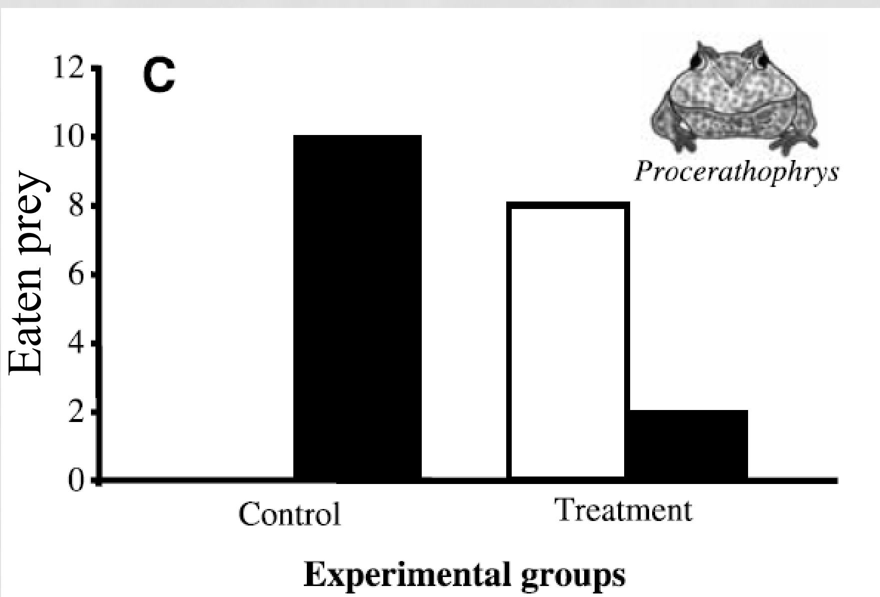
- hydrogen cyanide, alkaloids – Oribatid mites
- nicotine, anabaseine – Opiliones

Pheromones

- Alarm – Opiliones

Machado et al. (2005)

- release droplets from tubercles
- secretion diffuses, covers harvestmen body, sprayed or transferred to the enemy by legs
- benzoquinones prevent approach by predators – chemical shield
- benzoquinones treated prey was rejected by ants, spiders, frogs



Iporangaia

- sac-like glands on metasoma
- vaporised spray to a big distance
- acetic acid, ketones, esters
- repelled Solifuges, mice, shrews, racoons

Schmidt et al. (2000)

- glandularia of water mites produce proteinaceous substances
- repellent against fish

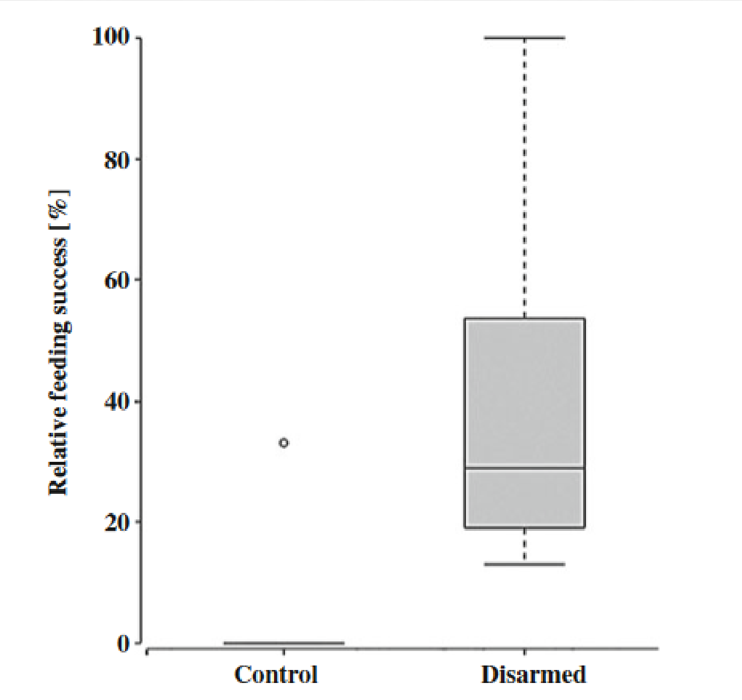
Kerfoot et al. (1980)

Mastigoproctus

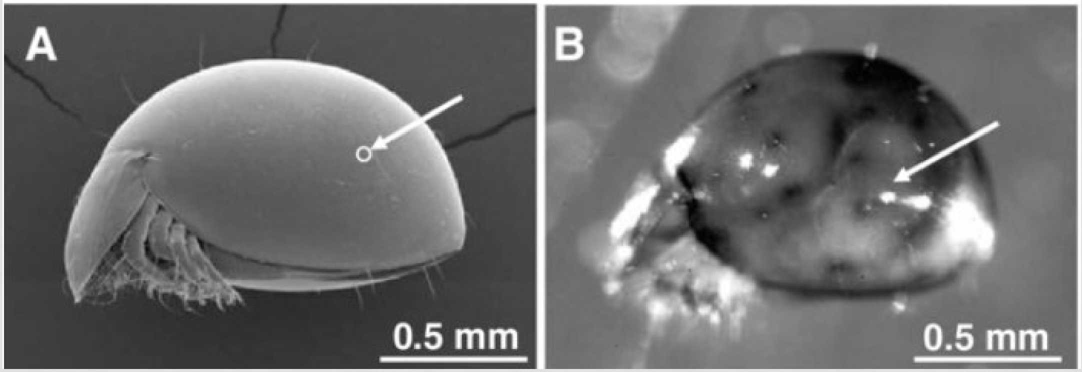
Limnochares

Heethoff et al. (2011)

- paired oil glands in opisthosoma of Oribatid and Astigmatid mites
- produce diversity of substances - hydrocarbons, terpenes, aromatics, and alkaloids
- function as alarm pheromones
- beetles rejected mites with full glands



Oribotritia



Mechanical defences

- spines – Opiliones, Araneae, Acari
- urticating hairs – Araneae

- effective against badgers, skunks, racoons

- strong cuticle – Acari, Araneae

- effective against beetles (Heethoff et al. 2018)

- silk – Araneae

- effective against arthropod and vertebrate predators (Vetter 1980)

Laniatores

Oribatida

Grammostola

Nasua

Behavioural defences

- aggressive stance, counterattack – Araneae, Scorpiones, Solifuges, Thelyphonida,
- fleeing, dropping – Araneae, Pseudoscorpiones, Opiliones
- freezing – Araneae, Opiliones

Cyrtophora

mygalomorph

Mastigoproctus


Warning displays

- in species with effective secondary defences – potent venom, spines, hard cuticle, chemicals
- advertised by a visual, acoustic or chemical (aposematic) signals
- visual signals – always on, used during day, perceived at longer distance
- acoustic and chemical signals – deployed after attack, used during night, perceived at short distance
- signal is conspicuous against background – contrasting colours, deterring sounds and chemicals

Leiobunum

Trombicula

Benefits:

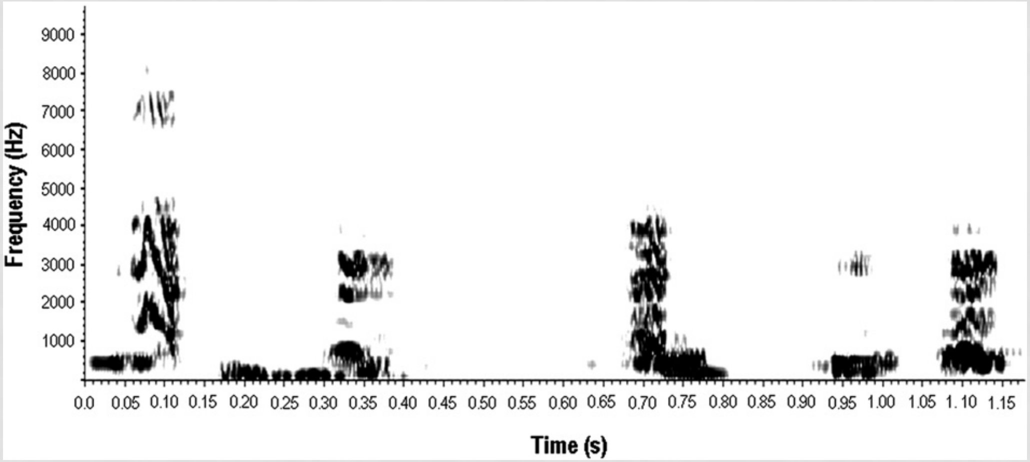
- unconstrained opportunities

Costs:

- production of the signal

Pomini et al. (2010)

- visual signals - used by Opiliones, Araneae, Acari
- acoustic signals (stridulation) - used to advertise chemical defences in Opiliones, urticating hairs in spiders

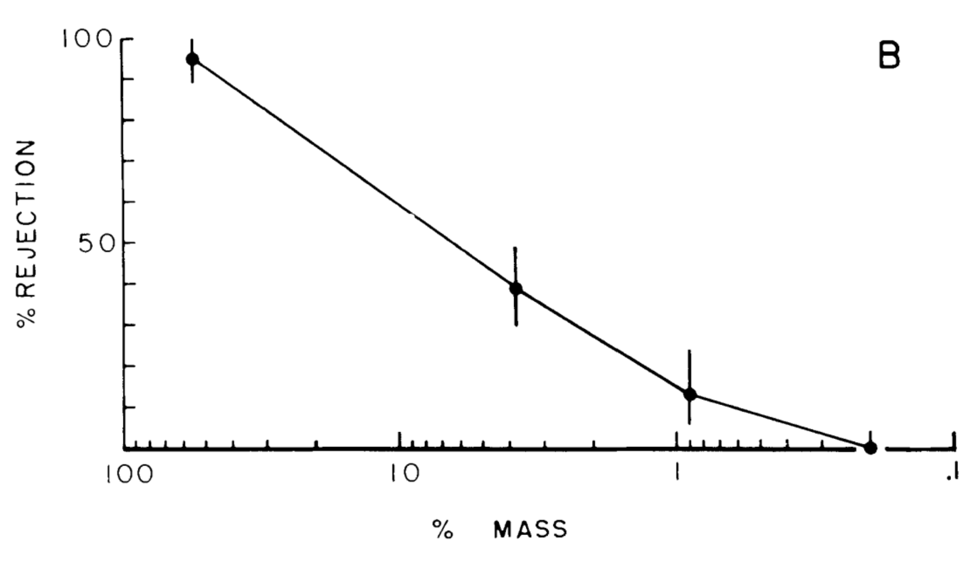


Sclerosomatidae

- aposematic colouration evolved from cryptic in species with defences (pre-adaptations to defences)
- followed by shift in habitat preference

Kerfoot (1982)

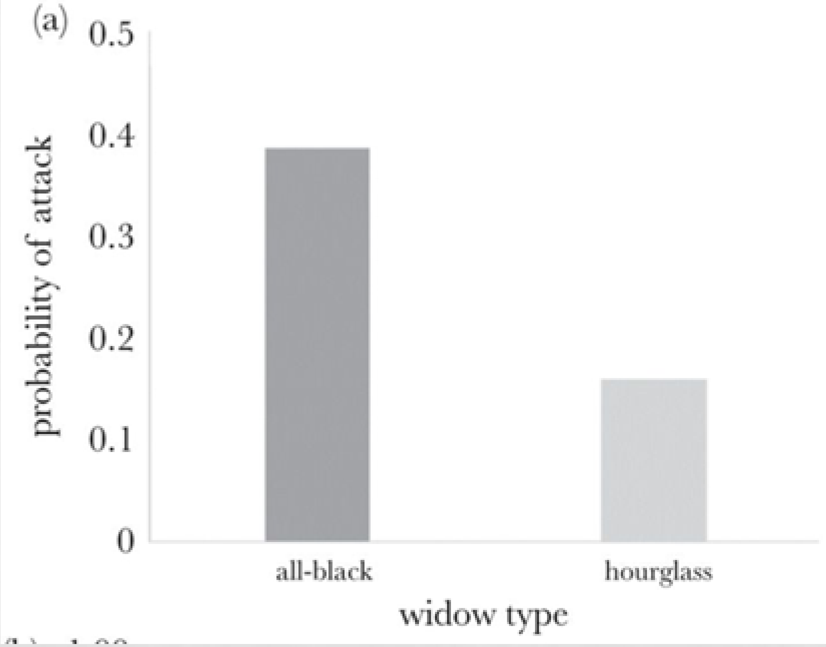
- wasps avoided *Micrathena* spiders due to hard cuticle
- fish rejected water-mites (produce mucus-like substance)
- in food



Micrathena

Brandley et al. (2016)

- American *Latrodectus* species differ in red colouration on abdomen
- defended by sticky silk and powerful venom
- ventral red marking is conspicuous to birds
- birds attacked more dummies imitating completely black than red species




Mullerian mimicry

- related or unrelated species sharing similar aposematic signal
- form Mullerian rings
- unpalatability vary within rings
- all species share costs of predator learning – minimised by increasing species number
- absence of polymorphism due to frequency-dependent selection
- possibly used by Acari, Araneae, Opiliones

- in Malaysia - several species of spiny spiders with sympatric distribution

Actinocantha globulata

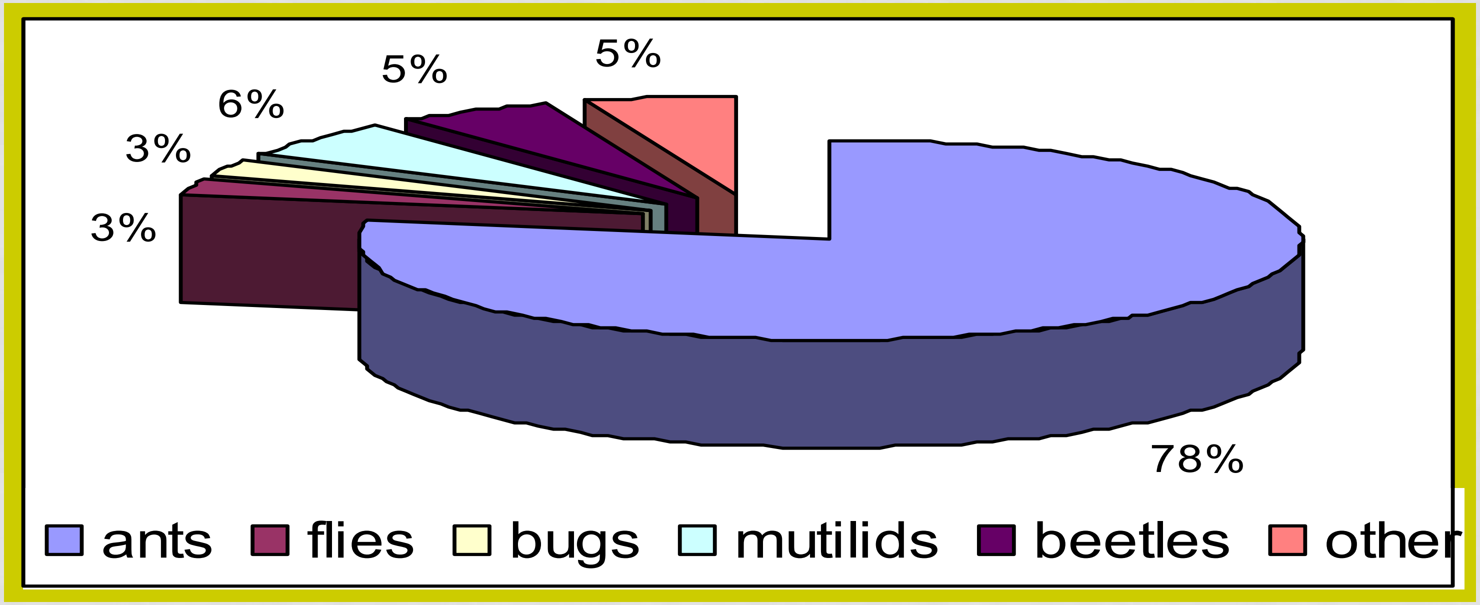
G. hasselti

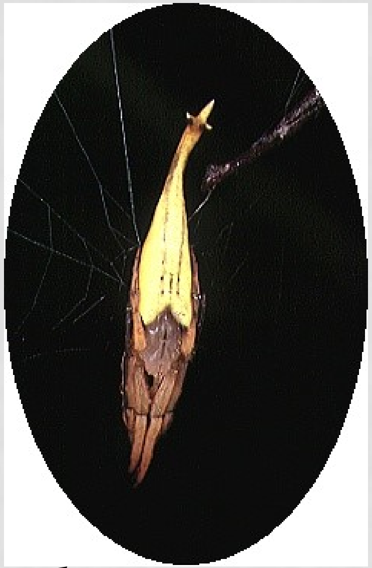
Gasteracantha diardi

Batesian mimicry

- imitation of low-profitable (noxious, unpalatable, toxic) model by palatable species
- imitation of aposematic signal (visual, acoustic, olfactory)
- Resemblance is multi-trait – colouration, shape, size, behaviour, ecology
- mimics parasite on models
- used by Araneae and Solifuges

Models of mimetic spiders





Arachnura

Poecilopachys

Cyrtarachne

Paraplectena

Graptartia

solpugid

Myrmecomorphy

- defended (bite, sting, communal attack, formic acid, hard integument, spines)
- numerous and occur in many habitats
- similar morphology (body size, wingless)

Morphological resemblance

- 3 body parts – head, thorax, gaster
- presence of antennae
- 3 pairs of legs

Synemosyna

anburia

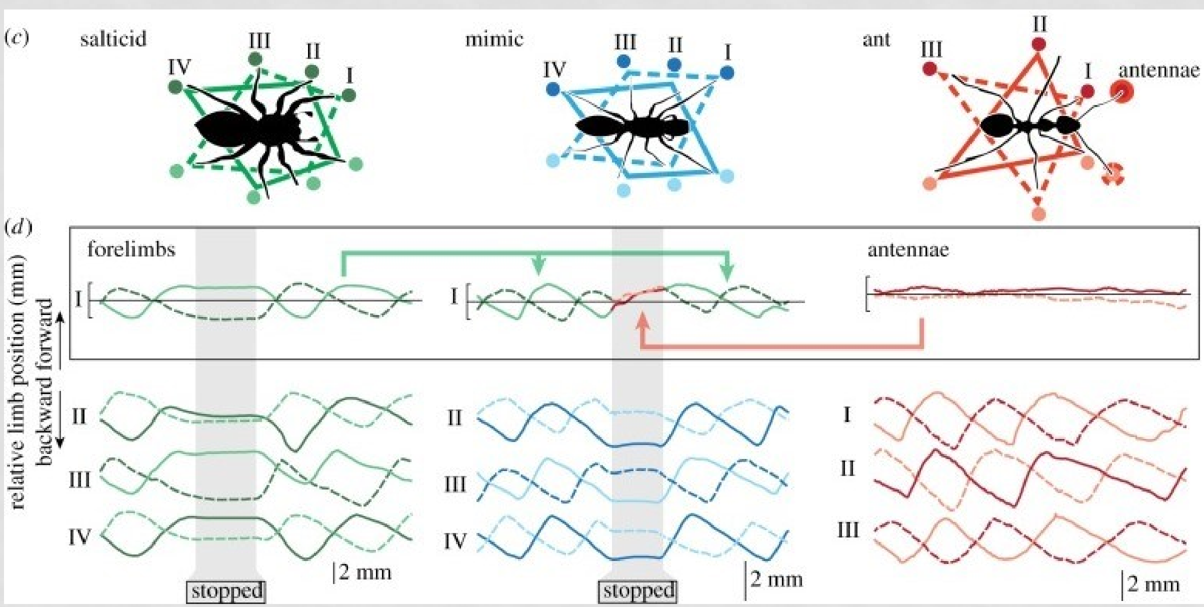
Myrmecium

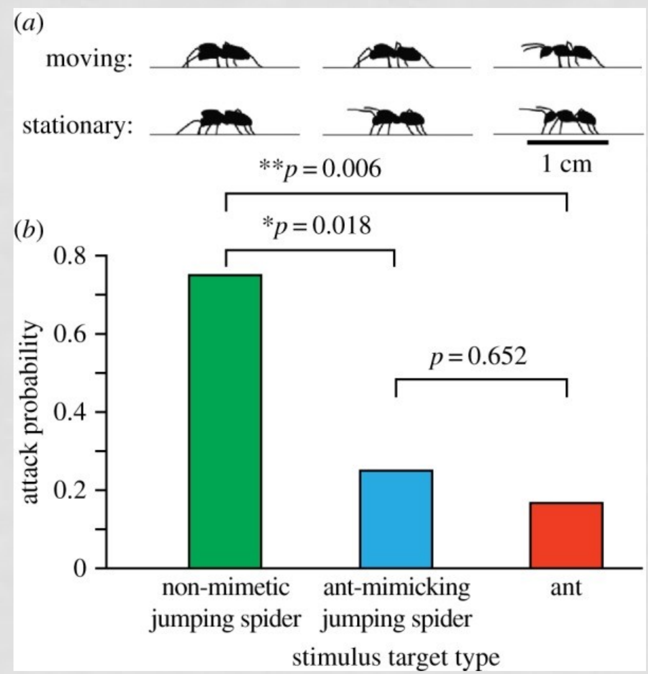
Behavioural resemblance

- Circadian activity, locomotion, legs movement

Shamble et al. (2017)

- *Myrmarachne* walks on 4 legs, wave forelegs only when stationary
- exhibited winding trajectory similar to ants
- spiders pounced on payback of ant-mimics less than on spiders





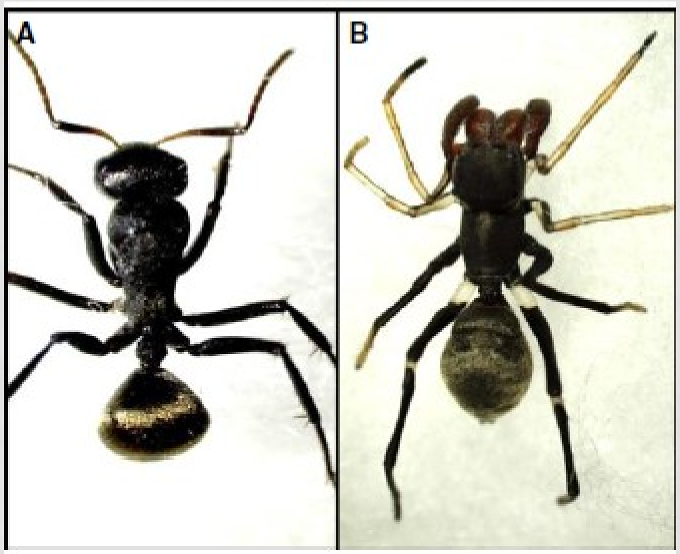
Synemosyna

A RIDDLE

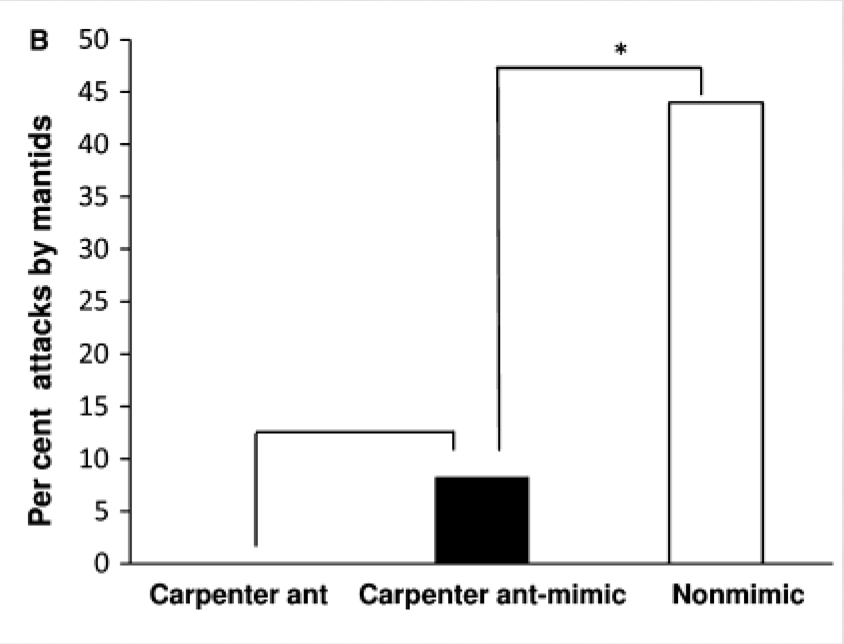
- **Frequency-dependent selection -** rate of predation on mimics depends on the relative abundance of models and mimics: the more models the less attacks on mimics

Ramesh et al. (2016)

- birds, lizards, wasps, spiders avoided to catch ant-mimics
- mantids have innate aversion to ants – avoid to catch ant-mimics too



Camponotus *Myrmarachne*



Mimetic accuracy

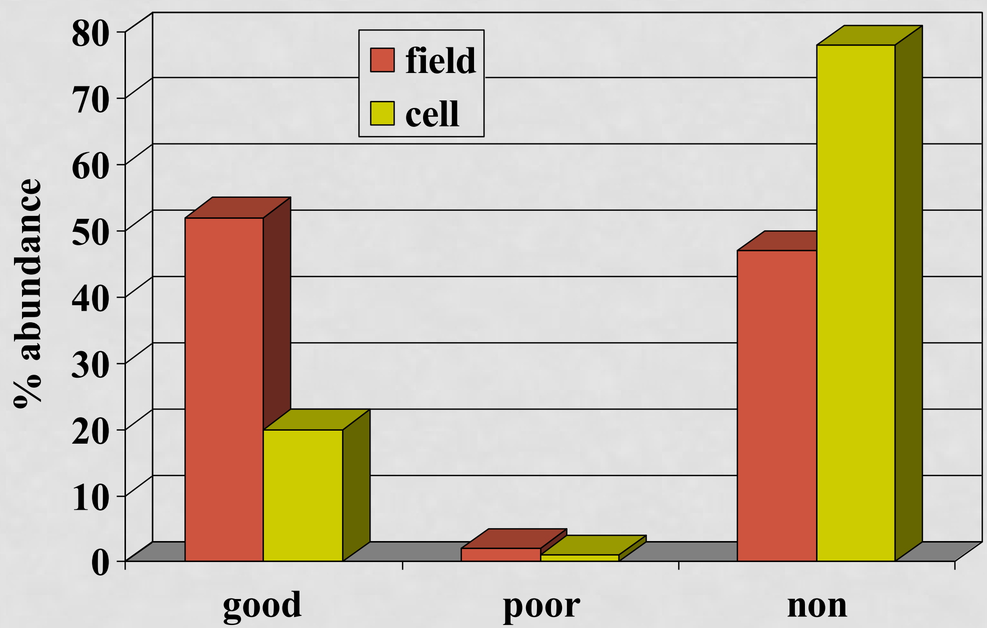
- Accurate mimics – imitate all traits
- Inaccurate mimics – imitate size and colouration

Evolutionary models

- <u>Multi-model hypothesis</u>: resemble more than one model inaccurately – can co-occur with all models
- <u>Multi-predator hypothesis</u>: accurate mimicry will evolve if the selection from visually-oriented predators is strongest, inaccurate mimicry will evolve if selection from other types of predators is strongest
- <u>Noxiousness hypothesis</u>: accurate mimics resemble less defended species than inaccurate mimics
- <u>Relaxed selection hypothesis</u>: predators do not perceive details of resemblance

Edmunds (1993)

- *Pison* wasps are spider parasitoids
- of 873 spiders in wasp cells 870 were salticids
- wasp take fewer ant-mimics than non-mimics
- wasp do not forage near ant nests



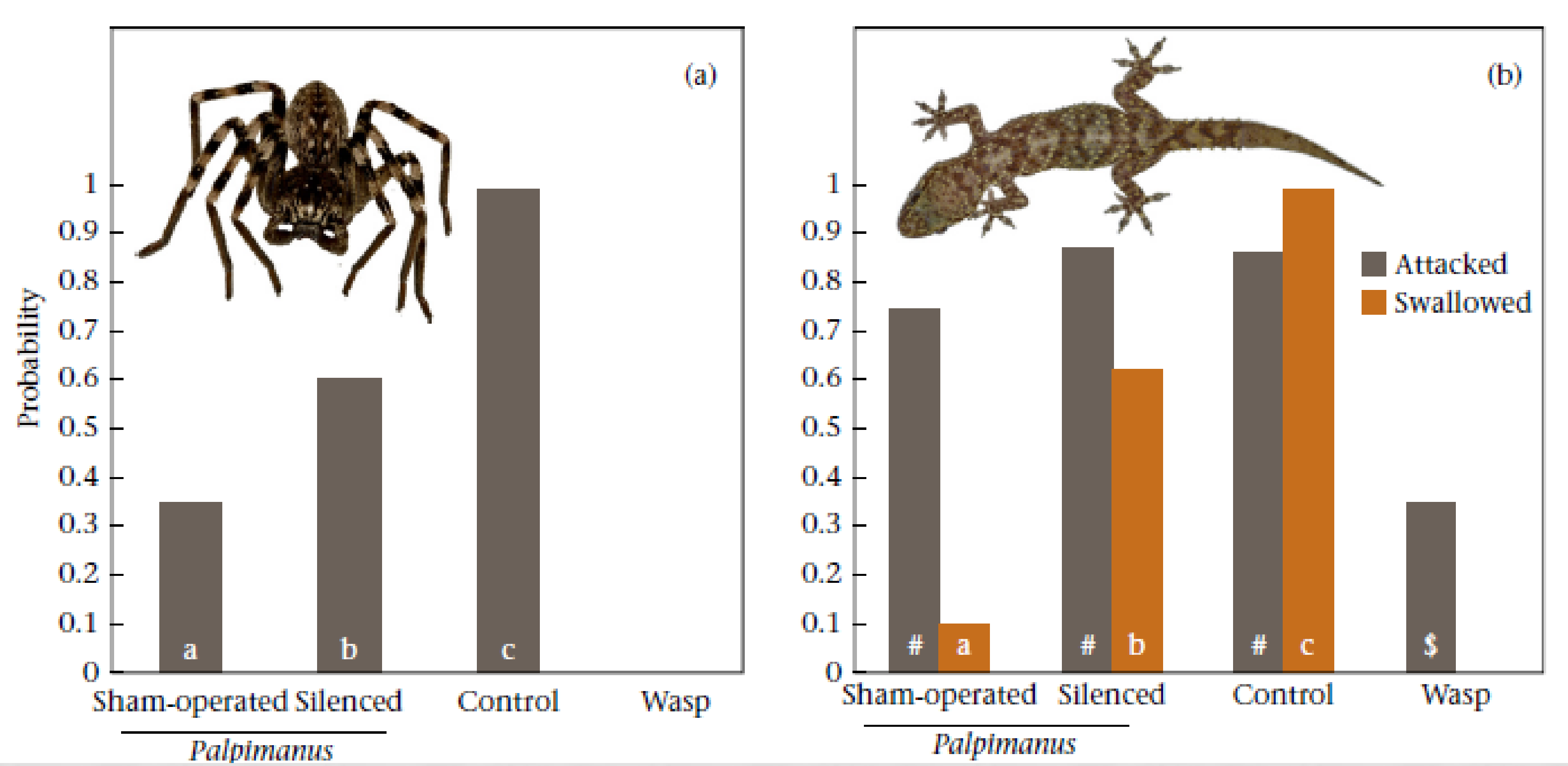
Pekár et al. (2020)

- acoustic signals are important at low-light conditions
- *Palpimanus* spiders co-occur with mutillid wasps under stones
- *Palpimanus* spiders can fall prey to nocturnal predators
- mutillids are defended by powerful sting and strong cuticle
- *Palpimanus* is palatable
- both use defensive stridulation of similar characteristics

Palpimanus

Mutilla

- *Eusparassus* spiders and geckoes avoided mutillids
- *Eusparassus* spiders attacked *Palpimanus* at lower frequency than control
- geckoes attacked but dropped stridulating spiders
- stridulation protects *Palpimanus* from nocturnal predators



Camouflage

- imitation of inedible objects (bud, branch, seed, flower, poo)
- imitated objects are extremely common
- do not imitate signals (aposematic) but cues
- resemblance is multi-trait – visual and chemical cues
- effective for sit-and-wait strategy, often have nocturnal activity
- used by Opiliones and Araneae

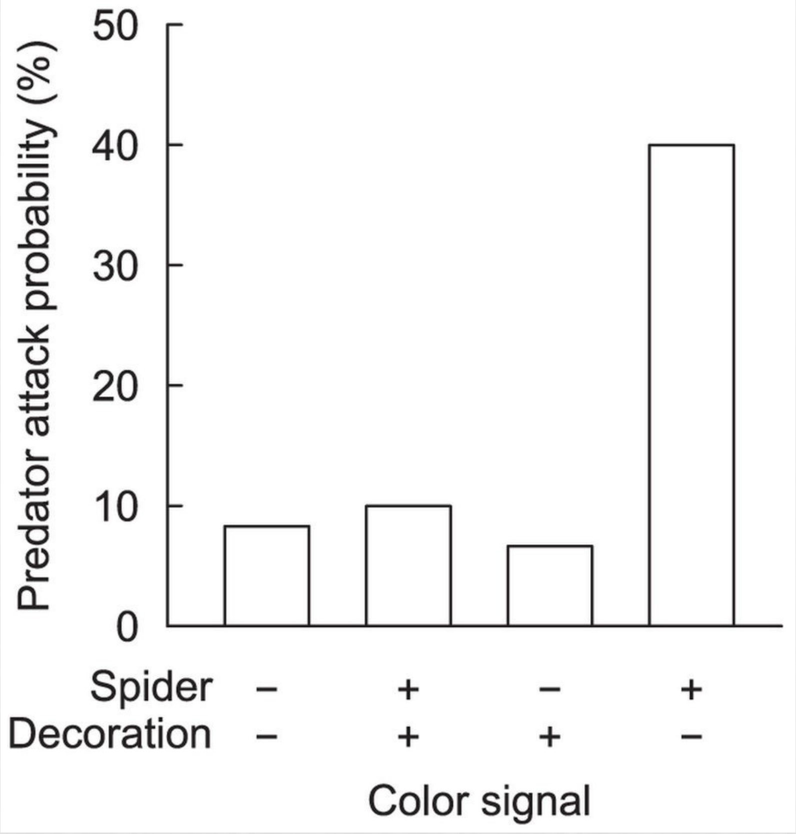
Poltys

Epicadus

Caerostris

Liu et al. (2014)

- *Cyclosa ginnaga* on the stabilimentum resembles a bird-dropping
- spectrometric profiles were similar between spiders and bird droppings
- birds attacked more spiders with blackened decorations than other treatments



Startle

- signals (acoustic, visual) produced after
attack by undefended prey
- signals are hidden and triggered by predators
- after display prey relies on fleeing or hiding
- stimulates predator's sense to delay subjugation
- used against rare predators
- used by Acari, Amblypygi, Araneae, Opiliones, Scorpiones, Solifuges

<u>Visual displays</u>
- posture displays (increase body size)
- aposematic markings underneath
- body jerking (difficult to focus)

<u>Acoustic display</u>
- stridulation (disturbance)

Phoneutria

Pholcus

Deflection

- prey influences position of the initial contact of the predator to decrease risk of harm (chance of escape)
- based on sensory exploitation of predator’s perception
- in the form of appendotomy:
    - Autotomy – reflex action
    - Autotilly – self-removal
    - Autospasy – restrained by extranal force
- detached lesg/telson may twitch
- used by most orders

Costs:

- some body part is sacrificed

– it might/not be regenerated

Philodromus

Thanatosis

- adoption of an immobile state reminiscent of dead animal
- reduces risk of detection/capture after primary detection
- last-resort defence alike fleeing, counter-attack
- remain in thanatosis for few minutes
- used by Acari, Opiliones, Ricinulei, Araneae

Costs:

- loss of opportunities

Latrodectus

Hoplobunus