Sex specific plasticity in life-history and the mating system of *Trichonephila senegalensis*
Acknowledgements

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Sex differences

Sexual selection is responsible for many sex specific traits

- however, it is not always that simple ....
- e.g. size differences are more complex to explain

Peacock spiders (genus Maratus): Males look and behave different from females

Photos: Jürgen Otto
Sexual Size Dimorphism in spiders

Argyroneta aquatica

Maratus spec.

Nephila clavipes
Sexual size dimorphism (SSD)

- Genes underlying body size are usually correlated between sexes
- To achieve SSD, selection must act on both sexes in opposite directions
Nephilidae: giant females & dwarf males

Genera: Clitaetra, Nephilengys, Nephilingis, Herennia, Trichonephila, Nephila
Recent analyses of Nephilidae:

Phylogenetically independent contrasts analyses using a variety of body size metrics:
Female and male size evolution = INDEPENDENT (n=28; $r^2=0.0008; p=0.886$).
Males are „normal“ size, females are giants
**Nephila**: Golden orb-web spiders

Our study species:

*Trichonephila fenestrata*
*Trichonephila senegalensis*

Occur sympatrically in Central and Southern Africa
Sexes are size dimorphic + highly variable

Trichonephila senegalensis

CV$_{\text{males}}$ (n=213) = 31%
39 +/− 12 mg

CV$_{\text{females}}$ (n=210) = 25%
965 +/− 243 mg
Female gigantism and male dwarfism

Why are females so large?
Why did males remain small?
Where does size variation come from?

- Trade-offs & selection pressures should be revealed in individual responses to variable conditions
Effects of nutrition on adult body size

**Split-brood design**

- High-High
- High-Low
- Low-High
- Low-Low

**Switch after 4 weeks**

**8 families, 1256 individuals**

- X = SEX, TREATMENT, FAMILY
- Y =
  - Adult body size
  - Duration of development
  - Female fecundity
  - Hatching success
  - Longevity post-maturity

Neumann, Ruppel & Schneider 2017 PeerJ
All families produce all sizes

Female offspring

Male offspring

Neumann, Ruppel & Schneider 2017 PeerJ
Body size at maturation

Differences in prey availability shift the mean but not the variance

Adult size = tibia-patella length
Female development

High food: females maximise body size and developmental speed
Restricted food: delay of maturation, not necessarily reduced body size

**HH – LH: no difference**
Poor conditions in early life can be compensated fully

**LL – HL: no difference**
High prey early in life does not increase adult size

Neumann, Ruppel & Schneider 2017 PeerJ
Female catch-up growth

LH Females prolong the duration of development and completely catch-up in body size

Selection maximises body mass and size

Traded-off against time

Neumann, Ruppel & Schneider 2017 PeerJ
No apparent costs through catch-up growth

High-High and Low-High females are not different in their fecundity

Supports hypothesis of fecundity selection on females

No differences in hatching success and adult longevity
Summary

**Strong directional selection on female size**

Females maximise body size and fecundity

Females compensate poor conditions in early life through catch-up growth at the cost of delayed maturation

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Natural selection
Male development

- Mixed feeding treatments (HL, LH) have different effects on males and females.
- Maturation becomes asynchronous: extreme protandry or synchronous maturation.

Neumann, Ruppel & Schneider 2017 PeerJ
SCAP – fine tuning of maturation

Socially cued anticipatory plasticity

• Fine-scale adjustment to variation on fine temporal & spatial scales
• Variation in availability of mate and/or competition for mates
• Can help males to adjust maturation to females in the direct vicinity

Kasumovic & Brooks 2011 Quarterly Review of Biology
Methods

In a split-brood design, males were kept in two identical climate chambers

- one group kept without females and cues,
- males in the other chamber received fresh silk from adult, virgin females once a week
Males respond to female cues

- Males that received female cues developed a few days sooner than males without cues
- Males that did not perceive cues delayed maturation
  - By remaining in the penultimate stage, males can still hunt & feed
  - Adult males survive by scavenging in female webs

- Results support selection for protandry
- SCAP may help to speed up and/or to wait

Neumann & Schneider 2016 BMC Evol Biol
Why is male adult body size so variable?

Large males only occur under conditions that produce large females.
Male catch-up growth

- Male catch-up less than females
- No body mass compensation in males

Selection acts stronger on optimising the timing of maturation than body mass/size.
**Summary – growth plasticity**

- *Nephila senegalensis* shows highly opportunistic life-history
- Both sexes respond plasticially to different prey regimes
- Body size determined by family and environment
- FEMALES: show catch-up growth and maximise body size
- MALES: optimise the timing of maturation and respond to female cues for fine-scale adjustment (SCAP)
- Results support fecundity selection on females and protandry selection on males
Extreme SSD in Spiders

associated with:

- **Monogynous mating system**
- Sexual cannibalism
- Self sacrifice
- Genital mutilation

*Herennia multipuncta, Nephila pilipes, Nephilengys malabarensis*
Monogyny

Definition:
- Males actively limit their mating rate to one
- Females may mate multiply
- No paternal care

Adaptive benefits through
Increased paternity share
= best supported explanation

Theory predicts monogyny requires male-biased sex ratio
- Well supported in many spiders
BUT certain conditions allow for alternative strategies
under frequency-dependent selection
- Either genetically or conditionally plastic

Rare overall but taxonomically widespread

Known in
- Annelids
- Echiura-Bonellia
- Rotifers
- Honeybees
- Stingless Ants
- Anglerfish

Particularly common in spiders

Fromhage, Elgar & Schneider 2005 Evolution, Fromhage & Schneider 2012 EcolEvol
Trichonephila fenestrata = monogynous

Genital damage
- Conductor tip breaks during copulation
- Pedipalp dysfunctional
- Blocks the entrance of the insemination duct
- Rivals can bypass plug

Mate guarding by eunuchs
- Males can escape sexual cannibalism
- Mated, sterile males win fights
- Mated males escalate fights
- Mated males cause a higher incidence of injury

Tips remain stuck in female genital openings

*used pedipalp is damaged

ONE-SHOT GENITALIA

Fromhage & Schneider 2005a,b AnBehav, Fromhage & Schneider 2005, 2006 Behav Ecol
Trichonephila senegalensis

• No genital damage, no plugging
• Males mate repeatedly
• Fertilise between 2 and 7 females
• After 4 copulations, many matings resulted in unfertilised eggs
• WHY?
  permanent sperm depletion

Schneider & Michalik 2011 BMC EvolBiol
Termination of spermatogenesis

- Following sperm induction (Phase 3) there are no sperm cells in the testes
- Males can charge their pedipalps ONCE
- Stored sperm will be portioned
- Males invest sperm differently!

PSD also demonstrated in:
- *Nephila clavipes*
- *Argiope keyserlingi*
- *Tidarren*
Trichonephila senegalensis

- No genital damage, no plugging
- Males mate repeatedly
- *Despite permanent sperm depletion*

  - Mating system likely derived from monogyny
  - Some typical traits are lost, but not all

**Males doubled potential mating rate**

Schneider & Michalik 2011 BMC EvolBiol
Size related male mating strategies

Large variation in male size/mass

Why?

- double mating study
- males of all size classes compete
- paternity with sterile male technique

Male adult body mass (mg)

Neumann & Schneider 2015 Anim Behav
Size related paternity success

- Average paternity does not differ between size-classes

- Large males are most successful with large females
- Medium sized males do better with small females
- Small males do well independent of female size

Neumann & Schneider 2015 Anim Behav
Size related paternity success

- Average paternity does not differ between size-classes
- Likely explained by size dependent mating investment strategies
- Supports theoretical model (Rittschof et al 2012)
- Large males invest less sperm in copulations with small females

Neumann & Schneider 2015 Anim Behav
Summary

Selection favours protandry

- Particularly large males must mature early
- Sexual selection favours large male size especially under conditions that also produce large females

Size dependent mating strategies result in equal fitness

Variation maintained under negative frequency dependent selection
Take home message

- *Trichonephila senegalensis* shows highly opportunistic life-history
- FEMALES: perform catch-up growth; MALES: can fine-tune the timing of maturation
- Males show size dependent mating tactics: Large males defend large females, small males sneak copulations
- Males evolved polygyny despite heritage of PSD

WHY?
Thank you for your attention