



National University of Singapore

LSM1303 Animal Behaviour

Lecture 08: Courtship and Mating



Courtship display of Rhinoceros Hornbill
in Borneo by Nara Simhan @ Flickr



N. Sivasothi aka Otterman

What is Courtship?

- all behaviour that precedes and accompanies
- the sexual act
- leading to the conception of young

What is Courtship?

- the function of a behavioural pattern is its contribution to the survival of that animal or its offspring.
- Courtship creates the circumstances in which successful mating is possible.
- It also results in reproductive isolation, intra-sexual competition and mate assessment

Observation: Synchronicity

- To achieve simultaneous release of sperm and egg (external fertilisation)
- To indicate readiness to mate to enable the approach of an aggressive female
- To invite a female to adopt a vulnerable position with an aggressive male.



Mating Lions, Etosha National Park, Namibia by Frank.Vassen @ Flickr

Why have sex?

Costly exercise

Advantages, disadvantages

Advantage of asexual reproduction?

Clones pass on all of their genes to their offspring
(budding, fragmentation, regeneration, parthenogenesis)

No loss of genetic information

Cf. the cost of sexual reproduction = the loss of half its genome



Watts, P. C., Buley, K. R., Sanderson, S.,
Boardman, W., Ciofi, C., & Gibson, R., 2006.
Parthenogenesis in Komodo dragons.
Nature, 444(7122), 1021-1022.

Parthenogenesis - ‘virgin birth’ Komodo dragons (2006)

Remember Jurassic Park?

Facultative parthenogenesis in **wild** North American pitvipers



Virgin births

- 10 species of snakes
- four species of shark
- several monitor lizards
(including the Komodo dragon)

The concern in zoos?
The concern in
conservation of species?

Great if you stay in an
unchanging environment and
it's tough to find a mate!

What if the
environment changes?

Advantage?

What advantage over asexual reproduction?

Variability

With sex, there is mixing of genes
Genetic recombination, genetic diversity
Loss of harmful genes

“Asexual clones” versus the
“lucky draw of reproduction”

“Genetic diversity is
essential for a species to
evolve”

Trials of reproduction

A long process with many selection mechanisms

Male-male competition and Female choice

Trials of reproduction

I. Attracting a mate (inter-sexual)

- Sensory cues attract a potential mate.
- Locate and identify potential mates.

2. Stereotyped courtship and mating activities (inter-sexual):

- Specific cues (isolating mechanisms) prevent crossbreeding and wasted energy on infertile matings.

Trials of reproduction

3. Demonstration of greater fitness than rivals (intra/inter-sexual)

- Monogamous species - demonstrations that reflect nutrition and strength. E.g. bird song, nuptial gifts, hunting displays
(90% of bird species are monogamous).
- Polygamous species - forceful retention of females, fending off rivals (in mammals e.g. elephant seals) and exaggerated displays (birds

Trials of reproduction

4. Arouse sexual motivation (inter-sexual)

- Sensory cues enhance sexual arousal.
- Overcome aggression/predation, persuade to mate.
- Synchronize behavior to allow mating.

5. Copulation.

6. Post copulation competition (intra-sexual) - amongst sperm.

1. Attracting a Mate

Scent, visual, displays, sound

I.I Attracting a mate by scent

Social odours - insect

The “Trilobite larvae”



Alvin Loke



Mating adult beetles – here
both genders of the beetle are
adult forms with wings

Metriorrhynchus rhipidius (Lycidae)
[Benjamint444 @ Wikimedia]

In trilobite beetles, the females retain the juvenile form (neotenous) and adults look like larvae



Tan Heok Hui



Alvin Wong

Female

Male



Trilobite beetle, undergoes a final moult and wafts pheromones into the air

Duliticola hoiseni

Alvin TC Wong (MSc thesis)





Alvin
Wong

Wong, A.T.C., 1998. A revision of the neotenous 'trilobite larvae' of the genera Duliticola and Platerodrilus (Coleoptera: Cantharoidea: Lycidae). M. Sc. Thesis. School of Biological Sciences, Faculty of Science, National University of Singapore, Singapore. 168 pp.

The male beetle was found tightly attached to the female's gonopore via its long curved genitalia for at least five hours before releasing the female.

The male died 3–4 hours later. The female laid a batch of 200 eggs the following day and died a week later



I.2 Attracting a mate by visual displays

Bower building



Bowerbirds

- Twenty species in the Austro-Papuan region
- Males build a courtship structure (not a nest),
- decorate it with sticks and brightly coloured objects
- to attract a mate.

Female satin bowerbird



Bowerbird | BBC | 5:02



I.2 Attracting a mate: visual



Baya weaver
(Ploceus philippinus)



Firefly displays

Kuala Selangor, Malaysia



I.3 Attracting a mate by sound

I.3. I Birdsong (nocturnal)

- Nightingale



I cannot see what flowers are at my feet,
Nor what soft incense hangs upon the boughs,
But, in embalmed darkness, guess each sweet
Wherewith the seasonable month endows
The grass, the thicket, and the fruit-tree wild;
White hawthorn, and the pastoral eglantine;
Fast fading violets cover'd up in leaves;
And mid-May's eldest child,
The coming musk-rose, full of dewy wine,
The murmurous haunt of flies on summer eves.

Ode to a Nightingale
BY JOHN KEATS

Straw-headed bulbul

(Lee Shiou Ming, 2015)



Birdsong (nocturnal)

- Large-tailed Nightjar (*Caprimulgus macrurus*)



I.2 Attracting a mate: sound

I.3.2 Cicada

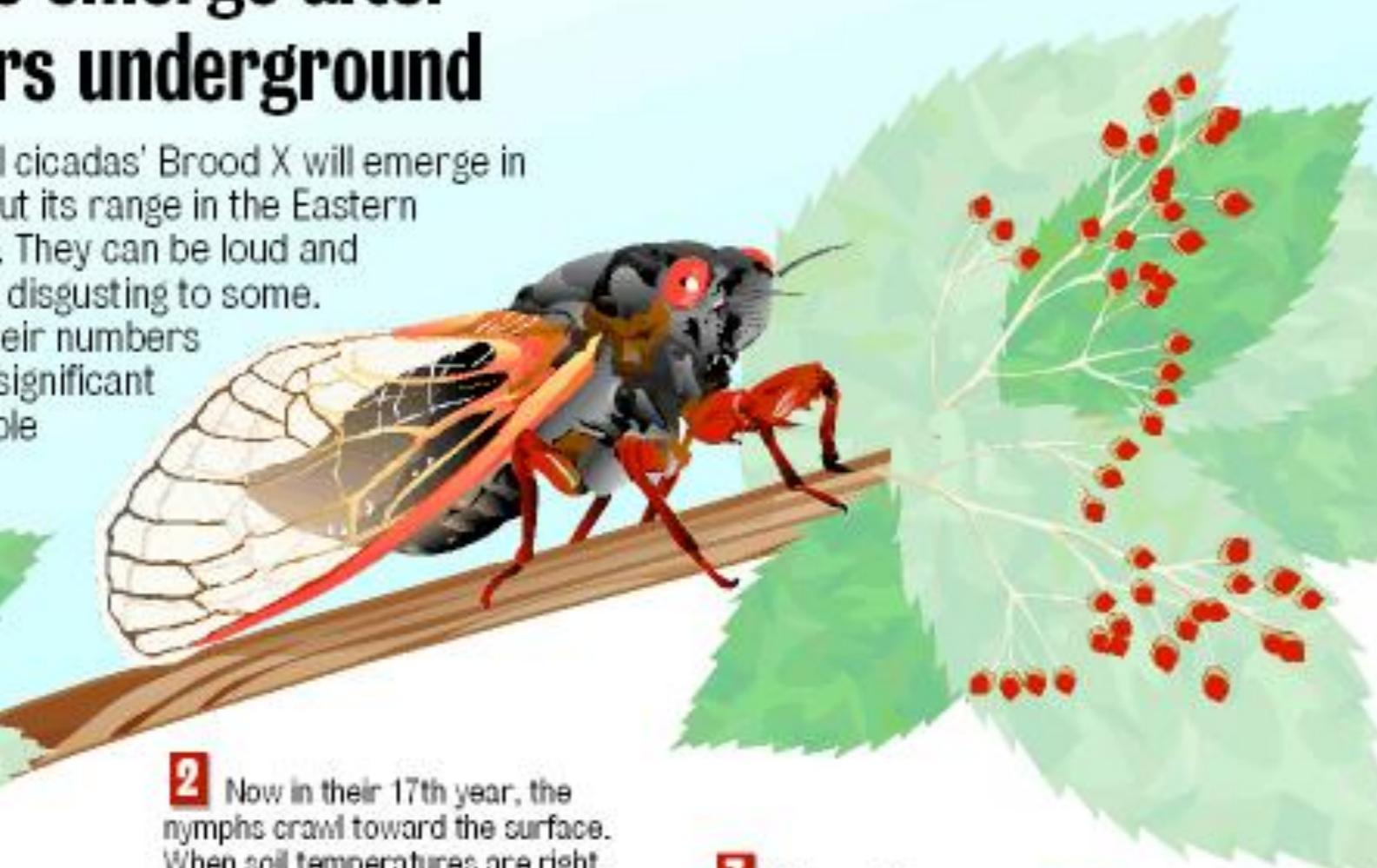


Moultling Cicada



Cicadas emerge after 17 years underground

The periodical cicadas' Brood X will emerge in May throughout its range in the Eastern United States. They can be loud and annoying, and disgusting to some. But despite their numbers they pose no significant threat to people or animals.



2 Now in their 17th year, the nymphs crawl toward the surface. When soil temperatures are right, they emerge by the millions, climbing trees or vertical surfaces. After shedding their skin, the adults spread their wings. The males fly into the trees and begin to call to the females with loud buzzing.

3 After mating, the female cuts slits in the bark of twigs and deposits more than 400 eggs, 24 to 48 per slit.

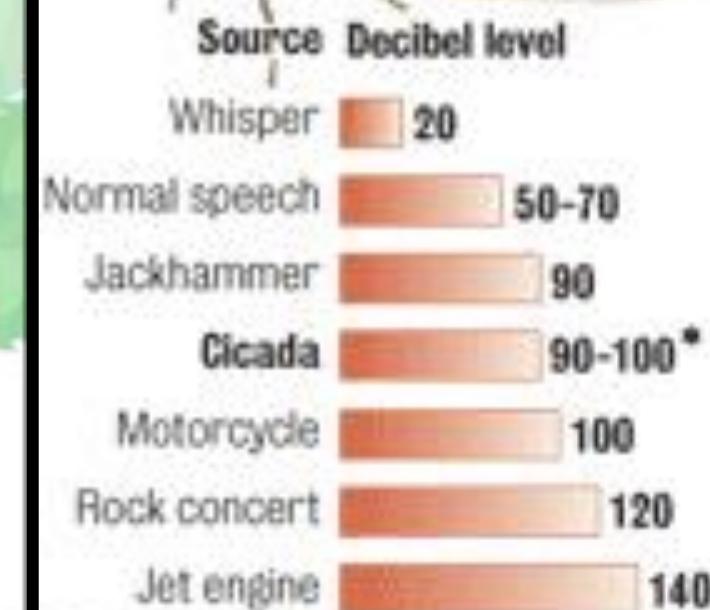
4 The eggs hatch in six to 10 weeks. The antlike nymphs drop to the ground and burrow several feet into the soil. There, they will feed and await their next emergence, in 2021.

Life cycle

1 Deep underground, the cicada nymphs have fed on the sap in tree roots since 1987.



Sound comparisons



*Typical range

Source: Sun staff researcher

SHIRDELL McDONALD ; SUN STAFF

Baltimore Sun



Photo courtesy of
Amanda Hevel.



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Thu 31 Mar 2005

Hundred(s) of cicada moults on Pulau Ubin

Category : [nature](#)

Most of us have heard the drone-like calls of cicadas in our forests but rarely seen them. They have an interesting life cycle which takes them from tree root to tree-top.

Eggs are laid in small grooves cut into tree bark or shoots. When the eggs hatch, the larvae drop to the ground and burrow into the soil. Feeding on the sap of tree roots, the larvae or nymphs grow each time they shed their exoskeleton (moult). Unlike butterflies, they do not undergo complete metamorphosis so there is no pupal stage, and the nymphs look very much like the adults.

Upon maturity, the cicada nymphs emerge from the soil as a group and climb up trees. They shed their exoskeleton for the final time (terminal moult) and emerge as winged-adult cicadas, leaving behind moult skins we may see on tree trunks in forest, which are light-weight, translucent, and which retain the morphological details right down to the fine hairs!

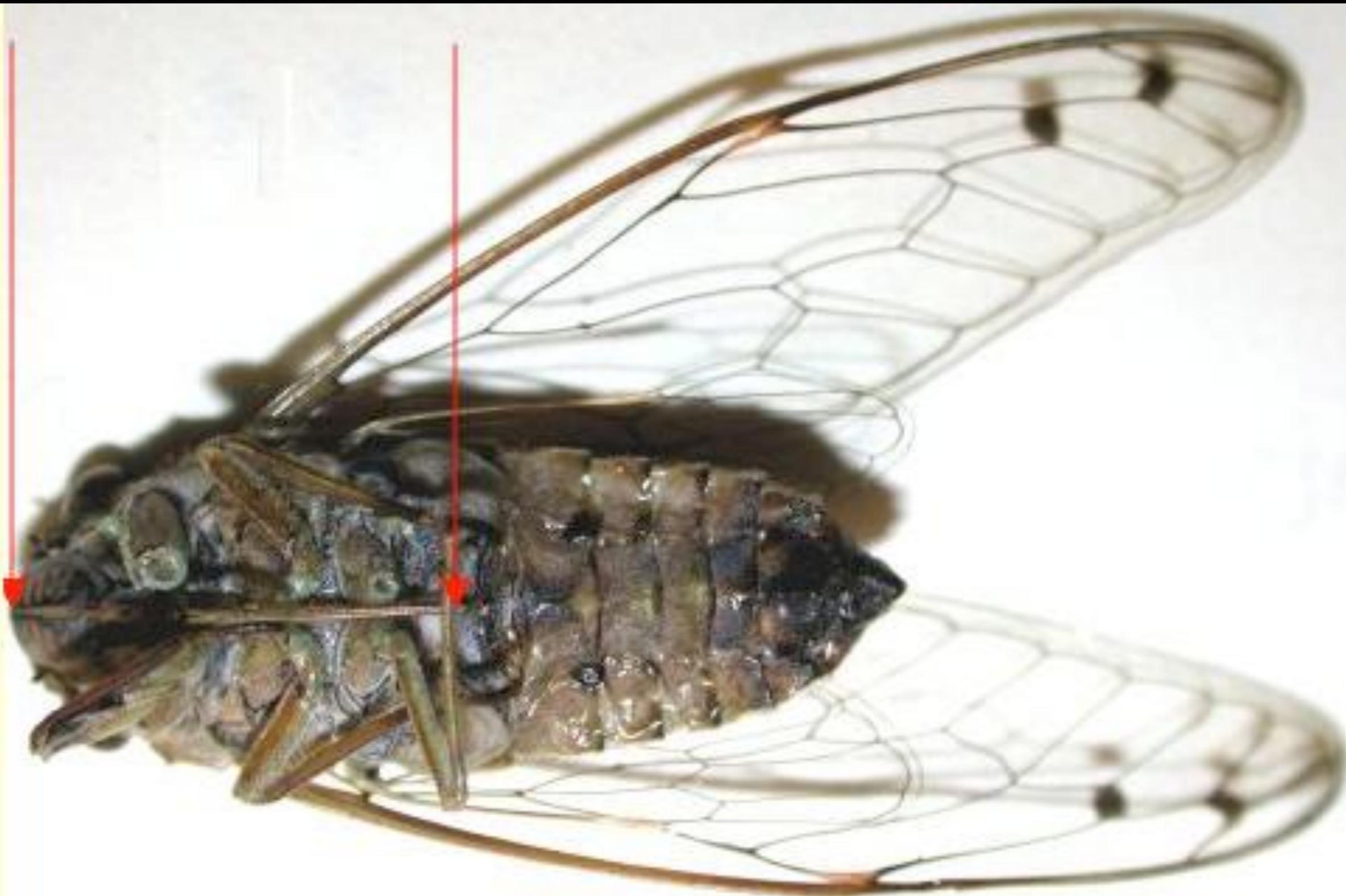


Up in the tree canopy, the cicadas feed and the resulting spray can be quite noticeable - see this report from [Labrador Park](#) from June 2004.

Meanwhile, the din we hear are of the males calling for a mate - hence we hear cicadas rather than see them. We do see moults once in awhile and very rarely see the actual insect.



© Chim Chee Kong





Cicadas at Labrador Park

I.4 Hazards of sexual advertisement

Tungara frogs







Bats echolocate, frogs see



Which is the male?



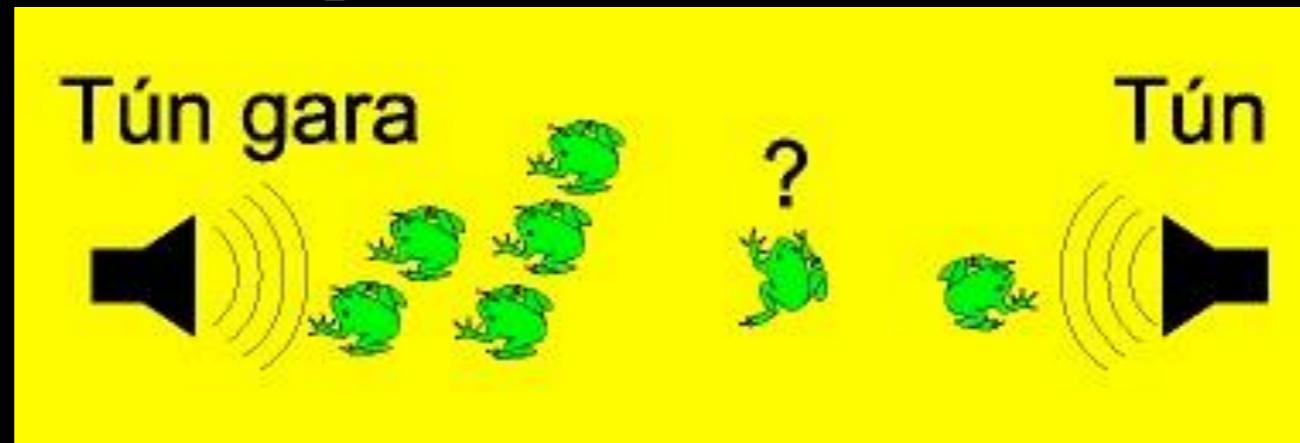
Tungara frogs: Two types of calls



Gravid females (swollen with eggs) hear potential consorts
and they will swim to the males they choose.

The selected male climbs aboard a female's back.
She carries him off to fertilize the eggs she will eject.

Which do females prefer?



Females prefer males with the more complex call:

= whine + chuck

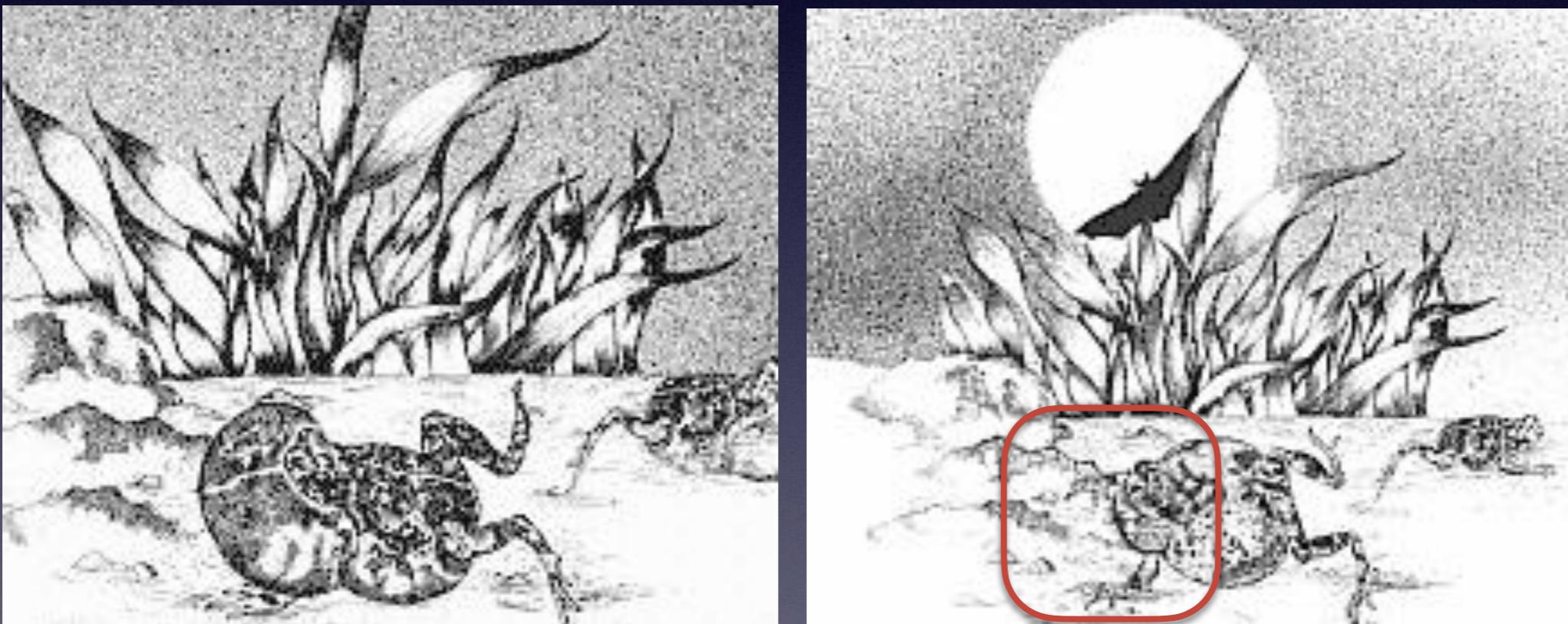
Chuck = lower frequency = larger male;
larger male more compatible with female

Which do bats prefer?

Eavesdropping on frogs



Call less when bats can be seen



http://striweb.si.edu/forest_speaks/english/fauna/frogs/index.html

Frogs which see approaching bats stop calling, deflate their vocal sac, immerse deeper into water and finally dive and swim away

Ripples give away location



Generating the call creates a circle of ripples in the water.
(Photo by Ryan Taylor/Salisbury University)

Bats dove at ripple
ponds 36.5% more often
than still ponds

Halfwerk, W., Jones, P. L., Taylor, R. C., Ryan, M. J., & Page, R. A. (2014).
Risky ripples allow bats and frogs to eavesdrop on a multisensory
sexual display. *Science*, 343(6169), 413-416.

May call less also
when bats
cannot be seen
(i.e. no surprise attack)

Call less in small groups, call more in larger groups

Cost-benefit balance

Attraction of mate

vs

Attention of predators

Hence males exhibit **facultative calling!**

Not all bats eat frogs



Green tree frog (*Litoria cerulea*) eating a bent-wing bat (*Miniopterus australis*), Australia

2. Intra-sexual competition

May the best genes win

The best one mates with partner; but a partner may want choice

2. I Theory of natural selection is stumped by prominent displays - risk?



"The sight of a feather in a peacock's tail,
whenever I gaze at it, makes me sick."

--Charles Darwin 1887

So costly?!

How could it benefit the animal
and its offspring?

New theory - **sexual selection!**

evolutionary process that
favours adaptations that increase
an animal's chances of mating

Sexual selection

- two kinds

I. Male competition

Males compete fiercely with each other
for access to females.

- favours characters such as large size, armaments
 - which enhance a male's ability to fight.

Sexual selection

- two kinds

II. Female choice

Males compete to win over mate.

- characters that heighten a male's attractiveness to the opposite sex.

E.g. vivid color patterns,

- intricate courtship displays,

2.2 Male competition

Fighters are larger,
egged on by testosterone

Bighorn sheep (*Ovis canadensis*)



Lance and Erin @ Flickr

Bighorn sheep

- Prior to the mating season or "rut", rams attempt to establish a dominance hierarchy that determines access to ewes for mating.
- Testosterone peaks during the pre-rut (when social relationships are established).
- Declines from the pre-rut to the rut.
- **Testosterone levels was correlated with social rank.**

Pelletier, F., J. Bauman & M. Festa-Bianchet, 2003. Fecal testosterone in bighorn sheep (*Ovis canadensis*): behavioural and endocrine correlates. *Can. J. Zool.*, 81(10): 1678–1684.



Heavy weight males:
Elephant Seals



Beachmaster Elephant Seal Fights off Rival Male |
BBC Earth | “Beachmasters may control
harems of 100-plus cows.” | 2:03

BBC



2.3 Female Choice

Males work hard to impress

Common Myna (*Acridotheres tristis*)

The courtship display of the male is characterized by head bowing and bobbing, fluffed plumage and vocalisations



The Bowerbird's Grand Performance! | Life Story | BBC

BBC



3. Courtship (sexual arousal)

Enabling approach; readiness to mate

Who needs this?

3.I Three-spined stickleback



Male courts female,
stimulates egg deposition by female,
male then fertilises eggs

3.2 – 3.5 Courting solitary,
aggressive females

3.2 The conflicted male approach of female Spotted Hyaenas



Photo by Kay E. Holekamp

Courting dominant females in the spotted hyaena matriarchy
is dangerous business | Animal Planet | 2:36



Spotted hyenas (*Crocuta crocuta*)

- Male hyenas initiate most courtship interactions with larger and more aggressive females.
- Males display unique “approach-avoid” and “bowing” behaviours - approach/flee behaviours.
- Males also show signs of fear when trying to mount the females.

Spotted hyenas (*Crocuta crocuta*)

- Males prefer higher ranking females.
- Female receptivity is subtle and they are less threatening when receptive, adopting a stance that signals the male.
- Females are more aggressive to the advances of immigrant males but they father 97% of all cubs!

3.3 Sexual cannibalism

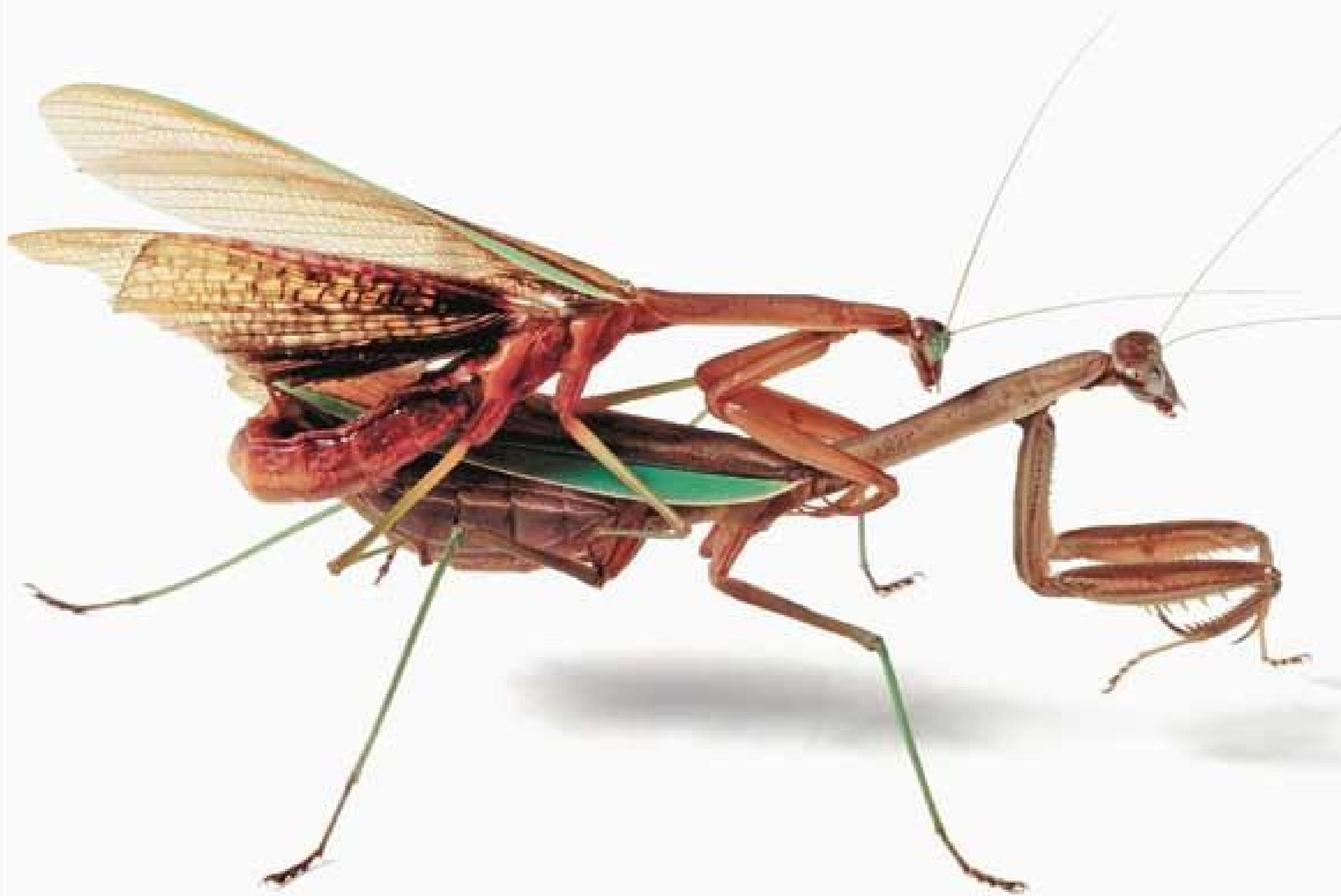
Female's food, fact or fiction?



Praying mantis



4.3 Sexual cannibalism in praying mantises





Catherine Chalmers





Cannibalism as a means of terminal parental investment

- Sexual cannibalism by female hunters with predatory response during courtship.
- Body of male contributes nutrition (successful courtship)?
- Biasness of laboratory experiments

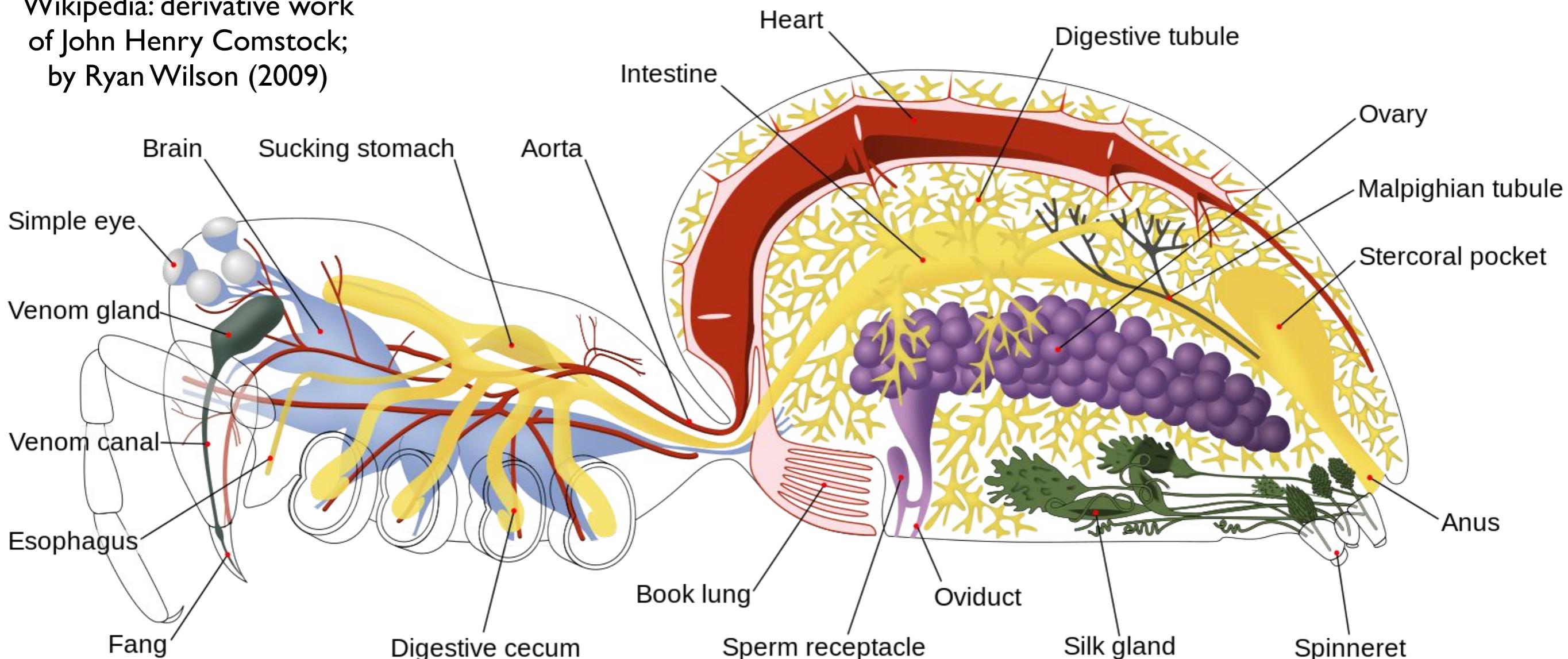
What really happens?

- Hungry females attract fewer males than satiated females; males more cautious too
- Dismounting is dangerous - cannibalisation often happens then; males spent a longer time on a hungry female before dismounting
- Male submissiveness may not inherently increase male reproductive success
- Instead, cautious and fit males escape to mate with multiple females

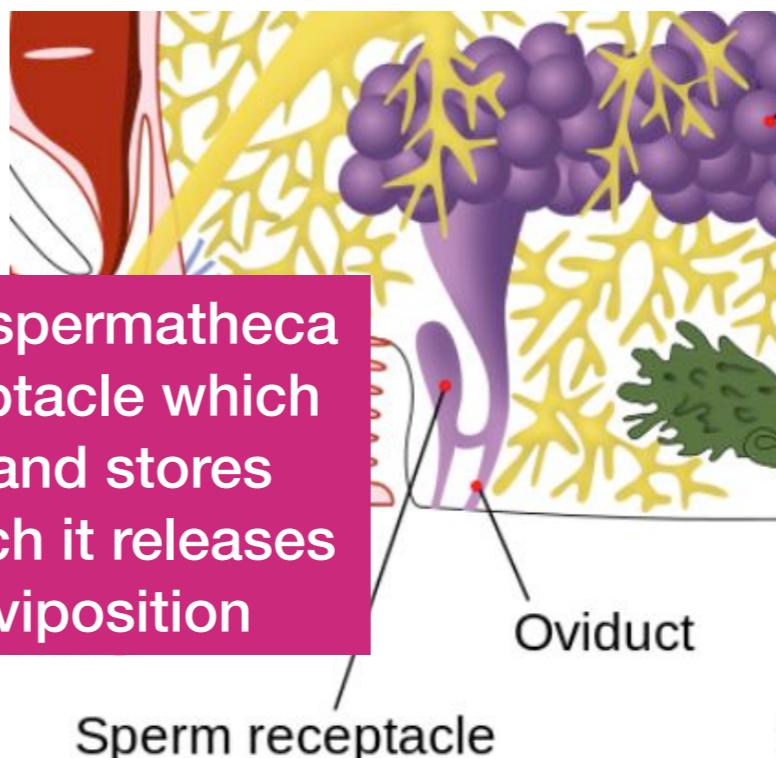
J. P. Lelito & W. D. Brown, 2006. Sexual conflict in a praying mantis. *The American Naturalist*, 168. Lelito J. P. & Brown W. D., 2006. "Complicity or Conflict over Sexual Cannibalism? Male Risk Taking in the Praying Mantis *Tenodera aridifolia sinensis*". *The American naturalist* 168 (2): 263–9.

3.4 Sexual cannibalism in *Latrodectus hasselti*, the Australian red-backed spider





The paired spermatheca is the receptacle which receives and stores sperm, which it releases during oviposition



Sexual cannibalism in the Australian red-backed spider (*Latrodectus hasselti*)

- Paired independent spermatheca.
- Male inseminates one organ.
- Somersaults 180-degrees, presents its abdomen.
- Female begins to devour the male,
 - male success with a second insemination higher
- Most males do not survive this process (2/3; survivors mostly die of injuries)

Red-backed spider (*Latrodectus hasselti*) sacrifice increases fertilisation success (2:02)



Sexual cannibalism in the Australian red-backed spider (*Latrodectus hasselti*)

- Cannibalised males copulate longer.
- Fertilise more eggs than males that survive.
- Females are more likely to reject subsequent suitors after consuming their first mate.
- Thus redback males facilitate sexual cannibalism by shifting their abdomen above the female's fangs during copulation.

Sexual cannibalism in the Australian red-backed spider (*Latrodectus hasselti*)

- However, males are not always successful.
- Females often cannibalize smaller males during first copulation.
- I.e. limiting paternity to 50% (one spermatheca).
- Female control of paternity - mates with subsequent suitor

Forster, L. M. (1992). "The Stereotyped Behavior of Sexual Cannibalism in *Latrodectus hasselti* Thorell (Araneae, Theridiidae), the Australian Redback Spider". *Australian Journal of Zoology* 40: 1.

Males also bite through the exoskeleton of juvenile females to deliver sperm without somersaults!

3.5 The self-mutilating male *Nephila fenestrata*

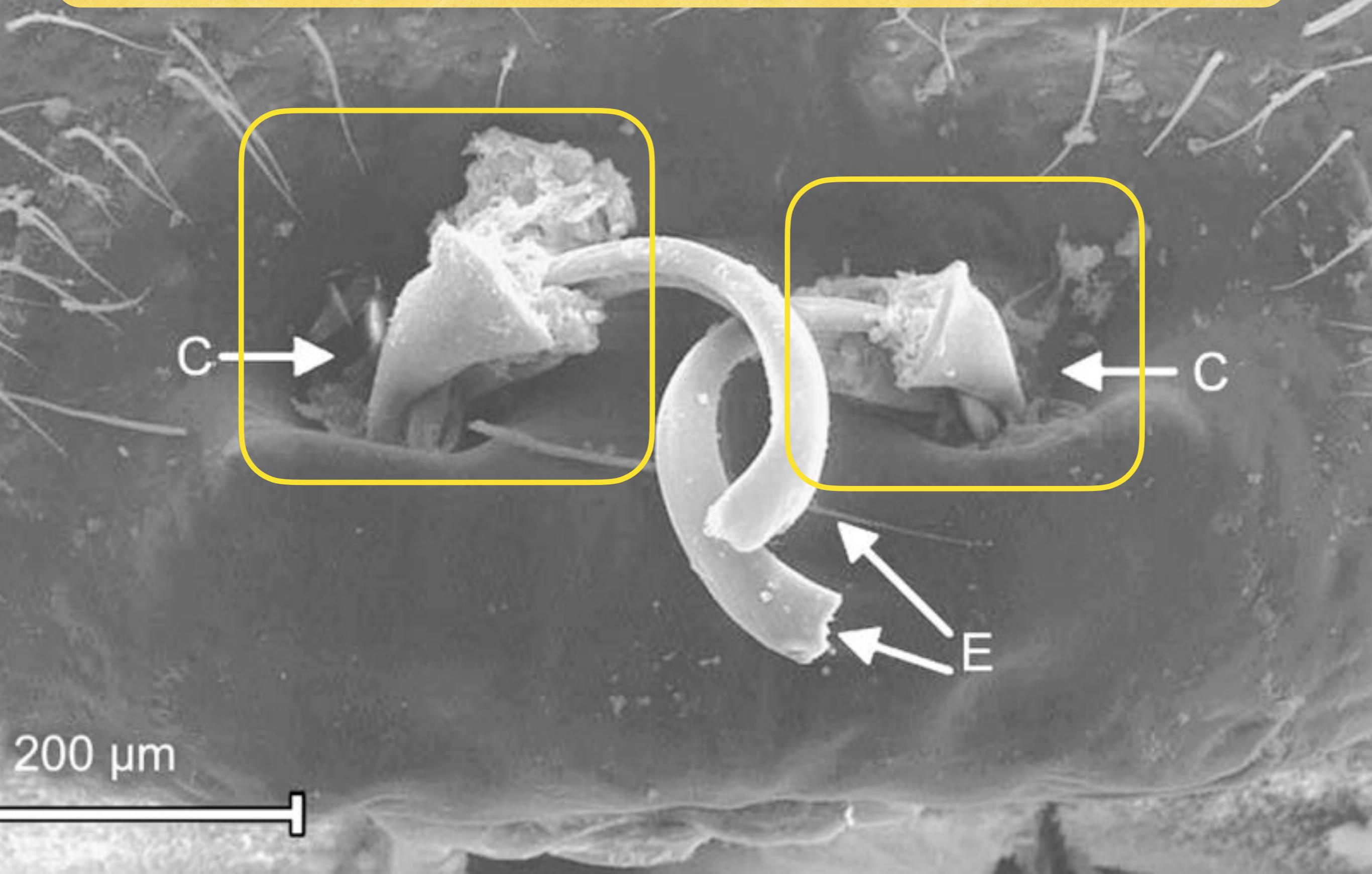
Seminal plugs in *Nephila fenestrata*
(also engages in post-copulatory mate guarding)

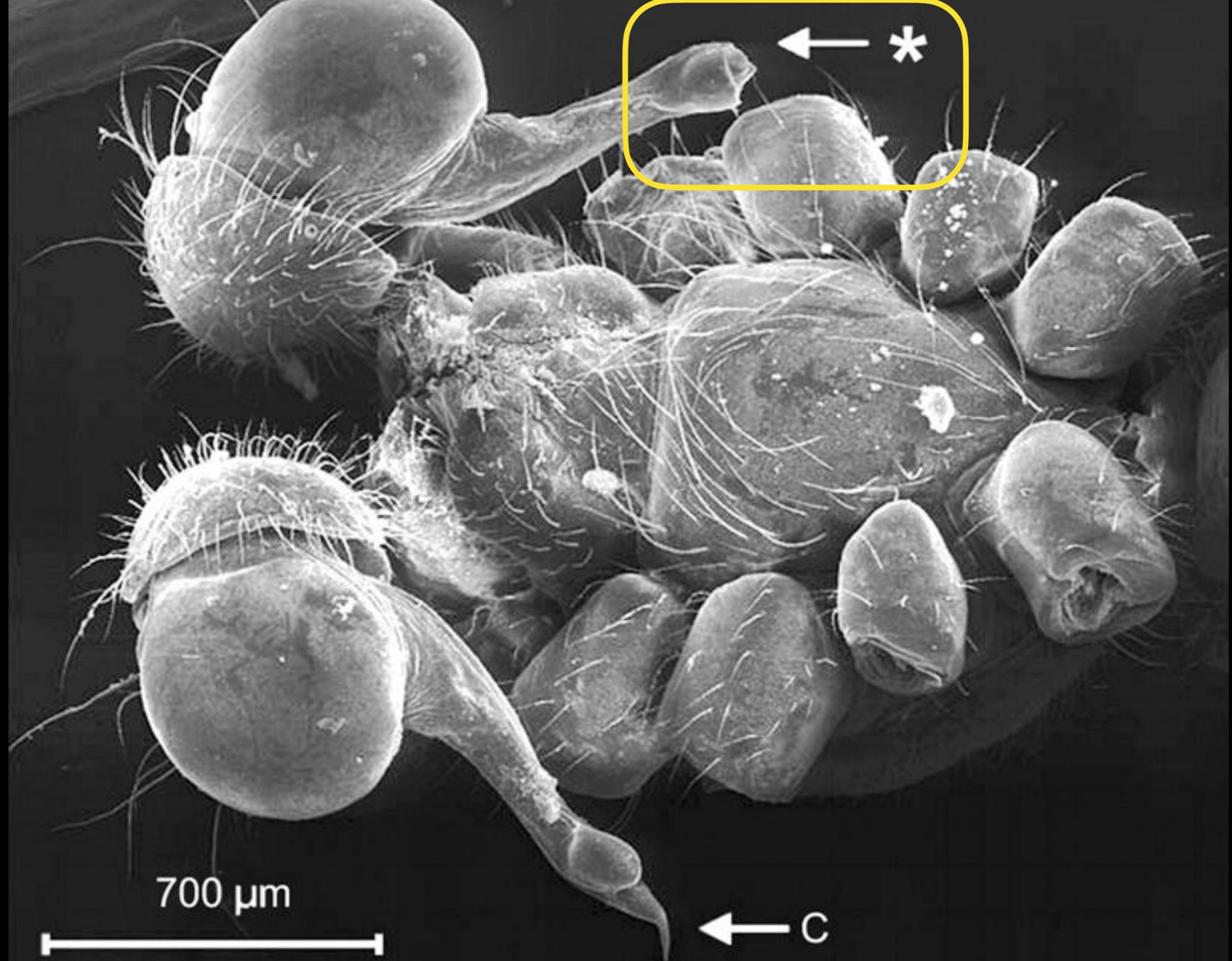


Nephila fenestrata
(Hairy Golden Orb Weaver)

Photo from Lutz Fromhage, Flickr

Genital region of mated *Nephila fenestrata* female. Each genital opening is plugged by a conductor (C) and its corresponding embolus (E).





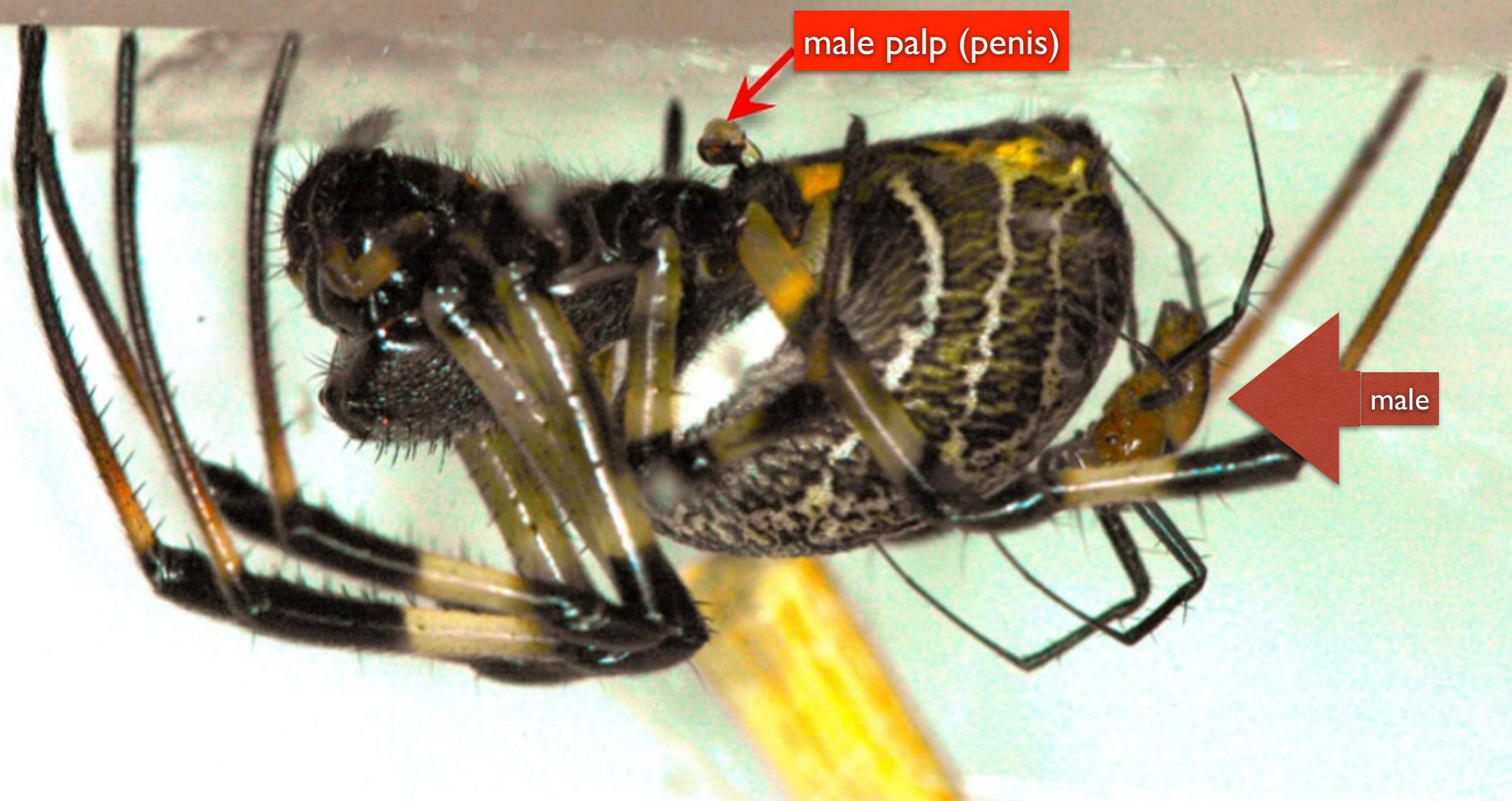
Mated *Nephila fenestrata* male, ventral view (legs removed). The conductor (C) is intact on the right pedipalp but missing on the left side (asterisk).

Eunuch spiders are superior fighters!

- Male spiders which have broken off their palp (eunuchs) and which survive female cannibalism
- stay nearby to prevent competitors from dislodging their palpal plug
- These eunuch males usually win fights with other, intact, males.
- The 9% "palp weight poses significant physical costs to males."

Lee, Q. Q., Oh, J., Kralj-Fišer, S., Kuntner, M., & Li, D. (2012). Emasculation: gloves-off strategy enhances eunuch spider endurance. *Biology letters*, rsbl20120285.

Orb web spider (*Nephilengys malabarensis*): male much smaller than the female!
Here, the much smaller male is resting on the female's abdomen after escaping from
female cannibalism via emasculation during copulation.
The self-emasculated male palp (red arrow) is lodged in the female's epigynum.





Nephila pilipes
(Giant Golden Orb Weaver)
Can be seen on Kent Ridge

4. Post copulatory choice

Female choice

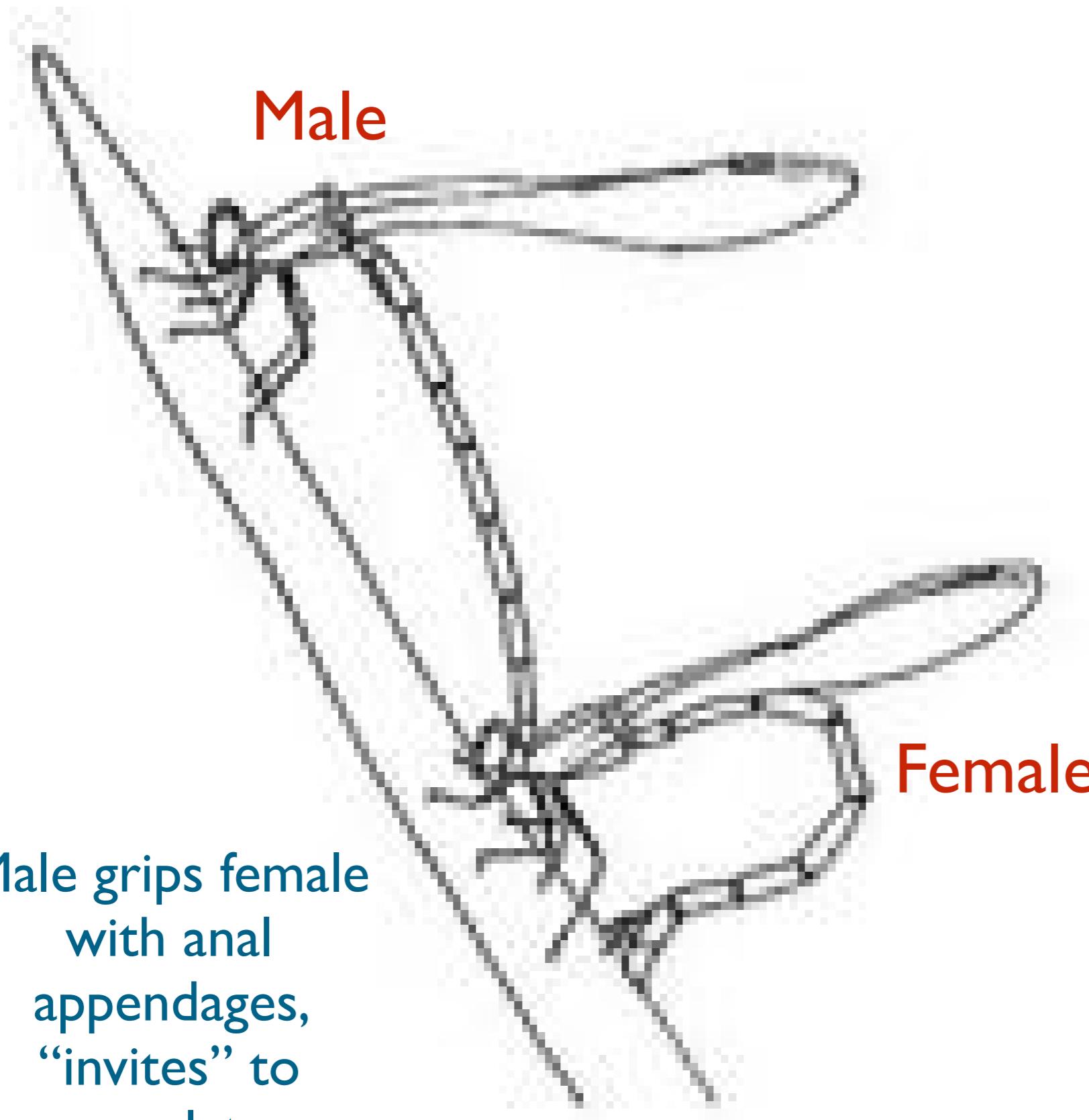
It ain't over until...

Competition between
males does not
end at mating!

4. I Mate guarding

Black-winged damselfly





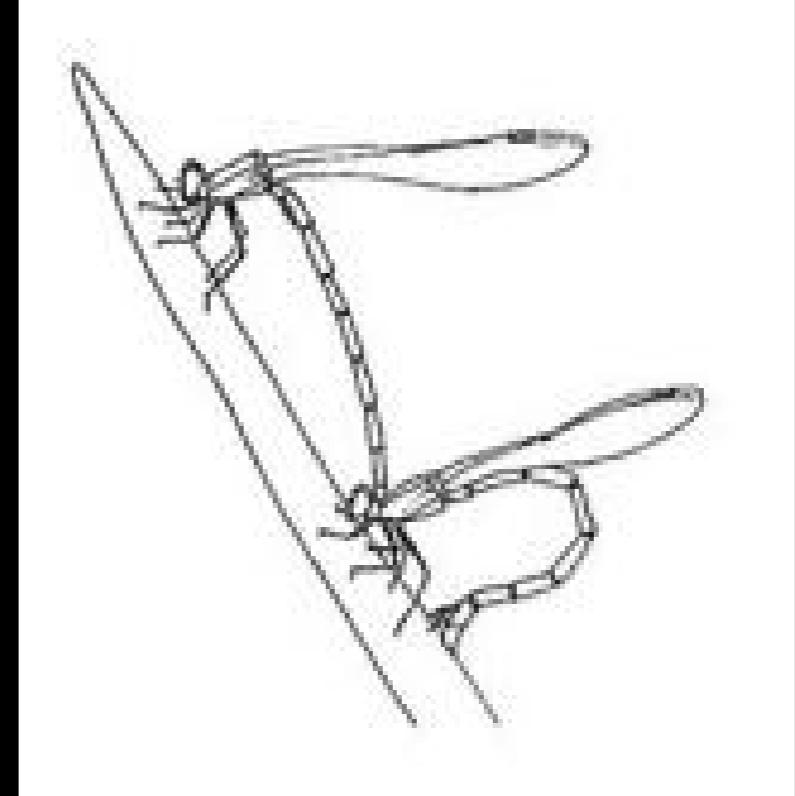
Male

Female

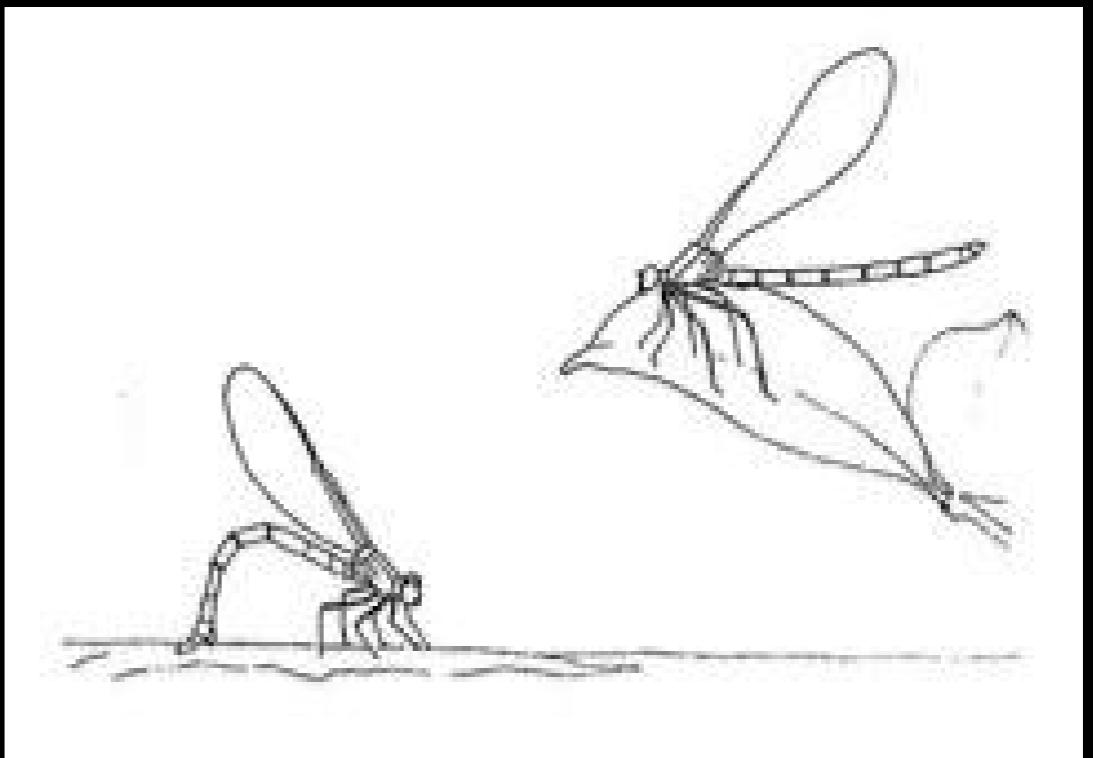
Male grips female
with anal
appendages,
“invites” to
copulate

Post copulatory guarding

Remain in tandem after mating



Mate guarding in *Calopteryx*



Why guard?

Mate guarding

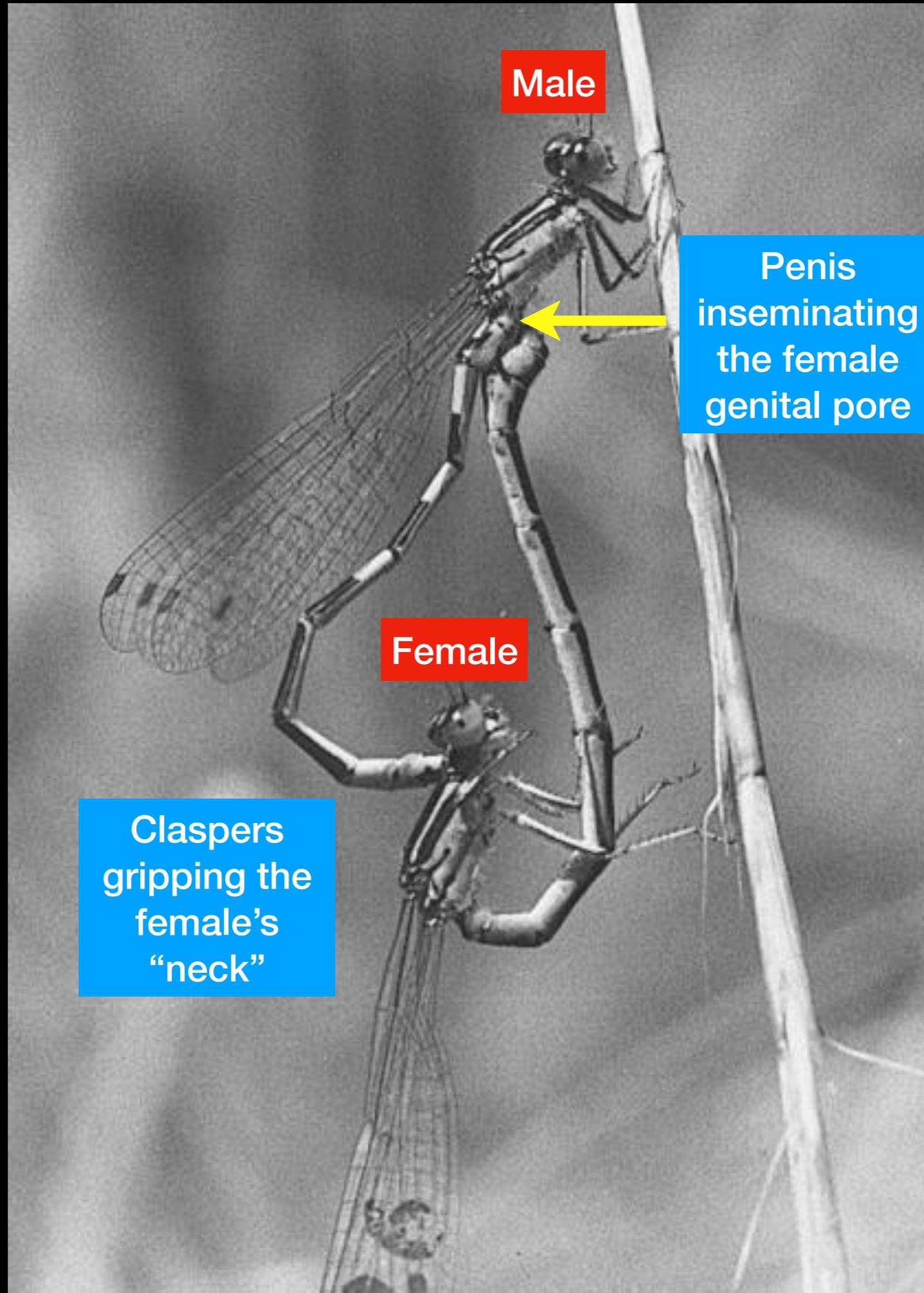
Black-winged damselfly

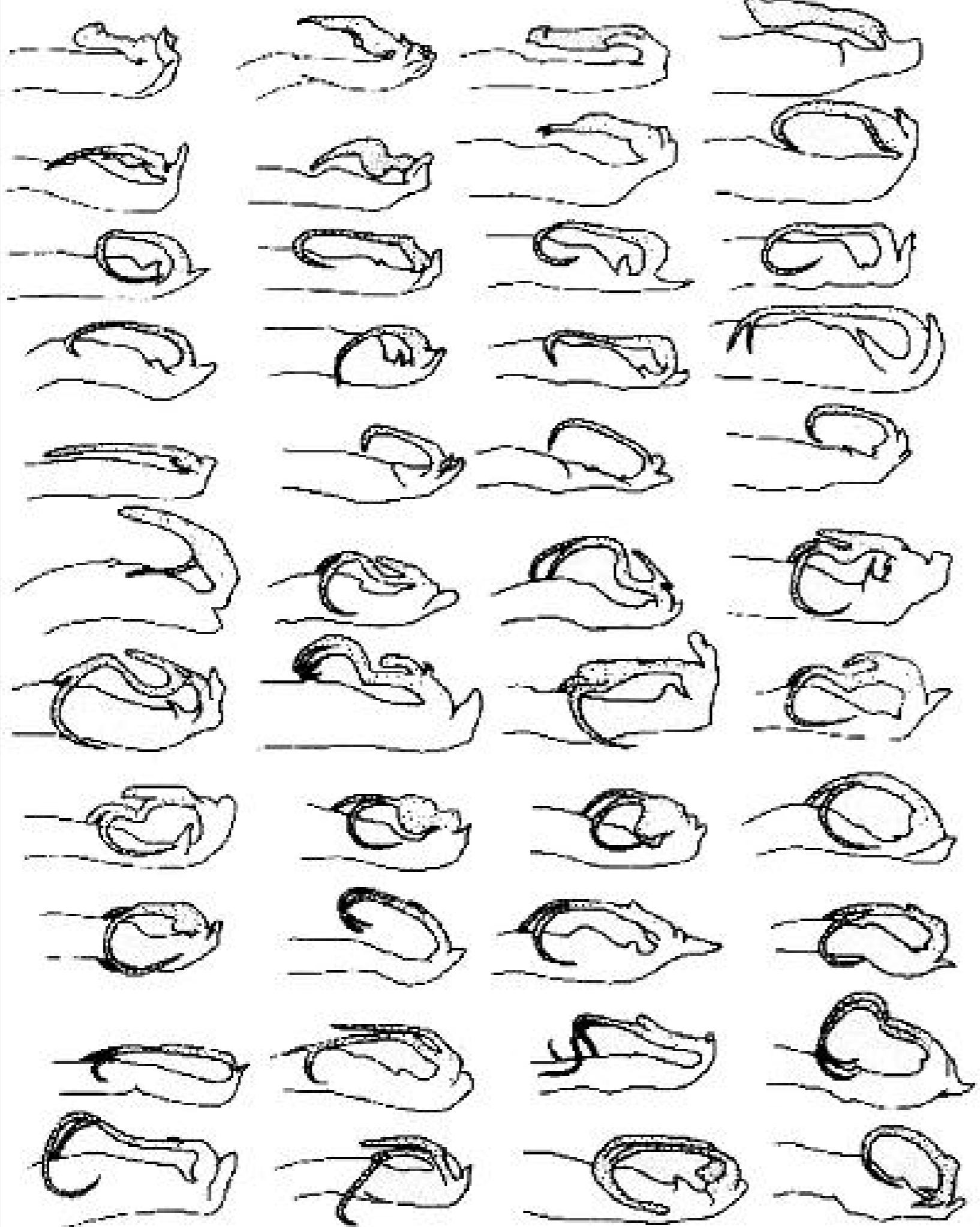
- * Females are promiscuous (multiple partners)
- * Males guard a territory
- * Ensure she lays eggs in his territory
- * It is important that she lays eggs
- * before meeting another male

4.2 Sperm removal

Black-winged damselfly







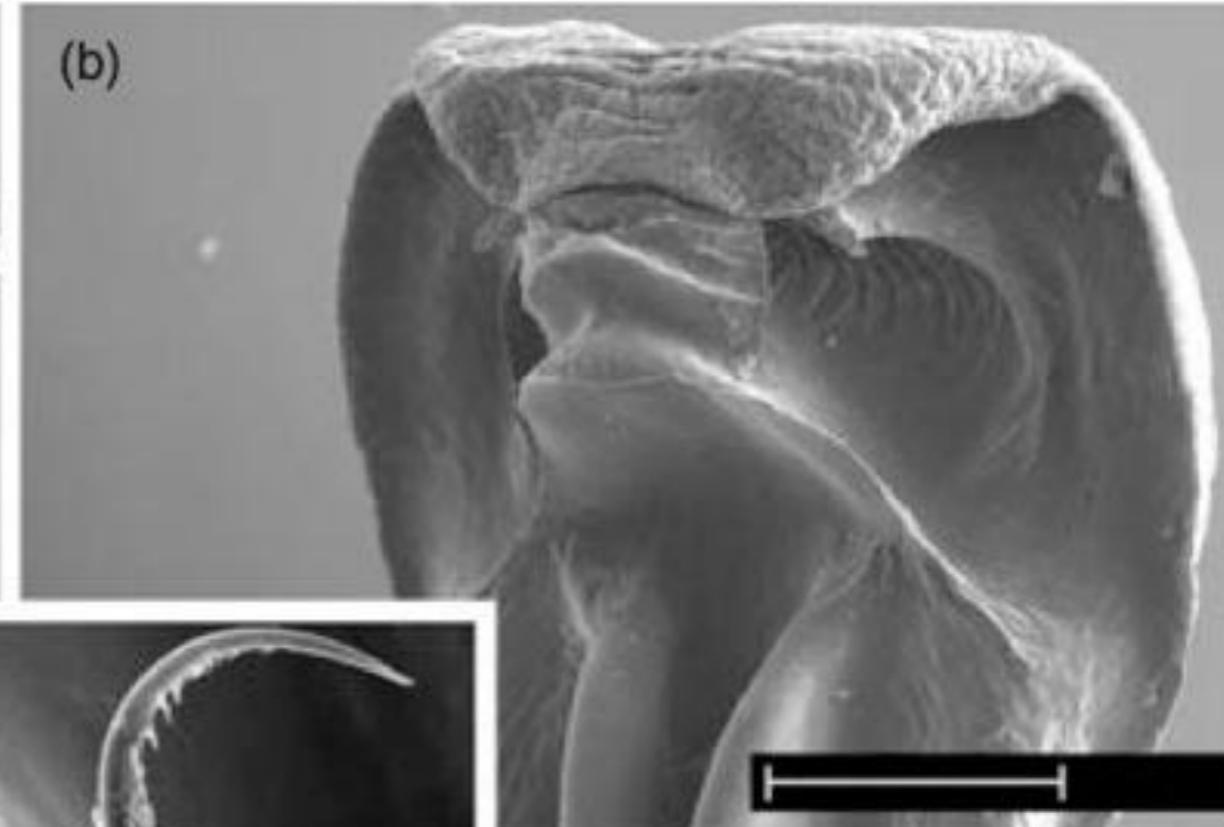
**Diversity of
damselfly
penises**

Sperm competition in Odonata

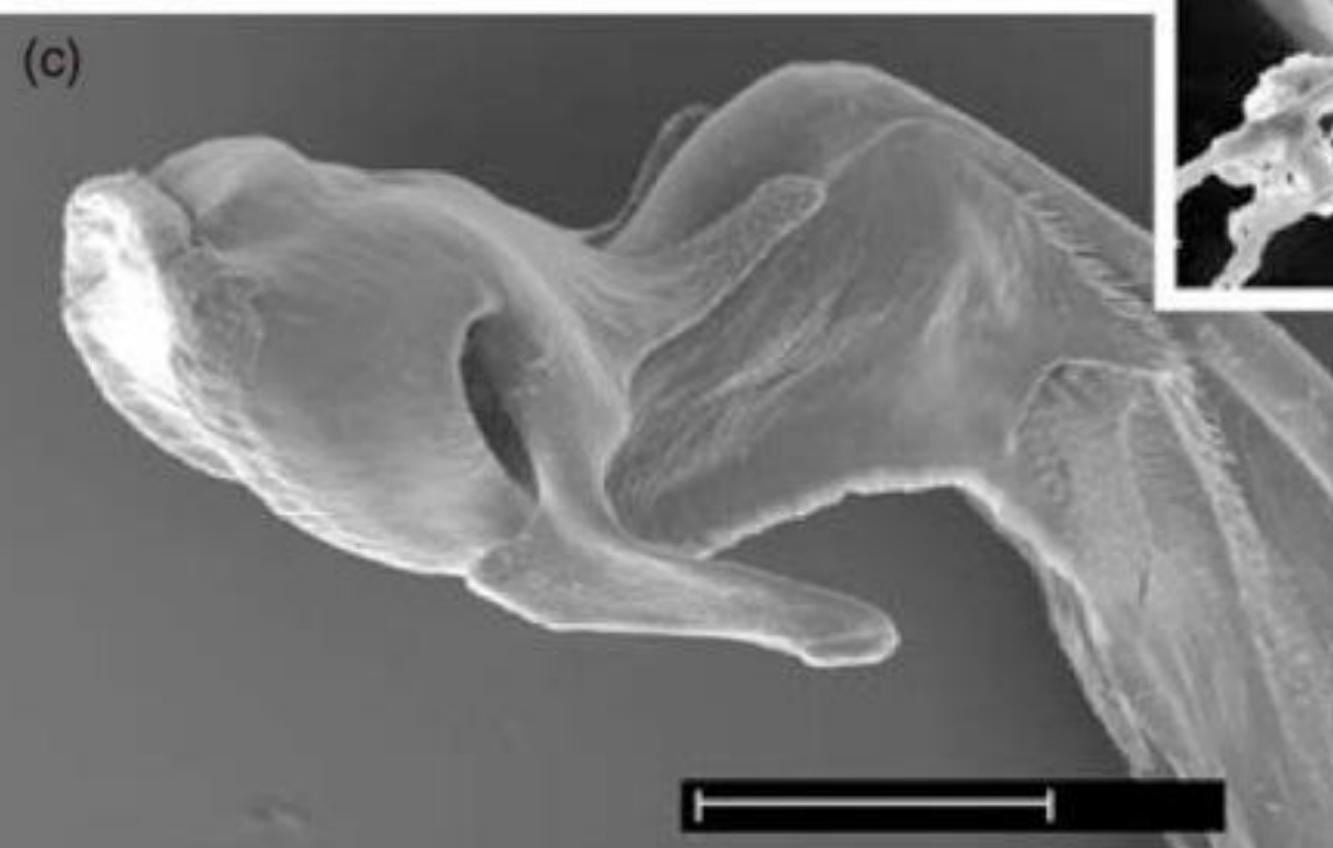
(a)



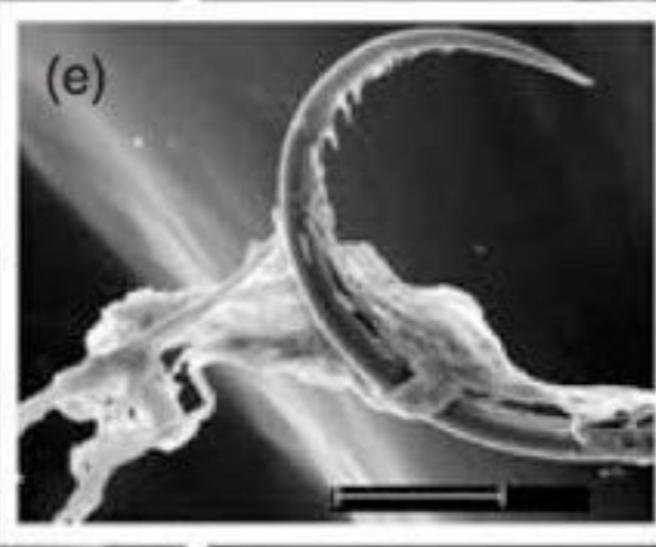
(b)



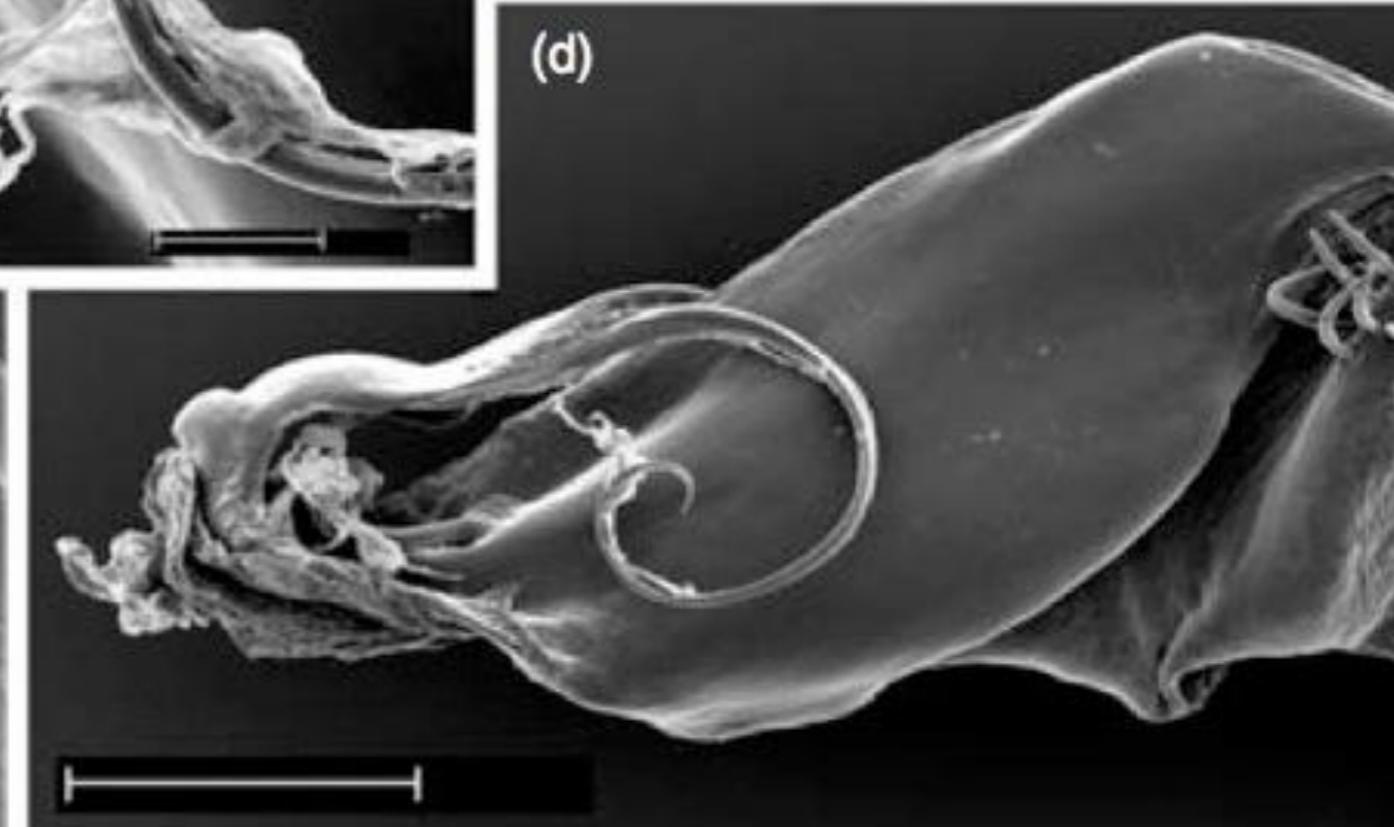
(c)



(e)



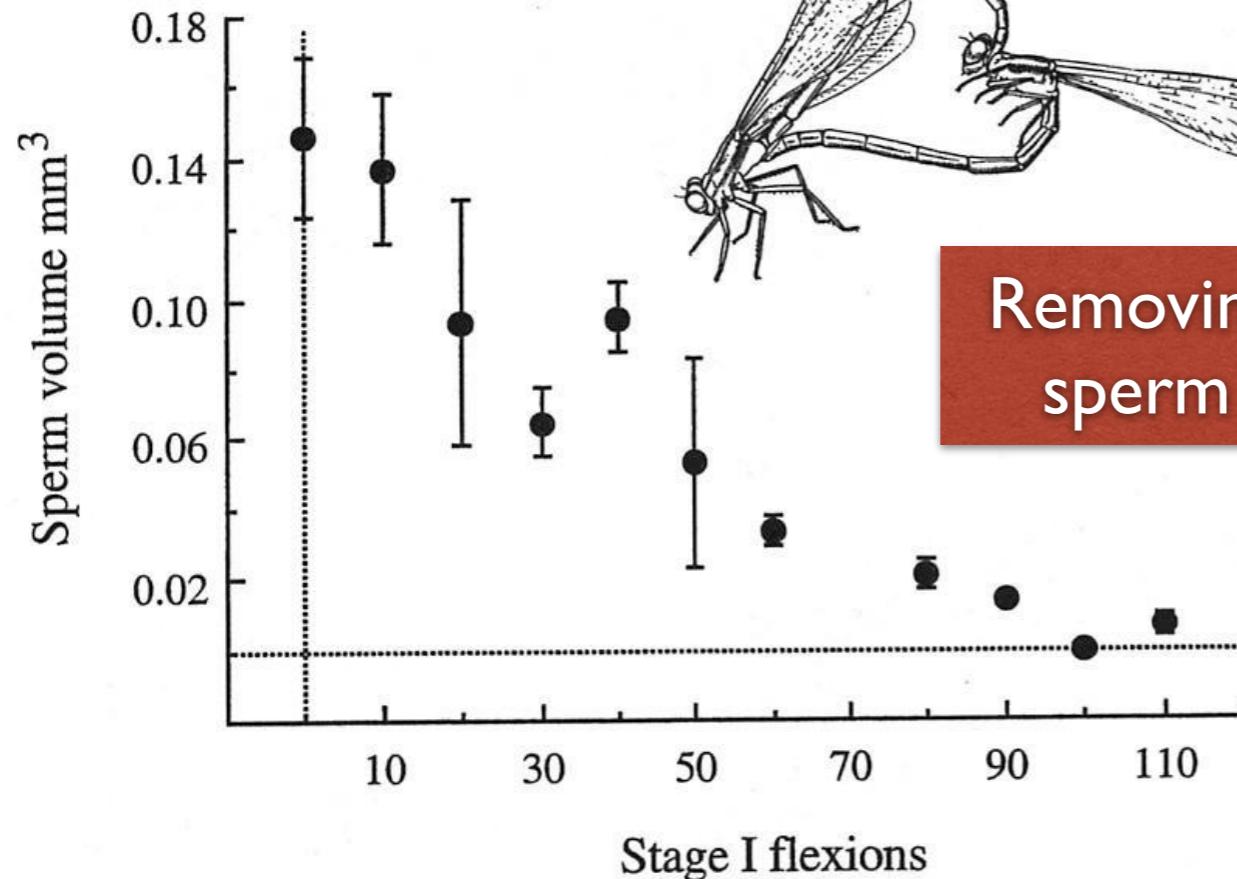
(d)



Damselfly A Battle for Paternity - Battle of the Animal Sexes | BBC | 1:20



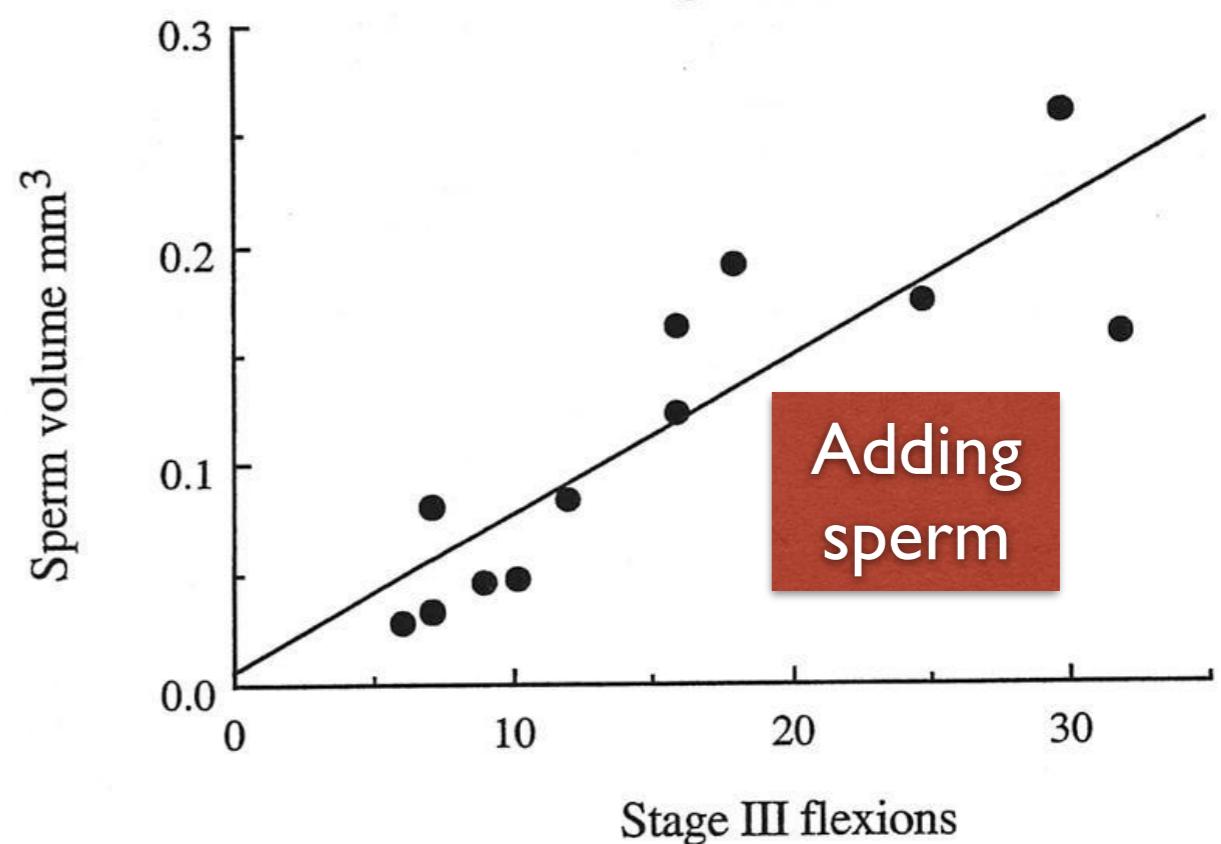
Dragonfly/damselfly mating systems are characterised by sperm removal



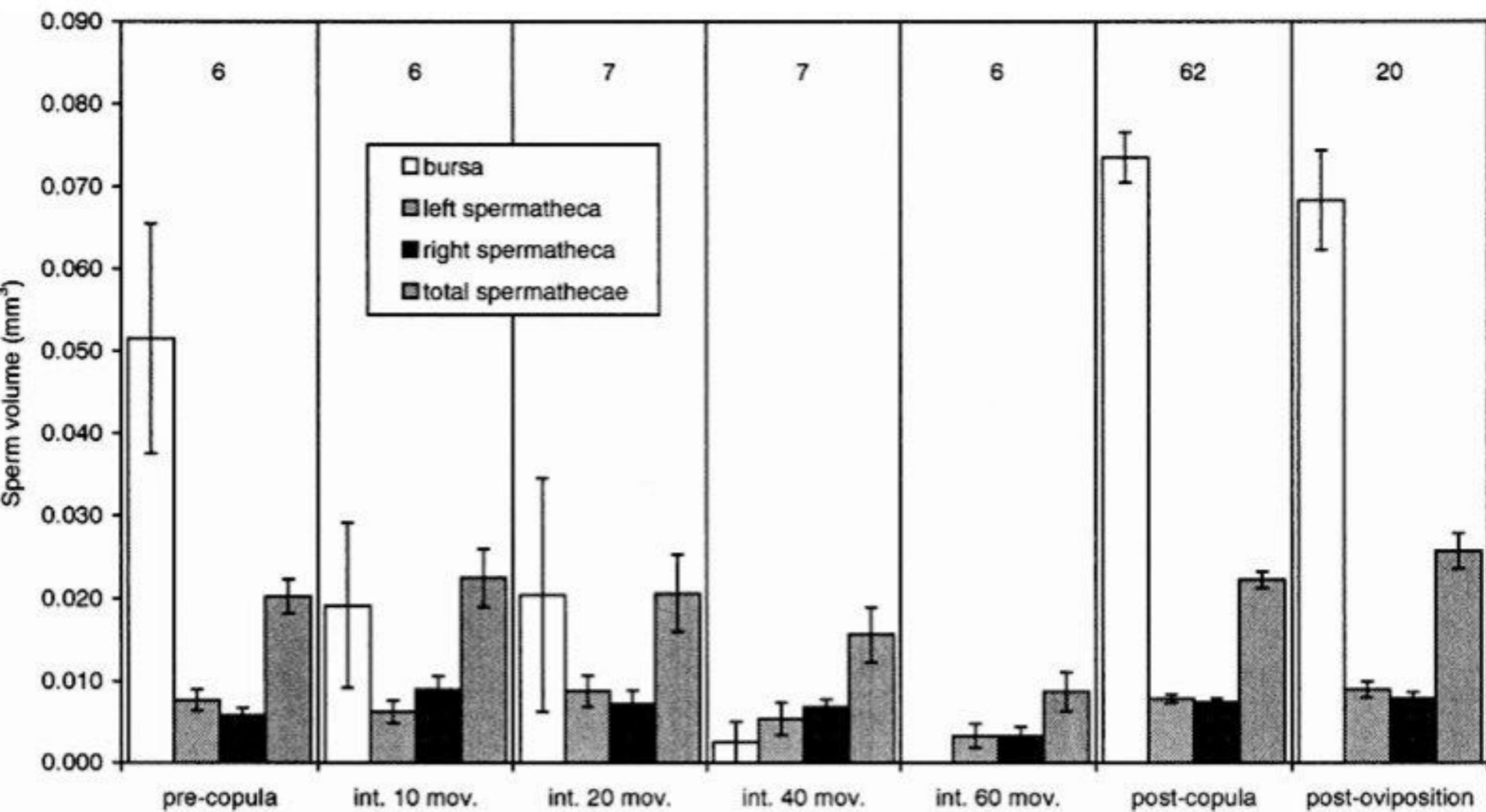
Siva-Jothy & Tsubaki 1989
Behav Ecol Sociobiol
24:39

Insemination
sperm volume in
female genital
opening increases
with repeated
flexions later

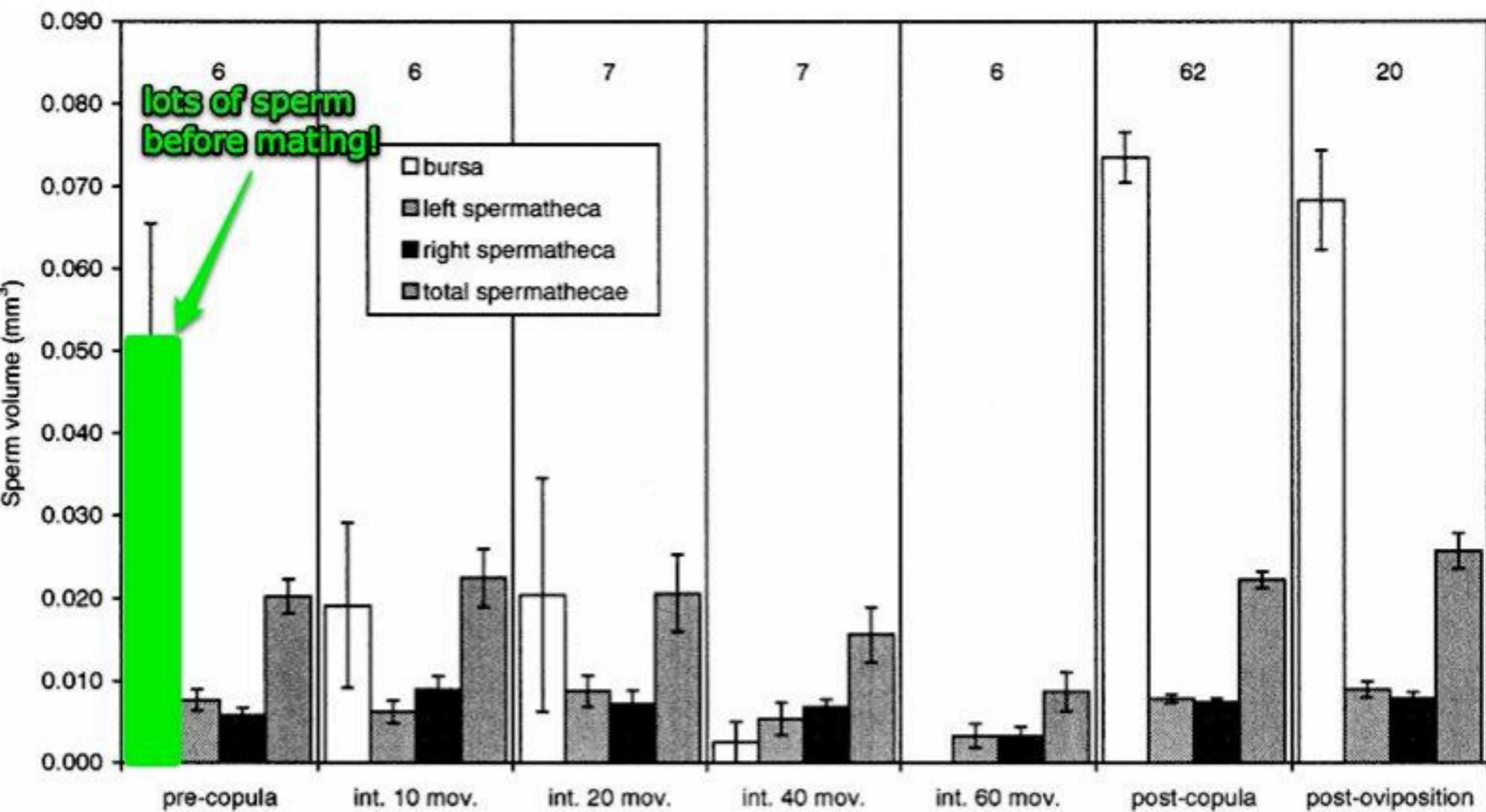
Sperm removal:
sperm volume in
female genital
opening decreases
with repeated
flexions



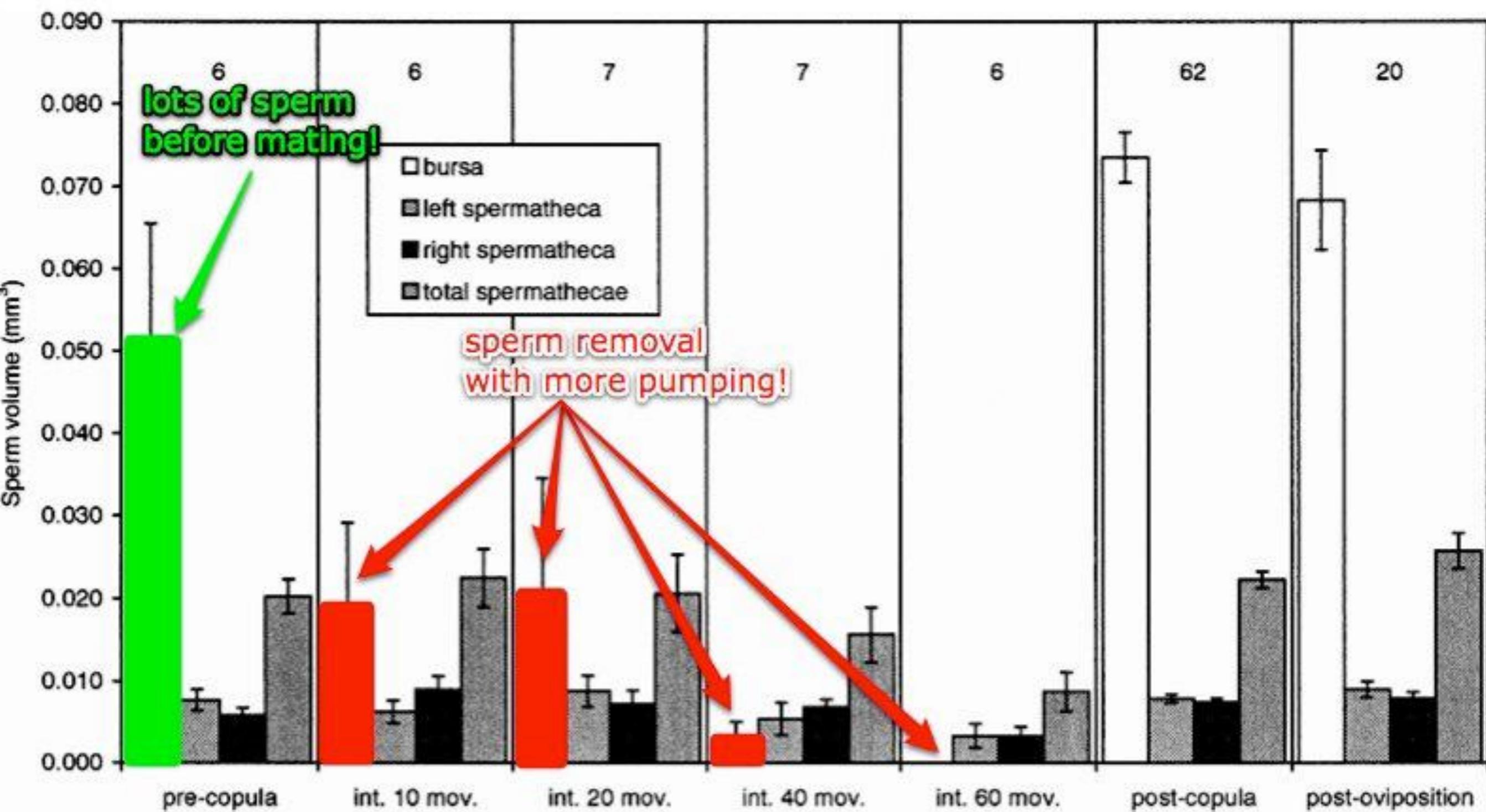
ALLOPATRIC EVOLUTION OF SPERM COMPETITION TRAITS



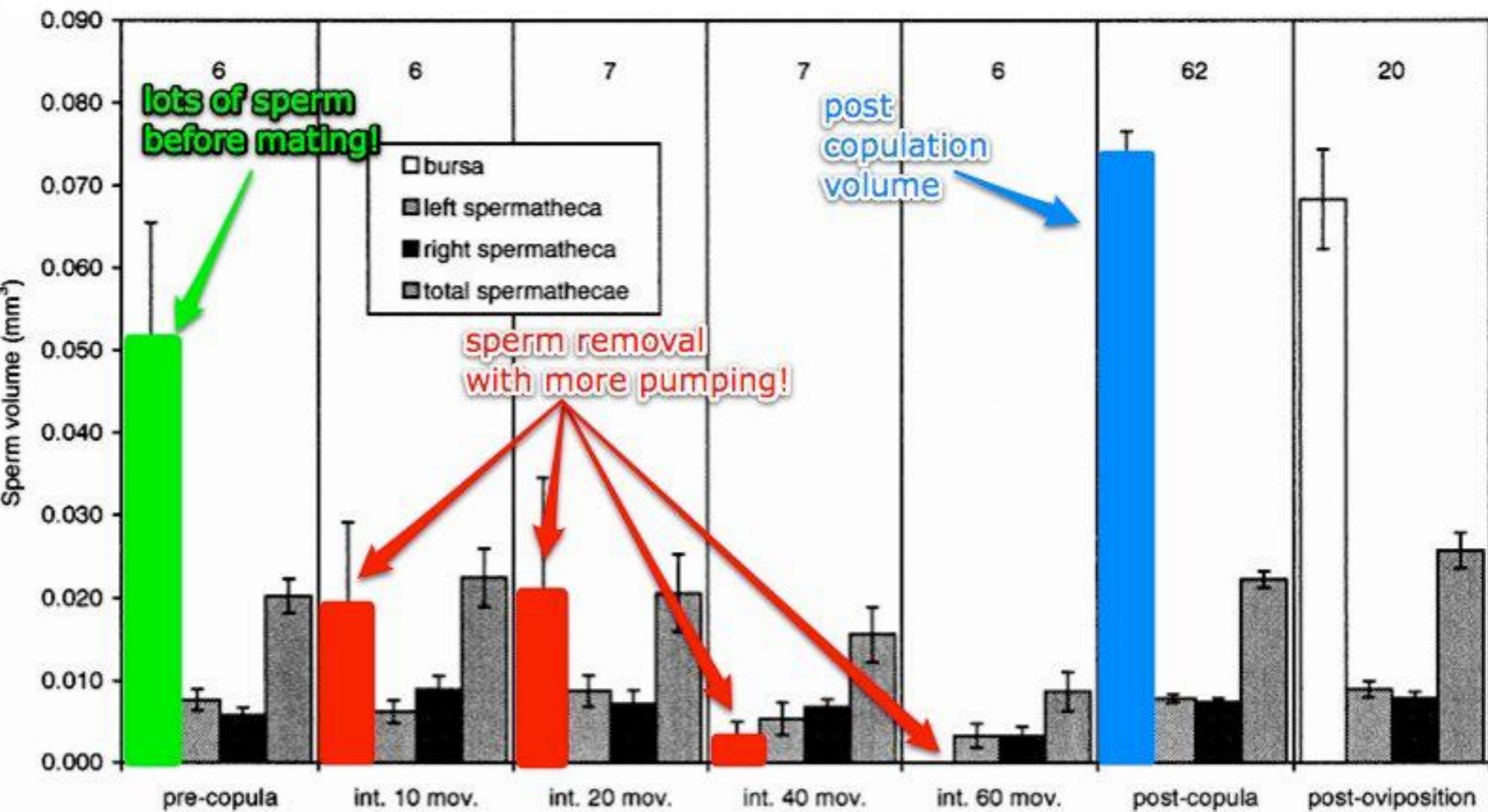
ALLOPATRIC EVOLUTION OF SPERM COMPETITION TRAITS



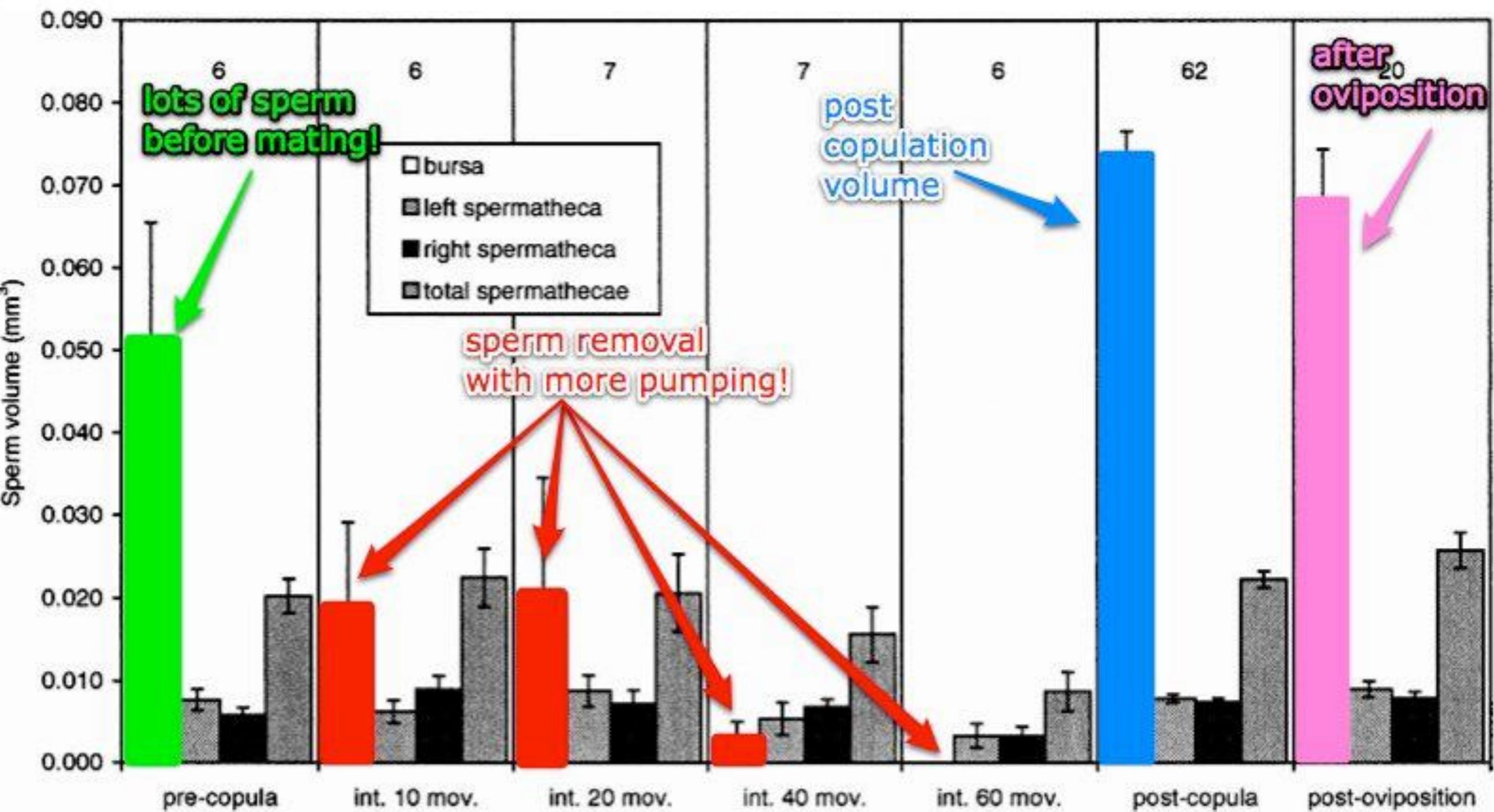
ALLOPATRIC EVOLUTION OF SPERM COMPETITION TRAITS



ALLOPATRIC EVOLUTION OF SPERM COMPETITION TRAITS



ALLOPATRIC EVOLUTION OF SPERM COMPETITION TRAITS



Male strategies

Sperm removal (mechanical),

Sperm removal (female stimulation)

Sperm displacement (mechanical)

Sperm flushing (abundant ejaculate)

SUMMARY

Males and females of different species use different tactics
to increase their reproductive success

Mating advertisement can be costly

These tactics/behaviours have evolved over time
and are probably suited for the species
in its environment.

Animal courtship performed by humans
Act of Love advertisement (2:16)

Animal Courtships Performed by Humans

にんげんによって表現された、どうぶつたちの求愛。