

The design of a beautiful weapon

[resolving the paradox of the weakening combatant]



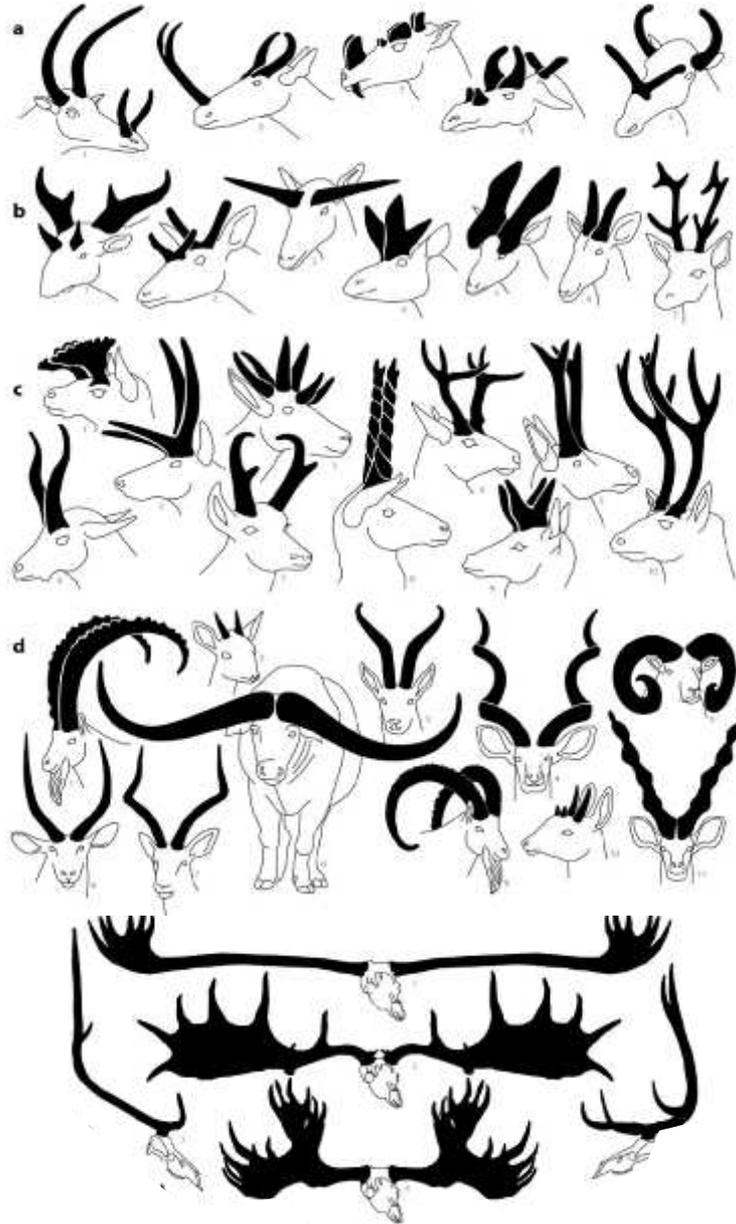
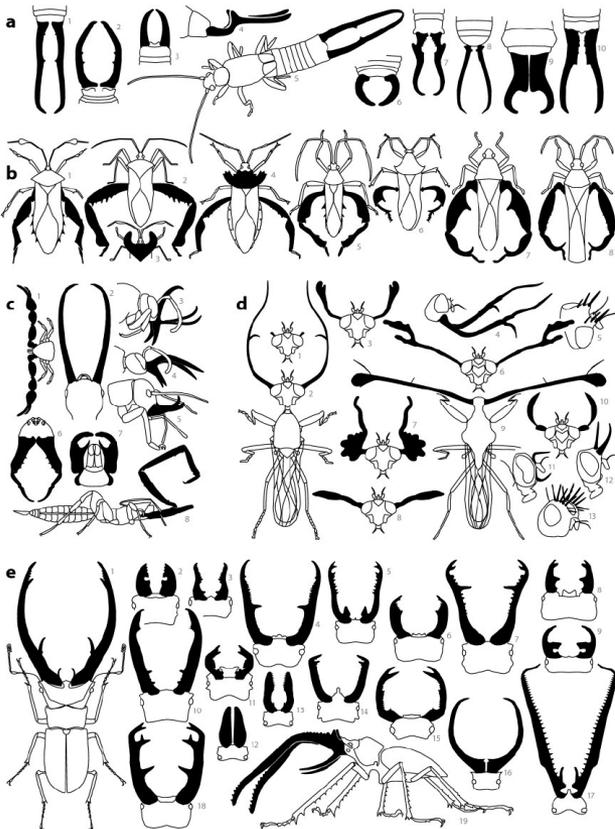
Stefan Dennenmoser

Francesca Gherardi Memorial Award

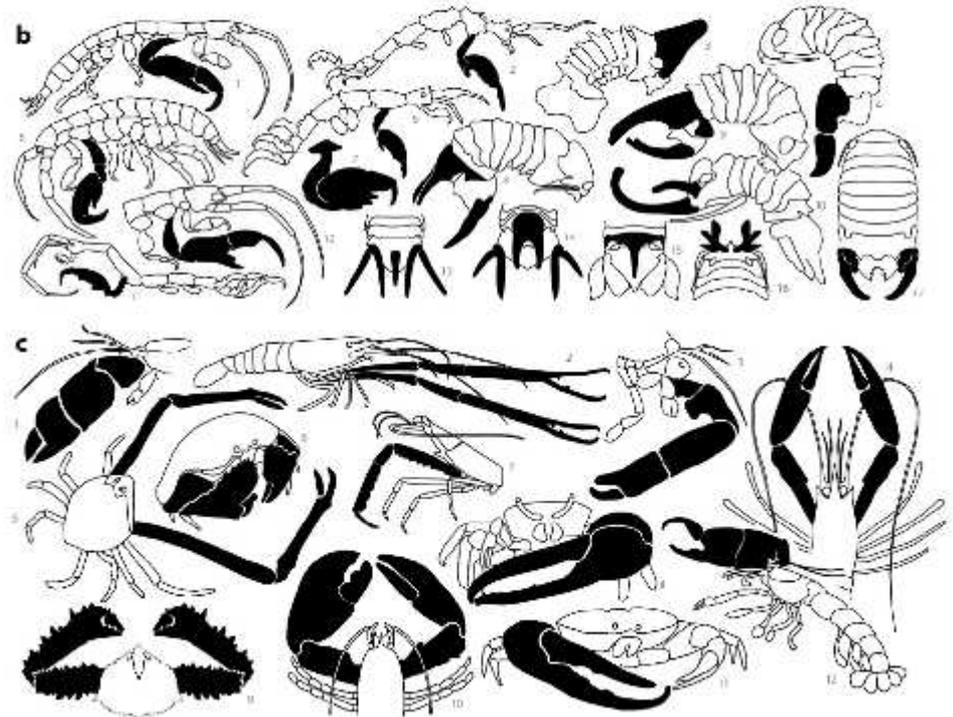
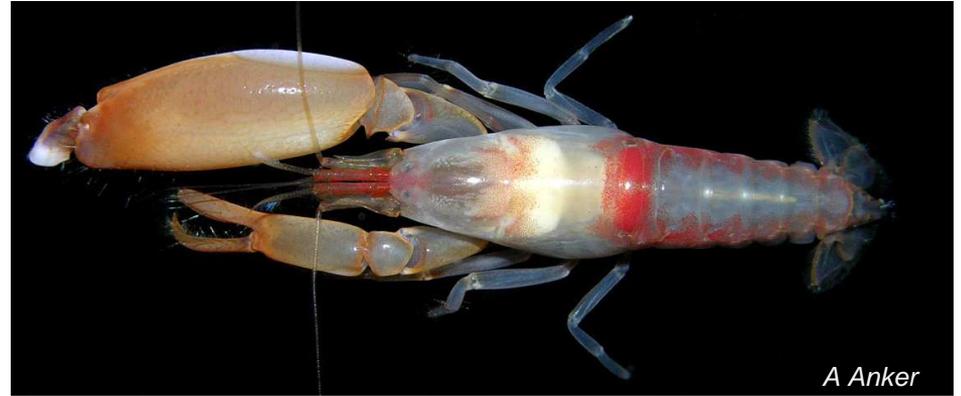
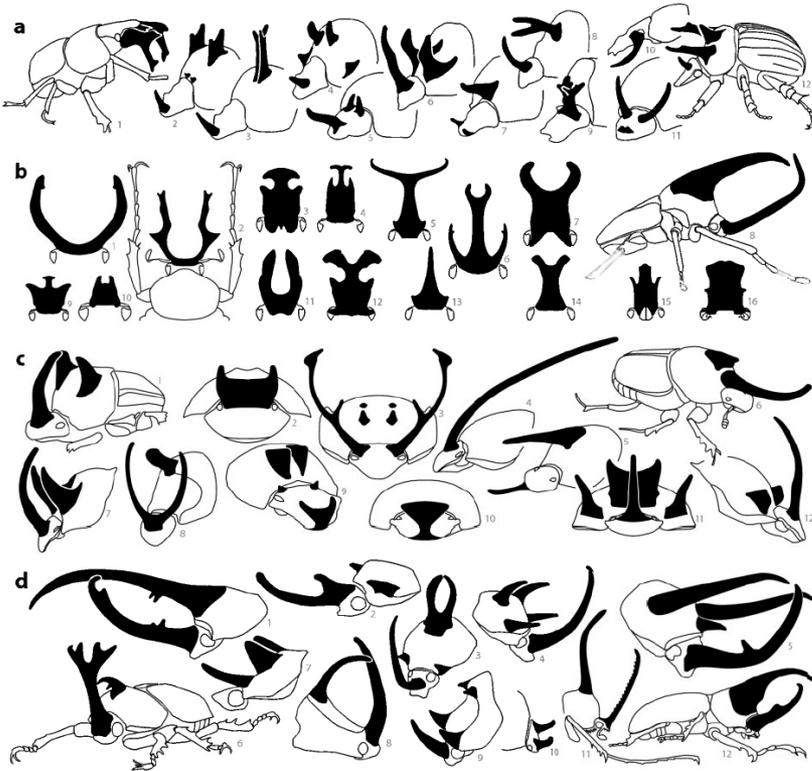
University of Florence (May 12, 2016)



Animal weapons are highly diverse



Animal weapons are highly diverse

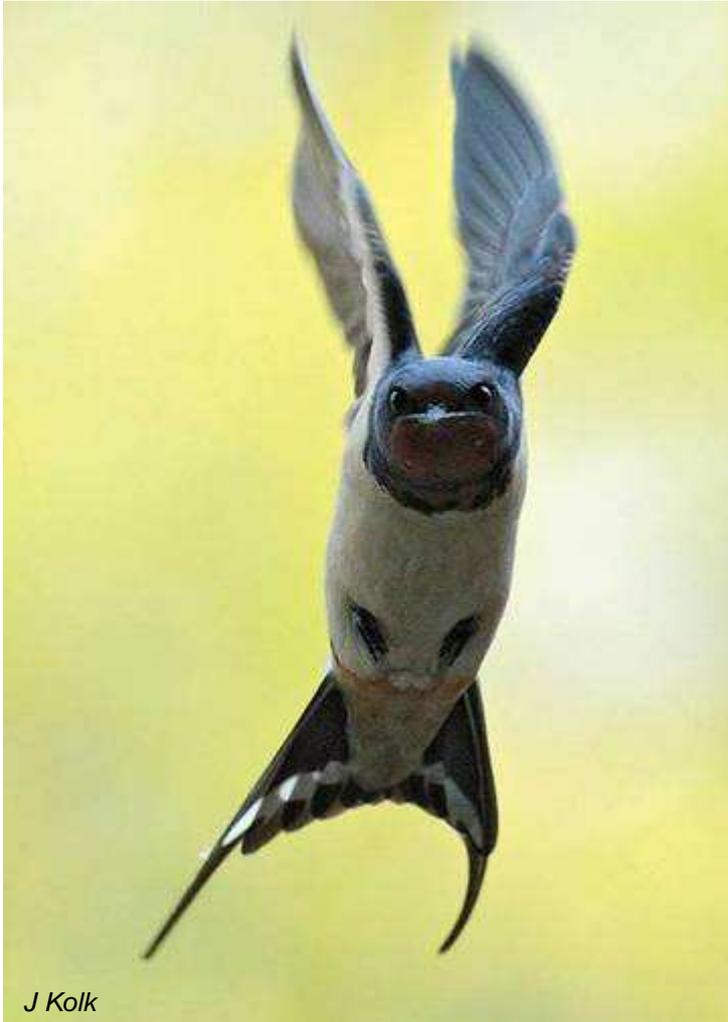


Emlen 2008

Exaggerated growth is common



Compensatory traits



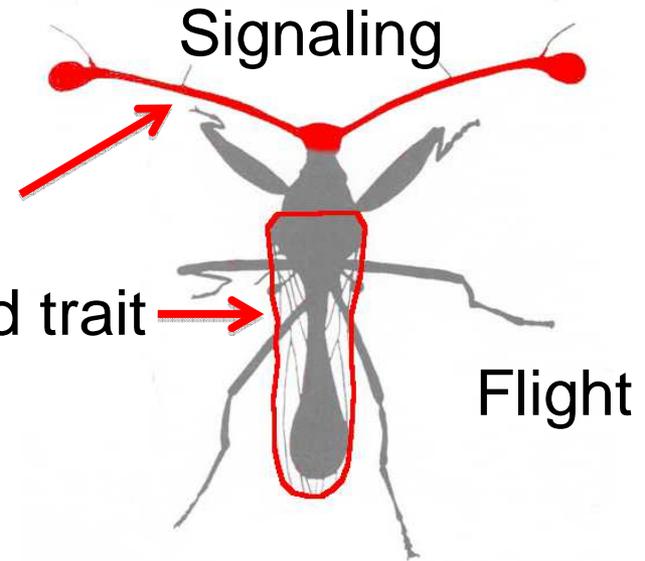
Tomkins et al. 2005, Husak and Swallow 2011

Selectional conflict in multi-functional traits?

Conflict among structures

Reduce costs of exaggerated trait

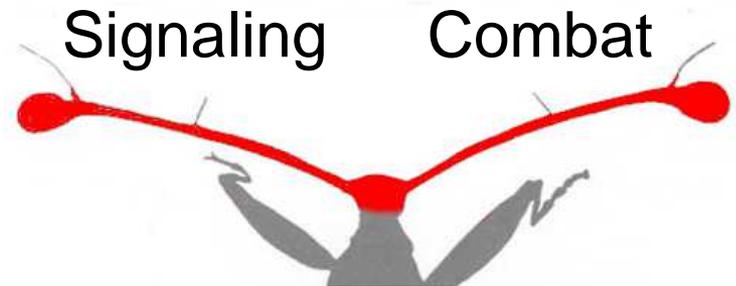
Enhance performance of conflicted trait



Conflict within structures

Different functions may perform best at different trait expressions

... change trait design?



Selectional conflict in multi-functional traits?

Hunt et al. (2009):

Assessed multi-functional traits in 51 species
(mostly body size and signaling structures)

Male competition and female choice aligned: 82%



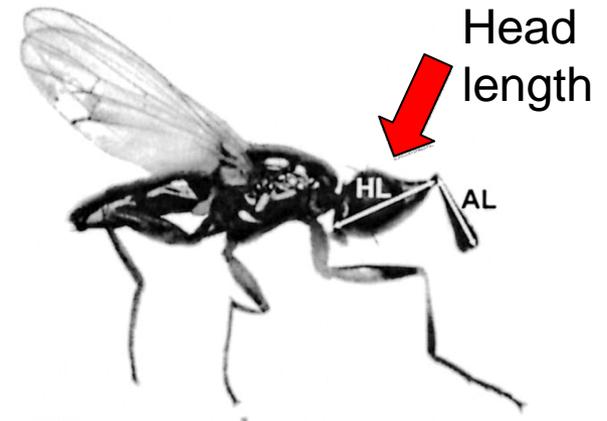
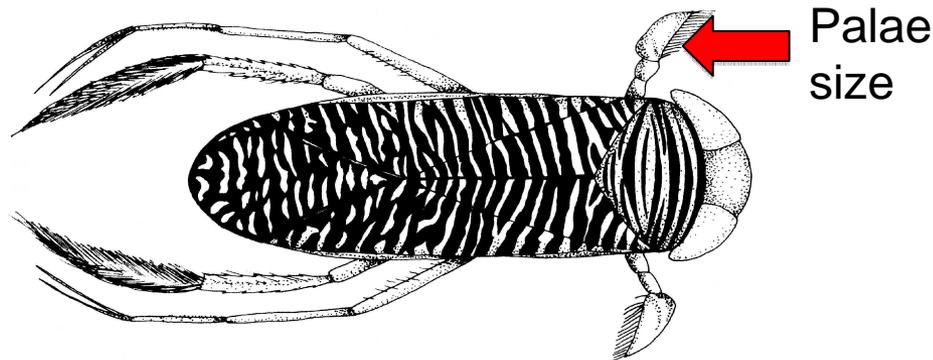
No Conflict..

Selectional conflict in multi-functional traits?

Hunt et al. (2009):

Assessed multi-functional traits in 51 species
(mostly body size and signaling structures)

Male competition and female choice opposed: 18%



Selectional Conflict!

**Compensation for
opposed sexual selection
on multi-functional traits?**

Male Fiddler Crab's Major Claw

Mate attraction

Claw waving display
(e.g., McLain and Pratt 2007)

Weapon

Male-male combat
(e.g., Levinton and Allen 2005)

Conflict?

**Longer claws
are more attractive**

**Longer claws
are weaker**



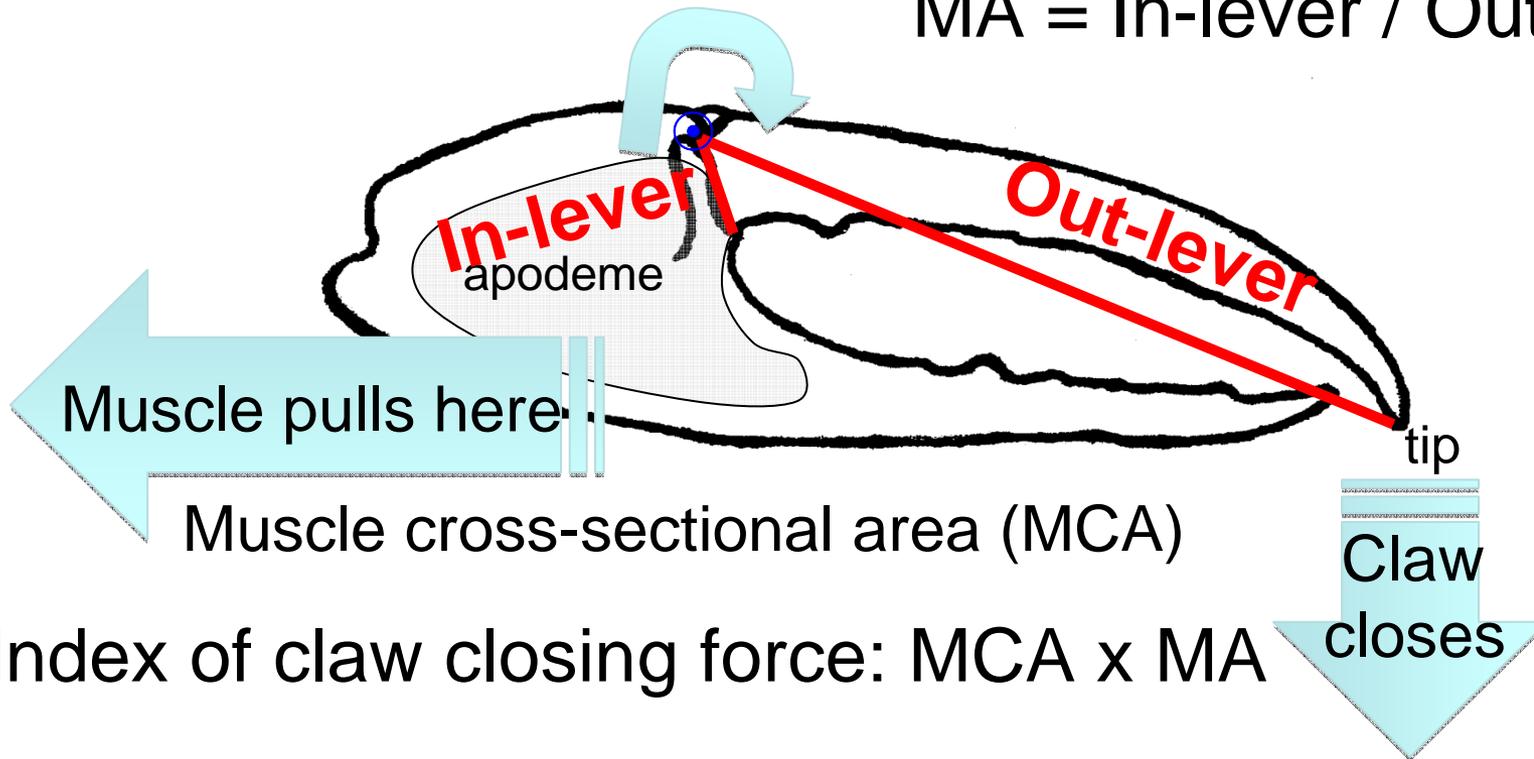
Paradox of the weakening combatant

Levinton and Allen (2005)

As claws grow and get longer fingers, they get relatively weaker because mechanical advantage decreases.

Claw as a lever system:

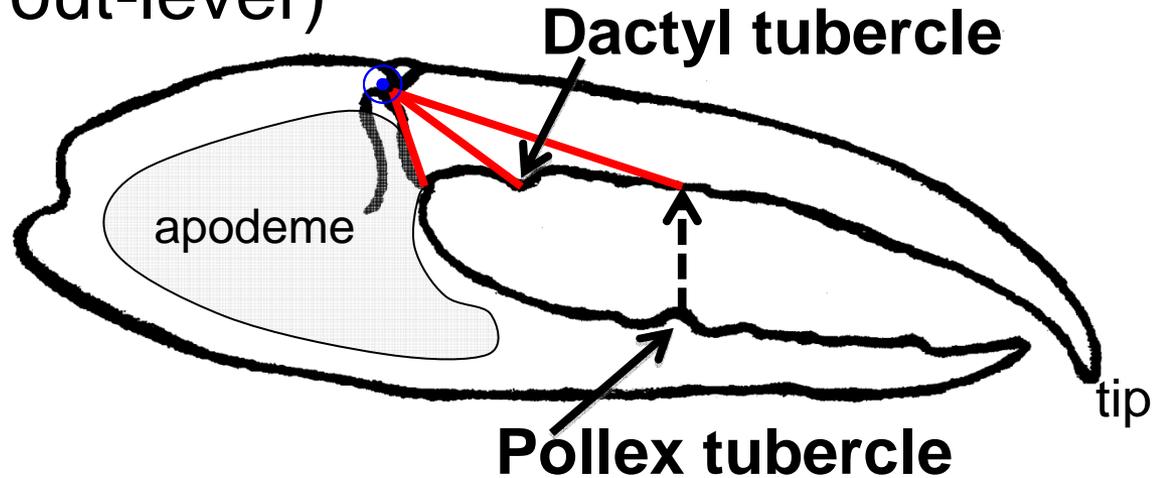
$$MA = \text{In-lever} / \text{Out-lever}$$



Index of claw closing force: $MCA \times MA$

A possible two-part solution

- 1) Crabs deliver force at tubercles instead at claw tip:**
Better MA (shorter out-lever)



- 2) Slower loss of MA at tubercles during growth:**

Tubercles could maintain their position close to pivot

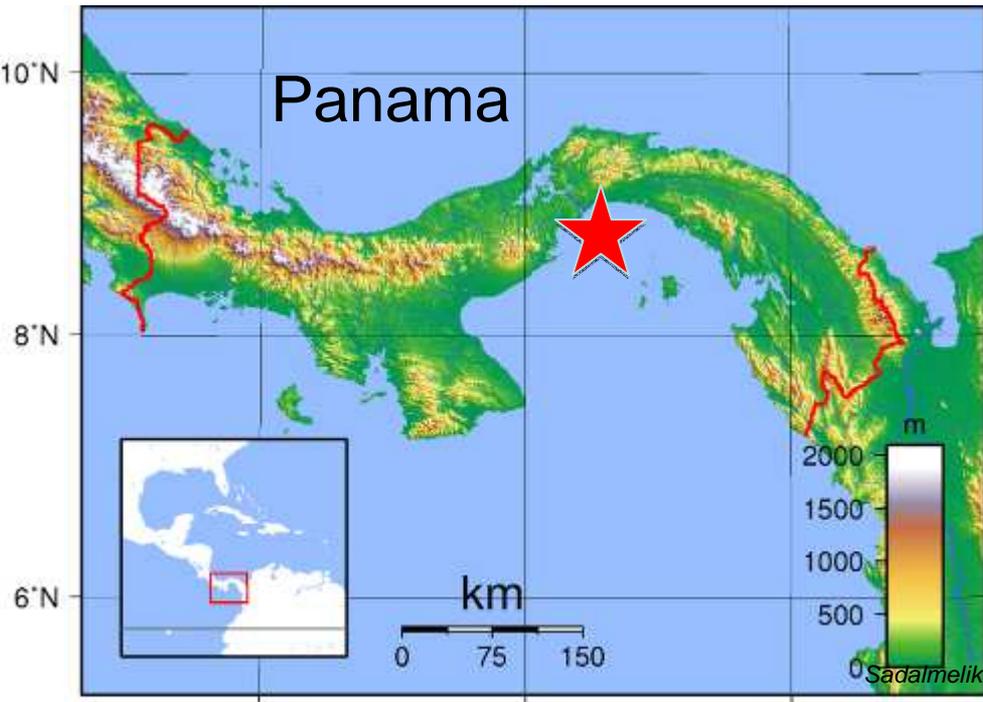
Preserves MA of shorter claws

Study area and species

Smithsonian Tropical
Research Institute



Smithsonian



Rodman

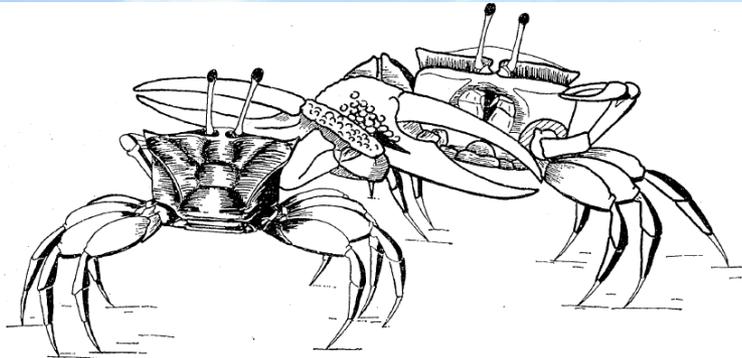
Uca terpsichores

Uca beebei



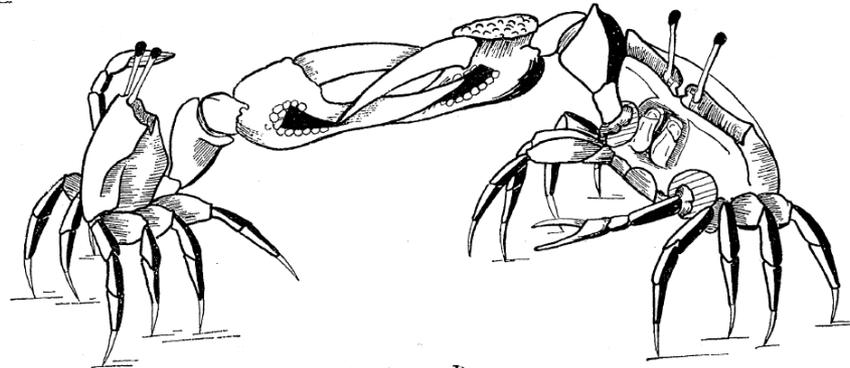
Culebra

Part I: How do fiddler crabs fight?



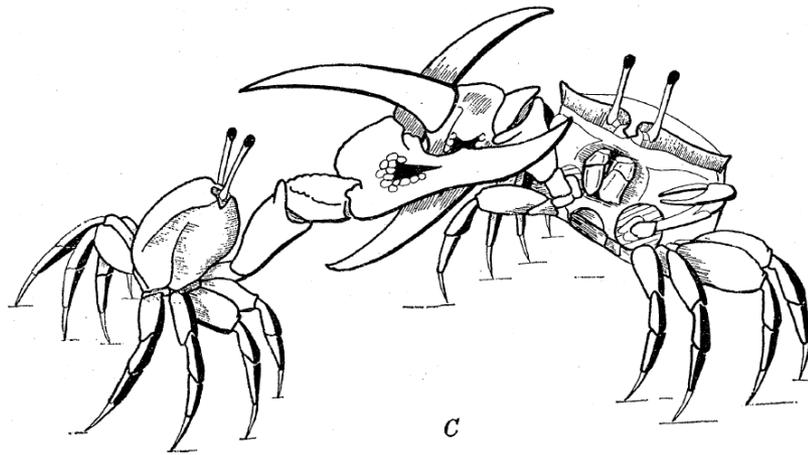
A

Low Intensity
Manus push



B

Medium Intensity
Dactyl slide



C

High Intensity
Fully Interlaced claws

Crane 1966; Hyatt and Salmon 1978

Part I: How do fiddler crabs fight?



<https://www.youtube.com/watch?v=hvsfNOtUfNA>



Part I: Gripping force: delivered by tubercles

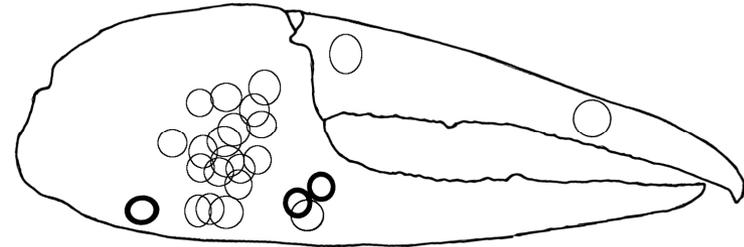
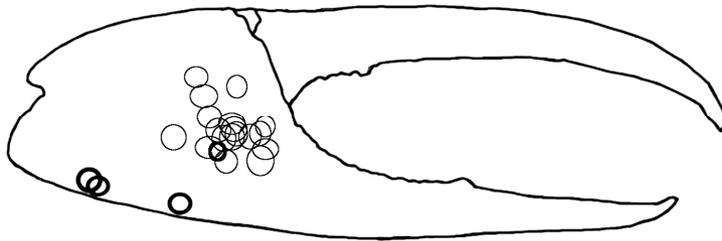
Uca terpsichores

22 recorded fights
18x dactyl tubercle
4x pollex tubercle

Uca beebei

24 recorded fights
21x dactyl tubercle
3x pollex tubercle

Contact points of tubercles:

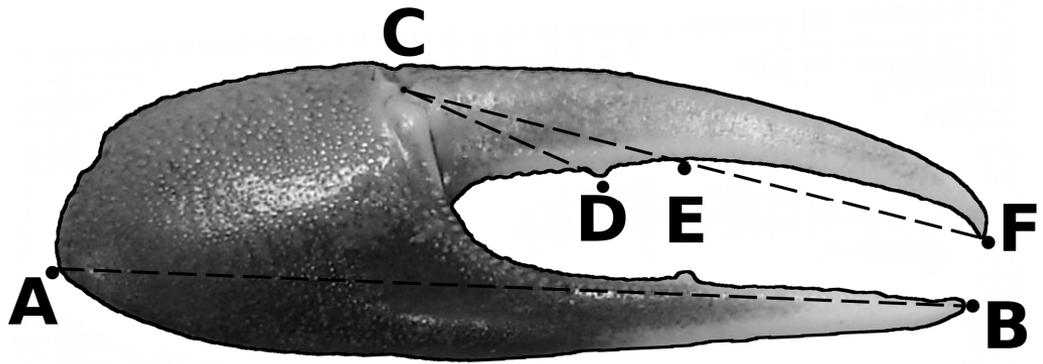


Crabs deliver force at tubercles instead at claw tip

Part 2: Slower loss of MA at tubercles?

Collected claws in the field (94x *U.terpsichores*; 121x *U.beebei*)

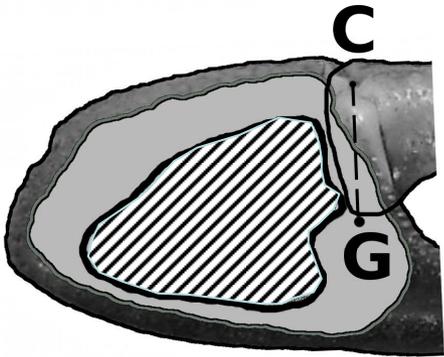
Measurements:



Out-lever lengths:

- Dactyl tubercle (C-D)
- Pollex tubercle (C-E)
- Claw tip (C-F)

Claw Length (A-B)

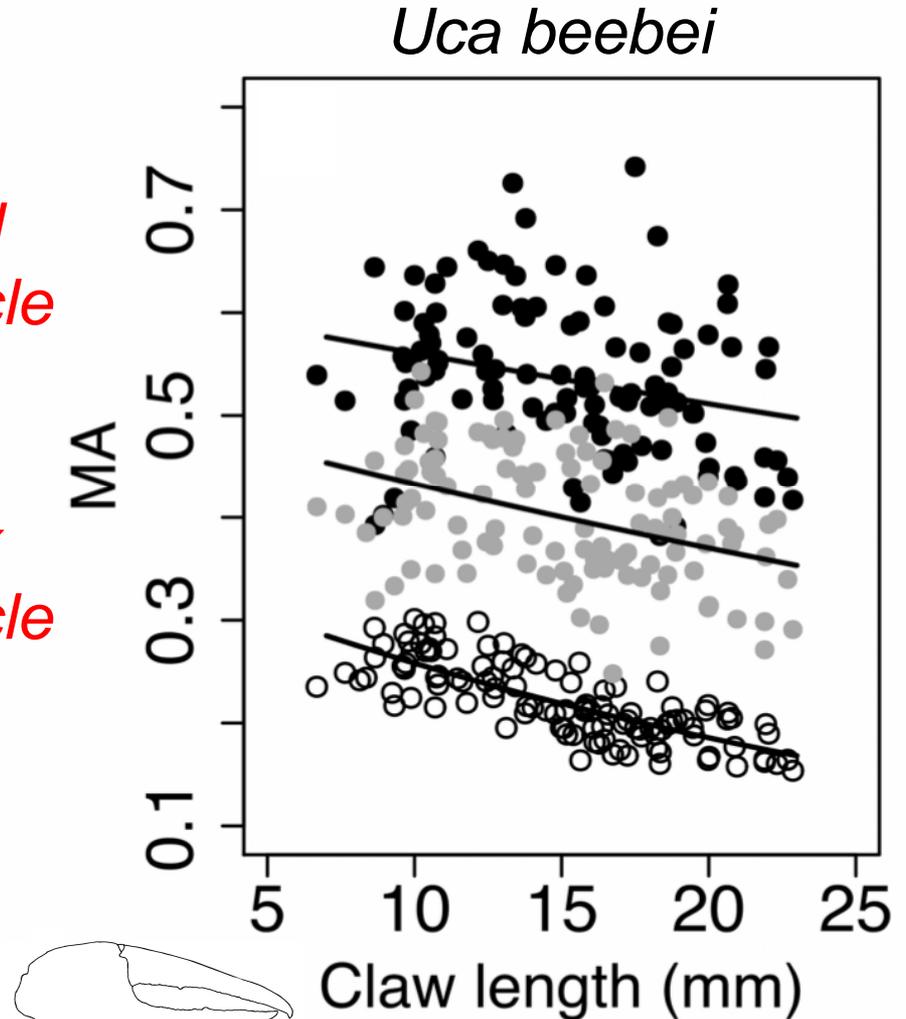
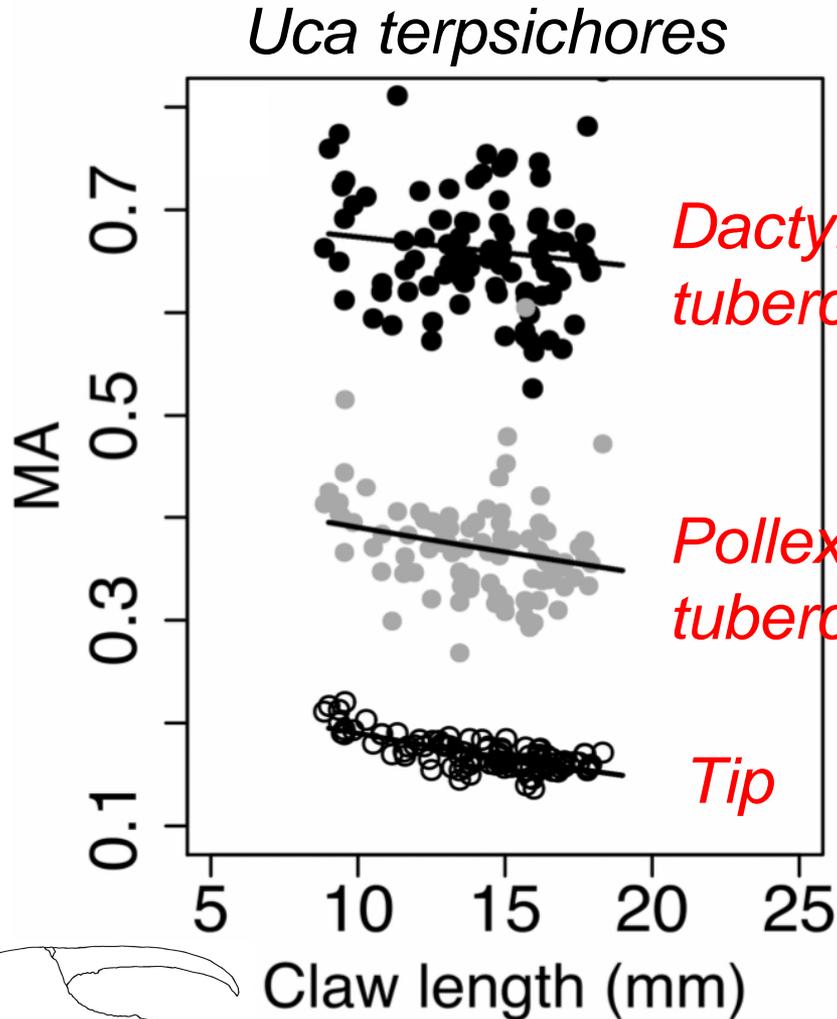


In-lever length: Dactyl height (C-G)

Apodeme area (~muscle cross sectional area)

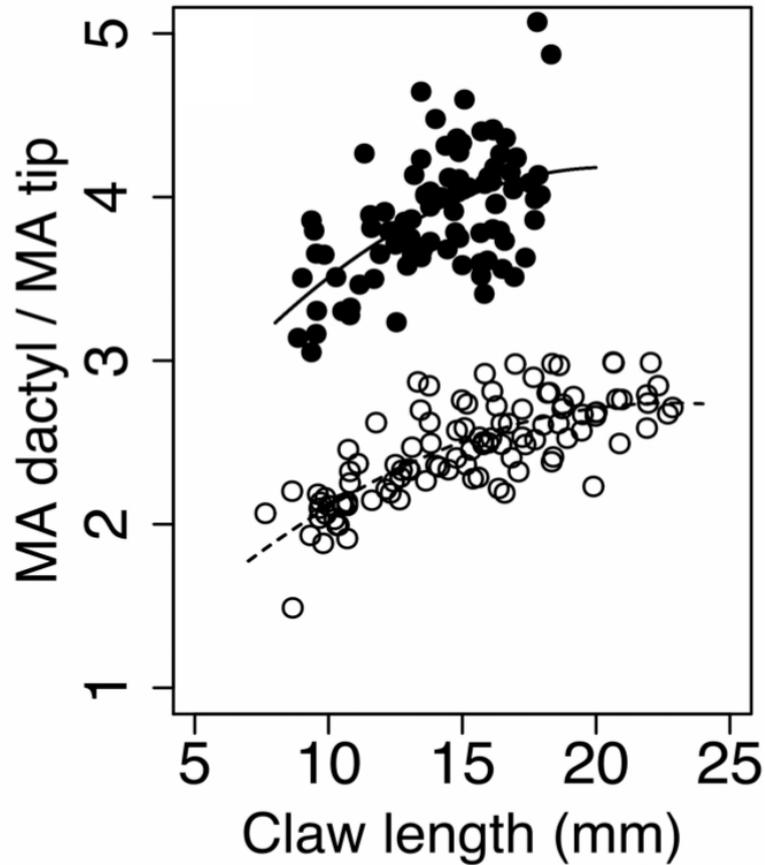
Loss of MA: lower at tubercles

Tubercles stay relatively close to the pivot as the claw grows

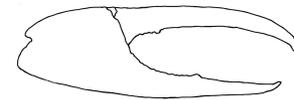


MA compensation at dactyl tubercle

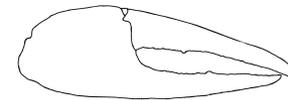
Compensation increases with claw length



Uca terpsichores



Uca beebei



No paradox but a beautiful weapon

Mate attraction

Long, conspicuous claw

Low MA

vs.

High MA

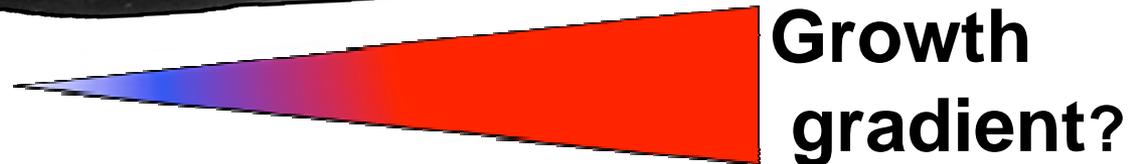
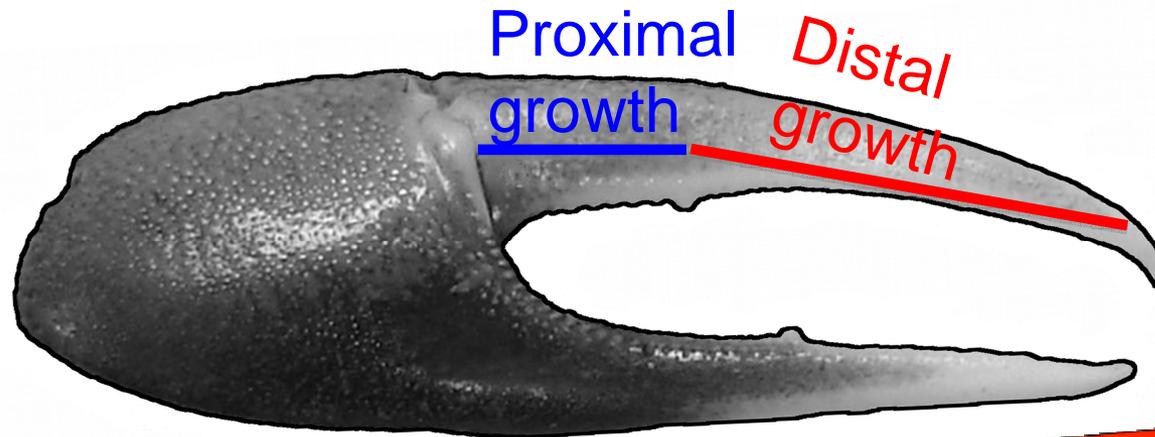
Weapon

Strong gripping force

Tubercles

Compensatory trait: Use of tubercles to deliver gripping force

High MA is maintained during growth



Animal weapon diversity

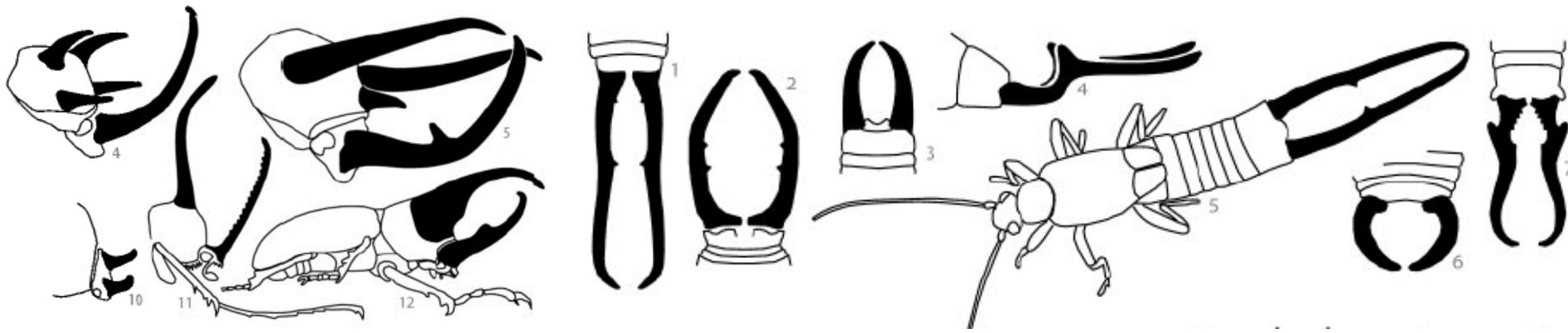
Exaggerated size (female choice; male-male combat)

Fighting style matters (e.g., levering, pinching, gripping)

Functional conflicts through opposed selective forces

Elongated structures vs. mechanical advantage
(signaling, levering) (gripping, pinching)

Compensation features can be integrated in weapon design



Thank you to Francesca Gherardi for many great inspirations!



Behav Ecol Sociobiol (2006) 59: 500–510
DOI 10.1007/s00265-005-0074-z

ORIGINAL ARTICLE

Francesca Gherardi

Fighting behavior in hermit crabs: the combined effect of resource-holding potential and resource value in *Pagurus longicarpus*



biology
letters

Biol. Lett. (2008) 4, 163–165

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Animal behaviour

Evidence of female cryptic choice in crayfish

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Via Romana 17, 50125 Florence, Italy*

Thank you!



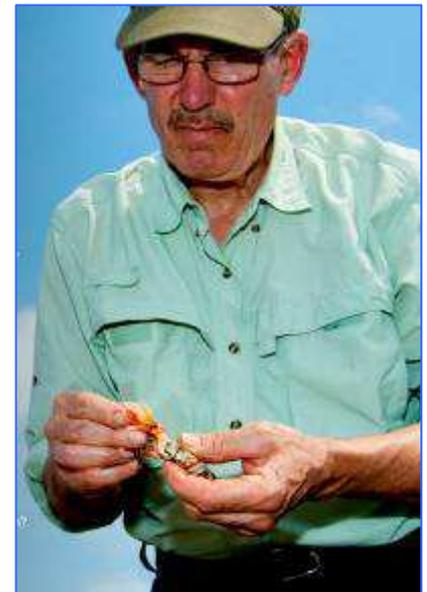
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Smithsonian Tropical Research Institute



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... questions?