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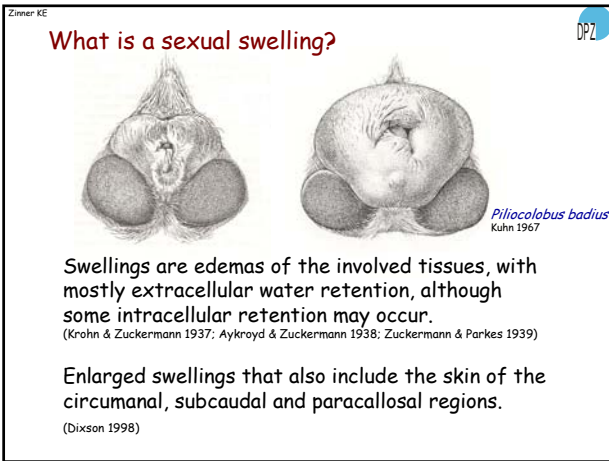
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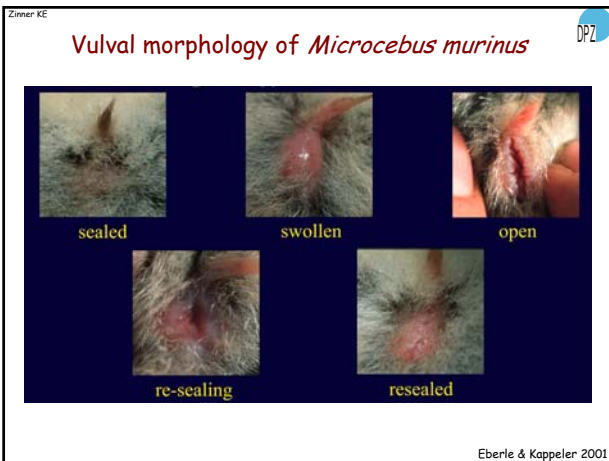
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Zimmer KE

### Non-exaggerated sexual swellings

Swelling size categories distinguished: (a) no, (b) partial, and (c) full swelling.

Shelmidine et al. 2007

*Trachypithecus cristatus*

*Hylobates lar*

Barelli et al. 2007

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Zimmer KE

### Extreme case of „Sexual Skin“ in *Callithrix*

DPZ

Russel & Zuckermann 1935

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Zimmer KE

### Exaggerated sexual swellings

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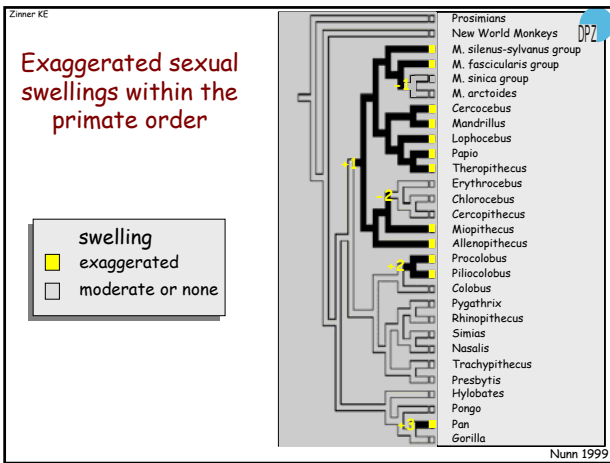
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Zimmer KE DPZ

Swellings are not permanent, but rather fluctuate in size and coloration.

Maximum swellings are temporally associated with increased sexual activity (estrus).

↓

**Hypothesis:**  
Swellings are affected (controlled) by hormones

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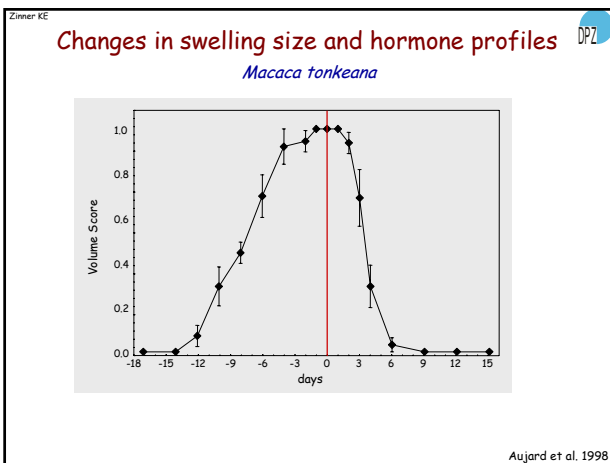
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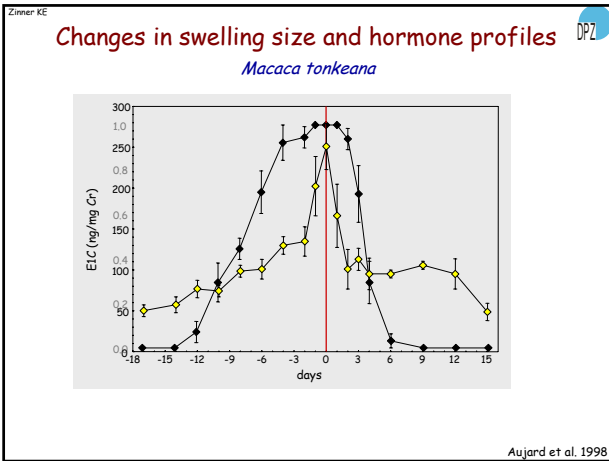
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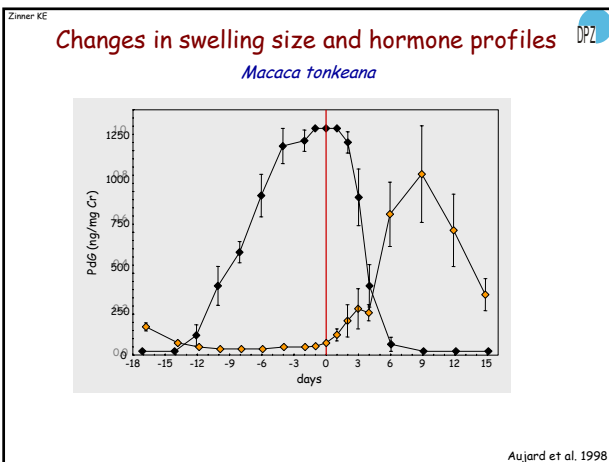
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Sexual swellings show a strong temporal and physiological relation to the cyclical hormonal changes in females (Endocrinological and experimental evidence).

↓

**Hypothesis:** Sexual swellings indicate receptivity (ovulation) of the female.

➡ but, swellings may also occur during gestation and in other situations when ovulation is very unlikely (situation dependent swellings).

e.g., obligatory post-conception swelling in mangabeys, after group take-over by new male in lactating hamadryas baboon females

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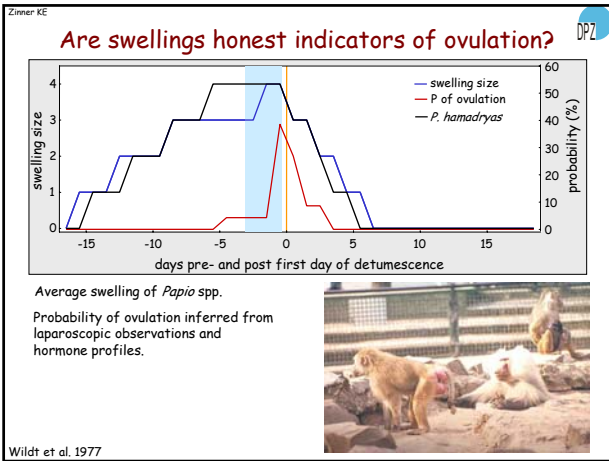
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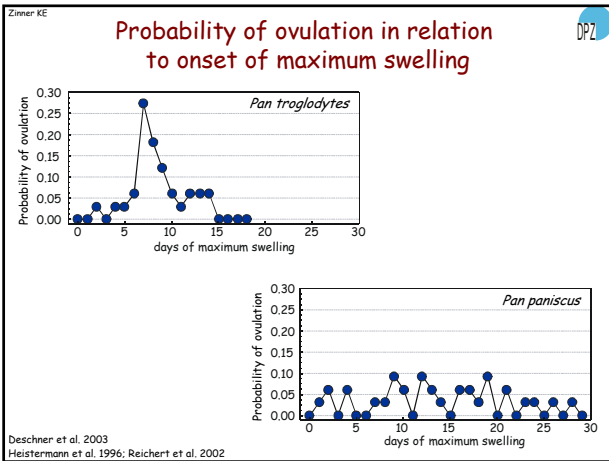
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### Costs of exaggerated swellings

Females with large swellings may suffer from a higher predation risk.

Turgescient swellings are prone to injuries. (Hausfater 1975)

Large swellings increase female body mass:  
up to 14%, chacma baboon, *Papio ursinus* (Bielert & Busse 1983)  
up to 17%, pig-tailed macaques, *Macaca nemestrina* (Dixon 1983)

↓

may lead to higher travel costs

However, no data on actual costs are available.

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## Response of males towards swellings

Swellings attract males for mating independently of olfactory or behavioral cues.

Observational and experimental evidence  
e.g. Bielert and colleagues 1982, 1985, 1986, 1989



*Macaca silenus*

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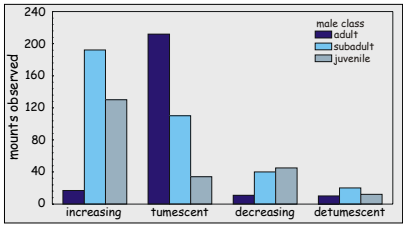
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## Male mating preference

Mounting rates by male *Papio ursinus* in relation to swelling state



Swelling State	Adult	Subadult	Juvenile
increasing	~10	~190	~130
tumescent	~210	~100	~40
decreasing	~10	~40	~45
detumescent	~10	~20	~15



Saayman 1970

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## Male response

(Dominant) Males concentrate their mating effort on times when females show maximum swellings.

Males behave as if swelling size indicates times of high probability of ovulation (conception).

### Evolution

Males that are able to recognize swellings, to discriminate swelling sizes and to mate when swellings are largest, would have higher chances to sire an infant.

↓

High selection pressure on males to react in correspondence to swelling state.

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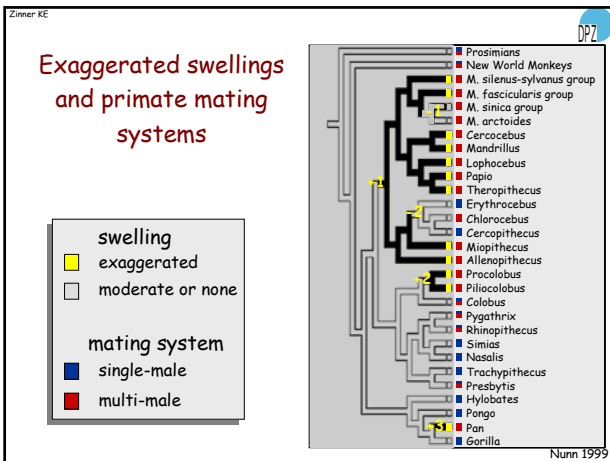
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### Research questions on the ultimate level:

What is the function of exaggerated sexual swellings?  
(proximate level: to attract males)

What are the underlying evolutionary mechanisms?  
(in the framework of sexual selection theory)



Sexual conflict: male hamadryas baboon gives neck bite to an estrous female

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Various hypotheses have been proposed to account for the function and evolution of sexual swelling. These hypotheses have to be confronted with the facts.

### Facts about swellings:

- Swellings are hormone dependent and signal ovulation only more or less precise. (Probability of ovulation)
- Swellings may also occur when ovulation is very unlikely.
- Swellings are most likely costly signals.
- Swellings last up to 2/3 of a cycle.
- Swellings attract males and stimulate their sexual arousal.
- Swellings are linked to multi-male, multi-female mating systems in certain catarrhine lineages.

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## Commonly cited hypotheses

**Obvious-ovulation hypothesis** Hamilton 1984  
Swellings pin-point ovulation and increases paternity confidence for the mating male, hence increase paternal investment.

**Best-male hypothesis** Clutton-Brock & Harvey 1976  
Swellings incite male-male competition so females can identify, and then mate with, the male with "best" genotype.

**Many-males hypothesis** Hrdy 1981; Hrdy & Whitten 1987  
Swellings attract multiple males as mating partners. Mating with multiple males facilitates paternity confusion, which reduces risk of infanticide.

**Reliable-indicator hypothesis** Page 1994  
Females compete for certain "best" males. Swellings indicate female quality and females with larger swellings incite more male-male competition so females can identify, and then mate with, the male with "best" genotype.

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## Obvious-Ovulation & Best-Male Hypotheses

expected characters of swelling

Explains:

- long duration -
- large size -
- ovulation probability -
- multi-male +/-

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## Mating activity in relation to sex ratio

*Macaca mulatta*

Wallen 1982

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### Cycle length and receptive period in two populations of Hanuman langurs

	Jodhpur, India <small>Sommer et al. 1992</small>	Ramnagar, Nepal <small>Ziegler 2001 Borries et al. 2001</small>
mating system	single-male	multi-male
duration of receptive periods (days)	4.0	9.6 7.6
mean cycle length (days)	24.1	24.7

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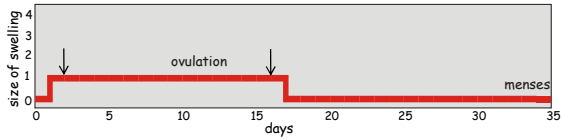
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### Many-Males Hypothesis

expected characters of swelling



size of swelling

days

Explains:

- long duration            +
- large size                -
- ovulation probability   +
- multi-male               +

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### Reliable Indicator Hypothesis

Page1 1994

(Pavo cristatus)

(Papio hamadryas)

Swellings are costly, and therefore honest indicators of female quality and are a product of some form of female-female competition and male mate choice.

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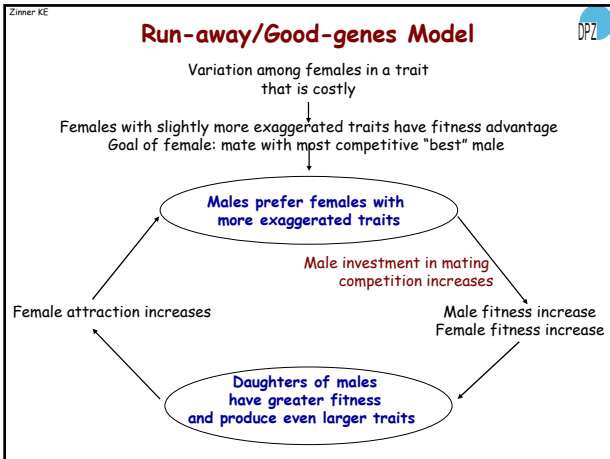
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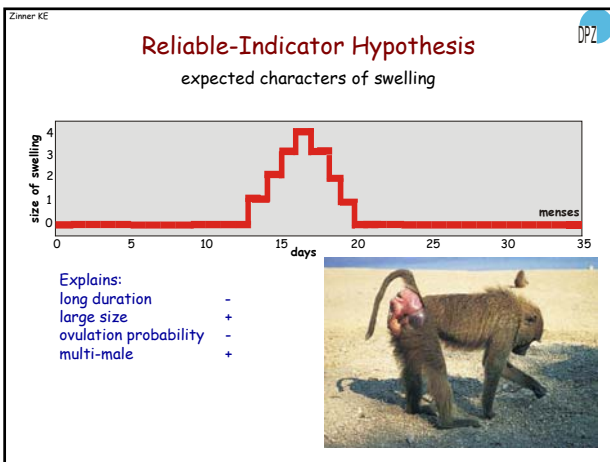
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- Zimmer KE DPZ
- ### Predictions of RIH
- Swelling are costly!
  - Females with larger swellings mate with "better" males!
  - The trait (large swelling) is an enduring character of an individual female!
  - Males are choosy! They prefer females with larger swellings and are willing to invest more in competition!
  - Males increase their fitness from reproducing with the female with largest swellings!

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### Evidence for the RIH

Domb & Pagel (2001) evidence in support of RIH - females olive baboons at Gombe with larger swellings had better life time reproductive success than females with smaller swellings

Setchell & Wickings (2004) no evidence - no correlation of lifetime reproductive success and swelling size in mandrills in Gabon

Deschner et al. (2004) no evidence - male chimpanzees in Tai Forest do not prefer females with the largest swelling

Setchell et al. (2006) no evidence - no correlation of swelling size with general measures of parasitism and immune status in mandrills in Gabon

Gesquire et al. (2006) no evidence - no evidence for swelling size as an enduring individual-level character

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### Female-female competition and exaggerated swellings

Female:Male Ratio

Canine Residuals

Mean sex ratios (females/male) for catarrhine species without and with exaggerated swellings and results for evolutionary contrasts

Mean canine residuals for catarrhine species without and with exaggerated swellings and results for evolutionary contrasts

Nunn et al. 2001

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### Female ultimate reproductive goals in multi-male mating systems

- 1) to mate with many males (paternity confusion, infanticide avoidance)
- 2) to mate with males of her choice ("best" male, paternity insurance)

Male and "swollen" female Guinea baboon

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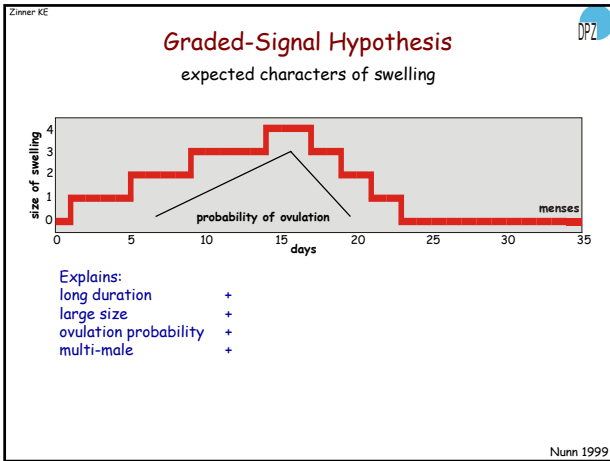
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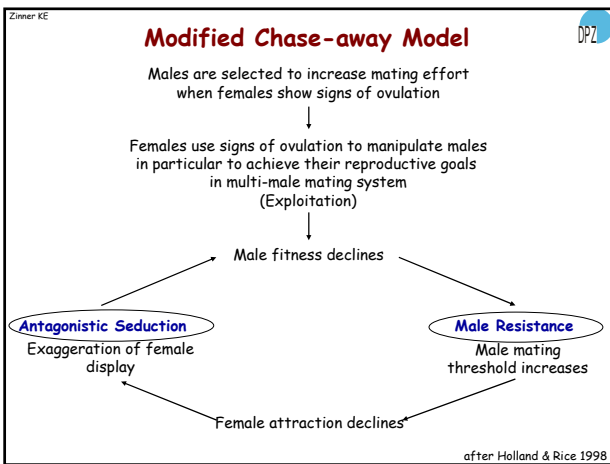
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### Conclusions

Existing data suggest that females obtain multiple benefits from exaggerated sexual swellings.

Thus, hypotheses focusing on a single benefit are unlikely to explain all aspects of this exaggerated trait.

Secondary benefits may superimpose the original benefits and may have helped to change or maintain exaggerated swellings.

Including aspects of "sexual conflict" and antagonistic co-evolution might help to better understand the function and evolution of swellings.

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