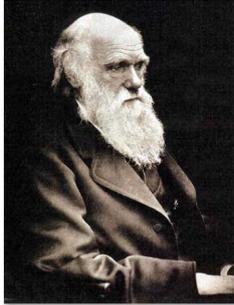


## Sexual selection

Introduction, key concepts, examples.

ENS – Master 1 EBE – UE Comportement, population, adaptation (E2)  
Octobre 2011  
David Laloi (david.laloi@upmc.fr)





### Darwin's hypothesis

Natural selection (in its basic form) does not explain appropriately the evolution of many traits, dimorphic sexual ornaments in particular:

→ other selective pressures?

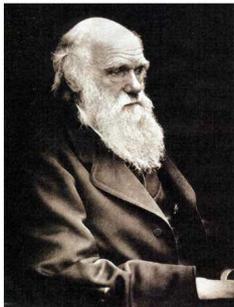
1859 *The origin of species by means of natural selection*

1871 *The descent of man and selection in relation to sex*

### Sexual selection

Selection that results from differences in reproductive success due to competition for mate acquisition.

*In other words, some traits do not depend on a 'struggle for life' but on a 'struggle for mating'.*



### Darwin's hypothesis

Two main forms of sexual selection:

Males compete with each other to accede to females

→ **Intrasexual selection**

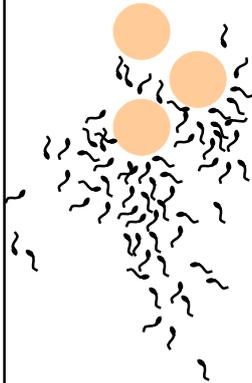
Females are choosy in which males to mate with

→ **Intersexual selection**

Sexual selection: asymmetrical processes...

Why males and females differ in trying to acquire mate?

- All individuals can obtain more offspring when mating with more mates.
- All individuals can obtain better offspring when mating with better mate.



But...

- ♀ gametes: large, non motile, swollen with reserves,  
High investment in each → small number.
- ♂ gametes: small, motile, with very few reserves,  
Low investment in each → very large number.

Bateman's principle

Sperm are cheaper and more numerous than eggs, thus:

- a single male can easily fertilize all a female's eggs; she will not produce more offspring by mating with more than one male,
- a male is capable of fathering more offspring if he mates with several females.

A male's potential reproductive success is limited by the number of females he mates with.

→ **Males compete with each other** (intrasexual selection).

A female's potential reproductive success is limited by how many eggs she can produce.

→ **Females become choosy in which males to mate with** (intersexual selection).

Bateman (1948), Trivers (1972)

## Intrasexual selection

Key questions :

How males increase their success in male-male competition?

Which traits have evolved as a result of intrasexual selection?

### 1. Direct competition between males

- For immediate mating.



- For the control of resources that are needed to reproduce: territories, nest sites...



E.g. some odonates: Males compete before mating to acquire sites for egg-laying.

### Traits that look like weapons

Other examples: horns of deers, stalk-eyed fly *Cyrtodiopsis whitei*, cephalic and thoracic horns of *Dynastes* beetles, tusk of narwhal, etc.

### Sexually selected traits or weapons to defend against predators?

Some indirect evidences:

- Horns of deers come off in winter, when predation risk is higher.
- Many correlations between traits and the intensity of intrasexual conflicts.
- The morphology of horns is often more suitable to defend against predators in females (in species where females have horns).



Overdeveloped weapons of males are sexually selected traits.

## 2. Sperm competition

Physical competition between sperms from different males to fertilize a female's eggs.

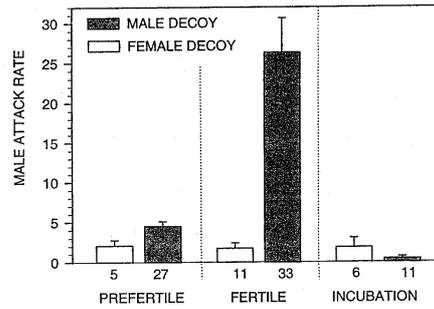
- Intrasexual competition goes on after copulation and sperm transfer.
- Sperm competition risk is a possible important selective force on any male trait that could either avoid competition or increase the probability of fertilizing egg.

### 3. Paternity assurance strategies

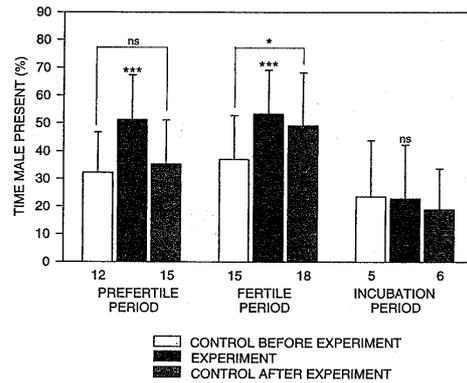
- Mate guarding



Montagu's harrier  
*Circus pygargus*



Mougeot *et al.* (2001) *Behav. Ecol.*



Mate guarding is costly, so males exhibit such a behaviour only when benefit → mate guarding is always correlated to risks of extra-pair copulation :

- when the female is fertile,
- when other males are in close proximity.

Mougeot *et al.* (2001) *Behav. Ecol.*

### 3. Paternity assurance strategies

- Mate guarding

Many others traits (anatomical, morphological, behavioural traits) may contribute to paternity assurance.

Some examples...

### 3. Paternity assurance strategies

- Mate guarding
- Frequent or prolonged copulations



*Parastrachia japonensis*  
Sperm transfer: 5 – 10 seconds,  
but copulation can prolonge up to 1 hour.  
Copulation is longer when there are other males in proximity



*Necroscia sparaxes*  
Anecdotal but stricly linked to paternity assurance : copulation  
can prolonge up to 79 days.

### 3. Paternity assurance strategies

- Mate guarding
- Frequent or prolonged copulations
- Copulatory plugs (physical or chemical barriers)



*Locusta migratoria*

Spermatophor bag remains in the female genital tract where it avoids transfer of other sperm.



*Dinoponera quadriceps*

Male sacrifices his genitalia.

### 3. Paternity assurance strategies

- Mate guarding
- Frequent or prolonged copulations
- Copulatory plugs (physical or chemical barriers)
- Repellents and antiaphrodisiac pheromones



*Tenebrio molitor*

Chemicals from the sperm package have a repellent effect on males.



Many mosquitoes (e.g. *Aedes*)

Male-produced chemicals reduce the females' attractiveness for subsequent mating.

### 3. Paternity assurance strategies

Paternal investment :

- territory defense / resource defense
- care to female / care to youngs
  - defense against predators
  - feeding

A male can gain from paternal investment if it is tuned to its own youngs → high benefit in evolving paternity assurance strategies when males invest in parental care.

→ Many correlations between both types of traits.

### Intersexual selection

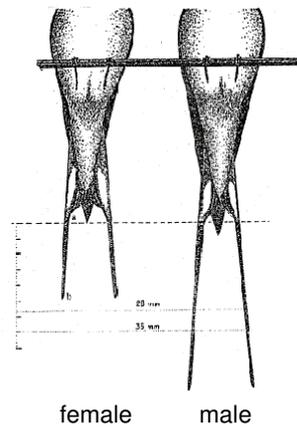
Key questions :

How females increase their fitness by choosing males?

Which traits have evolved as a result of intersexual selection?

Various traits can be intersexually selected, **extravagant male ornaments** (male secondary sexual traits) in particular.

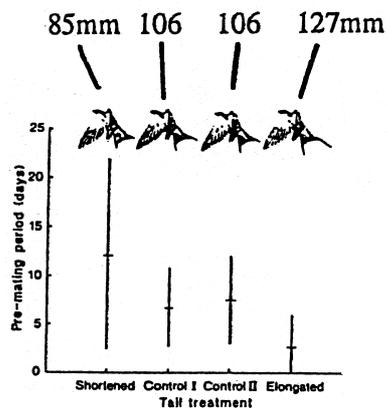
Barn Swallow  
*Hirundo rustica*



female male

Møller *et al.* (multiple references)

Empirical evidence : experimental manipulation (confounding factors do not affect the results) of tail ornaments.

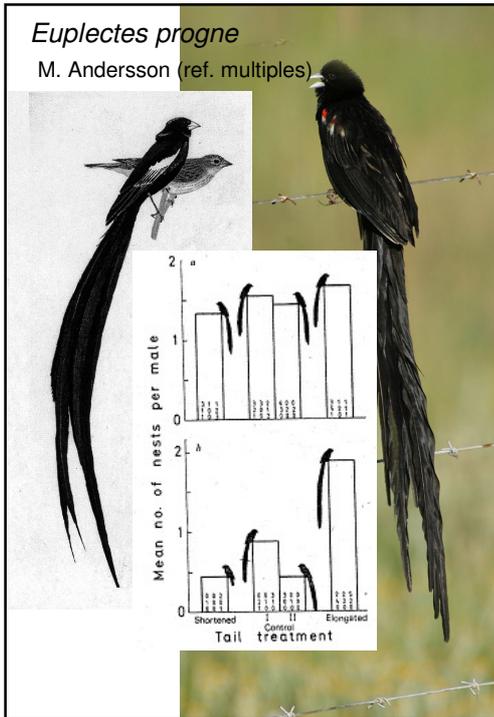


→ Males with elongated tails obtain mates more quickly, i.e. females prefer males with elongated tails.

Møller *et al.* (multiple references)

*Euplectes progne*

M. Andersson (ref. multiples)



Swallows are not alone...

→ Widespread female preference for ornamented males.

Traits that can be selected by female mate choice are highly diverse

- colour (entire body or patches)
- songs, calls
- display behaviour
- body size or size of some parts
- weight
- cuticular ornaments (spines, rostrum...)
- odours
- pheromones
- quality or size of territory
- nest site
- nuptial gifts
- social / hierarchical status, dominance, position in a lek

### Handicap hypothesis

(Zahavi, 1975)

- Ornaments are costly
- Their expression depends on male quality.

→ Honest signals of male quality.

- Predation, parasitism,
- energetic / physiological costs,
- constraint, embarrassment.

Key question:

What are the benefits of 'mate quality' for females?

### Good parent hypothesis

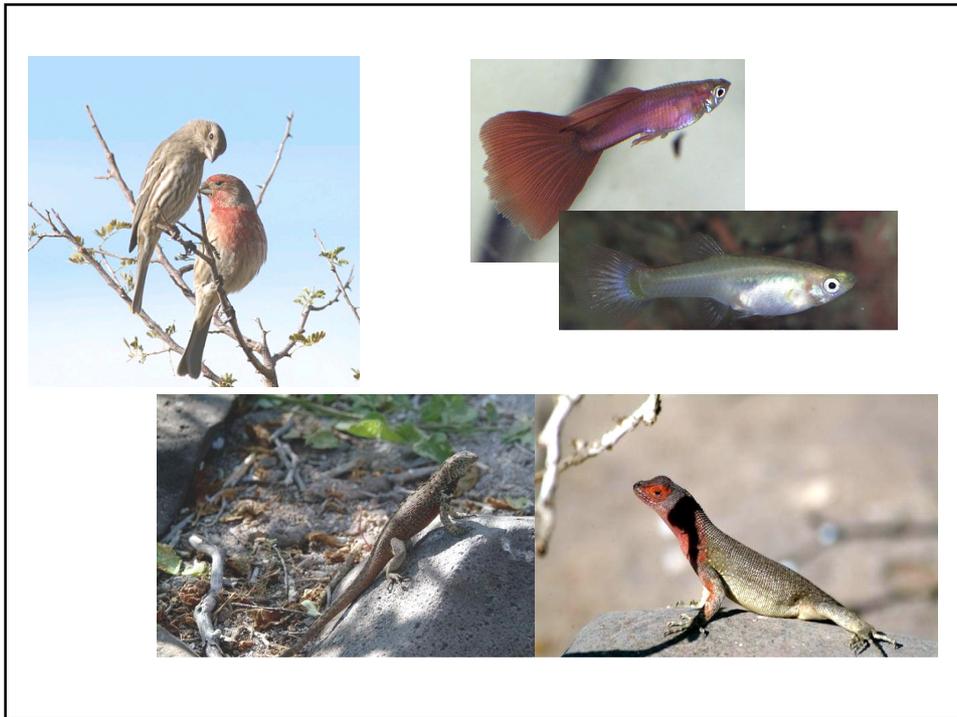
Offspring benefit from resources held / given by their father.

### Healthy mate hypothesis

Avoid pathogen transmission.

### Good genes hypothesis

Offspring inherit good genes from their father.



Do bright colours have particular properties that can fit with the 'honest signalling' hypothesis?

- Synthesis of all pigments: metabolic processes that are energetically costly.
- Main pigments are carotenoids, which are also strongly involved in immune response.

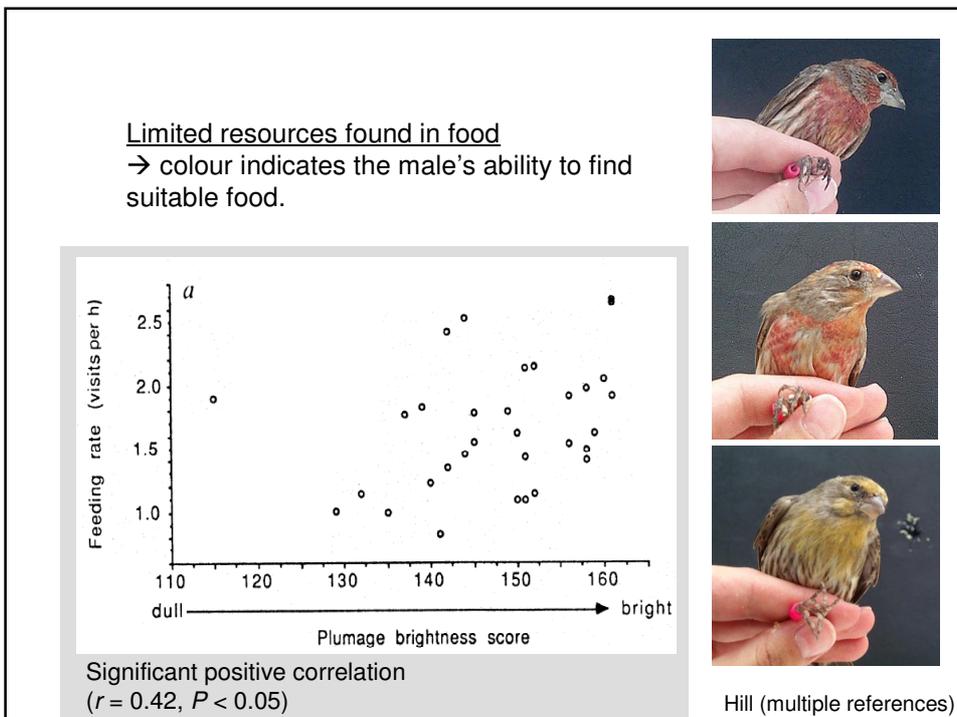
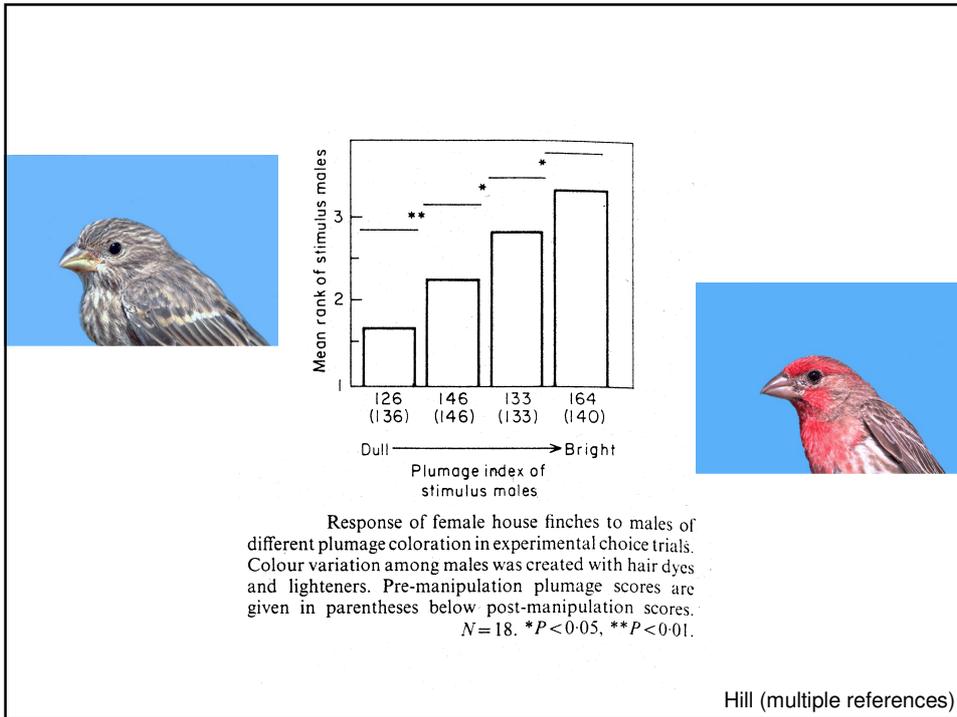
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Physiological roles of carotenoids

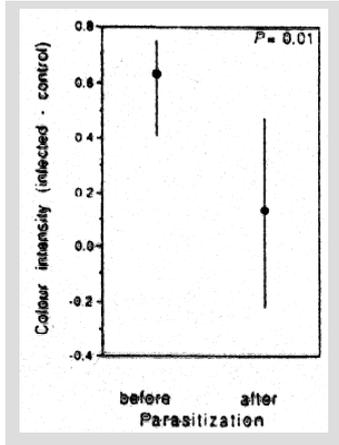
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- |   |  |
|---|--|
| <ul style="list-style-type: none"> <li>• synthesis of yellow-orange-red pigments</li> </ul> | <ul style="list-style-type: none"> <li>• stimulate the synthesis of lymphocytes, monocytes and macrophages</li> </ul> <hr/> <ul style="list-style-type: none"> <li>• stimulate the production of cytokines and interleukins</li> </ul> <hr/> <ul style="list-style-type: none"> <li>• contribute to capture free radicals (reduce oxydative stress)</li> </ul> |
|---|--|

- 
- Food origin → limited resource.

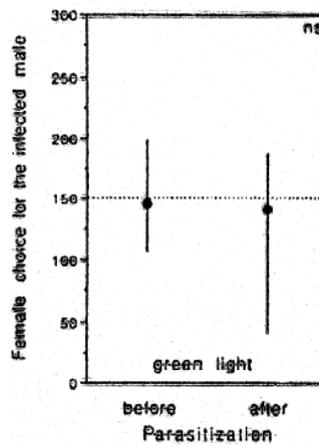
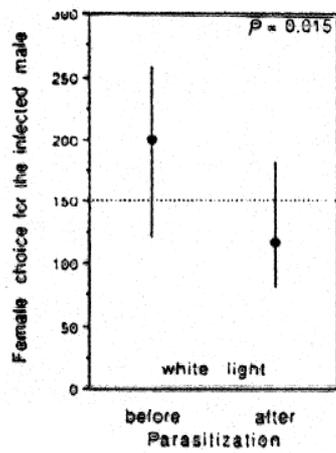
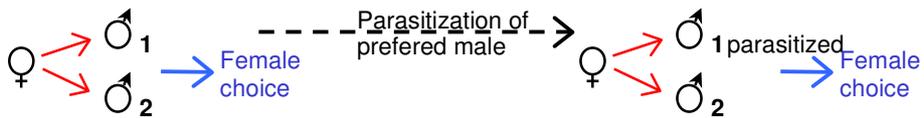


trade-off with immunitary respons  
 → colour indicates male's health

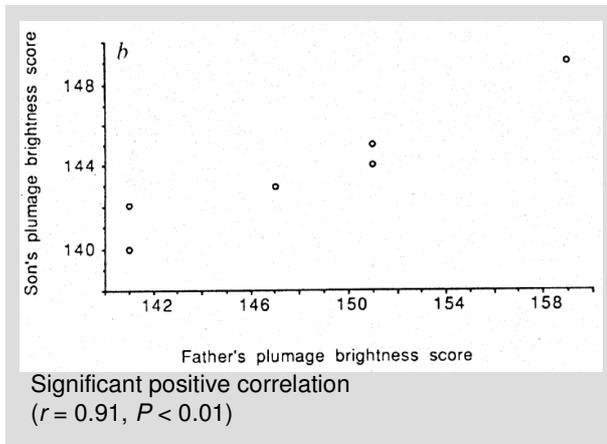


The intensity of carotenoid-based colouration is inversely proportional to pathogen load (Hamilton & Zuk, 1982)

Milinski & Bakker (1990) *Nature*



Milinski & Bakker (1990) *Nature*



- genetic determinism of colour
- performance in searching for food and feeding youngs

*May be both?*

Hill (multiple references)

Female mated to attractive (sexy) male



Sons will have an attractive phenotype  
(assuming that heritability of attractiveness  $\neq 0$ )

→ They will be preferred by females,  
so, they will have a higher reproductive success



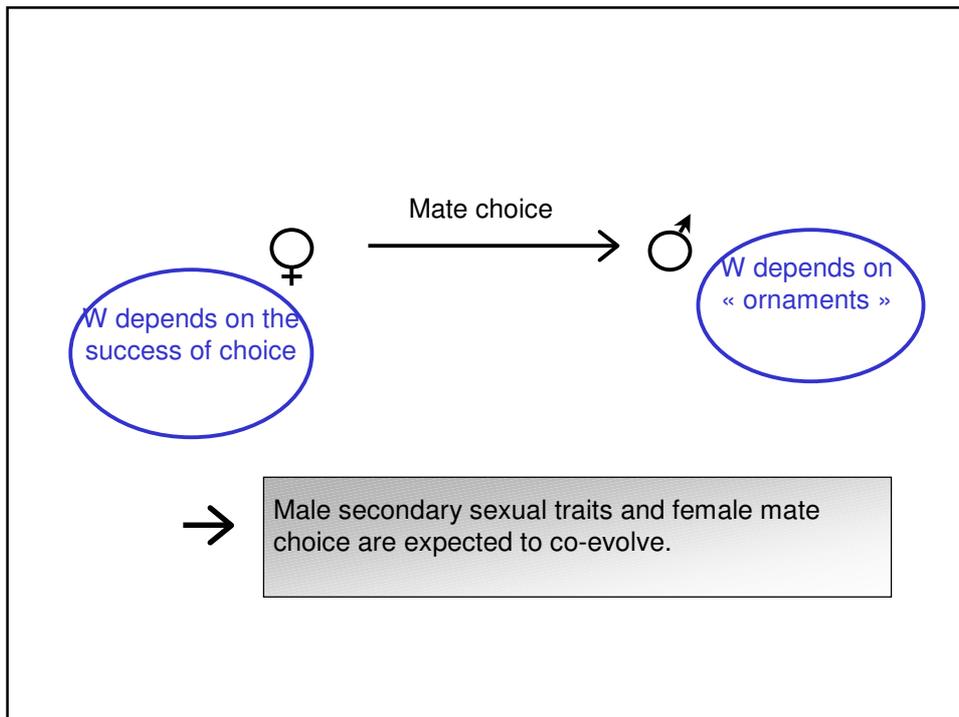
Which increases the transmission of mother's genes  
through the success of her sons.

Run-away

(Fisher, 1975)

By choosing an attractive male to mate with, a female will produce attractive sons, which increases the transmission of the female's genes in subsequent generations.

*Also known as Sexy-son hypothesis*



### Bateman's principle

Sperm are cheaper and more numerous than eggs, thus:

- a single male can easily fertilize all a female's eggs; she will not produce more offspring by mating with more than one male,
- a male is capable of fathering more offspring if he mates with several females.

→ Males should be polygamous (mating system is polygyny).

→ Females should be monogamous (mating system is monandry).

But this theoretical polygynous system is not as frequent as one can expect.



Social (apparent) monogamy does not always correspond to true (genetic) monogamy

Species	Extra-pair paternity % of broods	% of youngs
Kentish Plover	1,5	0,6
Western Sandpiper	8,0	6,6
Common Sandpiper	6,7	1,8



### Key questions

True (genetic) monogamy:

**Why males mate singly?**

Polyandry:

**Why females mate multiply?**

## Why males mate singly?

### 1. By-product of mate guarding



: an inevitable compromise

Paternal investment (care + mate guarding) in relation to mating that was already obtained

*versus*

Investment in search for other matings.

## Why males mate singly?

### 1. By-product of mate guarding

- 'Extreme' strategies.



*Dinoponera quadriceps*



*Apis mellifera*

Male sacrifices his genitalia (e.g. as a copulatory plug).

- Spending of time / energy to guard his mate can prevent a male to search for other females.

Particular cases when females are rare or scattered.

E.g. *Hymenocera picta*

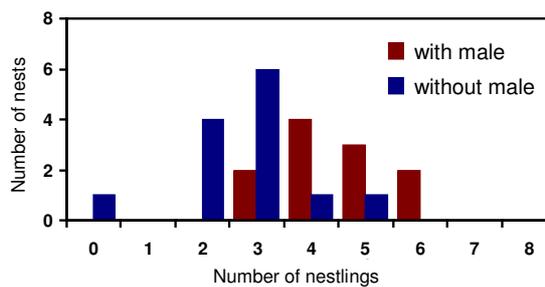
## Why males mate singly?

### 2. Link with paternal investment

- Incubation, brooding and care to young benefit strongly from male investment.



Comparison of reproductive success between nests without male (experimentally pulled out) and nests with male.



Lyon *et al.* (1987) *Behav. Ecol. Sociobiol.*

## Why males mate singly?

### 2. Link with paternal investment

- Incubation, brooding and care to young benefit strongly from male investment.

- Female can enforce monogamy:

- by refusing to copulate with already-mated males.
- by guarding male against other females.

## Why females mate multiply?

### 1. Fertilization assurance

- In some cases, contrary to Bateman's principle, sperm of one male can be insufficient (quantity, viability, decline of stocked sperm...) to ensure the fertilization of all a female's gametes.

## Why females mate multiply?

### 2. Direct (i.e. material) benefits of multiple mates

- Copulations with multiple males allow the female to obtain additional direct (material) benefits.

Male resources:

- nuptial gifts (food, nutrients)



Many Orthoptera:

Spermatophors contain not only sperm but also male secretions. Female can benefit from nutrients of male secretions that increase her reproductive success.

### Why females mate multiply?

Diversity of food resources brought by males to females (before, during or after copulation) in insects

<b>Male glandular secretions</b>	<b>Dorsal glands</b>	Some Orthoptera et Dictyoptera
	<b>Salivary glands</b>	some Diptera
	<b>Spermatophors</b>	Collembola, Orthoptera, Dictyoptera, Dermaptera, Psocoptera, Neuroptera, Lepidoptera, Hemiptera, Trichoptera, Coleoptera, Hymenoptera, Diptera
	<b>Copulatory plugs</b>	Lepidoptera, some Diptera, Coleoptera, Orthoptera and Isoptera
<b>Female feeding by male (nuptial gifts)</b>	<b>Preys</b>	some Mecoptera
	<b>Nectar</b>	some Hymenoptera
	<b>Seeds</b>	some Hemiptera
<b>Cannibalism (female eats male during or after copulation)</b>		Praying mantis, some Coleoptera, some Diptera

### Why females mate multiply?

#### 2. Direct (i.e. material) benefits of multiple mates

Male resources:

- nuptial gifts (food, nutrients)
- territory (nest sites, food)
- paternal care

### Why females mate multiply?



Dunnock  
*Prunella modularis*

	successful attempts / female / season	Mean number of young fledged / female		
		/ attempt (all attempts)	/ successful attempts	/ season
monogamy 1 Male - 1 Female	66,1%	1,95	2,95	5,37
polyandry 2 Males - 1 Female	84,6%	2,95	3,48	6,69
polygyny 1 Male - 2 Females	61,9%	1,43	2,31	2,62
polygynandry 2 Males - 2 Females	53,2%	1,29	2,44	3,61

Davies & Houston (1986) *J. Anim. Ecol.*

### Why females mate multiply?

#### 3. Genetic (indirect) benefits of multiple mates

- Multiple paternity (resulting from copulation with multiple males) can benefit genetically to offspring.

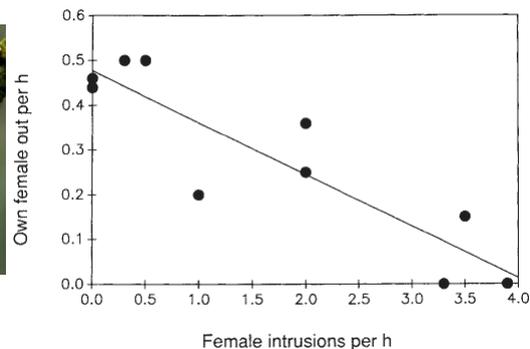
## Why females mate multiply?

### 3. Genetic (indirect) benefits of multiple mates

- Additional (extra-pair) matings with males of higher genetic quality than previous (social) mate.



Blue Tit *Parus caeruleus*  
40% of youngs come from extra-pair copulations.



Kempnaers et al. (1992) *Nature*

## Why females mate multiply?

### 3. Genetic (indirect) benefits of multiple mates

- Additional (extra-pair) matings with males of higher genetic quality than previous (social) mate.
- Increased genetic diversity of offspring can be benefit:
  - sib-competition avoidance / decrease,
  - inbreeding avoidance / decrease.
- Favoured sperm competition:
  - Multiple matings
    - increase quantity and diversity of sperm
    - increase 'selectivity' of sperm competition.
  - Females can obtain benefit from favouring sperm competition, assuming it increases offspring quality (described as a *female cryptic choice*).

## Why females mate multiply?

### 4. Other hypotheses

- In species where males harass the females, it could be less costly to accept multiple mating than to resist to harassment.
- An evolutionary correlation between male behaviour (selected for multiple mating) and female behaviour could (in theory) explain multiple mating by females (but a 'decorrelation' should be selected quickly if it is costly to females)

...many selective pressures act on mating behaviour, leading to the impressive diversity of mating systems.

## Some apparently more complex cases...

Sex-role reversion

Coexistence of alternative strategies

Red-necked Phalarope  
*Phalaropus lobatus*



**Males:**

- are choosy in which females to mate with,
- settle within a female's territory,
- take care of brood and offspring.

**Females :**

- larger-sized and more coloured than males,
- aggressive, defend territories,
- display.



**Sex-role reversion!**

Numerous cases in birds.

Large flightless bird (Ostrich, Rhea, Cassowary), Tinamous, Small Button-quail, some shorebirds (Phalaropes, Dotterel, Painted-snipes, Jacanas, Spotted sandpiper), some Woodpeckers, some passerines.

Very rare in other Vertebrates  
(but some cases in fishes, e.g. seahorses).

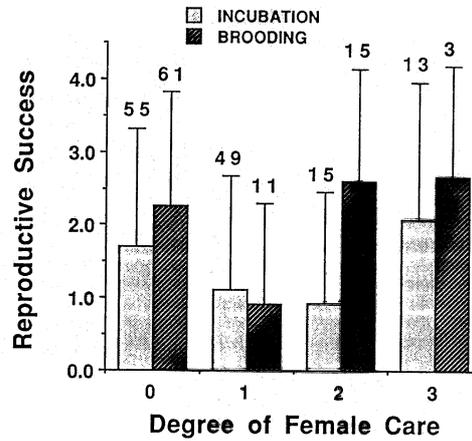
Why?

In birds: except egg-laying, males can ensure parental investment as well as females.

→ Initial asymmetrical investment (i.e. anisogamy) can be counterbalanced by later investment in incubation, brooding and care to young.



Spotted sandpiper  
*Actitis macularia*



Oring et al. (1992) *Behav. Ecol. Sociobiol.*

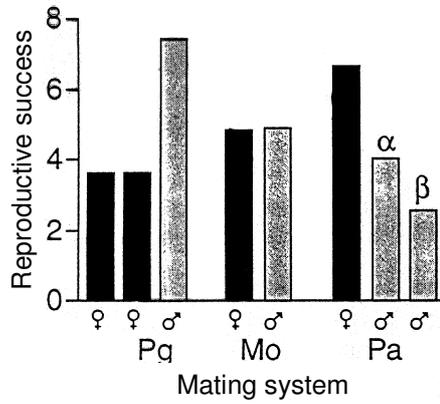
Dunnoek  
*Prunella modularis*



	successful attempts / female / season	Mean number of young fledged / female		
		/ attempt (all attempts)	/ successful attempts	/ season
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polygynandry 2 Males - 2 Females	53,2%	1,29	2,44	3,61

How different strategies with apparently different fitness outputs can coexist?

Davies & Houston (1986) *J. Anim. Ecol.*



**Pg** : polygyny (paternal care provided by one male is shared to two females)

**Mo** : monogamy (one male take care of one brood)

**Pa** : polyandry (one female benefits from paternal care provided by two males)

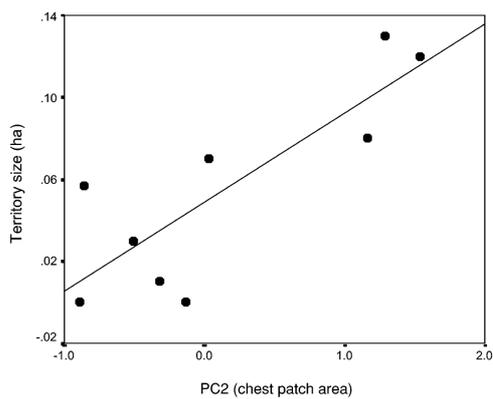
Alternative mating strategies could coexist in a population as the result of an evolutionary conflict between male and female interests.

Davies & Houston (1986) *J. Anim. Ecol.*

Ornate dragon lizard (Agamid)  
*Ctenophorus ornatus*



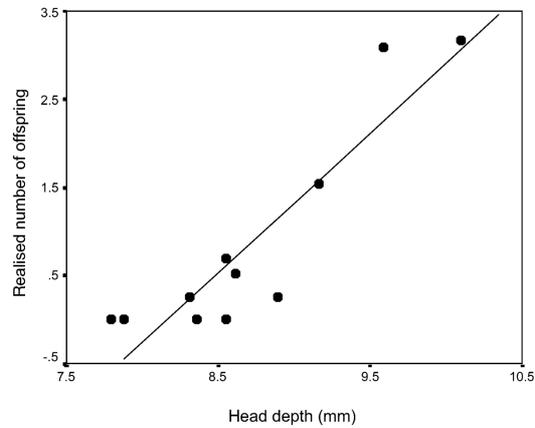
Territorial species



Male chest patch size predicts territory size and the number of females on the territory.

But chest patch size (and territory size) does not predict reproductive success...

LeBas (2001) *Molecular Ecology*



Larger body size males (body size is positively correlated to head depth) do not have a greater number of females in their territories, and instead have more extra-territorial copulations.

LeBas (2001) *Molecular Ecology*

- Males that have great territories
  - also have great numbers of females,
  - but they suffer from extra-territorial copulations.
- Larger body size males
  - have small territories and small numbers of females,
  - but enhance their reproductive success through extra-territorial copulations.

→ Alternative strategies can coexist since fitness outputs of both strategies are equal.

An 'extreme' but frequent situation in territorial species:

- territorial males obtain females in relation to territory size, but do not contribute to extra-territorial copulations (maybe due to time and energy expenditure in territory holding),
- floatter males do not hold territory, but gain reproductive success through extra-territorial copulations.

Side-blotched lizard  
*Uta stansburiana*



Throat-colour polymorphism associated with alternative male reproductive strategies.

Sinervo & Lively (1996) *Nature*



Males with orange throats  
**'ultra dominants'**:  
- very aggressive,  
- defend large territories.

Males with yellow throat  
**'sneakers'**:  
- do not defend territories,  
- search for matings in territories of other males.

Males with dark blue throat  
**'mate guards'**:  
- less aggressive, defend smaller territories,  
- do mate guarding.

As in a **dynamic 'Rock-paper-scissors' game**:  
- each strategy is defeated by only one of the two other strategies,  
- each strategy can invade when rare, but was invadable by another morph when common,

→ frequency-dependent selection maintains cyclic fluctuations, the **three strategies always coexist in an unstable equilibrium.**

Sinervo & Lively (1996) *Nature*