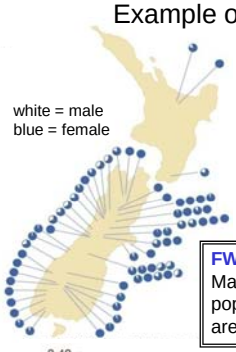
Maintenance of Sexual Reproduction, conclusion:

e.g., snails & trematodes

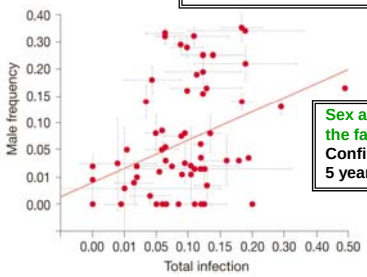
Through **antagonistic coevolution**, alleles of "future usefulness" remain in the sexual population longer, available to re-generate genotypes that had been useful in the recent past.

This applies to **Host-parasite interactions**, in particular:

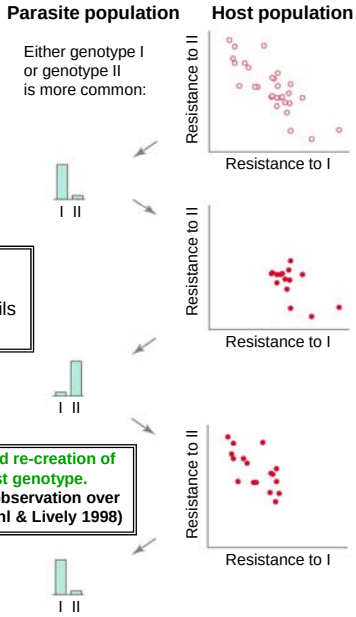
Example of **Antagonistic Coevolution**:
(Lively 1992, 2009, 2010, 2010, 2011)



FW Snail vs. Trematodes:
Males are more frequent in populations in which more snails are infected.



Sex allows rapid re-creation of the favored host genotype.
Confirmed by observation over 5 years (Dybdahl & Lively 1998)



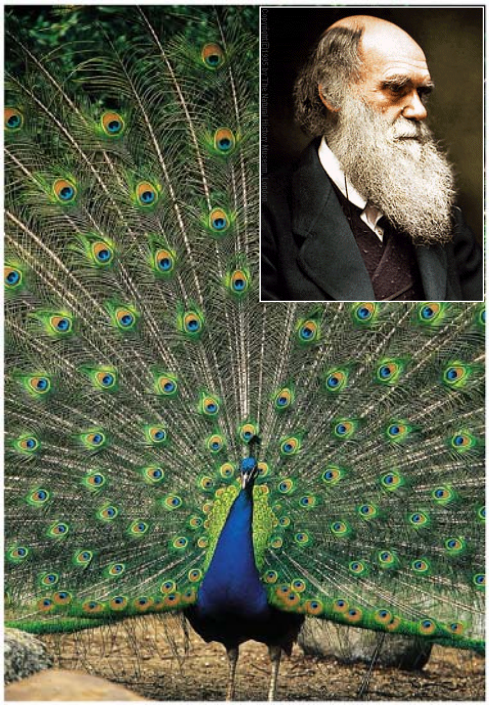
Characteristics of species that tend to be sexual vs. asexual generally **conform to predictions** of antagonistic co-evolution

Sexual Species		Asexual Species
Marine		Fresh water
Large bodies of fresh water		Small bodies of fresh water
More distant from shore in the ocean		Closer to shore in the ocean
Large organisms		Small organisms
Low latitudes		High latitudes
Low altitudes	**Asexual reproduction predominates in novel, disturbed habitats with low intensity of interspecific interactions.**	High altitudes
Wet		Dry
Undisturbed		Disturbed
Productive		Unproductive
Parasitic		Free-living

Note: Support from a recent model of Scheu & Drossel, 2007

So why is sex maintained despite the (oversimplified) two-fold advantage of asexual reproduction?

There's probably no single reason, but the ***combination*** of factors conspire to make sexual reproduction highly adaptive (the Pluralistic View – see Meirmans & Strand, 2010.

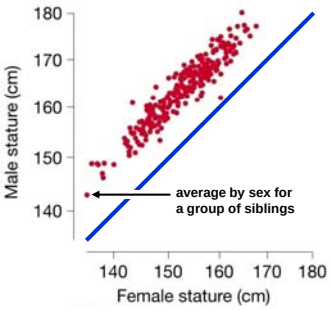


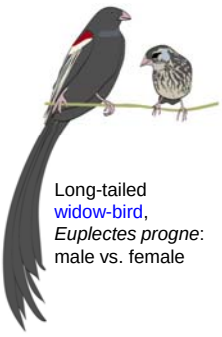
Sexual Selection

- Darwin (1871) first distinguished it from natural selection: selection for ***mating success*** rather than for viability & fitness.
- Far-reaching consequences:
  - intrasexual competition (male-male contests)
  - intersexual competition (female choice)
  - sexual dimorphism
  - runaway evolutionary change
  - evolutionary handicaps
  - antagonistic co-evolution
  - sexual conflict
  - speciation

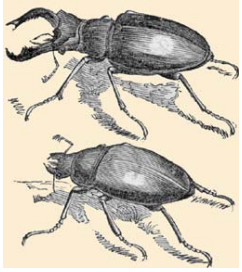
Secondary sexual characters

Sexual size dimorphism in humans
(Rogers & Mukherjee 1992)





Long-tailed widow-bird, *Euplectes progne*: male vs. female



Jaw hypertrophy in male Lucanidae (stag beetles)

- Darwin's question: Why weren't these obviously burdensome and energetically costly features eliminated by natural selection?
- His answer was the *theory of sexual selection*, that a male possessing such a feature *has an advantage over other males in the competition for mates*.

Flower dimorphism in *Wurmbea dioica*

Two types of sexual selection were identified by Darwin

1. ***Intrasexual competition***, in which members of one sex – usually males – vie with each other for access to females.
   - One sex constitutes a **rare resource** for the other.
   - This sets up male-male (or rarely female-female) competition.
2. ***Intersexual competition,*** in which members of one sex – usually females – exhibit discrimination in selecting their mates.
   - This is called mate choice…typically, *female choice.*
   - Here, males compete for the ***attention*** of females.

Both types lead to ***sexual dimorphism***

- *Intra*sexual competition leads to *weaponry* or other features that help males win contests with other males.
- *Inter*sexual competition leads to *ornaments* and other displays in males (see conceptual review by Prum, 2012).

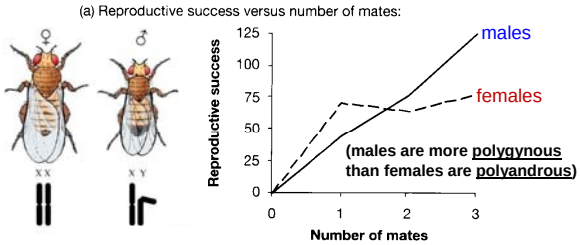
Underlying reason? ***Unequal investment of the sexes*** *in individual offspring*: expensive eggs (and care) vs. cheap sperm.

In sexual reproduction, asymmetries exist between the sexes

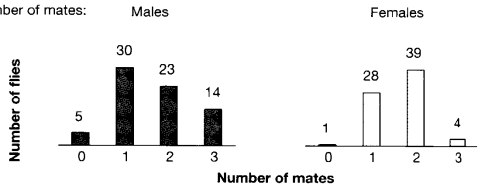
- ***Individual lifetime reproductive success*** of the sexes is different.
  - **Female's** = **low**, limited more by the number of eggs she can make or young she can nurture than by the number of males she can convince to mate with her.
  - **Male's** = potentially **high**, limited more by the number of females he can mate with than by the number of ejaculates he can produce.
- That's why (typically) females are a *rare resource* to the males, which sets up the two types of competition Darwin described.
- One male can mate with many females (*polygyny*), leaving many males with no females to inseminate.
- That is, the ***variance*** in lifetime reproductive success will be much greater in males than in females.
- **Angus John Bateman** developed these ideas further and tested them (1948) using *Drosophila melanogaster*.

(See **Wade & Schuster 2005** for full disclosure of the underlying logic)

Bateman's results (1948) on the relative strength of sexual selection



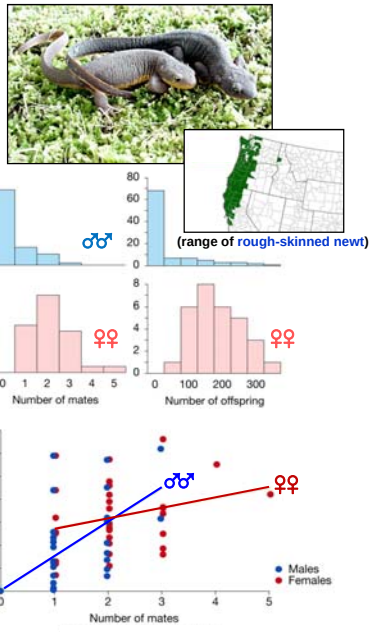
Angus John Bateman

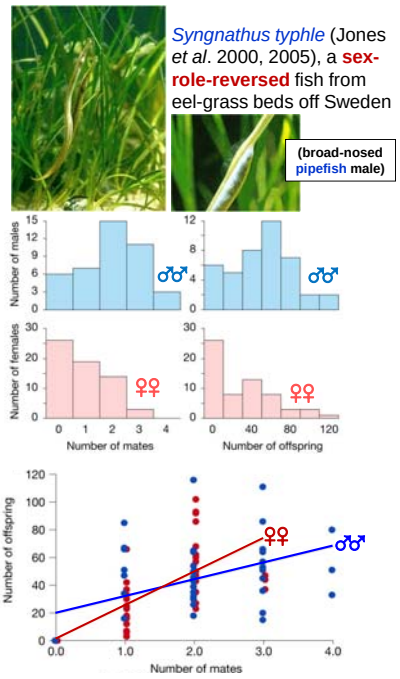


(c) Variance in reproductive success in four groups of experiments:

	Male Variance	Female Variance	Male Variance / Female Variance
Group 1	1604	985	1.63
Group 2	1700	209	8.14
Group 3	2798	993	2.82
Group 4	1098	277	3.97

Taricha granulosa (Jones *et al*. 2002)





Syngnathus typhle (Jones *et al*. 2000, 2005), a **sex-role-reversed** fish from eel-grass beds off Sweden

Other examples of sex-role-reversed organisms

Giant water bug (*Belostoma* spp) aerates his cargo of 150+ eggs for 1 month; stops feeding prior to hatching so he won't eat young.

Stickleback males build a nest and care for offspring of multiple females, aerating them and defending them against attack.

Panamanian poison-arrow frog hydrates the eggs by sitting on them and carries the hatchlings on his back to water.

Spotted sandpiper male incubates the eggs and tends the fledglings nearly exclusively.

Wilson's phalarope males incubate the eggs and care for the young while the mother flies south.

Females are larger and brighter and **compete for males and territories**.

Associated with **male-biased adult sex ratios** (Liker et al. 2013)

e.g. in Arthropoda, paternal care characterizes 15 lineages and at least 1500 species (Requena et al. 2013)**.**

Intrasexual selection

precopulatory

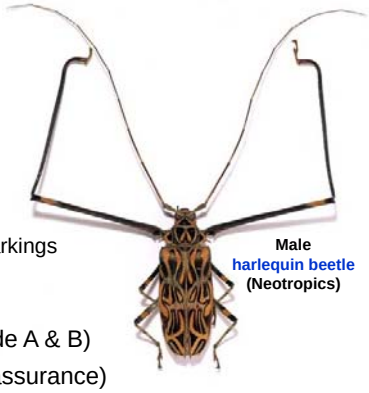
1. Male-male contests

A. Combat
- larger body size
- strength
- weaponry

B. Displays
- bright colors and markings
- posturing
- acoustic signaling

C. Territoriality (can include A & B)

Male fiddler crab, *Uca pugnax*



Male harlequin beetle (Neotropics)

postcopulatory

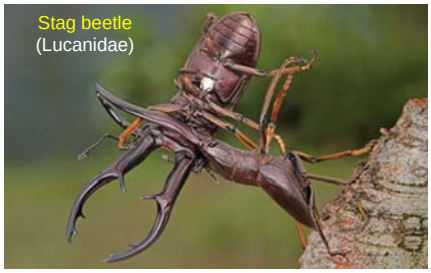
2. Mate guarding (paternity assurance)
- Attentive behavior, clasping genitalia or appendages
- Anti-mating fluids and plugs

3. Sperm competition
- Sperm amount, size, or ability
- Sperm scoops
- Spermicides
- "Helper sperm"

Male-male contests, A: Combat

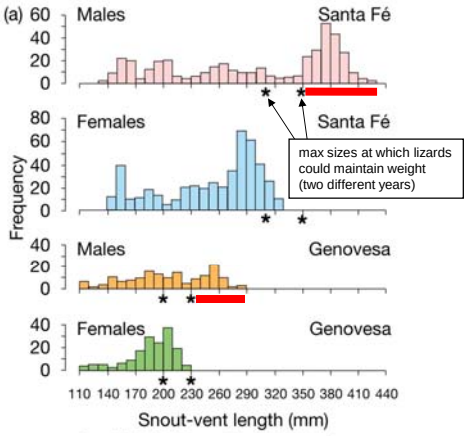
Northern elephant seal, *Mirounga angustirostris*

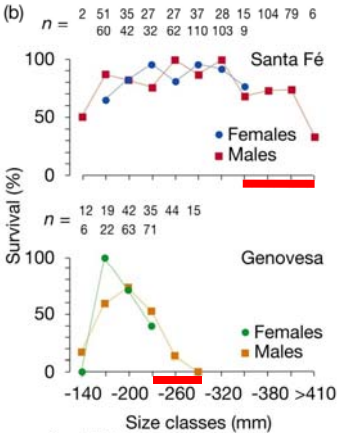
European red deer, *Cervus elaphus*



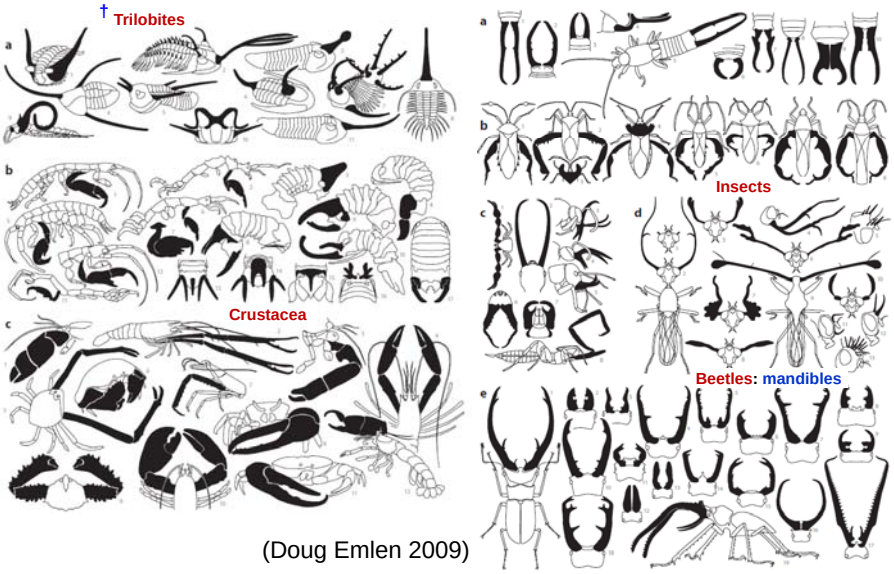
Male-male contests: Body size & combat

Bigger males get more matings, but sexual selection is *countered by natural selection* in **marine iguanas** on the Galápagos (Wikelski & Trillmich 1997)





Male-male contests: Combat weaponry I – Arthropoda



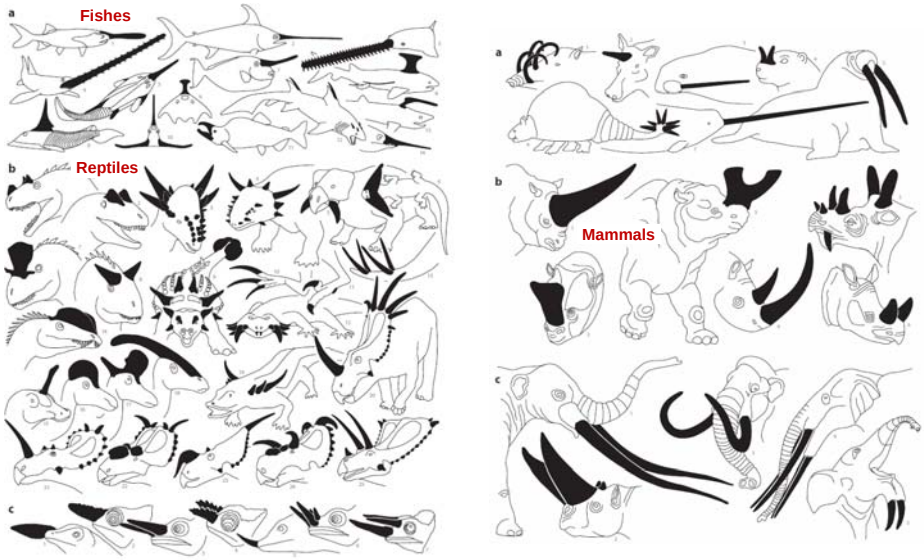
(Doug Emlen 2009)

Male-male contests: Combat weaponry II

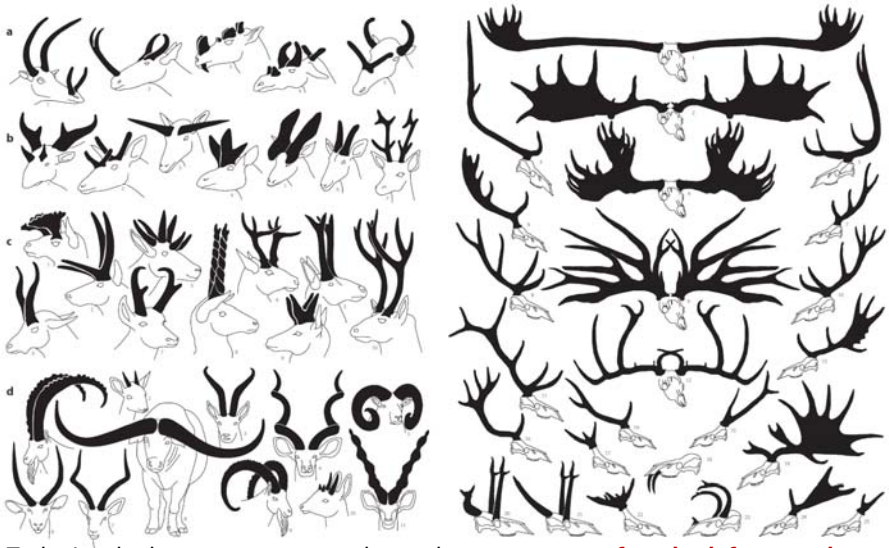
(Emlen 2009)

Beetles: horns, legs, etc. (non-mandibular)

Male-male contests: Combat weaponry III – Fishes, reptiles, mammals



Male-male contests: Combat weaponry IV – Ungulate mammals

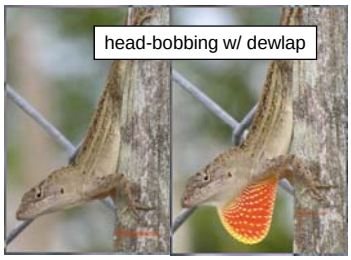


Emlen's take-home: weapons evolve under **resource-** **or** **female-defense polygyny**.

Note: only ***ornaments*** have evolved in sex-role-reversed females; is ***weaponry*** too expensive? (Berglund 2013)

Male-male contests, B: Visual displays (often territorial)

Cuban brown anole: (*Anolis sagrei sagrei*)

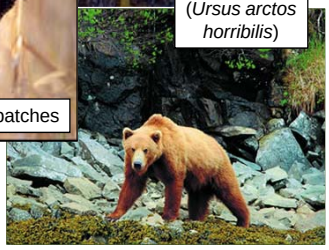


Canis lupus

Great Eggfly: (*Hypolimnas bolina*)

Red-winged blackbird:

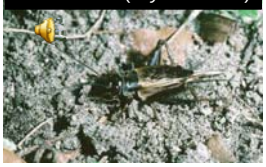
(*Agelaius phoeniceus*)



Male-male contests, B: Acoustic displays (often territorial, too)

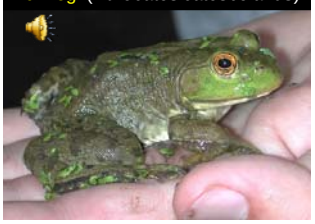
American toad: (*Bufo americanus*)

Field cricket: (*Gryllus firmus*)

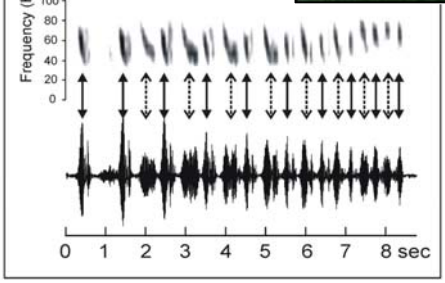


Katydid: (*Pterophylla camellifolia*)

Bullfrog: (*Lithobates catesbeianus*)



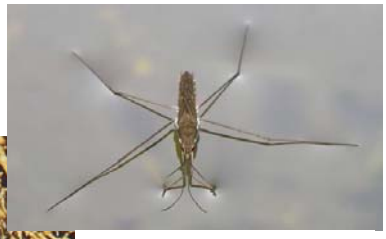
Lacewing: (*Chrysoperla plorabunda*)



Male-male contests, C: Territoriality

- Some types are best viewed as part of *contests* between males.
- Others are best interpreted as ways males keep other males away from their mates – more like pre- or post-copulatory *mate guarding*.

Wood duck (*Aix sponsa*)



water strider (*Gerris marginatus*)

Masked butterfly fish (*Chaetodon semilarvatus*)

- But DNA markers show the females of such species, esp. birds, nevertheless engage in high rates of ***extra-pair copulation***.

Postcopulatory male-male contests, 2: Mate guarding (paternity assurance)

Male tiger beetle grips female's thorax with his large mandibles.

Male damselfly grips female behind neck during copulation and oviposition.

Male blue crab guards female while she's still soft and able to mate.

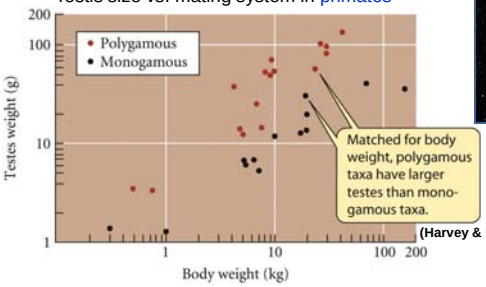
Male cranefly (Tipulidae) guards the female while she oviposits.

European frog (*Rana temporaria*) male clasps the female while she oviposits.

Postcopulatory male-male contests, 3:
Sperm competition (size matters)

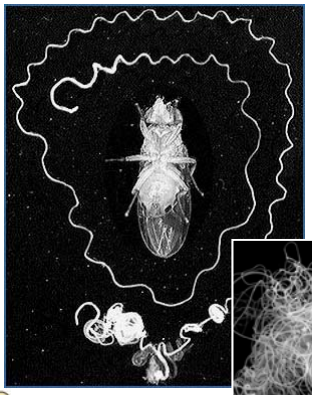
Alfrino rams

Testis size vs. mating system in primates

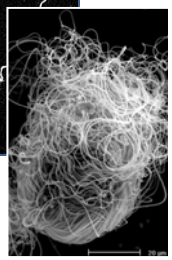


(Harvey & Pagel 1991)

Drosophila male surrounded by uncoiled testes (11% of body weight)



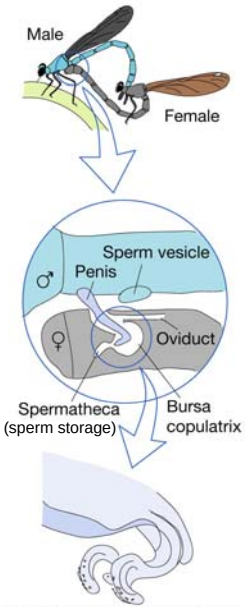
(our brains are 2%)



one spermatozoan

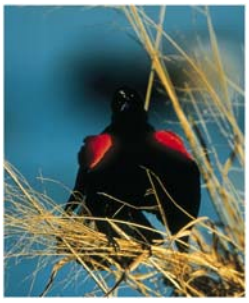
Sperm competition: Sperm scoops in damselflies (Odonata: Zygoptera)

Jonathan Waage 1979, 1984



Intersexual selection (mate choice; female choice; female preference)

1. **Direct benefits:** The male provides a direct benefit to the female or her offspring, such that selection favors females that recognize males that are ***superior providers*** via some correlated character.
   A. Nutrition (courtship feeding; nuptial gifts)
   B. Superior territory
   C. Freedom from disease or predators
   D. Superior parental care (greater vigor)



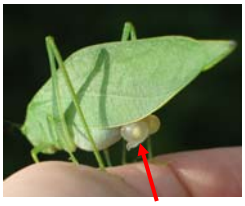
(benefits unclear)

2. **Sensory bias** and supernormal stimuli.
   - "Exploits" a pre-existing bias.
   - Due to the way the senses work.
   - Males evolve to match the preference.

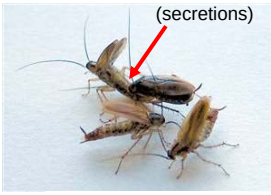
3. **Indirect benefits:** The male contributes only his genes, such that selection acts via the fitness of the female's offspring.
   A. Runaway sexual selection and the "**Sexy son**" hypothesis
   B. Handicaps and the "**Good genes**" hypothesis

Direct benefits of female choice: Nutrition

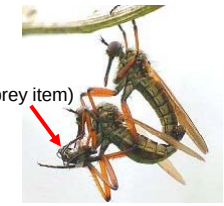
Microcentrum rhombifolium



(spermatophore & spermatophylax)



Courtship feeding in German cockroaches



Nuptial gift in empidid flies

Courtship feeding in Forster's terns

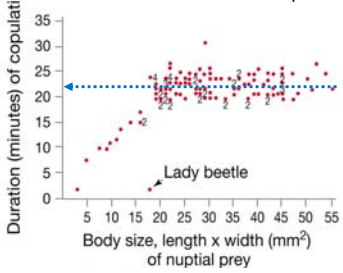
Nuptial gift is salivary ball secretion in scorpionflies (Mecoptera)

(becomes just an empty ball of silk in other Empididae)

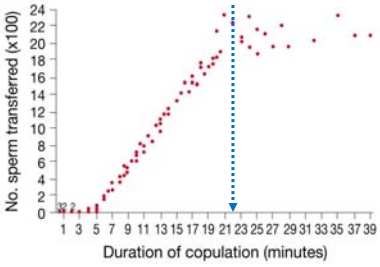
Experiments on direct benefits of **male nuptial gifts**

Bittacus apicalis
(Mecoptera)

Up to a point, the size of the nuptial gift determines the duration of copulation.



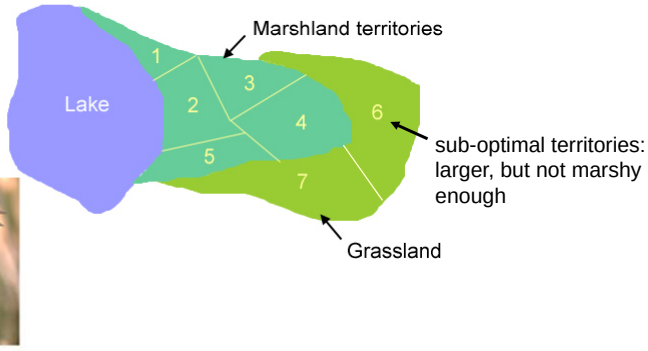
Cop. duration determines # sperm transferred.



Large nuptial gifts result in **longer copulations** (left), which in turn result in **more sperm** being transferred and **higher egg production** (Thornhill 1983).

Direct benefits of female choice: **Territories**

In the **red-winged blackbird**, limited habitat results in variable territory quality among males (w/ respect to food, protection, nesting sites, etc.).



Agelaius phoeniceus

Direct benefits of female choice: Disease-free mates & good fathers

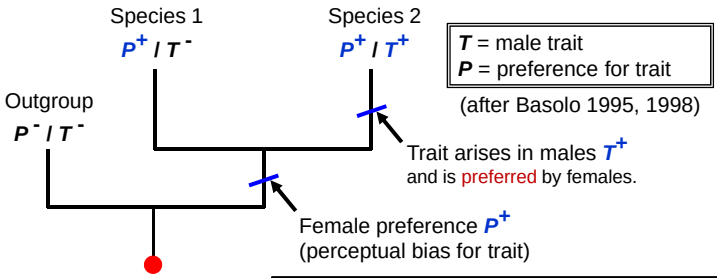
- **House finch** males (*Carpodacus mexicanus*) varies from orange to bright red.
- Brighter males are **preferred** by females, and also bring food to nestlings at a higher rate (Hill 1991).

- **Or**: female is *protected from* ***predators*** by male guarding behavior in ostracods (Cothran et al. 2012) and crickets (Rodríguez-Muñoz et al. 2011):

Female choice due to **sensory** or **perceptual bias** (Ryan & Rand 1990)

Priapella olmecae (male)

Xiphophorus helleri (male)



T = male trait
P = preference for trait

(after Basolo 1995, 1998)

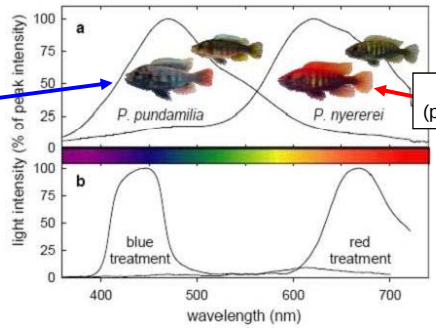
Direct or **indirect** benefits? Probably neither, or possibly ***direct*** benefits in response to the *environment* (Ryan & Cummings 2013).

Female choice due to **indirect benefits**: "**sexy sons**" and "**good genes**."
How does *runaway sexual selection* get started?

Fisher assumed a trait had to start with a *direct benefit*, as an ***adaptation***
– perhaps T_2 males have a slight mating advantage over T_1 males.

- their signal is easier to detect in nature (e.g., the color is easier to see in murky or deep water, or their song propagates better), or….
- their signal confers upon them some survival advantage (e.g., long tails might enhance flight ability in a bird).

deep-water species (only blue remains)

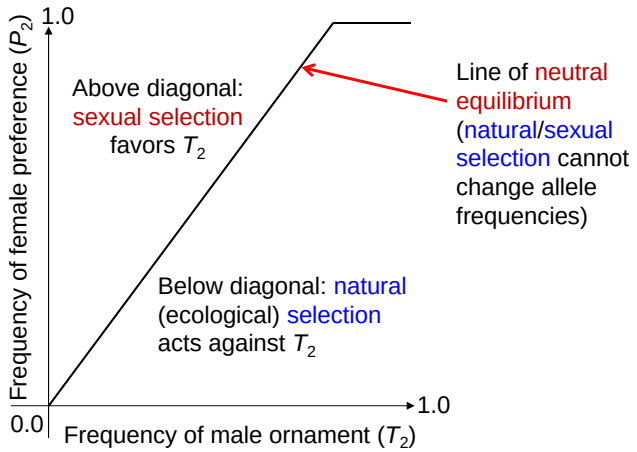


shallow-water species (plenty of red light present)

(see Endler 1993)

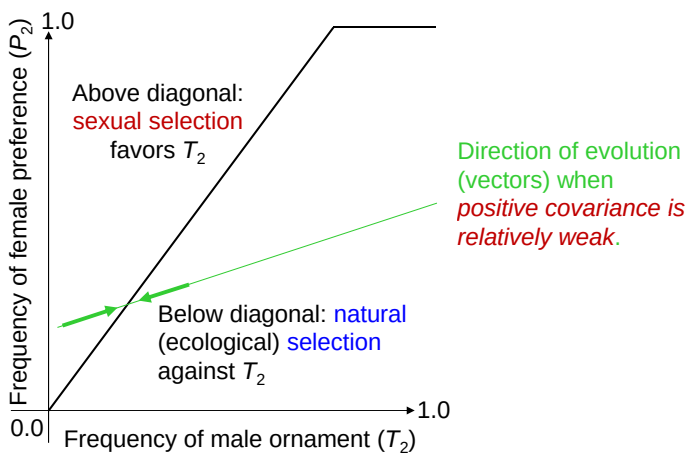
Runaway sexual selection (R. A. Fisher 1930)

1. So…a male trait originates as an adaptation – e.g., a long tail.
2. The evolution of a male trait and a female preference, once initiated, becomes a self-reinforcing, snowballing or "runaway" process.
3. Although the expression of genes ***P*** (*preference*) and ***T*** (*trait*) is sex-limited, both sexes carry both genes and transmit them to their offspring.
4. Assume T_2 is an allele for an exaggerated male trait and P_2 is an allele for the female preference for it.
5. Because P_2 females and T_2 males tend to mate with one another, their offspring of both sexes tend to inherit both the P_2 and T_2 alleles (*linkage disequilibrium* develops between the alleles).
6. The male trait and the female preference for it thus become ***genetically correlated***, so any increase in the frequency of the male trait is accompanied by an increase in the frequency of the female trait through hitchhiking (= *genetic covariance*).
7. The runaway process eventually runs up against viability (natural) selection.



Runaway sexual selection is due to a positive genetic correlation (covariance) of trait and preference.

This graph contains the allelic space for T_2 & P_2 occupied by all possible populations.



No runaway is possible: →→→