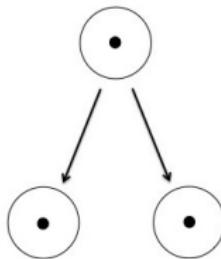


# Sexual selection

# Asexual reproduction

To introduce population and evolutionary dynamics we focused so far on **asexual reproduction** with **haploid** individuals.



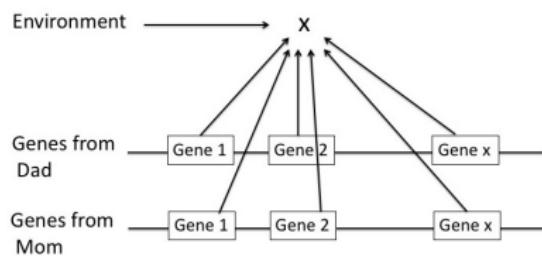
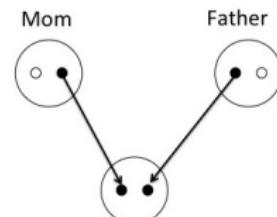
Asexual reproduction

Trees, bees, humans and other animals are **diploid**. These individuals have two **homologous** copies of each gene.

# Sexual reproduction

Diploids tend to reproduce **sexually**, by which offspring arise from the fusion of reproductive cells (called **gametes**) of two parents and thus inherit the genes of two distinct individuals.

The **ploidy** is the number of homologous sets of genes an individual has. For haploids this is one. For diploid, this is two. For tetraploids (as several plants are) this is four. Humans are diploid.



# Males and females: different allocation strategies

- Sexual reproduction often involves the presence of two types of individuals, **males** and **females**.<sup>1</sup>
- Females are by definition individuals that produce the largest reproductive cell or **gamete** (the egg or ovule is far larger than the sperm).

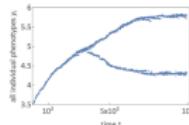


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<sup>1</sup>In hermaphrodites, male and female function is carried out by the same individual.

# Males and females are favored by disruptive selection

The fact that there are both males and females is thought to have resulted from **disruptive selection** on gamete size.



- There is a trade-off between number of gametes produced and their survival.<sup>2</sup> Quality-quantity trade-off.
- Due to physical constraints on motility, in a population where individuals produce intermediate gamete size, mutant alleles coding for smaller as well as mutant alleles coding for larger gametes than the resident allele can invade.

Hence, individuals producing smaller and larger gamete size will be favored by selection. **Two (and only two) sexes emerge.**

---

<sup>2</sup>In primitive marine ancestors, individuals produce a range of gamete sizes, and fusion between pairs of gametes is at random in the sea.

## Males and females: uninvadable sex ratio

In a population where there are males and females, the two sexes are produced in approximately equal number.

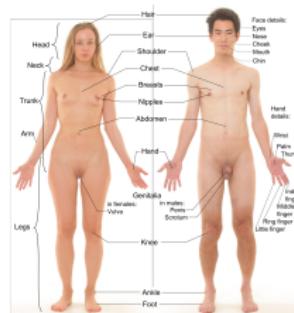
- Suppose males are less common than females. Then, a newborn male has high mating prospects (competition for mating is very low). Therefore parents genetically disposed to produce males tend to have more than average grand-children.
- Suppose females are less common than males. Then, a newborn male has a low mating prospect (competition for mating is very high). Therefore parents genetically disposed to produce females tend to have more than average grand-children.

Hence, at an evolutionary equilibrium the two sexes are produced in approximately equal number. In other words, **the sex-ratio is one half.**

# Sexual dimorphism

Several phenotypic traits are **sex-specific**. There are two types of such traits.

- **Primary sex traits.** Traits related to sex organs and are part of the reproductive system.
- **Secondary sex traits.** Traits appearing at sexual maturity (or at puberty in humans) and they are not directly part of the reproductive system.



# Sexual dimorphism in secondary sex traits: extravagant ornaments in males



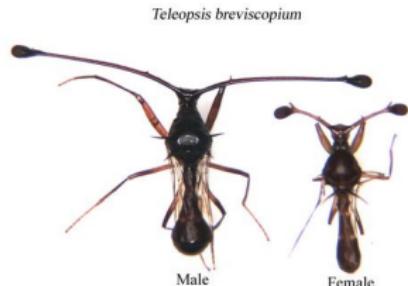
Peacock



Deer

- In many species males express extreme traits.
- These are somewhat puzzling traits, as they surely result in some survival cost.

# Sexual dimorphism: “impractical beauty”



Stalk-eyed flies: these flies distinguish themselves from most other flies by the possession of "eyestalks": projections from the sides of the head with the eyes at the end.

These extravagant traits<sup>3</sup> seem at first glance to hinder the males that express them and do not confer any advantage to them.

<sup>3</sup>Examples in humans are **Veblen goods**, luxury goods for which the quantity demanded increases as the price increases.

# Sexual dimorphism: “impractical beauty”

- Sexually dimorphic traits are very heterogeneous, they are found in animals as well as in plants.
- Morphologically distinct traits may be functionally equivalent.
- Is there is a general answer to why there is sexual dimorphism, and why it is mostly males that express extreme ornaments?



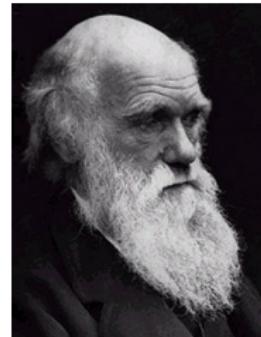
Male on the left



Male on the left

# Sexual dimorphism as an outcome of sexual selection

Under sexual reproduction, it is possible that members of one biological sex choose mates of the other sex to mate with, which induces competition in that sex.



Darwin surmised that ornament may function as a demonstration of the reproductive potential of their bearer (by displaying for instance genetic quality or parental investment) over which females may express preferences, whereby **female choosiness** and **male ornamentation** co-evolve.

# Why should females be the choosy sex?

- Owing to the asymmetry in gamete size, females “invest” more in offspring than males (and this is particularly true when there is gestation and lactation as in mammals). They are “saddled” with offspring. **Females tend to be limited by fertility.**
- Males can (theoretically) inseminate and run. **Males tend to be limited by the number of matings.**

Females should thus be choosy and males should spend considerable effort attracting mates and competing against others.<sup>4</sup>

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<sup>4</sup>In some species males provide the bulk of effort to rear offspring. In these species often the males are “choosy”, like in the seahorse.

# What should females be choosing in males?

Females are choosy, but what are they choosing for?

- Good genes, so that offspring inherit them? This is the “good gene” hypothesis.
- Sexy males, so that sons themselves inherit sexiness and get mating success? This is the “sexy son” hypothesis.
- Disease free males, so that offspring do not inherit parasite load?
- Males that will provide resources and paternal care?

The answer is yet not fully clear, but it is thought that paternal care should play a role in a number of species.

# Modeling sexual selection

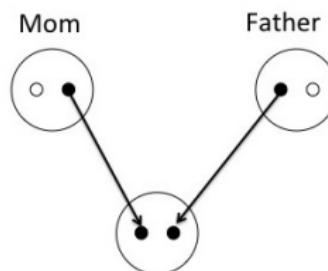
- We are now going to build a model for the co-evolution of male ornament and female choosiness, both formalized as quantitative traits.
- We will assume that the benefit of choice stems from paternal care.

To that end, we need to introduce a number of concepts and do a detour into the genetics of diploid individuals.

# Some further population genetic terminology

A diploid individual can be of two different types for a given gene.

- **Heterozygote.** An individual is said to be heterozygote at homologous genes if it carries two different alleles, i.e., the maternal and paternally inherited genes are in different states.
- **Homozygote.** An individual is said to be homozygote if its homologous genes carry identical alleles.



## Two-allele system: three genotypes for diploids

Consider that only two alleles segregate in the population: allele A and allele B. In a diploid population this produces **three genotypes**.

- ① Homozygote AA individuals.
- ② Heterozygote AB individuals.
- ③ Homozygote BB individuals.

We can thus no longer assume that an allele codes for a single phenotype (as we did under haploidy), since the phenotype of an individual depends on its paternal and maternal alleles and there may be interactions between these alleles.

## Two-allele system: phenotypes

With three genotypes, individuals can express three distinct phenotypes.

- ① Homozygotes AA with phenotype  $x_{AA}$ .
- ② Heterozygotes AB with phenotype  $x_{AB}$ .
- ③ Homozygotes BB with phenotype  $x_{BB}$ .

How should phenotype be determined as a result of allelic expression? What is the relationship between genotype and phenotype?

## Mode of gene action: co-dominance (or additive effects)

Under **co-dominance** or additive gene-action the phenotype of the heterozygote is half-way between the phenotypes of the two homozygotes.

$$x_{AB} = \frac{x_{AA} + x_{BB}}{2}$$

The effects of each allele add up and their contribution are clearly visible in the phenotype:



Heterozygote in Camelia

## Mode of gene action: complete dominance

Under **complete dominance** the expression of one allele dominates the other. If allele B is dominant we have

$$x_{AB} = x_{BB}$$

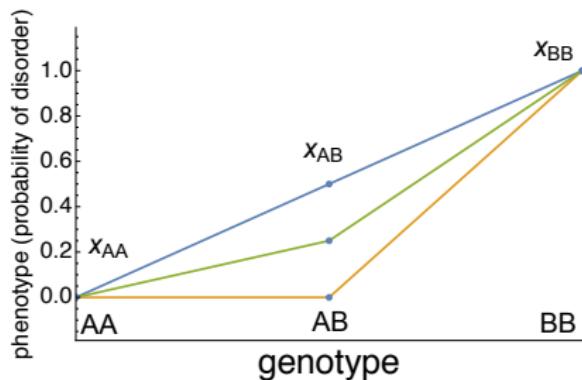
The effect of allele A is “hidden” or “masked” and is **fully recessive**.

Examples of recessivity includes many genetic disorders that expressed only in the homozygote:

- Cystic fibrosis (difficulty in breathing and lung infections).
- Spinal muscular atrophy.
- Dehydrogenase deficiency (inability to break down medium-chain fatty acids).

## Mode of gene action: partial dominance

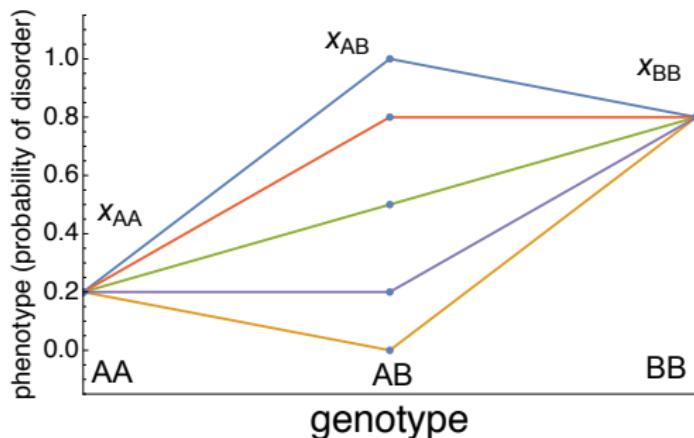
Suppose that allele A increase the probability of having a disorder, like say muscular dystrophy. Then in a graphical way one can represent the relationship between genotype and phenotype as



Full recessivity of A (yellow), co-dominance or additive gene action (blue) and partial recessivity of the A (green). The x-axes gives the genotype and the y-axes, the probability of getting the disorder (the phenotype).

# All modes of gene action in graphics

The following relationships between genotype and phenotype can be conceived.



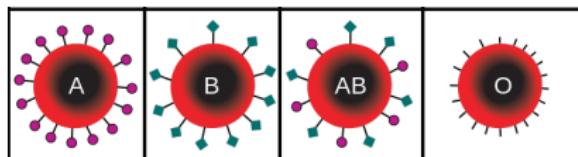
Overdominance (blue), dominance (red), co-dominance (green), recessivity (purple), and underdominance (yellow).

## Mode of gene action: overdominance in blood groups

Blood cells have signaling molecules at their surface that are recognized as antigens when in a foreign body. There are three main alleles: *A*, *B*, and *O*, which makes 6 genotypes:

Genotype:	AA	BB	AB	OO	AO	BO
Phenotype (blood type):	<i>A</i>	<i>B</i>	<i>AB</i>	<i>O</i>	<i>A</i>	<i>B</i>

Allele *O* is recessive and is the “universal donor”. An heterozygote *AB* has an advantage during blood transfusion (“universal receiver”).



Phenotype *A* can receive blood from *A* and *O* type individuals; phenotype *B* from *B* and *O*, phenotype *AB* from any individual, and *O* only from *O*.

# Mode of gene action

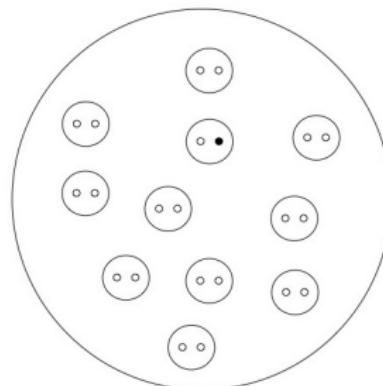
- Most gene action results in **partial dominance** with relatively small dominance effects.
- Not much examples of overdominance.
- We will assume additive gene action (co-dominance) to model the co-evolution of female choice and male ornament.

This assumption allows us to abstract away from genetic details and consider adaptive dynamics in the same setting as we have seen so far. In fact, all what saw so far about adaptive dynamics carries over to diploid genetics with co-dominant gene action.

# Involutionary invasion analysis for sex-specific traits

Suppose a mutation A appears in an otherwise monomorphic B diploid population.

Since any mutation arises as a single copy, this means that A necessarily arises in an heterozygote individual.

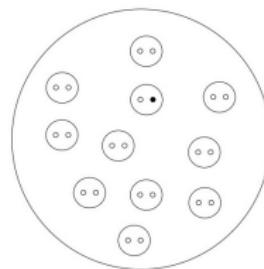


We want to characterize the condition under which A cannot invade.

## Evolutionary invasion analysis (female component)

The fitness of a **single** heterozygote AB female expressing phenotype  $x_f$  introduced into an otherwise monomorphic population for the B allele where homozygote BB females express a resident phenotype  $y_f$  is denoted

$$w_f(x_f, y_f)$$



A key point is that fitness is now defined at the **gene level**; namely,  $w_f(x_f, y_f)$  is the number of successful offspring produced by a female per haploid set of genes she carries (i.e., **per ploidy**).<sup>5</sup>

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<sup>5</sup>In other words  $w_f(x_f, y_f)$  is the successful number of offspring produced by a female divided by 2. We will refer to this as the gene fitness of an individual.

## Evolutionary invasion analysis (female component)

Denote by  $w_f(y_f, y_f)$  the gene fitness of BB individual in a monomorphic B population. Since at a demographic equilibrium each gene just replaces itself, gene fitness must be equal to one

$$w_f(y_f, y_f) = 1$$

Hence, allele A is disfavored by selection when

$$w_f(x_f, y_f) \leq 1$$

If this holds, then resident phenotype  $y_f$  cannot be displaced by mutant phenotype  $x_f$ .

# Uninvadability

We say that a phenotype  $y_f$  is an **uninvadable strategy** if

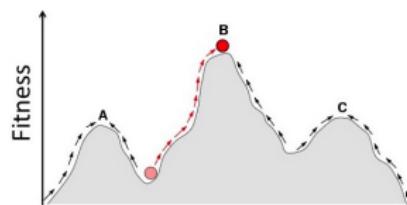
$$w_f(x_f, y_f) \leq 1 \quad \forall x_f \in \mathcal{X}_f$$

- Here,  $\mathcal{X}_f$  is the phenotype space in females, that is, the set of feasible alternative phenotypes (or “strategies”) that a female can implement in the heterozygote stage.
- An uninvadable strategy cannot be invaded by any alternative strategy in the phenotypic space and thus characterizes an evolutionary equilibrium for female trait expression.

# The selection gradient on female phenotype

In order to evaluate uninvadable strategies it is useful to define the selection on female phenotype

$$S_f(y_f) = \frac{\partial w_f(x_f, y_f)}{\partial x_f} \Big|_{x_f=y_f}$$

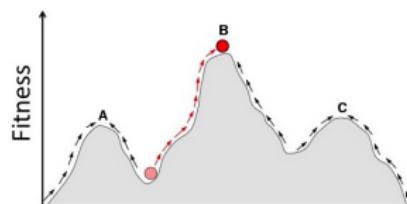


The selection gradient is the marginal change in the fitness of a female when she varies her strategy in a population expressing strategy  $y_f$ . It thus characterizes the direction of selection on the female trait in a population at  $y_f$ .

# The selection gradient on male phenotype

In complete analogy to the female case, we let  $w_m(x_m, y_m)$  be the successful offspring number (per ploidy) of a male expressing phenotype  $x_m$  when introduced into an otherwise monomorphic population for phenotype  $y_m$ . We can then obtain the selection gradient on male phenotype as

$$S_m(y_m) = \left. \frac{\partial w_m(x_m, y_m)}{\partial x_m} \right|_{x_m=y_m}$$



This is the marginal change in the fitness of a male when he varies his strategy in a population expressing strategy  $y_m$ . It thus characterizes the direction of selection on the male trait in a resident population expressing trait level  $y_m$ .

# The selection gradient on male phenotype

- The concepts of singular strategies, convergence stable strategies, and uninvadable strategies seen so far thus also applies to sexual reproduction and diploid populations.
- In general, males and females interact and thus the fitness of an individual of any sex will depend on the phenotypes expressed in the opposite sex.
- Hence, the fitnesses of males and females should be written as  $w_f(x_f, y_f, y_m)$  and  $w_m(x_m, y_m, y_f)$  to emphasize that female fitness depends also on the male phenotype  $y_m$  and male fitness also depends on the female phenotype  $y_f$ .

## Let us now consider sexual selection

- We assume that the trait  $x_f$  is the level of female choice of a mutant ( $y_f$  is for a resident female). It can be interpreted as the proportion of time, or fraction of energy budget devoted to choosing males to mate with.
- We assume that the trait  $x_m$  is male ornament size ( $y_m$  is for a resident male). Could be tail length or antler size.

We assume that there is a correlation between male provisioning of resources to offspring and ornament size, which is taken as an honest signal.



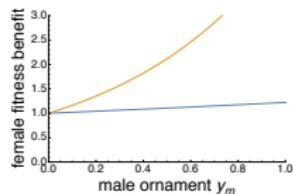
Hence, the ornament is an handicap and thus a honest signal.<sup>6</sup>

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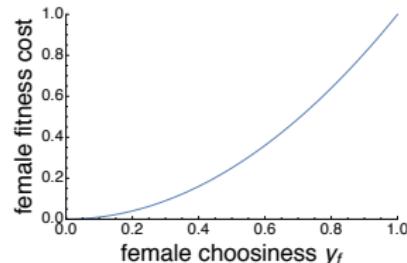
<sup>6</sup>The handicap principle suggests that reliable signals must be costly to the signaler, costing the signaler something that could not be afforded by an individual with less of a particular trait.

# Costs and benefits of female choosiness

- Benefit of choosiness:  $x_f e^{\beta y_m}$  where  $e^{\beta y_m}$  are the benefits of parental care, which is increasing with male ornament  $y_m$ .
- Cost of choosiness:  $x_f^2$  (concave function of resources allocated to choosing).



$\beta = 0.2$  (blue curve) and  $\beta = 1.5$  (blue curve), and  $x_f = 1$ .



The parameter  $\beta$  tunes the benefits of choosiness.

## Female fitness

Putting cost and benefit together, the fitness of a female with strategy  $x_f$  is a resident population where males and females have resident traits  $y_f$  and  $y_m$  is assumed to given by

$$w_f(x_f, y_f, y_m) = k_f \underbrace{\left( x_f e^{\beta y_m} - x_f^2 \right)}_{\text{fecundity}}$$

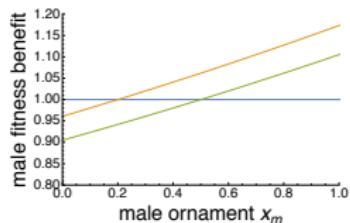
- The term in parenthesis is the females fecundity (increasing with male provisioning and decreasing with cost of choosiness).
- The constant of proportionality  $k_f$  is a regulating variable taking density-dependent competition into account.<sup>7</sup>

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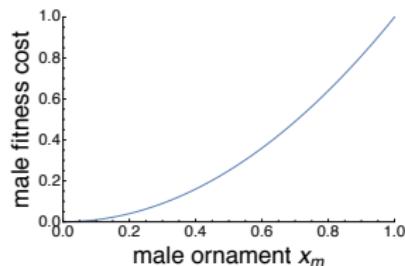
<sup>7</sup>This ensures that the population is regulated but will be considered as fixed, i.e., we assume density-independent selection, as in chapters 5 and 6.

# Costs and benefits of male ornamentation

- Benefit of ornamentation:  $e^{(x_m - y_m)y_f}$  gives the increase in mating success to a focal male “advertising more” (has a larger ornament) than males in the population. An individual with larger advertisement is more likely to be chosen for mating.
- Cost of choosiness:  $x_m^2$  (concave function).



$y_m = 0.2$  (yellow curve) and  
 $y_m = 0.5$  (green curve) and  
 $y_f = 0.2$ .



## Male fitness

Adding cost and benefit, the fitness of a male with strategy  $x_m$  in a resident population where males and females have traits  $y_f$  and  $y_m$  is assumed to be given by

$$w_m(x_m, y_m, y_f) = k_m \underbrace{\left( e^{(x_m - y_m)y_f} - x_m^2 \right)}_{\text{mating success}}$$

- The term in parenthesis is the mating success (increasing with male provisioning and decreasing with cost of choosiness).
- The constant of proportionality  $k_m$  captures (i) that males are subject to density-dependent competition and (ii) that male fitness is proportional to female fecundity, since the fitness of a male is necessarily linked to that of females it mates with.<sup>8</sup>

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<sup>8</sup>These two biological features do not affect the direction of selection on males ornament. So for simplicity we don't model them explicitly and subsume them into  $k_m$ .

# Coevolution of male and female choosiness

The selection gradient on female choosiness and male ornamentation are respectively given by

$$S_f(y_f) = k_f \left( e^{\beta y_m} - 2y_f \right) \quad S_m(y_m) = k_m (y_f - 2y_m)$$

These selection gradients say two things:

- ① Male ornament favors female choosiness.
- ② Female choosiness favors male ornamentation.

Hence the two traits will coevolve and may reinforce each other.

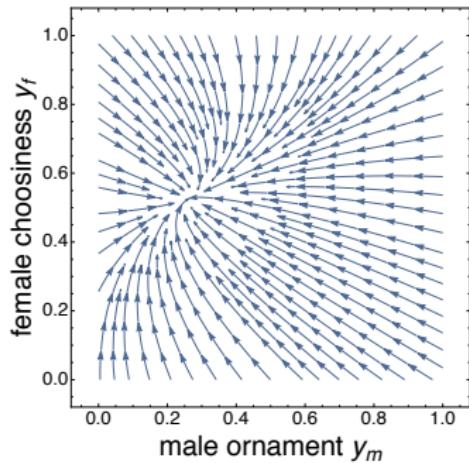
## Coevolution of male and female choosiness

When initially  $y_f = 0$  and  $y_m = 0$  (no ornamentation nor choosiness), the selection gradient on each traits are

$$S_f(0) = k_f \underbrace{e^0}_1 > 0 \qquad S_m(0) = k_m y_f > 0$$

- The selection gradient on the female trait is positive,  $S_f(0) > 0$ , which implies that female choosiness is favored by selection ( $y_f$  increases).
- The selection gradient on the male trait is positive,  $S_m(0) > 0$ , which implies that ornamentation is favored by selection ( $y_f$  increases)

## Coevolutionary outcome 1: **stabilizing selection** resulting in a stable interior equilibrium

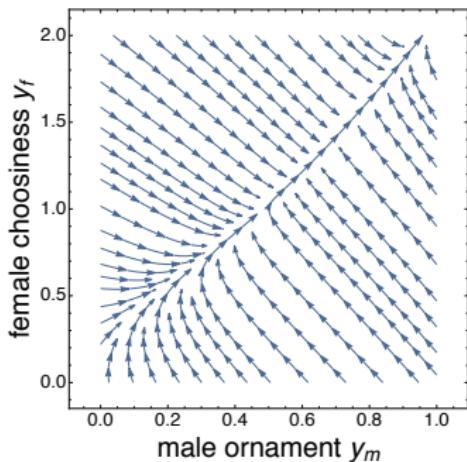


At each point in the graph, the vector  $(S_m(y_m), S_f(y_f))$  is plotted. This points in the direction of evolutionary change favored by selection, which favors an interior convergence stable strategy.<sup>9</sup>

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<sup>9</sup>Parameters in the graph are  $k_f = k_m = 1$  and  $\beta = 0.2$ .

## Coevolutionary outcome 2: constant directional selection resulting in a runaway



When  $\beta$  takes large values, a runaway is observed. That is, a positive feedback loop emerges, with choosiness selecting for ever increasing trait value in males, which in turn boosts fitness benefits in females that fosters choosiness.<sup>10</sup>

<sup>10</sup>Parameters in the graph are  $k_f = k_m = 1$  and  $\beta = 1.5$

# Runaway can lead to selection driven population extinction

Male trait can evolve to the point where the population is driven to extinction. In a resident population we have

$$w_m(y_m, y_m, y_f) = k_m \left( e^{(y_m - y_m)y_f} - y_m^2 \right) = k_m \underbrace{(1 - y_m^2)}_{0 \text{ if } y_m=1}$$

- This illustrates that what drives selection on ornament size is the relative (competitive) advantage of a male getting a mate.
- The gain in increasing ornament size for a population expressing a given strategy is captured by the the marginal benefit in the selection gradient on male ornament size.

# Extreme ornaments



Peacock



Irish elk who went extinct

# Human sexual selection

- There are clear differences in male and female secondary sex-traits, but sexual selection as a cause of these differences is not easy to establish.
- Both males and females tend to be choosy and choice can be unconscious.<sup>11</sup>
- It is pretty uncontroversial in the literature that male mate choice has been important for shaping female phenotypes (facial features, fatty breasts, hips, high-pitched voices); it is (surprisingly) less clear what is really the target of female choice.

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<sup>11</sup>Choice may be conducted without either admission or cognizance of their reproductive significance (e.g., choice may be based on status or reputation, which may correlate with power, which may correlate with wealth, which may correlate with access to the resources for reproduction)

# Human sexual selection

- Great apes (orangutans, gorillas, chimpanzees), tend to compete physically for access to females. **Ornament is armament** in these species. Males are far more muscular, more physically competitive and aggressive than females. Females prefer dominant males.
- But in humans these differences have decreased over time (we lost large canines). There has been a **de-weaponization of males** in humans. It is not clear what exactly is the cause.
- **Brain size**. It has been argued that brain size is a female sexually selected trait (it consumes up to a quarter of energy and the benefits are not so obvious). Large vocabulary (far larger than necessary to extract resources), music, humor may be sexually selected displays and are powered by brain size.

# Summary

- Strong sexual dimorphism in secondary sex-trait.
- Many of them in plants and animals are likely to be explained by sexual selection.
- Sexual selection tends to drive the evolution of traits that do not bring an absolute advantage to their carriers but a relative one.