

# EVOLUTION, NATURAL SELECTION, AND TINBERGEN'S 4 QUESTIONS



Primate Social Behavior  
8 September 2020

# TODAY

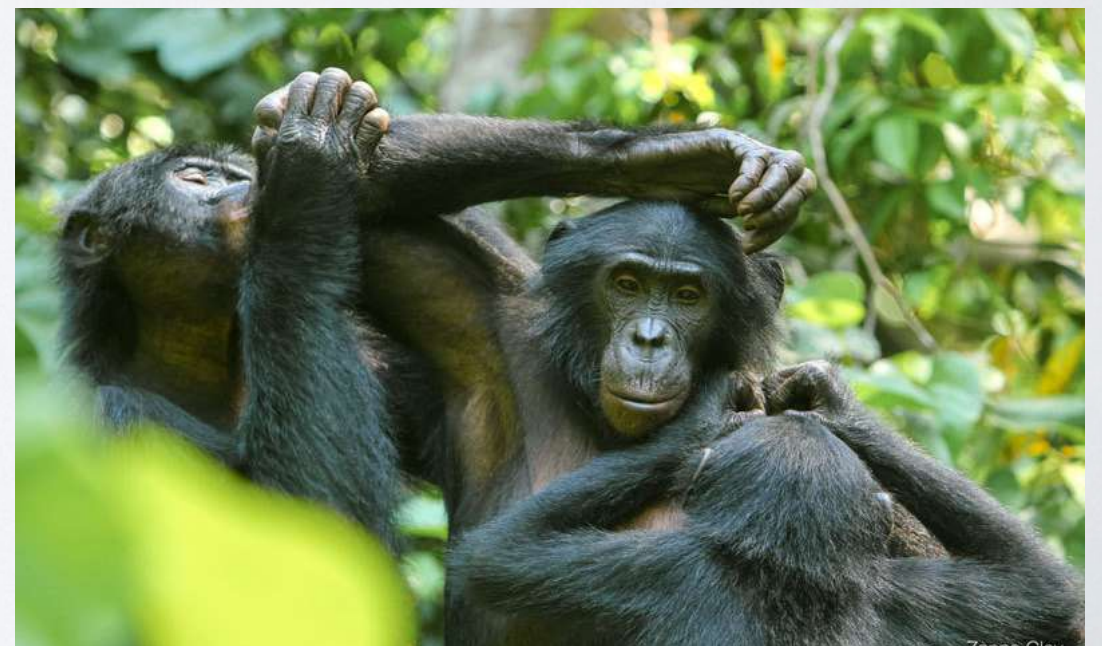
- Finish last lecture
- Practice quiz
- Evolution via natural selection
- Kin selection
- Tinbergen's 4 questions
- Write quiz questions for first quiz

# COURSE LOGISTICS

- Isaac's office hours: [tinyurl.com/y4ut584w](https://tinyurl.com/y4ut584w)
- Martin's office hours: [tinyurl.com/y2matwc5](https://tinyurl.com/y2matwc5)
- Module section on canvas has everything you need (readings, assignments, videos, etc)

# EARLY OBSERVATIONS BASED ON APES' RESPONSES TO BEING HUNTED

- Keen experimental probe or irrelevant behavior in response to unnatural event?



# EXPERIMENTS IN CAPTIVITY

- Professionalization of psychology in early 1900s
- Wolfgang Kohler interested in the evolution of insight
- Conducted some of the first experiments with non-human primates



# EXPERIMENTS IN CAPTIVITY



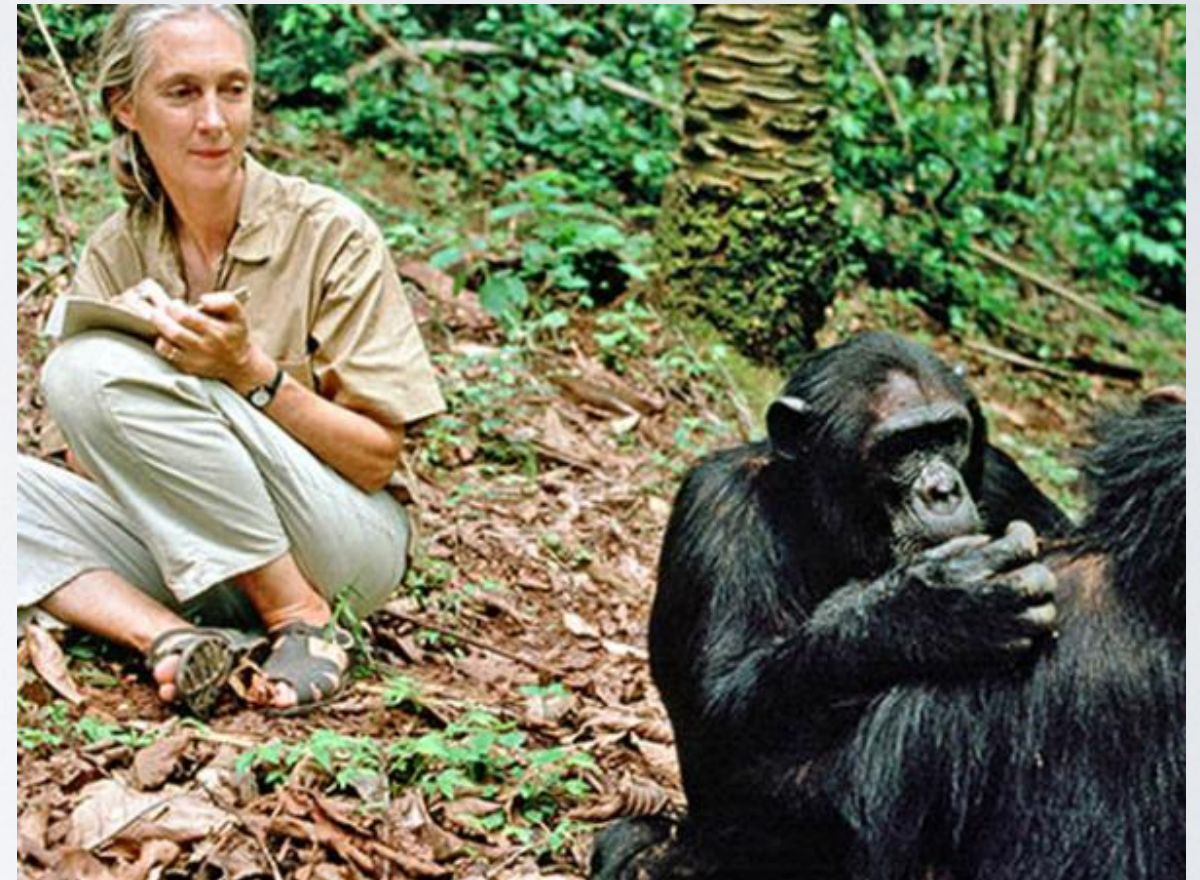
# EXPERIMENTS IN CAPTIVITY

- Experimental methods allowed for more control over research design
- Variable of interest can be isolated and tested directly



# LONG-TERM OBSERVATION OF WILD PRIMATES

- Jane Goodall et al. begin long-term studies in 1960s that continue to present
- Goodall criticized for anthropomorphizing chimps by giving them names
- Social and kinship structure of groups discovered
- Importance of social relationships becomes clear
- Behavior studied in context in which it evolved



# SUMMARY

- Three perspectives from which to study primates
- Political and social context of primate behavior research
- Observational vs experimental methods
- Captive vs wild studies

# PRACTICE QUIZ

1. Four minutes to complete (real quizzes will be 10 minutes)
2. Hand write answers on paper
3. Video on, showing paper
4. Pens down at 5 minutes
5. Take picture of your quiz, upload it to Canvas (assignment name: Practice quiz)

# PRACTICE QUIZ

1. List three advantages of conducting studies in the wild?
2. List three advantages of conducting studies in captivity?
3. How does the evolution of the keyboard help explain the contemporary QWERTY layout?

# WHAT IS NATURAL SELECTION?

- Differential reproduction based on phenotypic variation



**GENOTYPE: THE SET OF GENES THAT AN ORGANISM CARRIES.**

**PHENOTYPE: AN ORGANISM'S OBSERVABLE CHARACTERISTICS — WHICH ARE INFLUENCED BOTH BY ITS GENOTYPE AND BY THE ENVIRONMENT.**

<—Definitions from Berkley evolution website

# WHAT IS EVOLUTION?

- Change in a population over time



~1850, Manchester, UK:  
99% of peppered moths  
were white



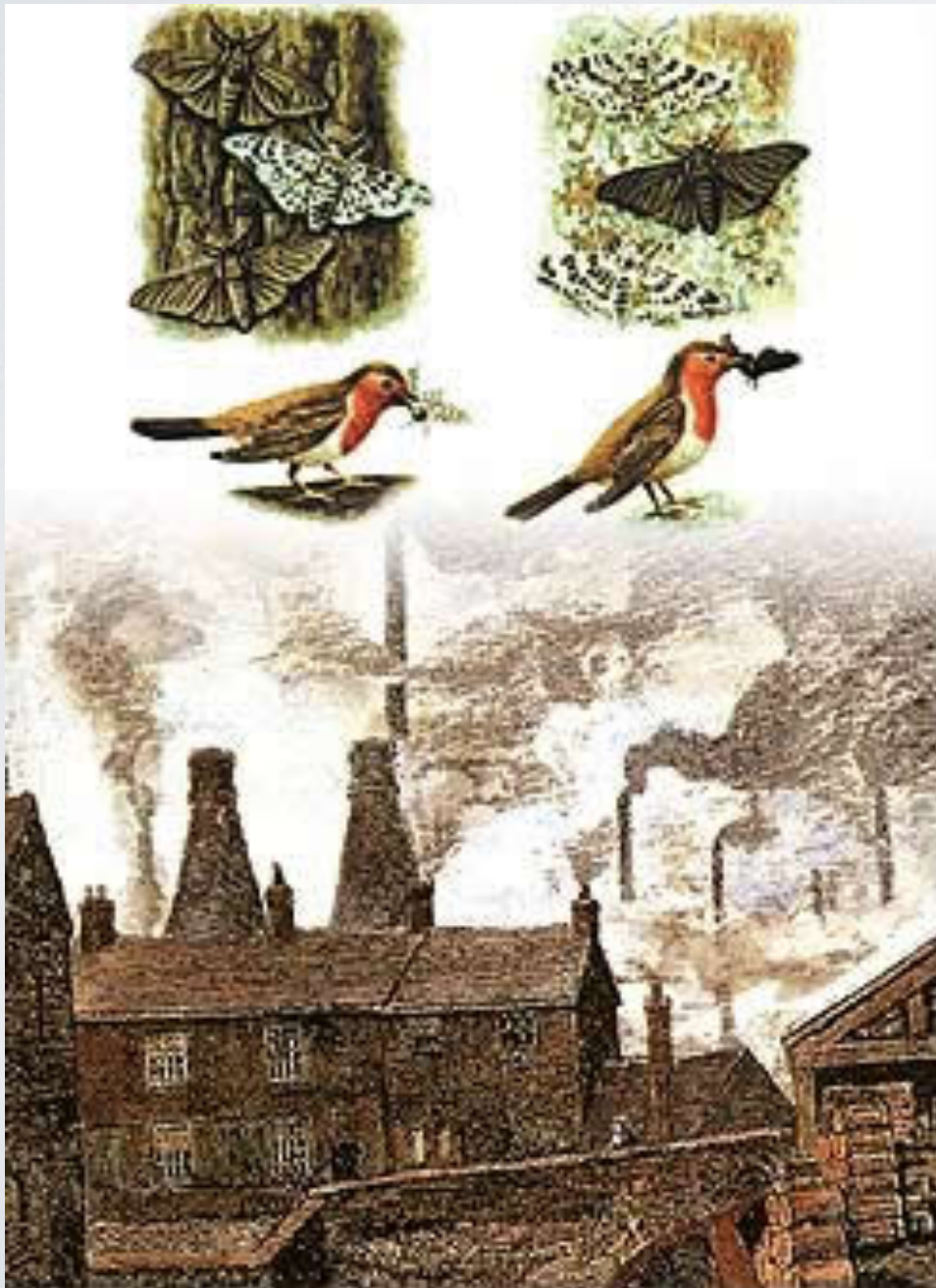
1895: 99% of peppered  
moths were black



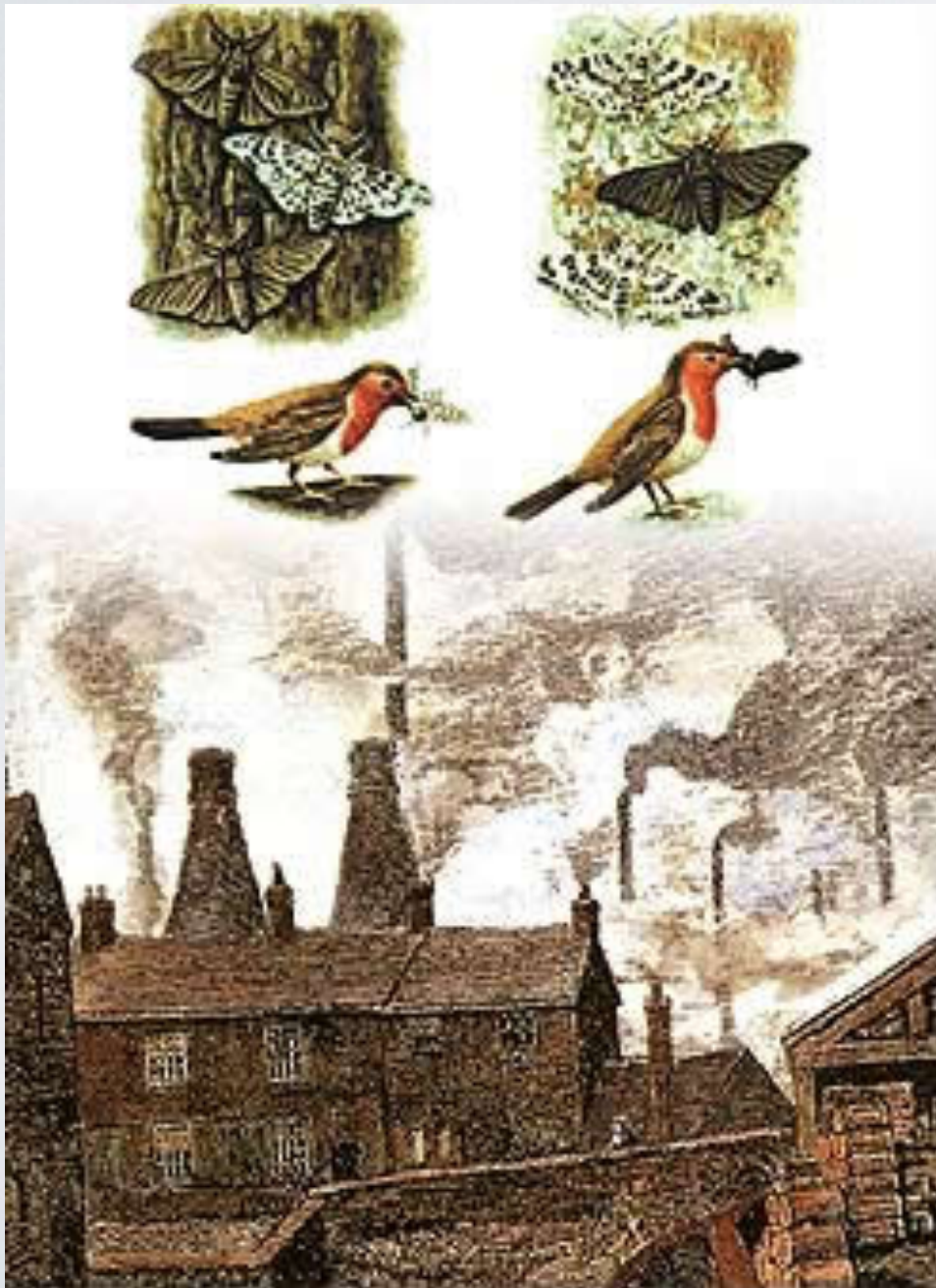
Post-1956 white morphs  
increase again

HOW DOES NATURAL SELECTION  
LEAD TO EVOLUTION?

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**Selection pressure:  
an agent of differential mortality or fertility**

# HOW DOES NATURAL SELECTION LEAD TO EVOLUTION?

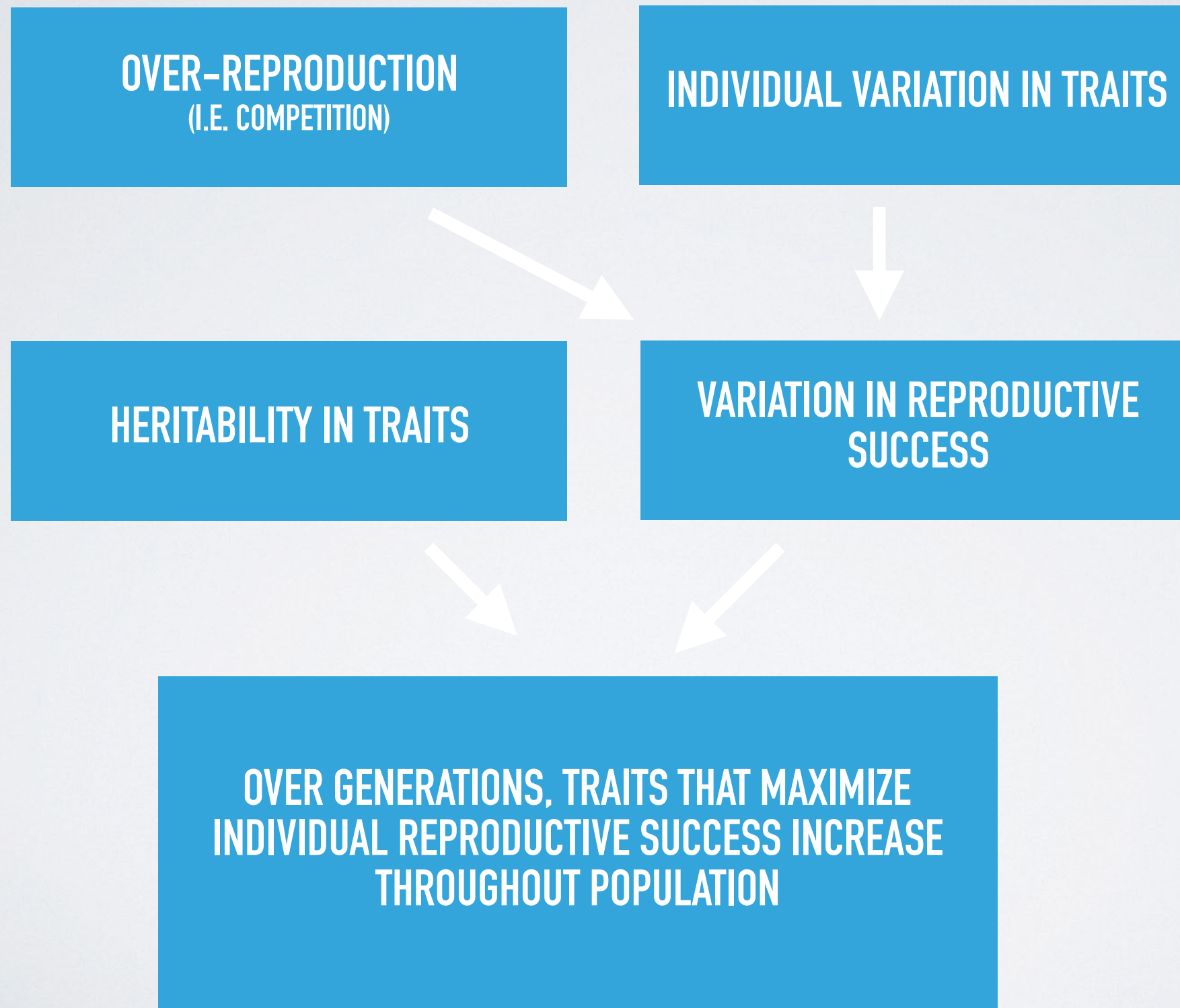
- Heritability of individual variation + differential reproductive success



# HOW DOES NATURAL SELECTION LEAD TO EVOLUTION?



# RECIPE FOR EVOLUTION VIA NATURAL SELECTION



# RECIPE FOR EVOLUTION VIA NATURAL SELECTION

(AND SEXUAL  
SELECTION)

OVER-REPRODUCTION  
(I.E. COMPETITION)

INDIVIDUAL VARIATION IN TRAITS

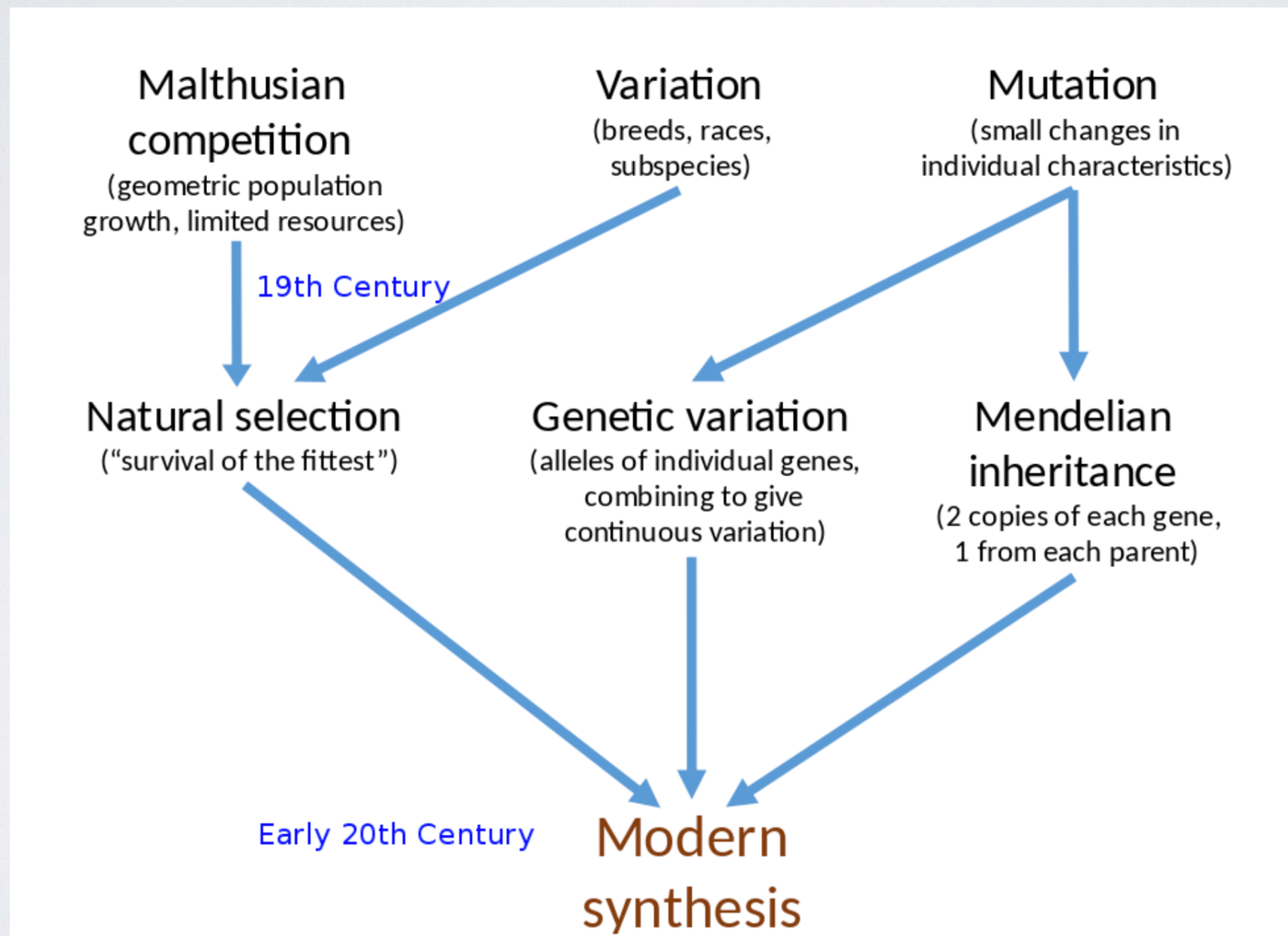
HERITABILITY IN TRAITS

VARIATION IN REPRODUCTIVE  
SUCCESS

OVER GENERATIONS, TRAITS THAT MAXIMIZE  
INDIVIDUAL REPRODUCTIVE SUCCESS INCREASE  
THROUGHOUT POPULATION

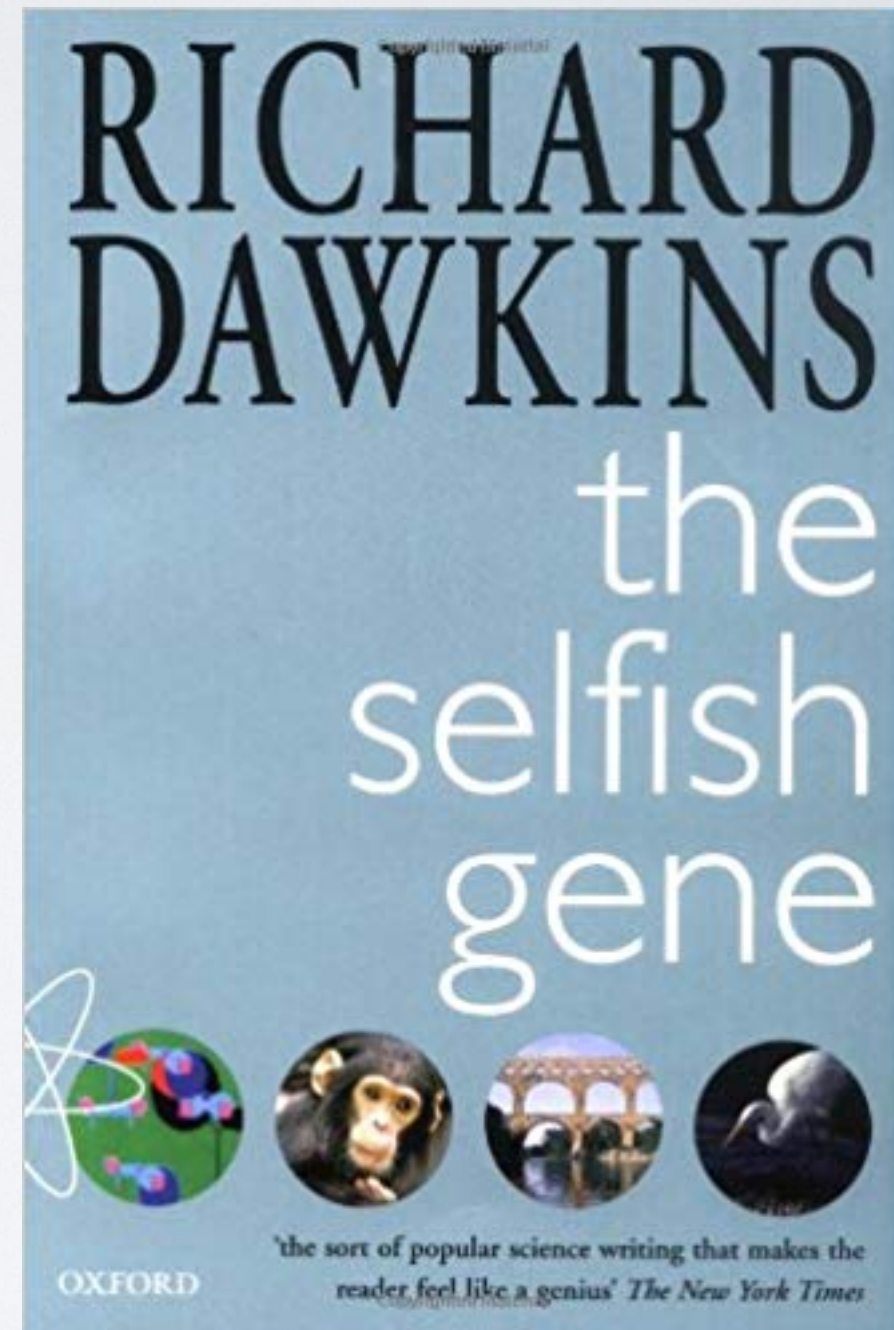
SEXUAL SELECTION: IS SUBSET OF  
NATURAL SELECTION THAT ACTS ON  
AN ORGANISM'S ABILITY TO OBTAIN  
OR SUCCESSFULLY COPULATE WITH  
A MATE.

# GENETICS + NATURAL SELECTION = MODERN SYNTHESIS



# GENETICS + NATURAL SELECTION = MODERN SYNTHESIS

- Gene-centered view of natural selection and evolution
- Individuals can be thought of as machines for gene propagation
- Evolution is change in allele frequency in a population from one generation to the next
- Kin selection an important insight from gene-level analysis



# KIN SELECTION

- Kin selection: the evolutionary strategy that favors the reproductive success of an organism's relatives, even at a cost to the organism's own survival and reproduction
- Relatives share large proportion of genes
- Relatives' reproductive success can also increase an individual's fitness

**FITNESS: ABILITY TO PASS GENES INTO FUTURE GENERATIONS. LUMPS TOGETHER MANY DOMAINS (E.G., SURVIVAL, MATE-FINDING, REPRODUCTION)**

# HAMILTON'S RULE

- Behavior that benefits relatives can evolve through natural selection, if:

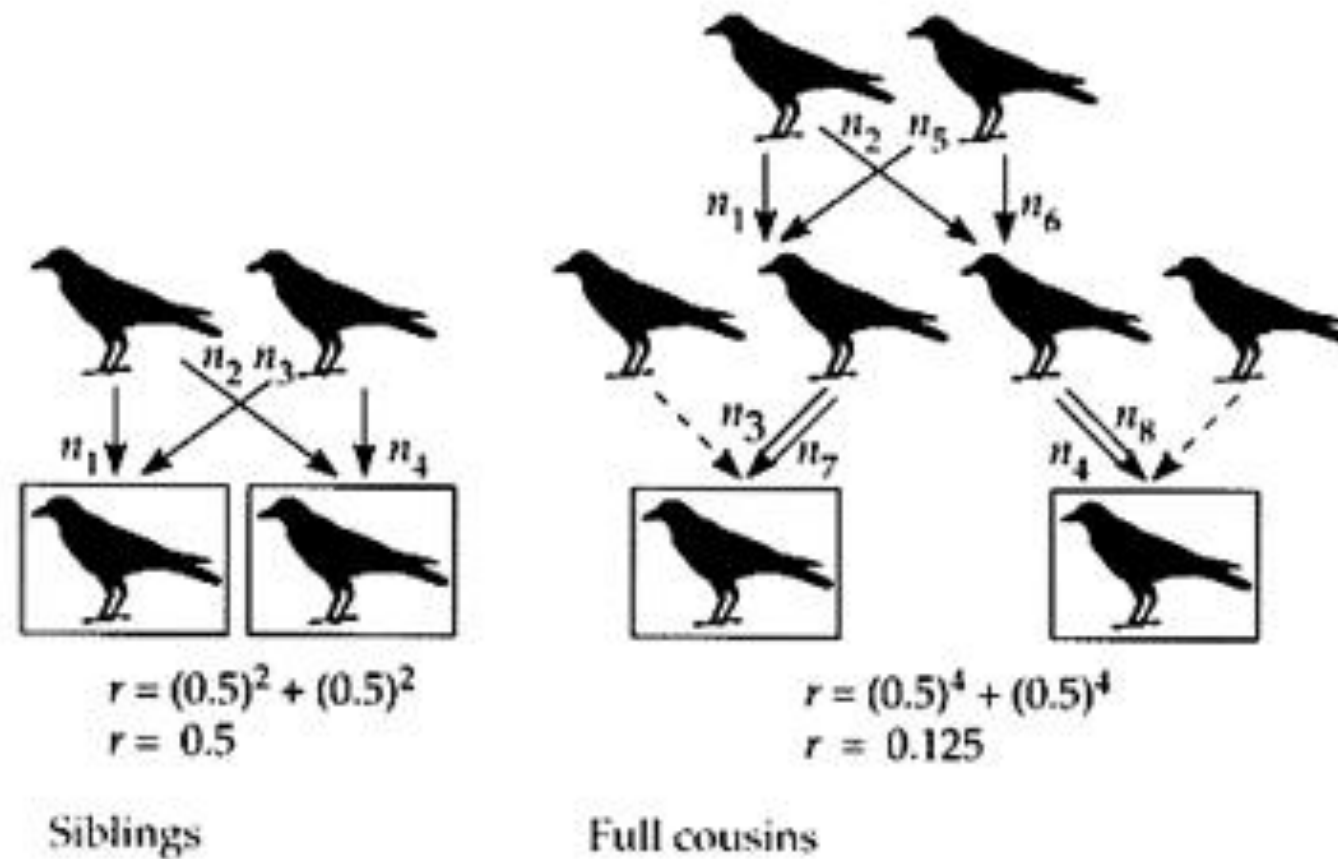
$$rB > C$$

$r$  = coefficient of relatedness (shared genes)

$B$  = Benefit to the recipient

$C$  = Cost to the Actor

# Calculating relatedness



$$r = \sum (.5^n)$$

where  $n$  is the number of "generational links"

- parents/offspring/full siblings=0.5
- Aunts/nephews/grandparents/grandchildren/half siblings=0.25
- 1st cousins=0.125

# HAMILTON'S RULE

- Behavior that benefits relatives can evolve through natural selection, if:

$$rB > C$$

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**A MAN SHOULD LAY  
DOWN HIS LIFE FOR TWO BROTHERS,  
FOUR NEPHEWS, OR EIGHT COUSINS**

JBS Haldane

# Fitness

A measure of an individual's success at spreading its genes

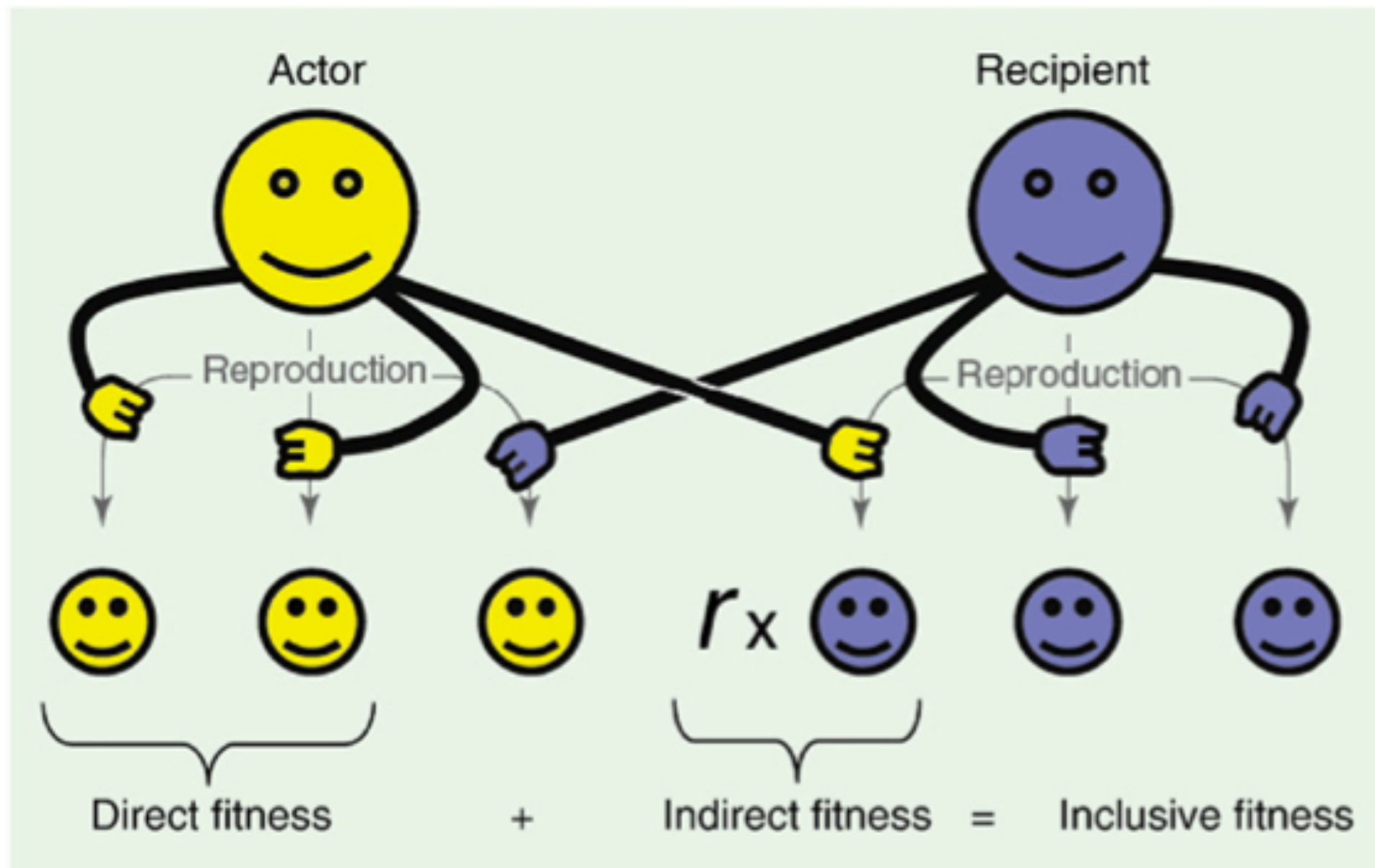


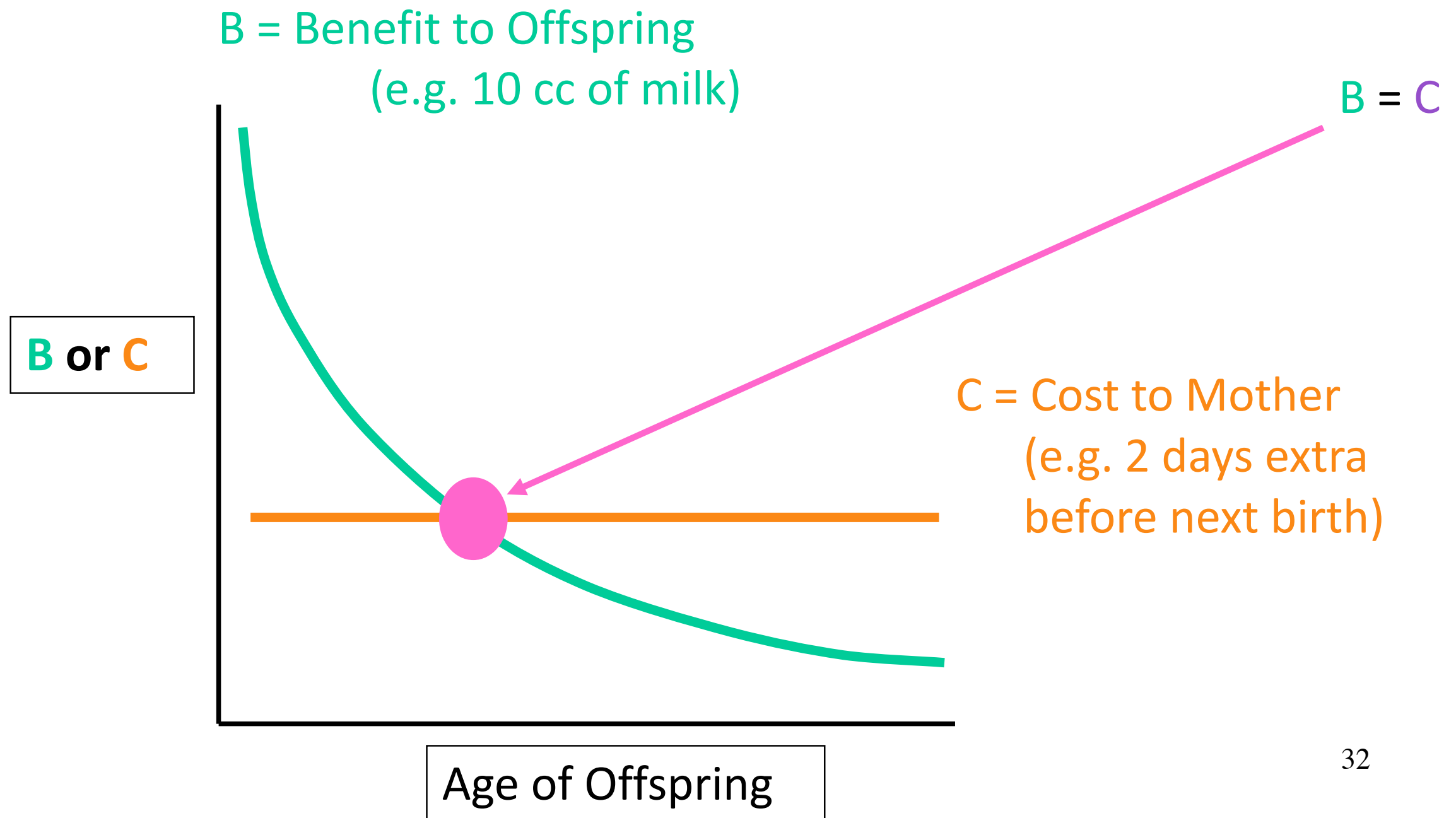
Fig. 1 (p. 233) in West et al (2011) *Evolution and Human Behavior* 32: 231-262

BUT HOW CAN KIN SELECTION  
EXPLAIN TURKEY MATING DANCES???



# Mother-Offspring Conflict

From the Observer's Perspective



# Mother-Offspring Conflict

From the  
Mother's  
Perspective



$B$  = Benefit to Offspring

$B$  or  $C$

$B/2$  = Benefit to Mother

$C$  = Cost to Mother

Age of Offspring

Wean when " $rB < C$ "  
i.e. when  $0.5(B) < C$

# Mother-Offspring Conflict

From the Offspring's Perspective



$B$  = Benefit to Offspring

$B$  or  $C$

$C$  = Cost to Mother

$C/2$  = Cost to Offspring

Age of Offspring

Wean when " $B < rC$ "  
i.e. when  $B < 0.5(C)$

# COMMON MISUNDERSTANDINGS

- Teleological thinking
- “For the good of the species (group)”
- Just-so stories

# TERMS

- Adaption - a feature that is common in a population because it provides some improved function.
- Exaptation - a feature that evolved by selection for one function but has been co-opted for another function
- Spandrel - 'a presently useful characteristic that did not arise as an adaptation ... but owe their origin to side consequences of other features'
- By-product - a characteristic that does not solve an adaptive problems and does not have to have functional design. It is carried along with characteristics that do have functional design because they happen to be coupled with those adaptations

# TERMS

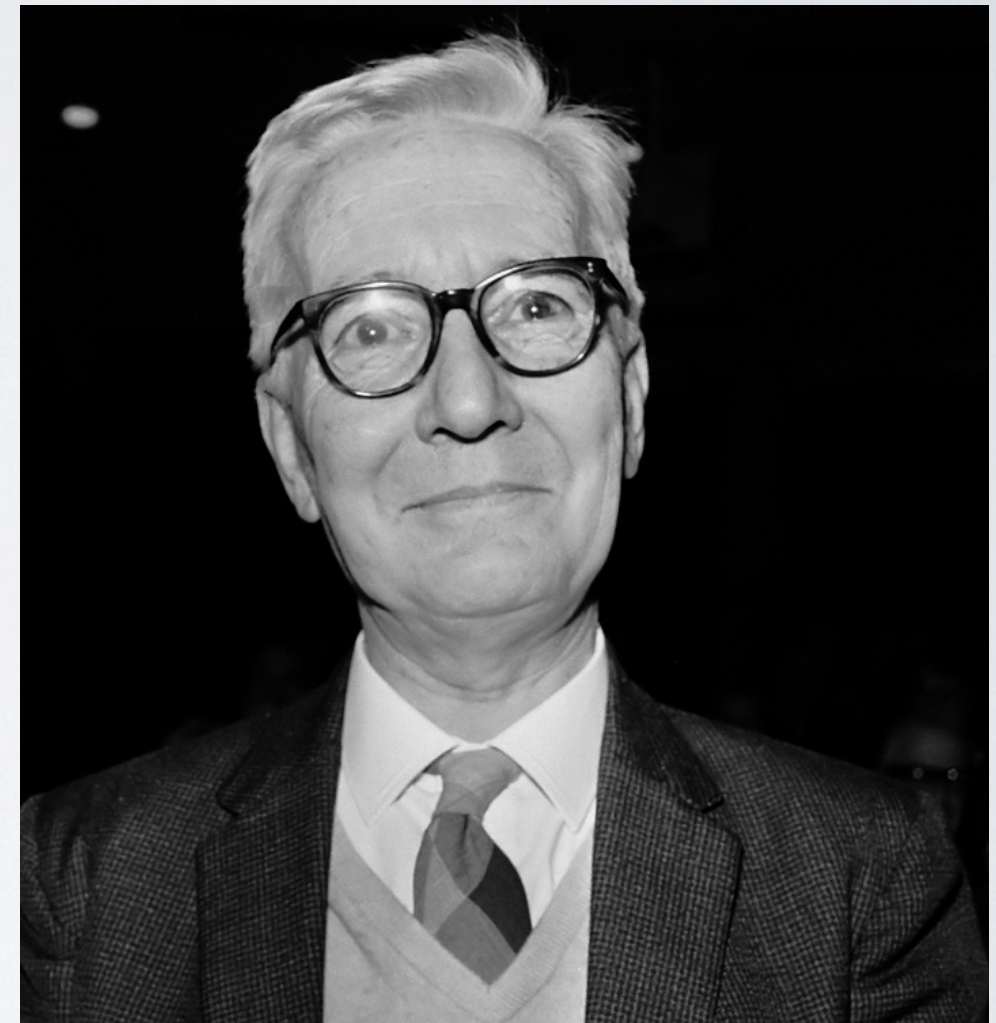
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**4 minutes in breakout rooms to come up with an example of each**

# NATURAL SELECTION AND BEHAVIOR

- How does an individual's behavior affects its survival and reproductive success?
- Individuals make decisions that are almost never explicitly based on evolutionary logic
- Then how does natural selection shape behavior?

# TINBERGEN'S FOUR QUESTIONS



Niko Tinbergen

# TINBERGEN'S FOUR QUESTIONS



Niko Tinbergen as the Riddler

# TINBERGEN'S FOUR QUESTIONS

- What is it for? (Survival value, function, adaptation, ultimate explanation)
- How does it work? (Causation, proximate mechanism, proximate explanation)
- How did it evolve? (Evolution, phylogeny, evolutionary history)
- How did it develop? (Ontogeny, development)



Niko Tinbergen as the Riddler

# TINBERGEN'S FOUR QUESTIONS

- Share/discuss your two examples in breakout room: 5 minutes
- Bring any questions/comments/disagreements back to main room



Niko Tinbergen as the Riddler

# TINBERGEN'S FOUR QUESTIONS

Table 1. Tinbergen's four questions, organized.

| FOUR AREAS OF BIOLOGY:<br>FOUR QUESTIONS |                                                                                                                                                                                     | Two objects of explanation                                                                                                                                                              |                                                                                                                                                                                                                                                       |
|------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                          |                                                                                                                                                                                     | <u>Developmental/historical</u><br>A sequence that results in the trait                                                                                                                 | <u>Single form</u><br>The trait at one slice in time                                                                                                                                                                                                  |
| Two kinds of explanations                | <u>Proximate</u><br>Explains how organisms work by describing their mechanisms and their ontogeny                                                                                   | <u>Ontogeny</u><br><br>Q: How does the trait develop in individuals?<br><br>A: Description of the trait's forms at sequential life stages, and the mechanisms that control development. | <u>Mechanism</u><br><br>Q: What is the structure of the trait; how does it work?<br><br>A: Description of the trait's anatomy, physiology, regulation, and how the trait works to accomplish a function.                                              |
|                                          | <u>Evolutionary</u><br>Explains how a species came to its current form by describing a sequence of forms, and how they were influenced by selection and other evolutionary factors. | <u>Phylogeny</u><br><br>Q: What is the phylogenetic history of the trait?<br><br>A: Description of the history of the trait as reconstructed from its phenotype and genotype precursors | <u>Adaptive significance</u><br><br>Q: How have variations in the trait interacted with environments to influence fitness in ways that help to explain the trait's form?<br><br>A: Description of how variations in the trait have influenced fitness |

# TINBERGEN'S FOUR QUESTIONS

## **Bat echolocation**

- Function/ultimate explanation?
- Proximate mechanism?
- Ontogeny?
- Phylogeny?

# TINBERGEN'S FOUR QUESTIONS

## **Bat echolocation**



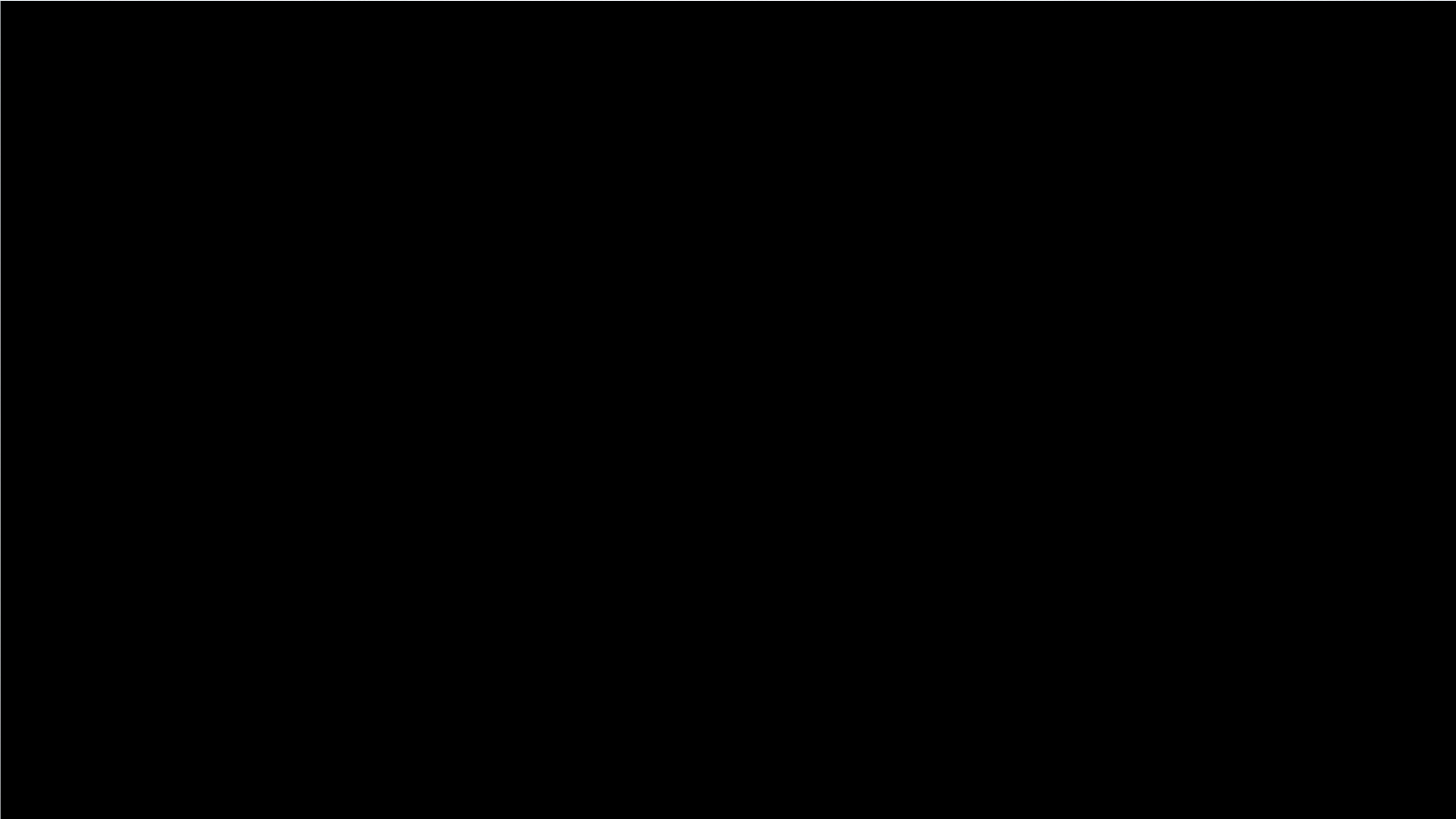
Video credit: OregonCavesNPS youtube channel

# TINBERGEN'S FOUR QUESTIONS

## **Bat echolocation**

- Function/ultimate explanation?
- Proximate mechanism?
- Ontogeny?
- Phylogeny?

# BROOD PARASITISM



# TINBERGEN'S FOUR QUESTIONS

## **Brood parasitism**

- How does Tinbergen help us understand brood parasitism?
- What is the adaptive significance of the reed warbler feeding the cuckoo

# QUIZ QUESTIONS

- Take 5 minutes in breakout room to come up with 2 or 3 questions for first quiz next Tuesday.
- We'll briefly reconvene in main room, in case you have any questions.

QUESTIONS?