Units of selection

Or distinguishing correlation from causation in evolutionary biology

Adaptation

A trait that has become prevalent because of a selective advantage due to an improvement of some function

At what level do adaptations act?

- genes
- chromosomes
- genomes
- individuals
- groups
- species
- species community
- ecosystem
- biosphere (-> “Gaia”)

At what level do we recognize adaptations?

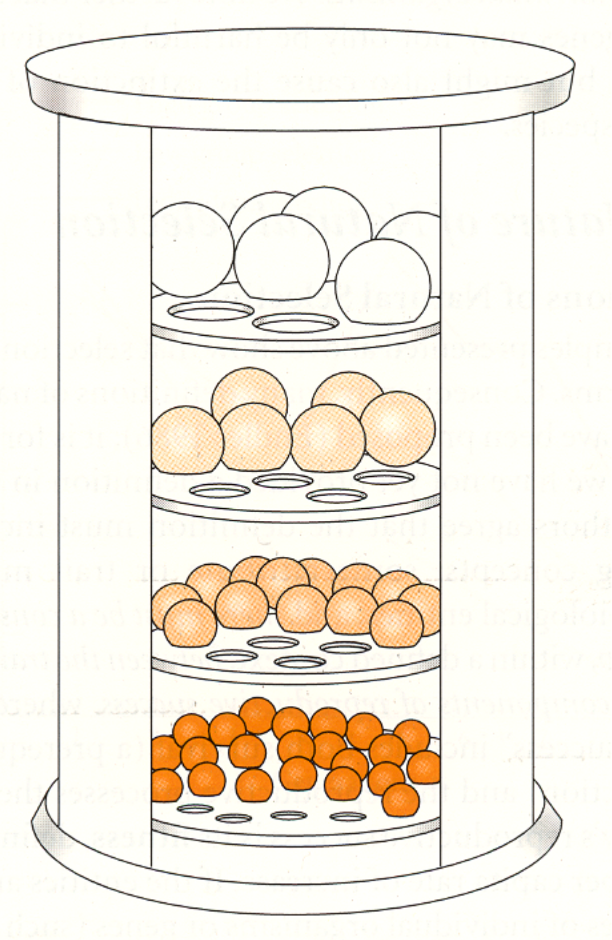
Herd of fast deer

vs.

Fast herd of deer?

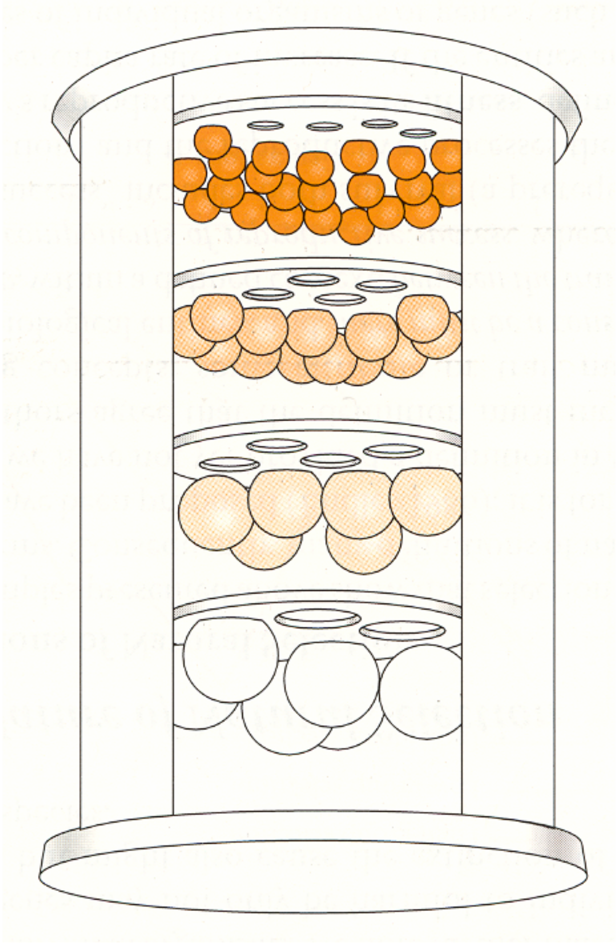
- Is speed the adaptation of the herd or the deer?

The distinction between natural selection
ACTING ON vs. SELECTING FOR



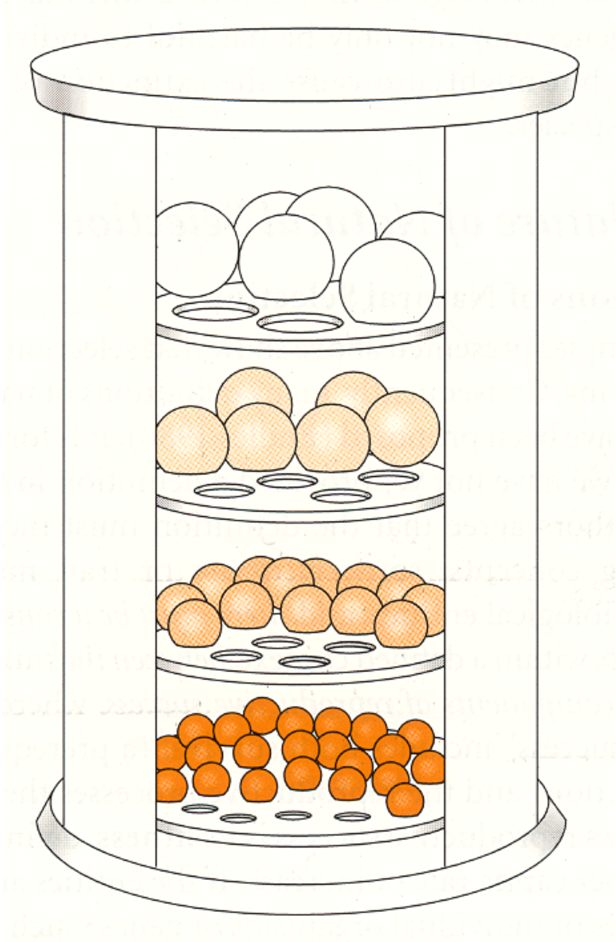
A famous
toy analogy
(Sober 1989; Futuyma 1998)

The distinction between natural selection <u>ACTING ON</u> vs. <u>SELECTING FOR</u>



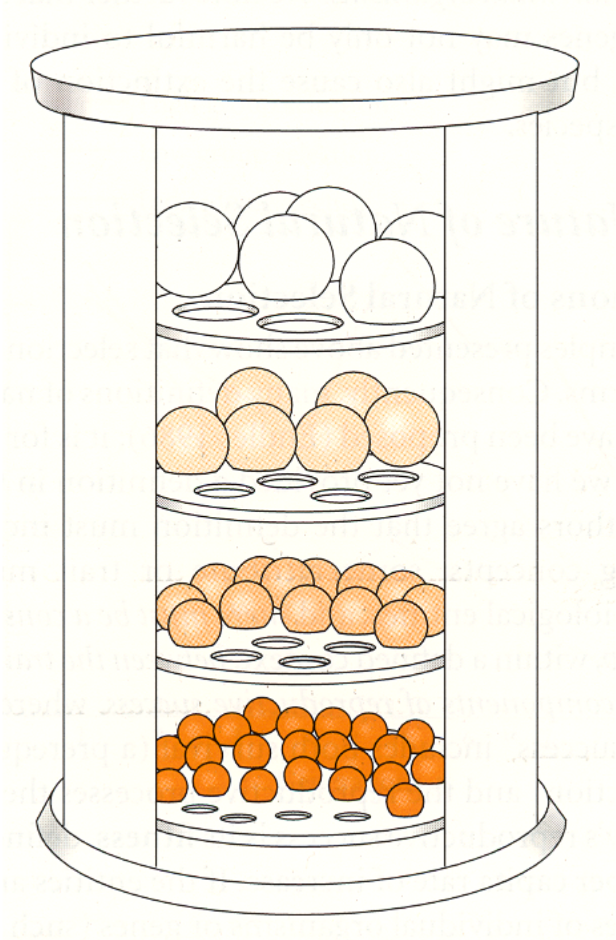
turn toy over;
what happens?

The distinction between natural selection
<u>ACTING ON</u> vs. <u>SELECTING FOR</u>



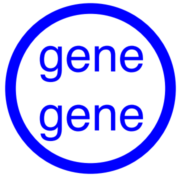
return toy;
what happens?

The distinction between natural selection
<u>ACTING ON</u> vs. <u>SELECTING FOR</u>



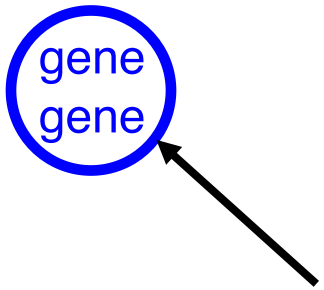
What does selection <u>ACT ON?</u>
What is <u>SELECTED FOR?</u>

The distinction between natural selection
ACTING ON vs. SELECTING FOR



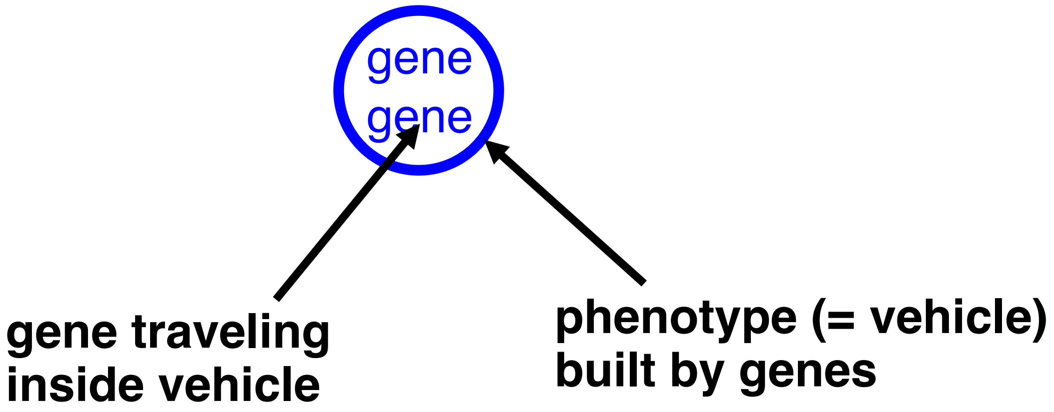
The more realistic gene-phenotype relationship

The distinction between natural selection
ACTING ON vs. SELECTING FOR

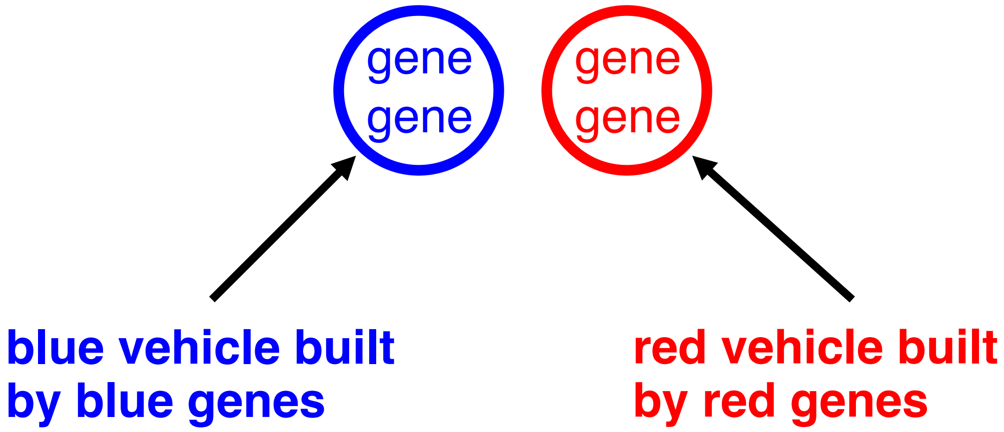


phenotype (= vehicle)
built by genes

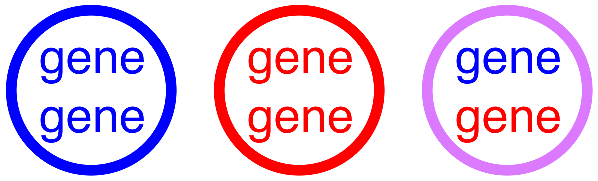
The distinction between natural selection
<u>ACTING ON</u> vs. <u>SELECTING FOR</u>



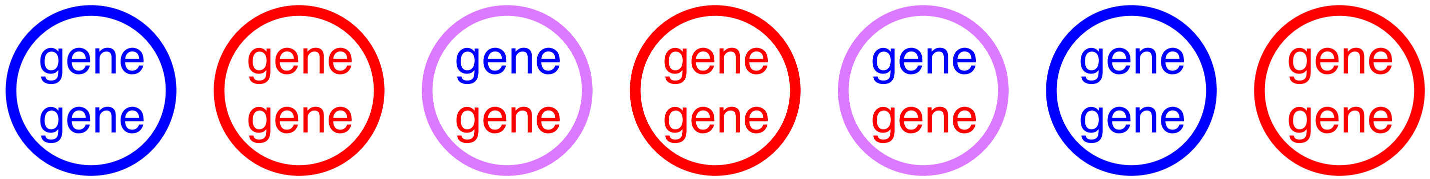
The distinction between natural selection ACTING ON vs. SELECTING FOR



The distinction between natural selection
<u>ACTING ON</u> vs. <u>SELECTING FOR</u>



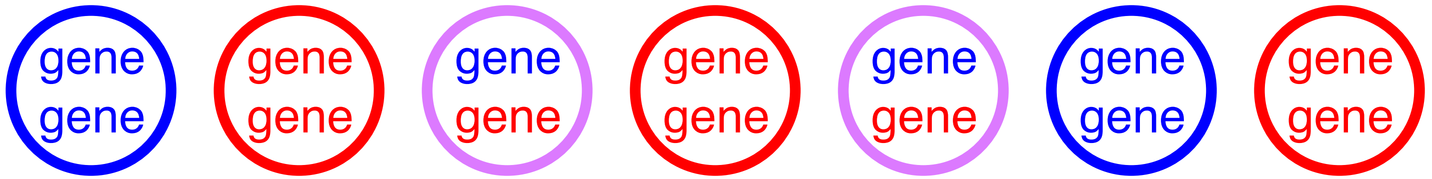
The distinction between natural selection
<u>ACTING ON</u> vs. <u>SELECTING FOR</u>



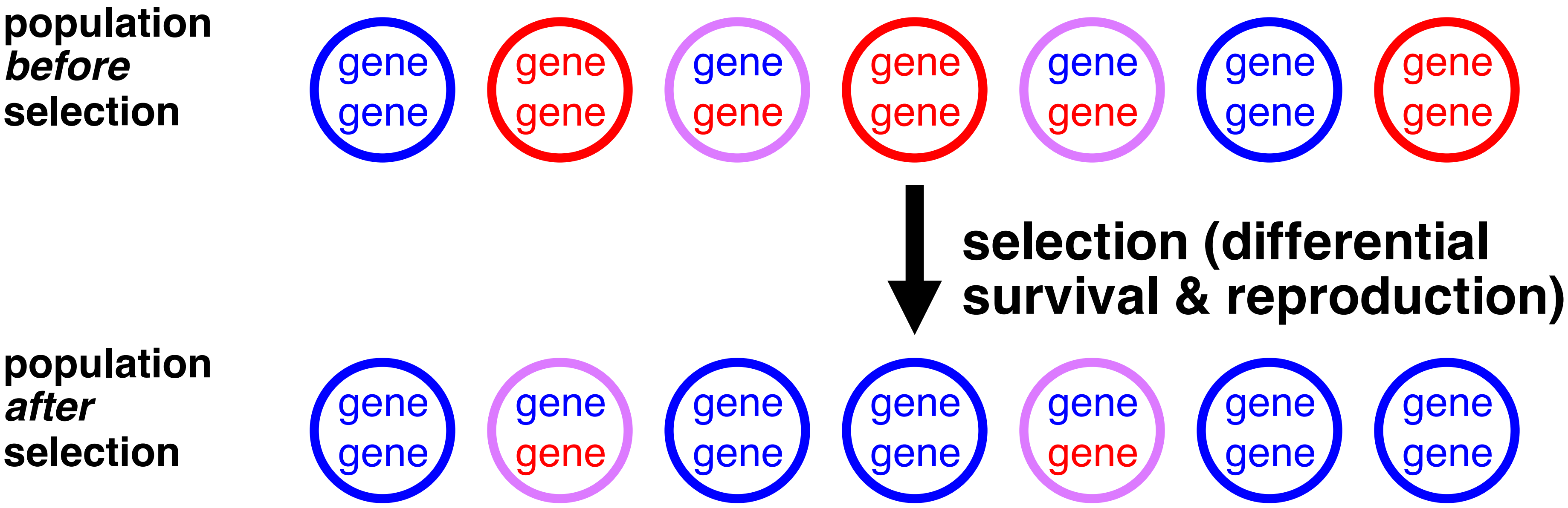
a population of vehicles built by genes

The distinction between natural selection
ACTING ON vs. SELECTING FOR

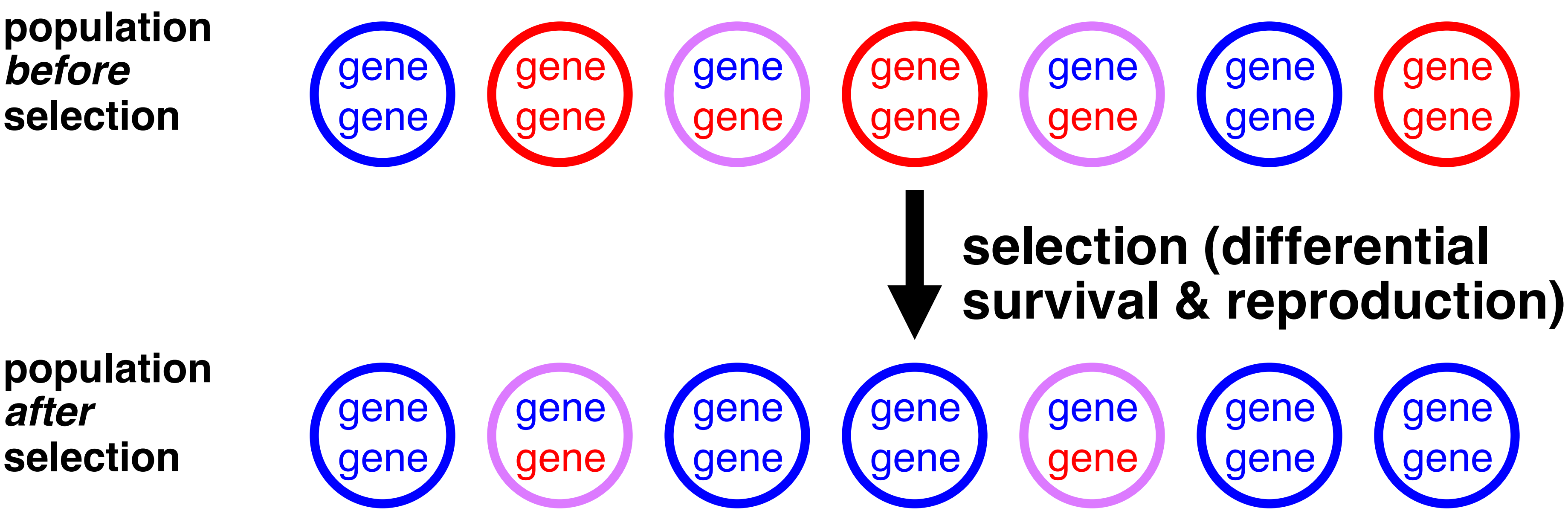
population
before
selection



The distinction between natural selection **ACTING ON** vs. **SELECTING FOR**

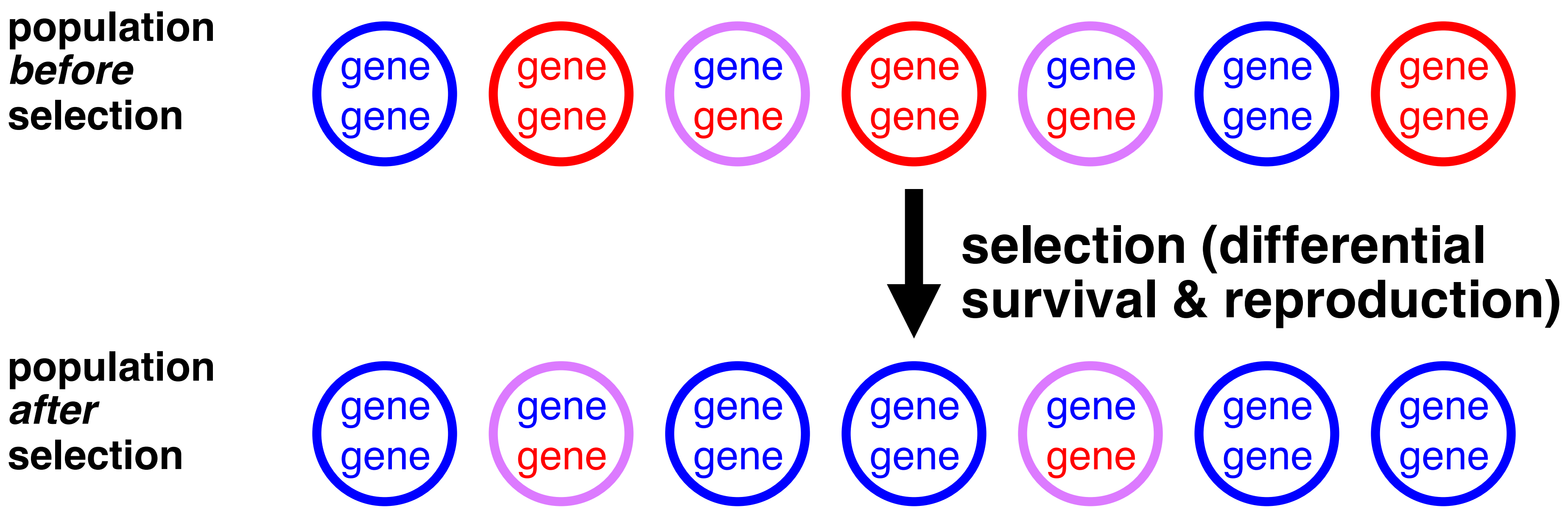


The distinction between natural selection __ACTING ON__ vs. __SELECTING FOR__



What does selection __ACT ON?__
What is __SELECTED FOR?__

The distinction between natural selection
<u>ACTING ON</u> vs. <u>SELECTING FOR</u>



Natural selection:

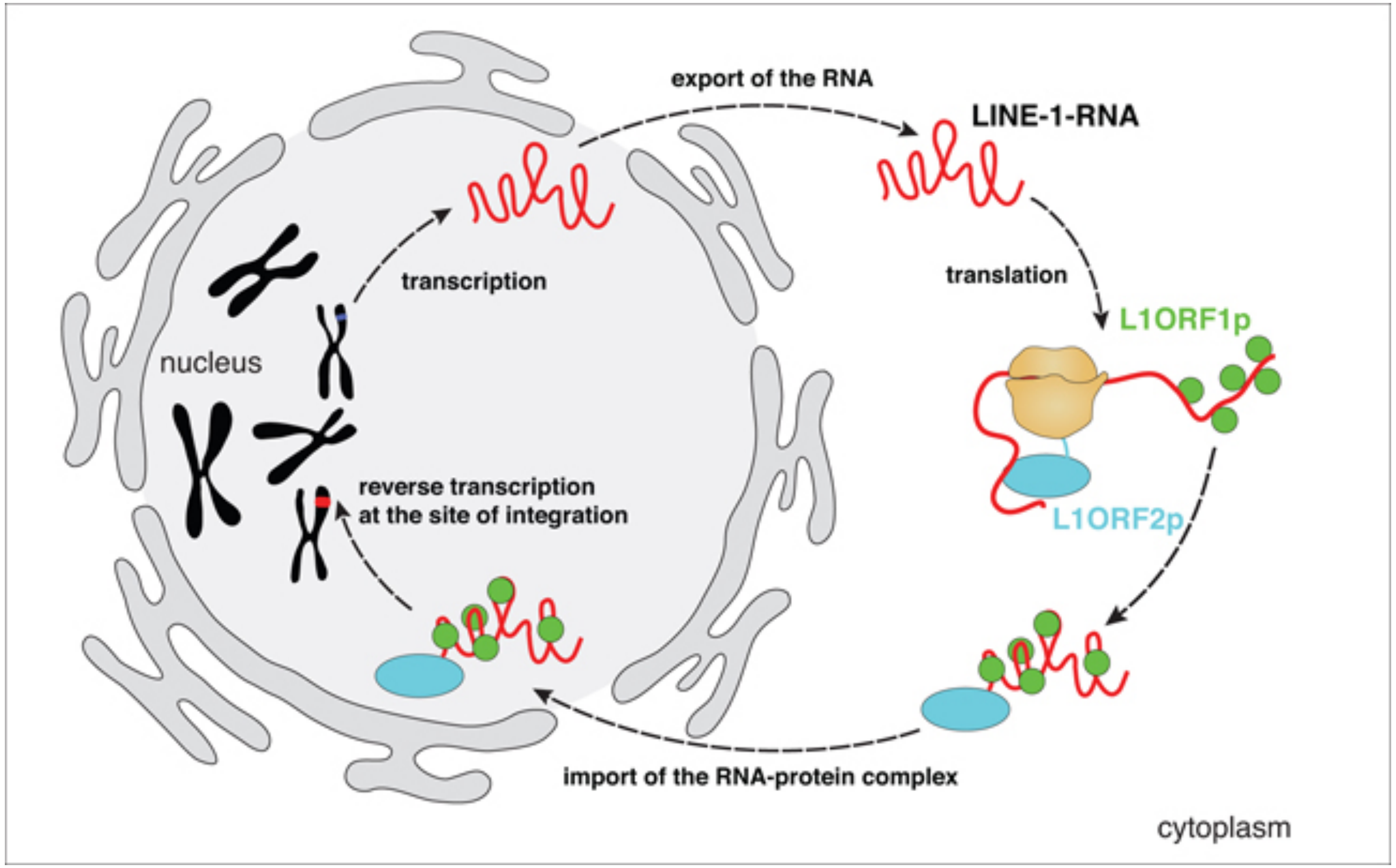
<u>ACTS ON</u> phenotype (= “vehicle” = unit of selective interaction)

<u>SELECTS FOR</u> genes (= “replicators” = unit of inheritance) that build the phenotype / vehicle

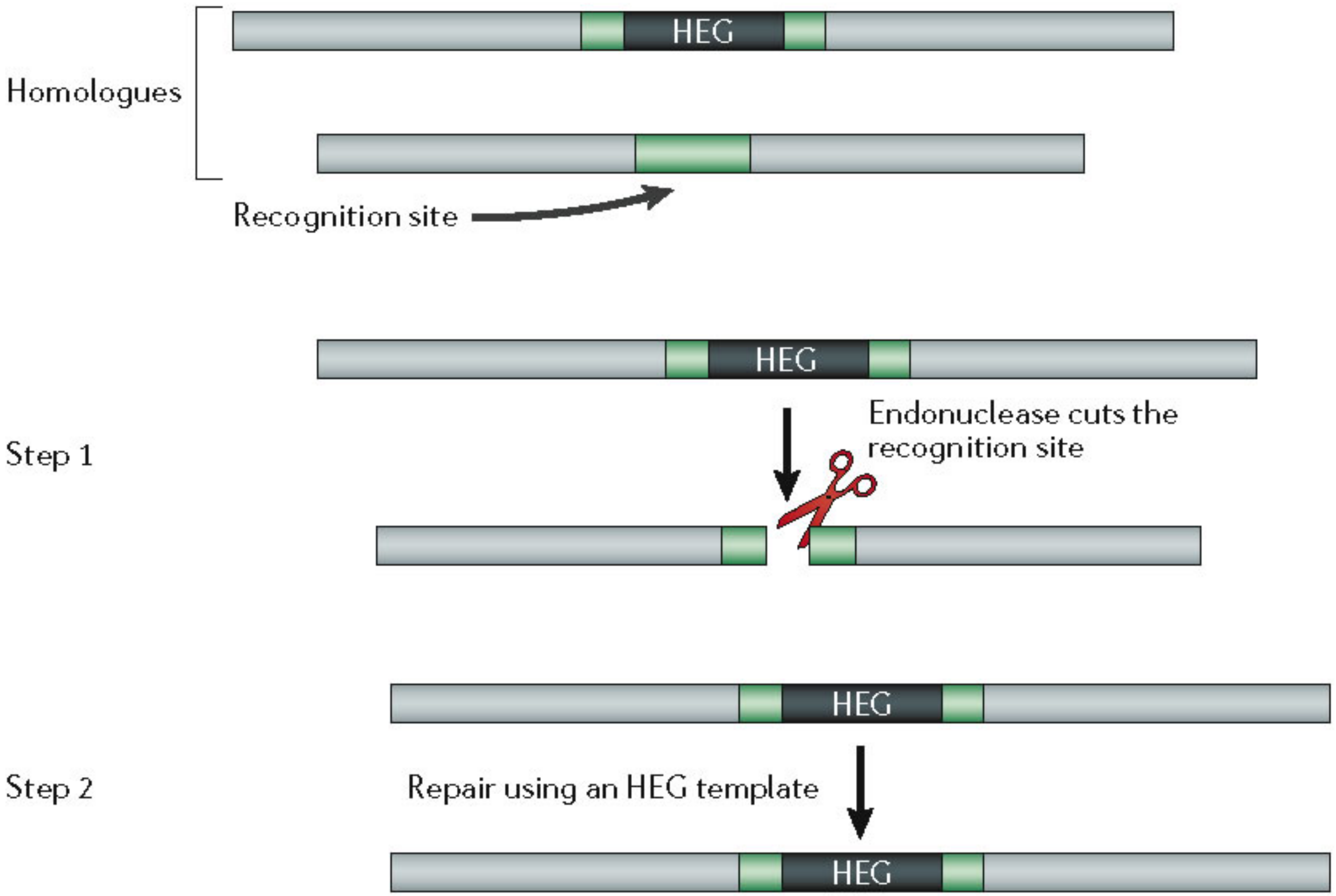
Selfish genes

- Transposons
- Homing endonucleases
- Segregation distortion
- Sex-ratio distorters
- Altruism by kin selection

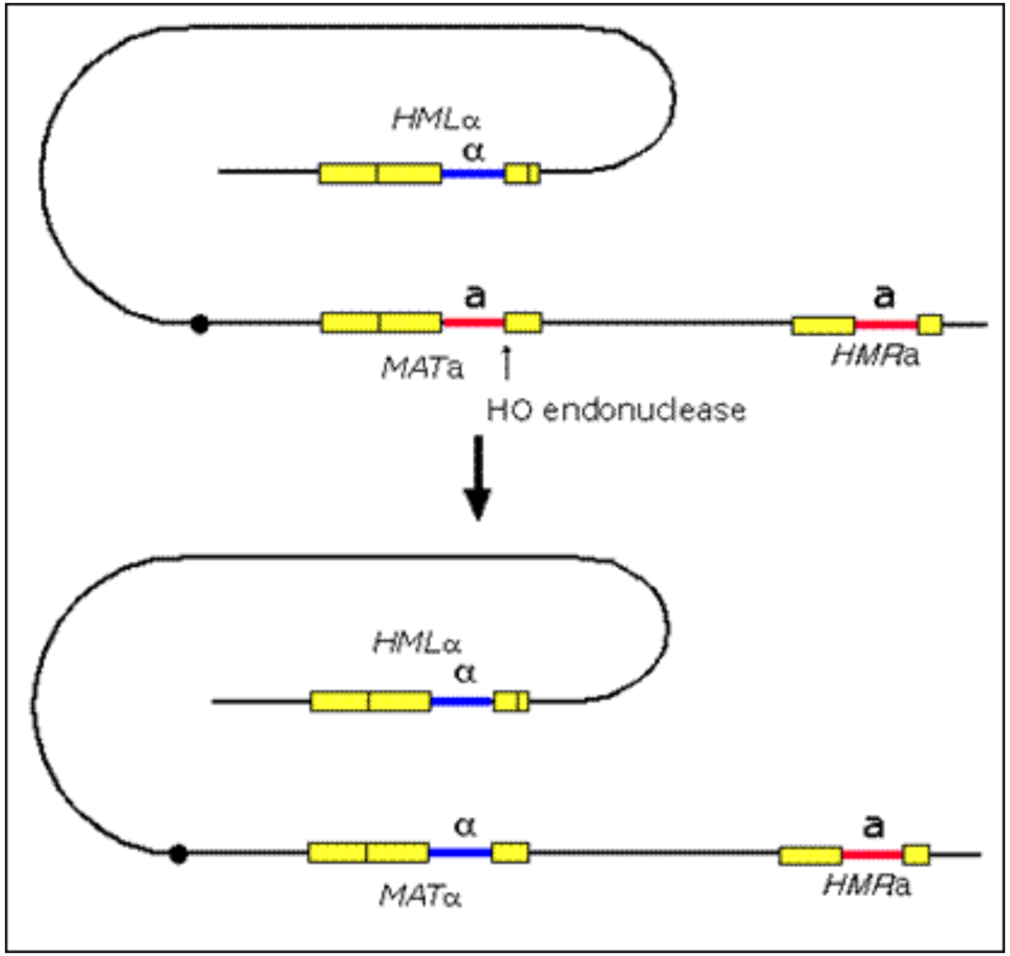
Transposons



Homing endonuclease

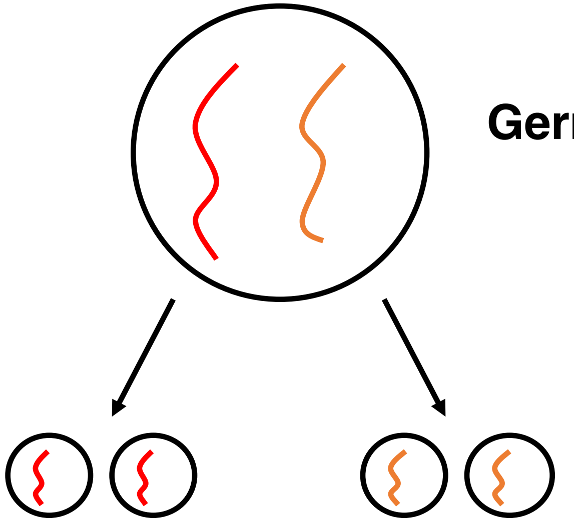


Fun aside: domestication of a selfish element



SELF-INTERESTED (SELFISH) GENES:

Segregation Distorters
e.g., meiotic drive in *Drosophila*

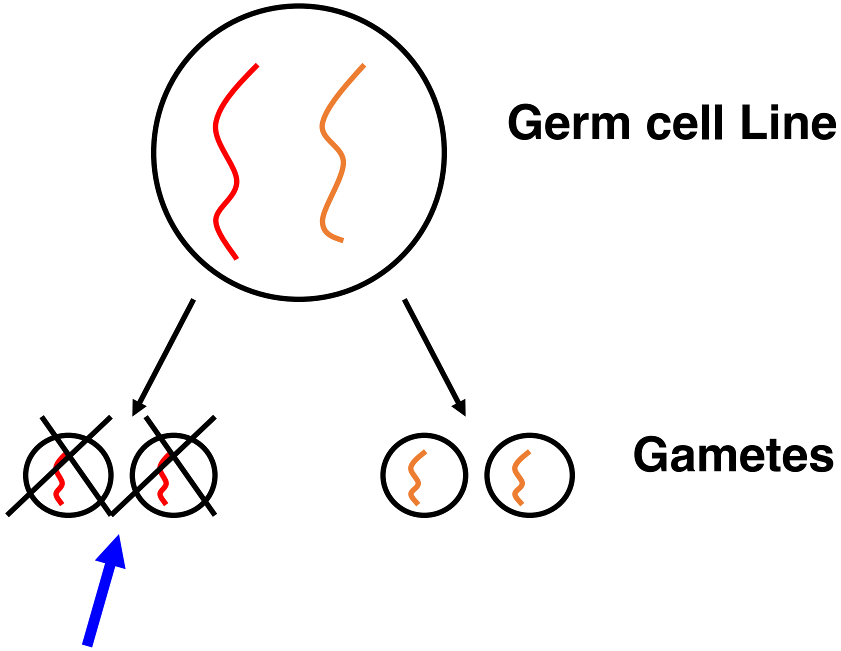


normal gamete production

SELF-INTERESTED (SELFISH) GENES:

Segregation Distorters

e.g., meiotic drive in *Drosophila*



Meiotic drive:

"blue" allele eliminates gametes carrying "red" allele

=> all suriving gametes carry "blue"

SELF-INTERESTED (SELFISH) GENES:

Sex-Ratio Distorters

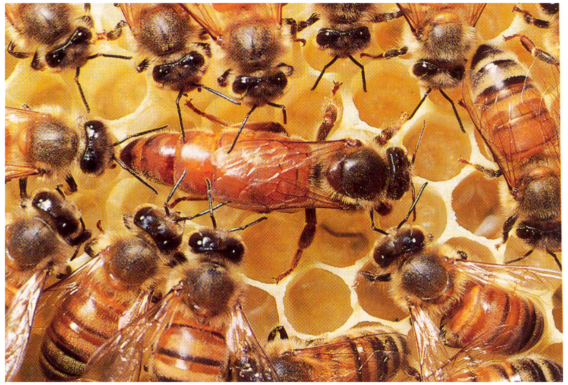
e.g., *psr*-gene in *Nasonia*

jewel-wasp
Nasonia vitripennis

Need to understand first:

<u>Haplodiploid Sex Determination</u>

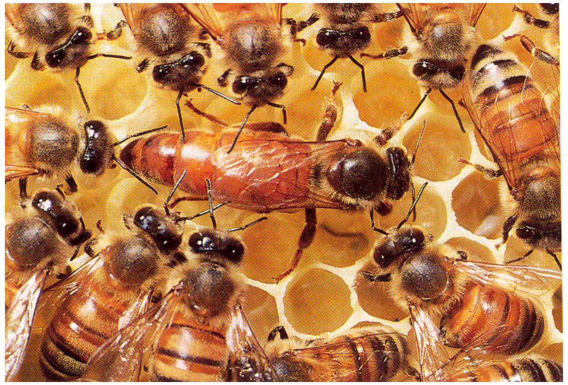
in the Hymenoptera (wasps, bees, ants)



Need to understand first:
<u>Haplodiploid Sex Determination</u>
in the Hymenoptera (wasps, bees, ants)

diploid ♀
2n

♂ haploid
1n



Need to understand first:

Haplodiploid Sex Determination

in the Hymenoptera (wasps, bees, ants)

diploid ♀

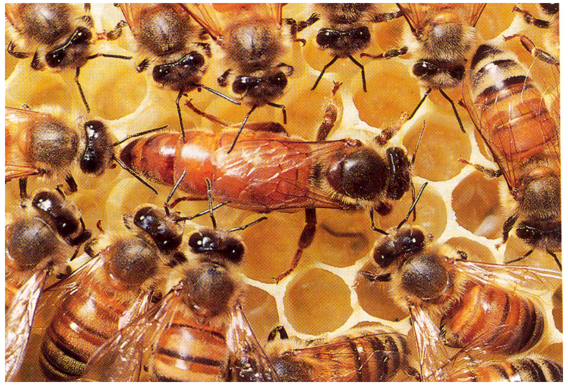
2n

meiosis
in female

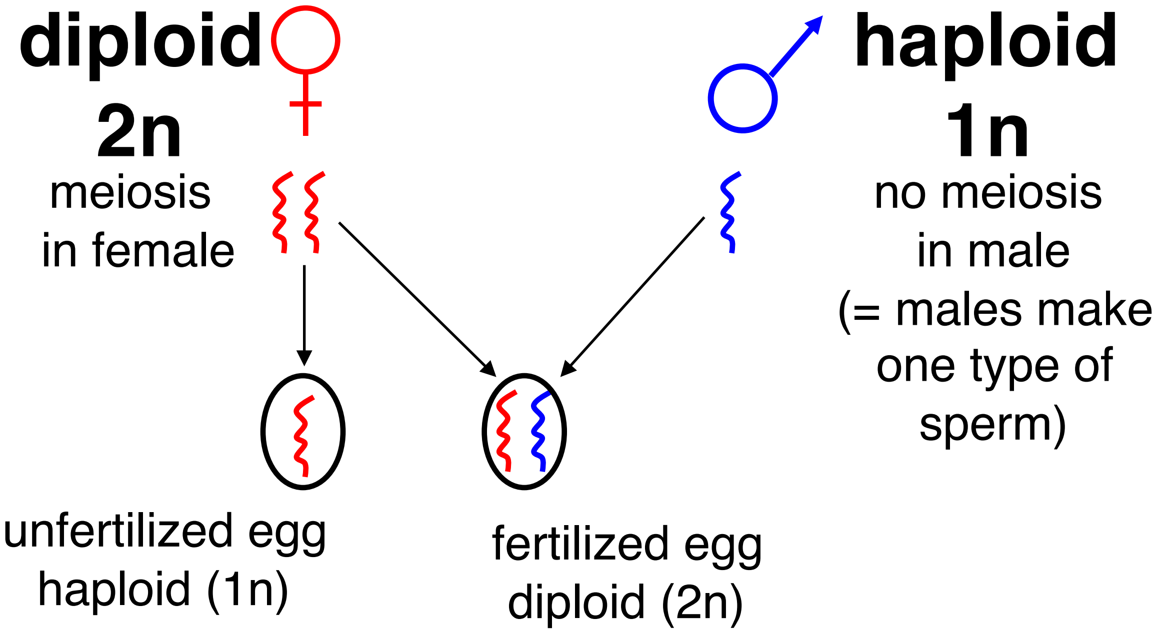
♂ **haploid**

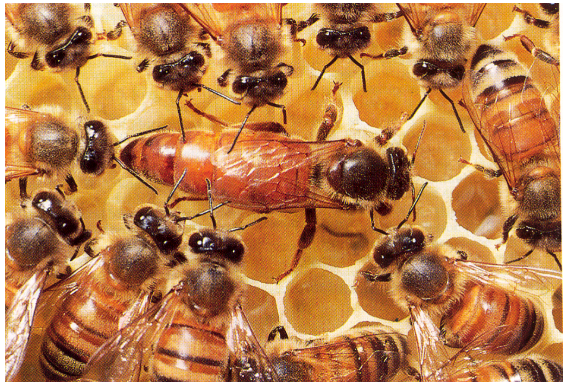
1n

no meiosis
in male
(= males make
one type of
sperm)



Need to understand first:
Haplodiploid Sex Determination
in the Hymenoptera (wasps, bees, ants)

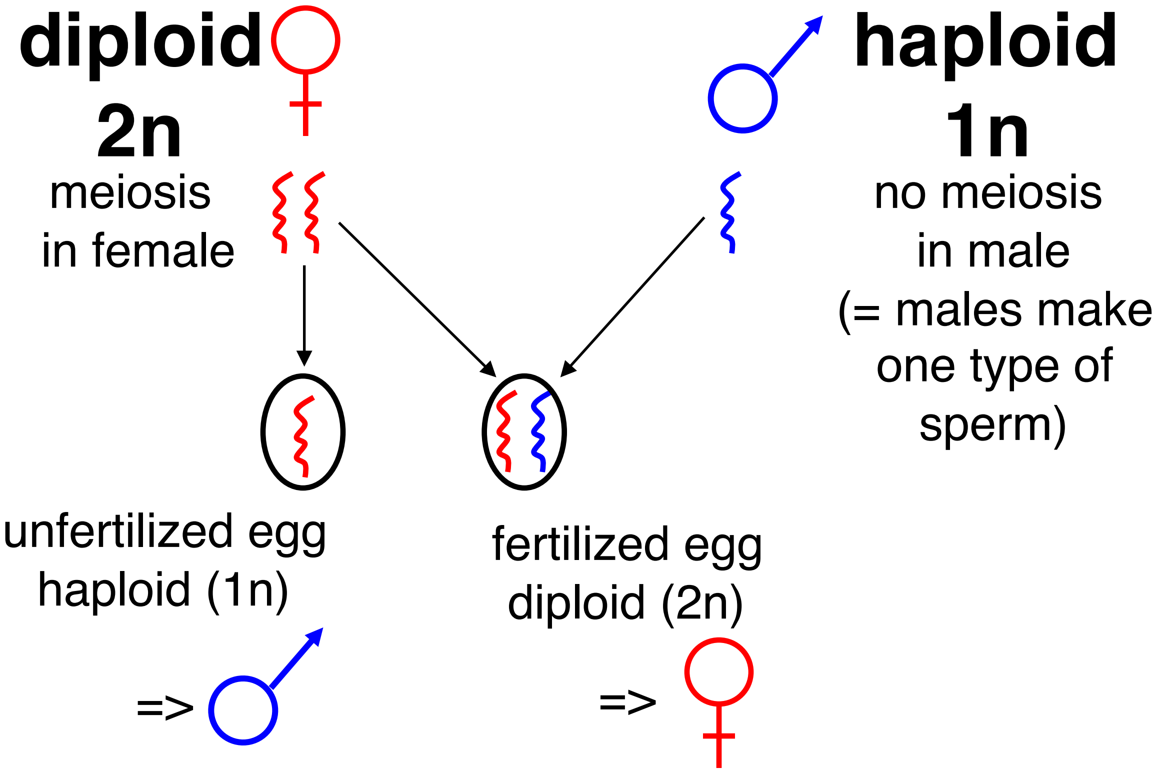


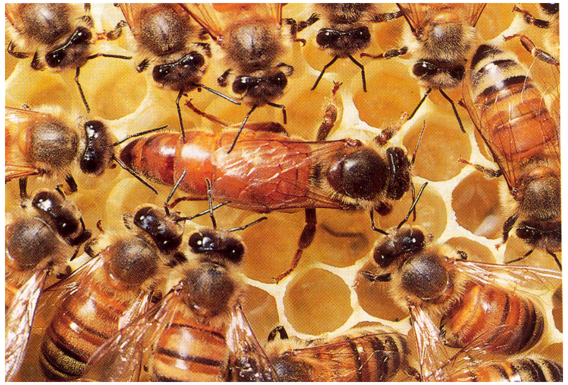


Need to understand first:

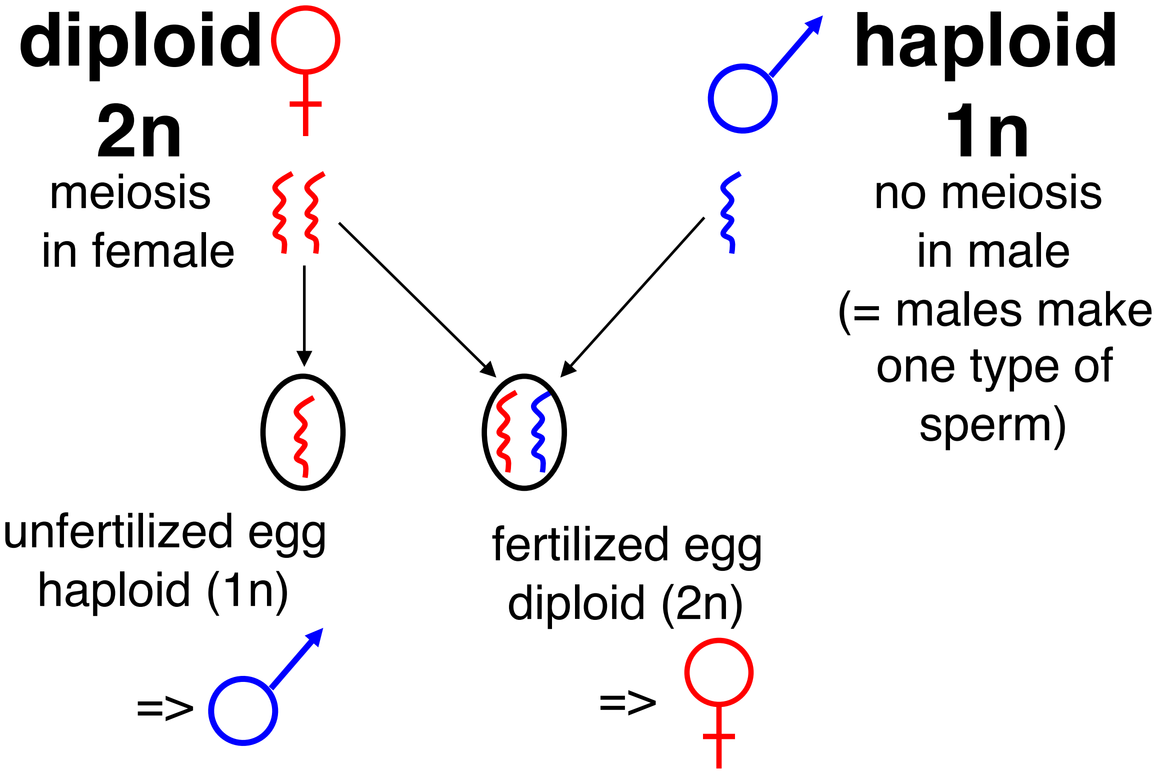
Haplodiploid Sex Determination

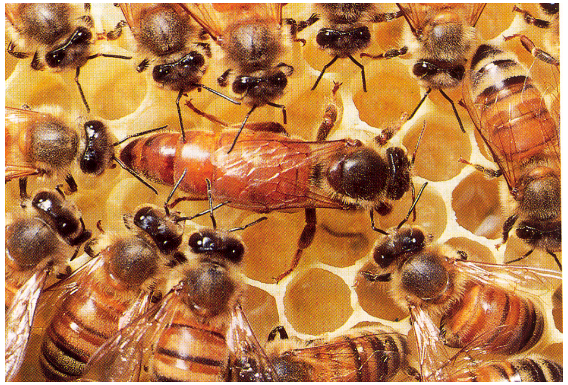
in the Hymenoptera (wasps, bees, ants)





Need to understand first:
<u>Haplodiploid Sex Determination</u>
in the Hymenoptera (wasps, bees, ants)





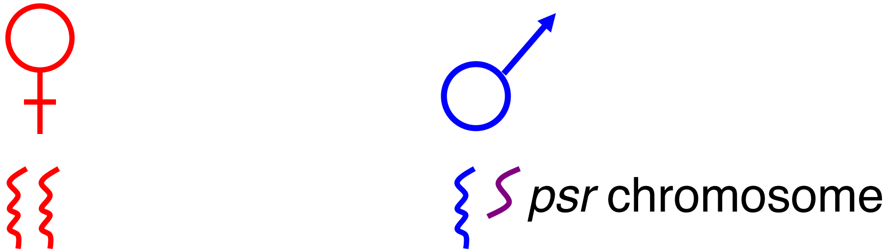
Only females have sons & daughters;

Males <u>do not</u> have sons, only daughters

SELFISH GENES: Sex-Ratio Distorters

psr-gene in *Nasonia vitripennis*

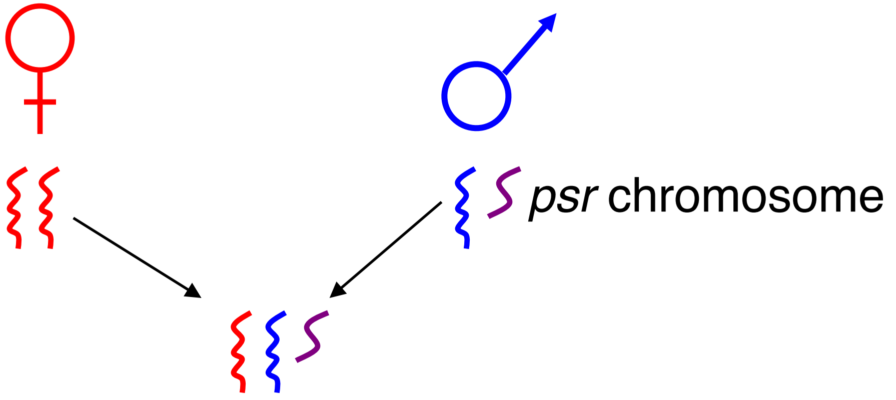
- supernumary chromosome (*psr*); found only in males



SELFISH GENES: Sex-Ratio Distorters

psr-gene in *Nasonia vitripennis*

- supernumary chromosome (*psr*); found only in males

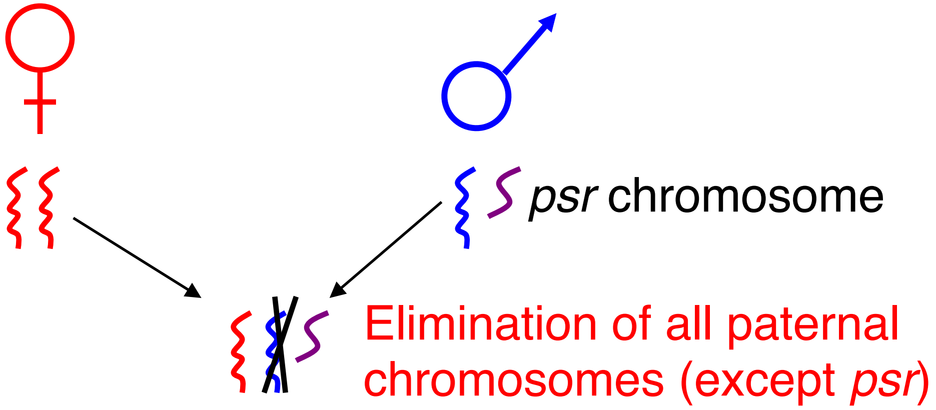


SELFISH GENES: Sex-Ratio Distorters

psr-gene in *Nasonia vitripennis*

- supernumary chromosome (*psr*); found only in males

- sperm containing *psr* causes paternal set of chromosome to condense (=> elimination), whereas *psr* survives

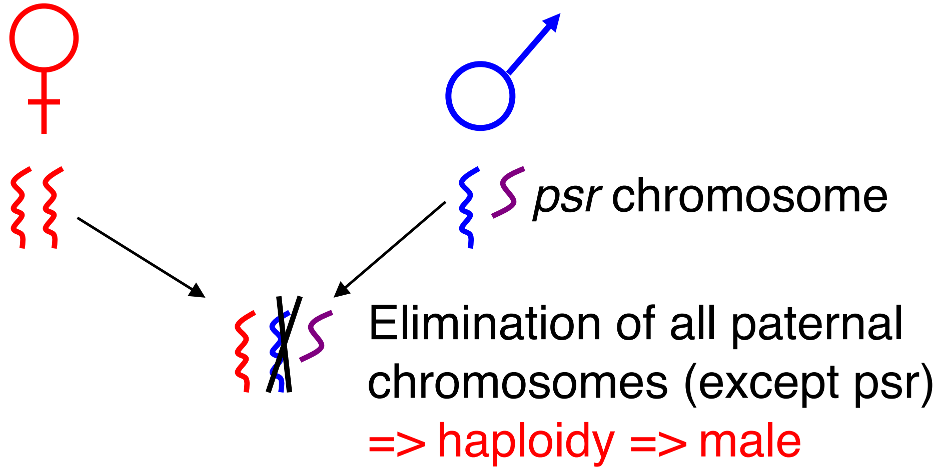


SELFISH GENES: Sex-Ratio Distorters

psr-gene in *Nasonia vitripennis*

- supernumary chromosome (*psr*); found only in males

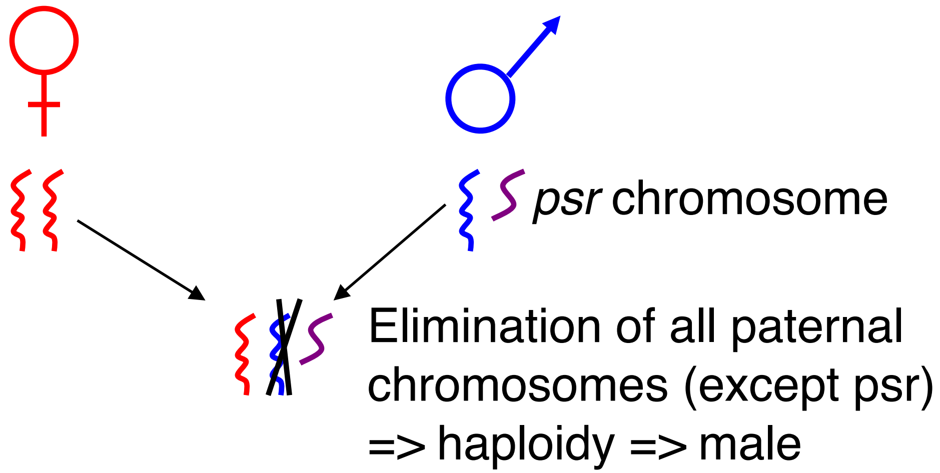
- sperm containing *psr* causes paternal set of chromosome to condense (=> elimination), whereas *psr* survives



SELFISH GENES: Sex-Ratio Distorters

psr-gene in *Nasonia vitripennis*

- supernumary chromosome (*psr*); found only in males
- sperm containing *psr* causes paternal set of chromosome to condense (=> elimination), whereas *psr* survives

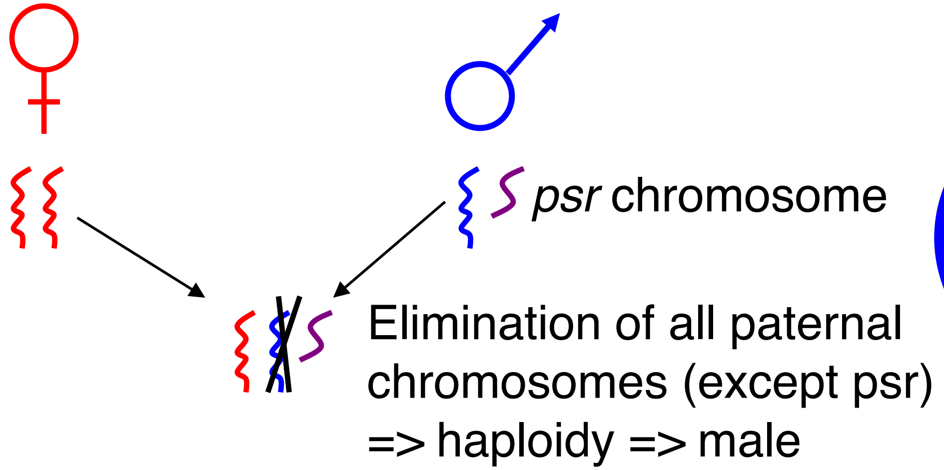


- *psr* causes chromosomal "fratricide", thus causing haploidy (=> offspring of *psr*-male are all male)

SELFISH GENES: Sex-Ratio Distorters

psr-gene in *Nasonia vitripennis*

- supernumary chromosome (*psr*); found only in males
- sperm containing *psr* causes paternal set of chromosome to condense (=> elimination), whereas *psr* survives



psr = "paternal sex ratio" because sex-ratio is determined by male in some matings

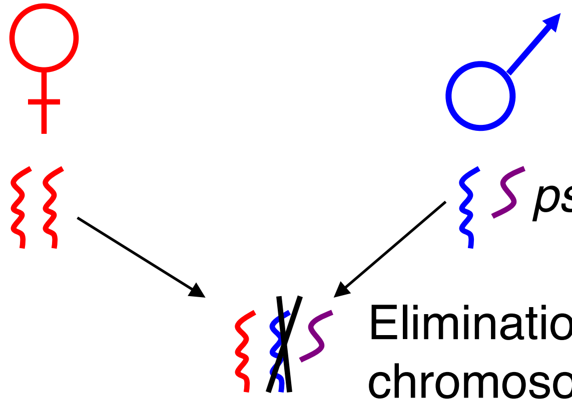
- *psr* causes chromosomal "fratricide", thus causing haploidy (=> offspring of *psr*-male are all male)

SELFISH GENES: Sex-Ratio Distorters

psr-gene in *Nasonia vitripennis*

- supernumary chromosome (*psr*); found only in males

- sperm containing *psr* causes paternal set of chromosome to condense (=> elimination), whereas *psr* survives



- *psr* causes chromosomal "fratricide", thus causing haploidy (=> offspring of *psr*-male are all male)

=> *psr* doubles its rate of reproduction, because it circumvents 50% chance of elimination during meiosis (i.e., *psr* manages to avoid the cost of meiosis)

SELF-INTERESTED (SELFISH) GENES:

Natural selection can select for genes against the interest of the individual

For example:

- **Repetitive DNA**

- **Spread of transposons in a genome**

- **Segregation distorters (e.g., meiotic drive in *Drosophila*)**

- **Sex-ratio distorters**
  (e.g., *psr*-gene in the jewel wasp *Nasonia vitripennis*)

SELF-INTERESTED (SELFISH) GENES:

Natural selection can select for genes against the interest of the individual

For example:

- Repetitive DNA

- Spread of transposons in a genome

- Segregation distorters (e.g., meiotic drive in *Drosophila*)

- Sex-ratio distorters
(e.g., *psr*-gene in the jewel wasp *Nasonia vitripennis*)

- Altruism and kin-selection

e.g., alarm calling in Belding's Ground Squirrel

e.g., helping in Florida scrub jays

Altruism

= fitness-reducing behavior that benefits another individual

Altruism

= fitness-reducing behavior that benefits another individual

Evolution of altruism / helping can be understood in terms of indirect fitness effects (effects on relatives)

Altruism

= fitness-reducing behavior that benefits another individual

Evolution of altruism / helping can be understood in terms of indirect fitness effects (effects on relatives)

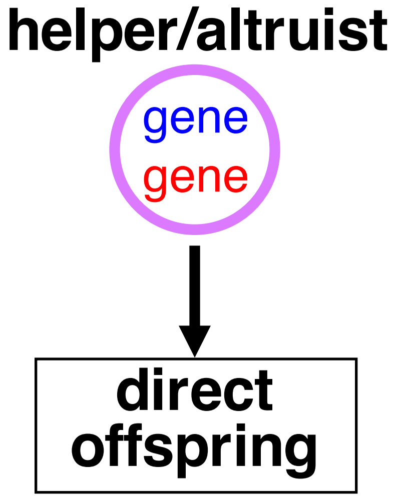
Direct Fitness = fitness gained through production of offspring
Indirect Fitness = fitness gained through effects on relatives (non-descendent kin)

Altruism

= fitness-reducing behavior that benefits another individual

Evolution of altruism / helping can be understood in terms of indirect fitness effects (effects on relatives)

Direct Fitness = fitness gained through production of offspring
Indirect Fitness = fitness gained through effects on relatives (non-descendent kin)



Altruism

= fitness-reducing behavior that benefits another individual

Evolution of altruism / helping can be understood in terms of indirect fitness effects (effects on relatives)

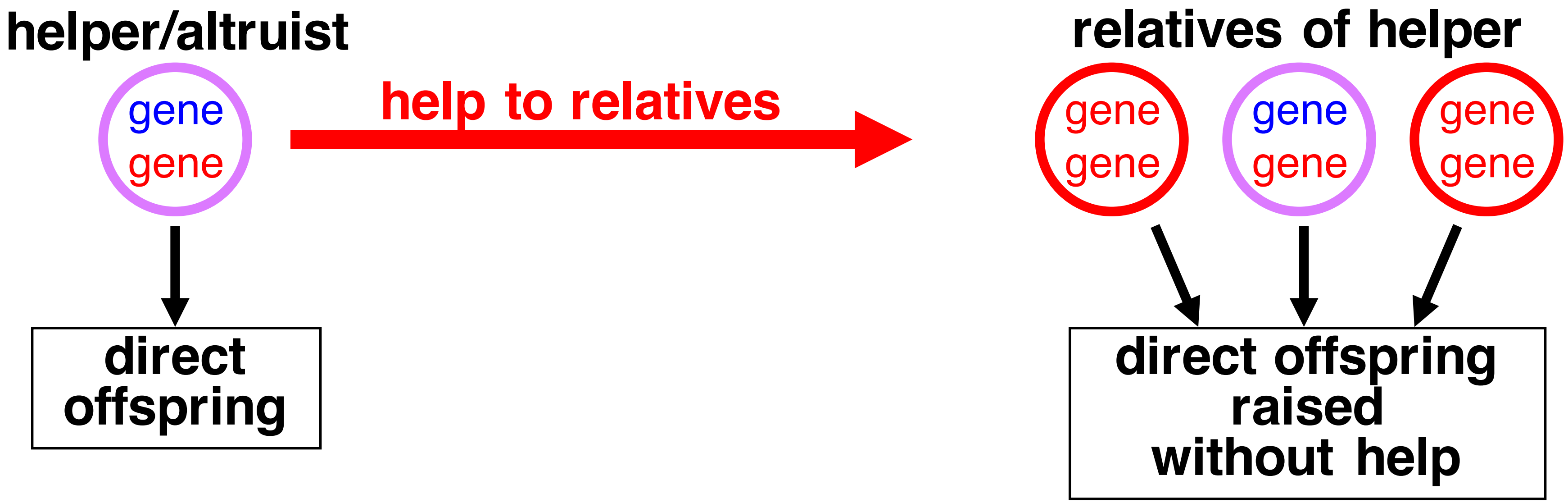
Direct Fitness = fitness gained through production of offspring
Indirect Fitness = fitness gained through effects on relatives (non-descendent kin)

Altruism

= fitness-reducing behavior that benefits another individual

Evolution of altruism / helping can be understood in terms of indirect fitness effects (effects on relatives)

Direct Fitness = fitness gained through production of offspring
Indirect Fitness = fitness gained through effects on relatives (non-descendent kin)

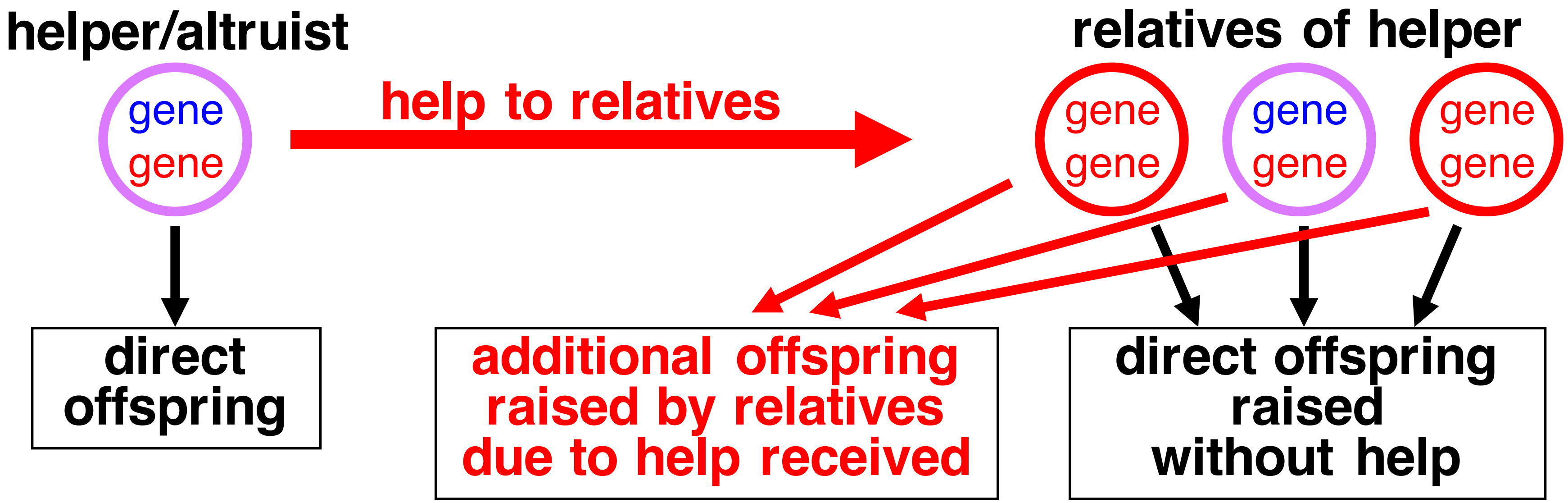


Altruism

= fitness-reducing behavior that benefits another individual

Evolution of altruism / helping can be understood in terms of indirect fitness effects (effects on relatives)

Direct Fitness = fitness gained through production of offspring
Indirect Fitness = fitness gained through effects on relatives (non-descendent kin)

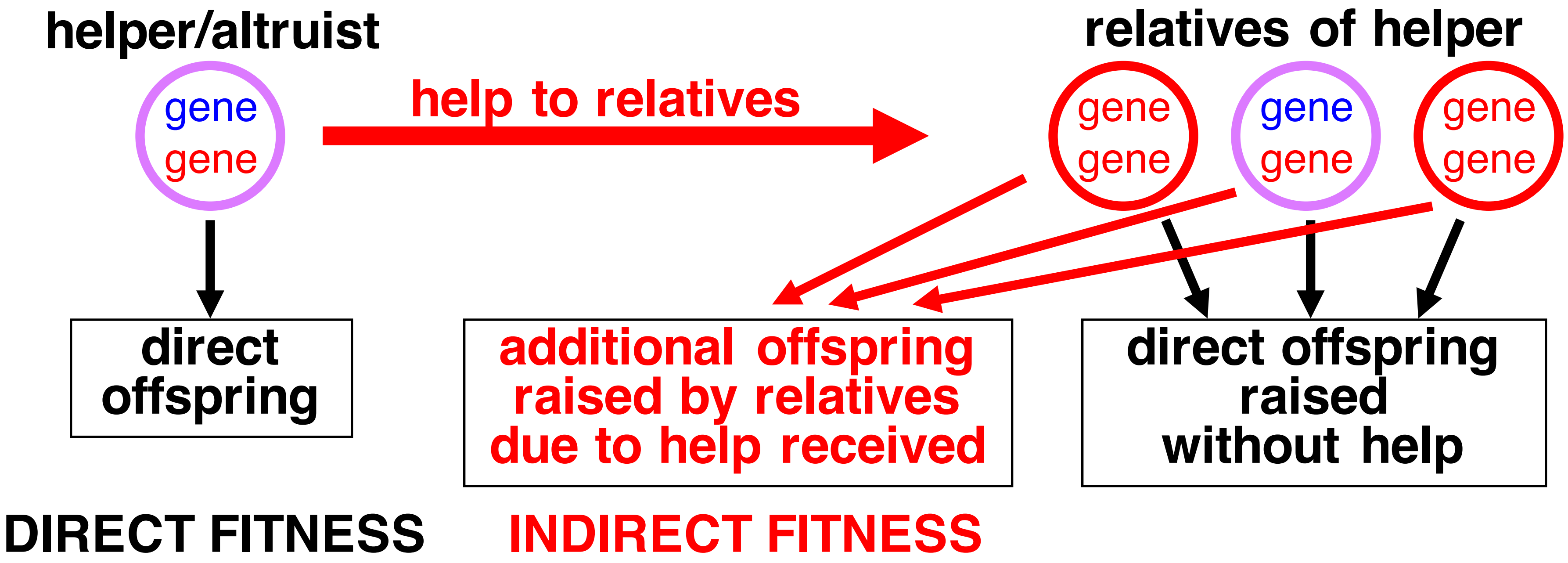


Altruism

= fitness-reducing behavior that benefits another individual

Evolution of altruism / helping can be understood in terms of indirect fitness effects (effects on relatives)

Direct Fitness = fitness gained through production of offspring
Indirect Fitness = fitness gained through effects on relatives (non-descendent kin)



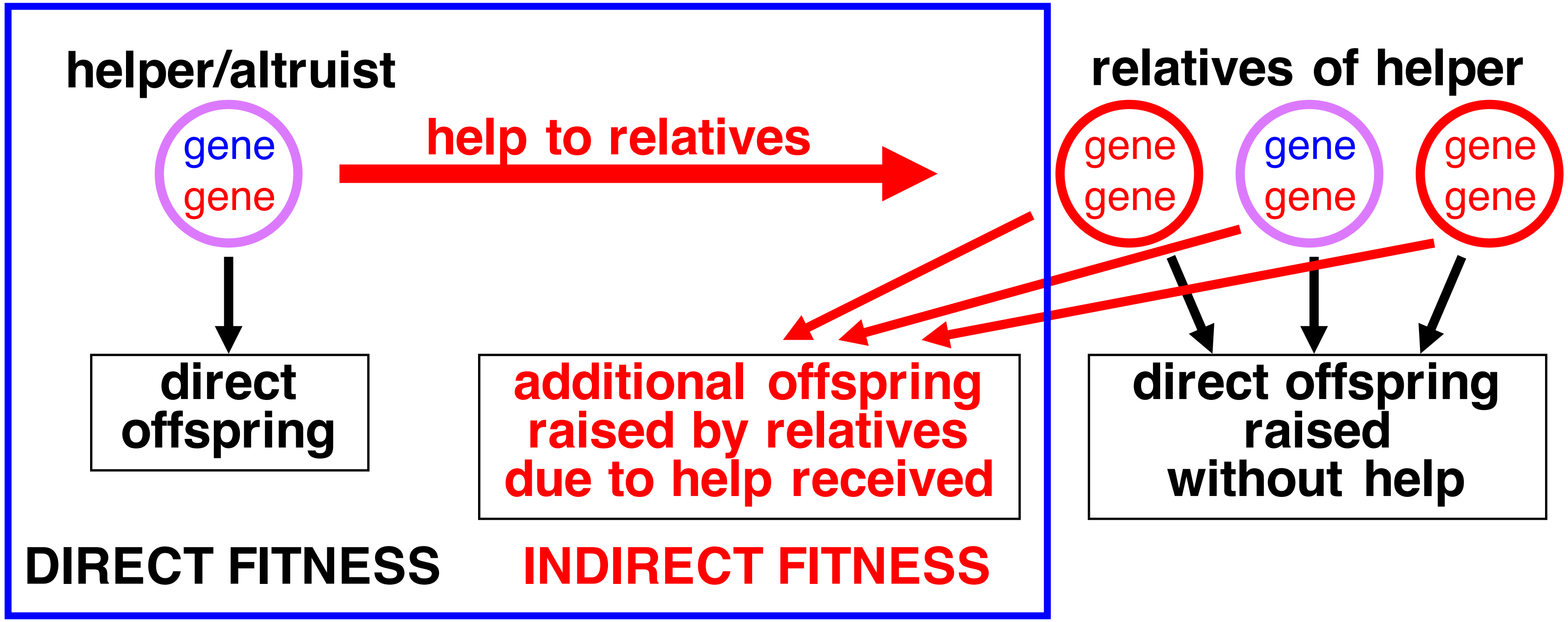
Altruism

= fitness-reducing behavior that benefits another individual

Evolution of altruism / helping can be understood in terms of indirect fitness effects (effects on relatives)

Direct Fitness = fitness gained through production of offspring
Indirect Fitness = fitness gained through effects on relatives (non-descendent kin)

INCLUSIVE FITNESS = DIRECT FITNESS & INDIRECT FITNESS



Altruism

= fitness-reducing behavior that benefits another individual

Evolution of altruism / helping can be understood in terms of indirect fitness effects (effects on relatives)

Direct Fitness = fitness gained through production of offspring
Indirect Fitness = fitness gained through effects on relatives (non-descendent kin)

INCLUSIVE FITNESS = DIRECT FITNESS & INDIRECT FITNESS

Altruism can evolve by kin-selection if:

$$rB > C$$

Hamilton's Rule

relatedness

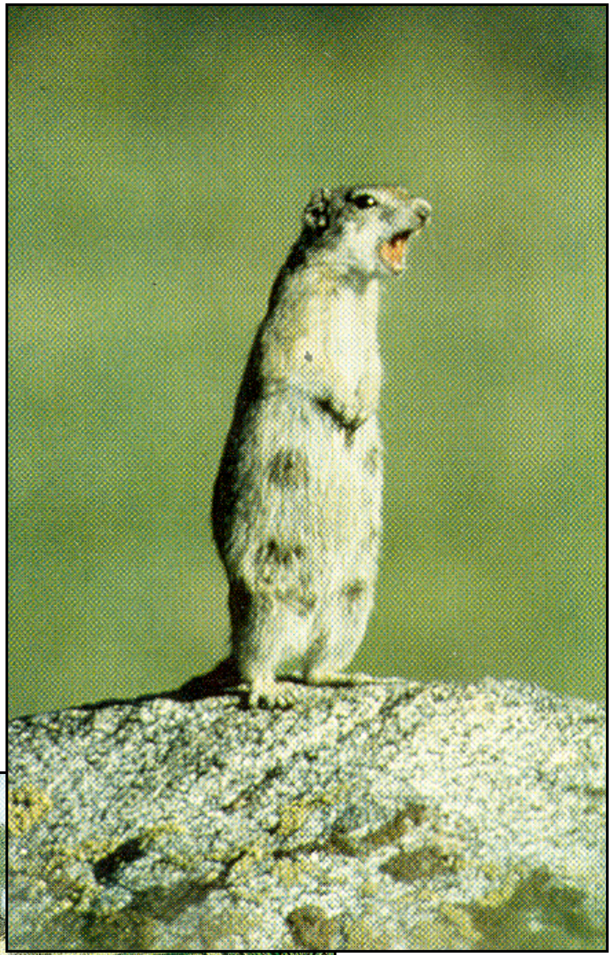
fitness benefit to relative

fitness cost to helper

Hamilton's Rule

$$r\,B > C$$

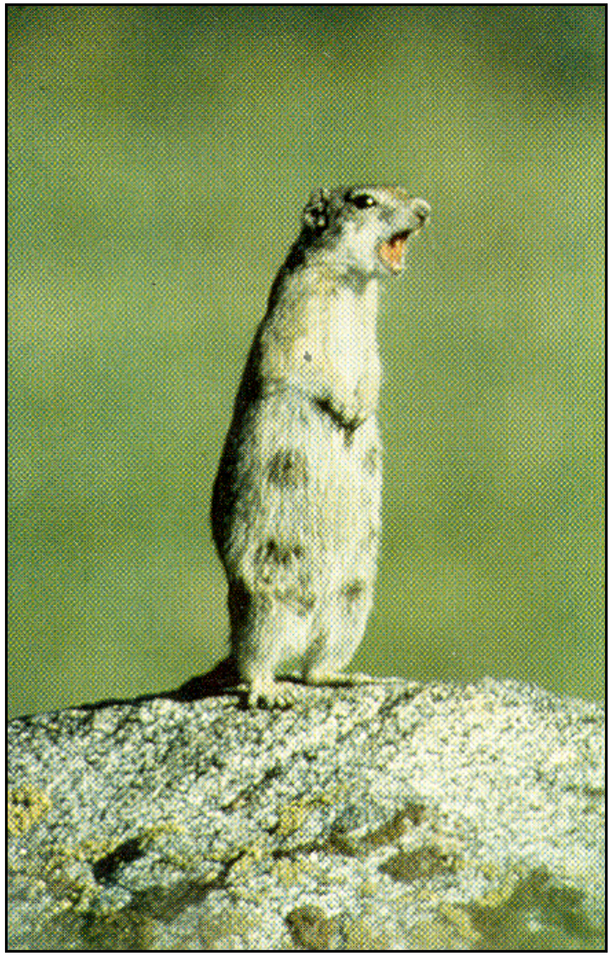
r = relatedness between helper and recipient
B = fitness benefit to recipient
C = fitness cost to helper



Hamilton’s Rule

$r\,B\ >\ C$

r = relatedness between helper and recipient
B = fitness benefit to recipient
C = fitness cost to helper



Kin-selection for Altruism

individual altruism is explained as genetic selfishness,
because genes in relatives benefit

kin-selection explanation: at the gene level, not at the
individual level;

SELF-INTERESTED (SELFISH) GENES:

Natural selection can select for genes against the interest of the individual

For example:

- Repetitive DNA

- Spread of transposons in a genome

- Segregation distorters (e.g., meiotic drive in *Drosophila*)

- Sex-ratio distorters
(e.g., *psr*-gene in the jewel wasp *Nasonia vitripennis*)

-Altruism and kin-selection: phenotypic altruism can be viewed as genetic selfishness

In the majority of cases, natural selection ACTS ON individuals, but SELECTS FOR genes

<u>Interesting cases</u>:

- Sometimes natural selection ACTS ON genes directly
  and SELECTS FOR genes (“selfish genes”)
  against the interest of the individual

- Sometimes natural selection ACTS ON organizational
  structures above the level of the individual
  (e.g., colony of some social insects)

In the majority of cases, natural selection ACTS ON individuals, but SELECTS FOR genes

Interesting cases:

- Sometimes natural selection ACTS ON genes directly
  and SELECTS FOR genes (“selfish genes”)
  against the interest of the individual

- Sometimes natural selection ACTS ON organizational
  structures above the level of the individual
  (e.g., colony of some social insects)

Evolution has build a nested-hierarchy of levels with emergent properties possible at each level

Nested Hierarchy

Social colony
Multicellular individual
Cell
Gene

Evolution has build a nested-hierarchy of levels
with emergent properties possible at each level

Nested Hierarchy

Social colony
Multicellular individual
Cell
Gene

these two levels are in conflict
in the case of "*selfish genes*"

Evolution has build a nested-hierarchy of levels
with emergent properties possible at each level

These emergent properties could serve as
adaptations for natural selection to ACT ON

Nested Hierarchy	Adaptation that could be acted on
Social colony	colony adaptations
Multicellular individual	individual adaptations
Cell	cellular adaptations
Gene	genic adaptations

Evolution has build a nested-hierarchy of levels
with emergent properties possible at each level

These emergent properties could serve as
adaptations for natural selection to ACT ON

Nested Hierarchy	**Adaptation that could be acted on**
Social colony	**colony adaptations**
Multicellular individual	**individual adaptations**
Cell	**cellular adaptations**
Gene	**genic adaptations**

=> Multiple-Level Selection Theory

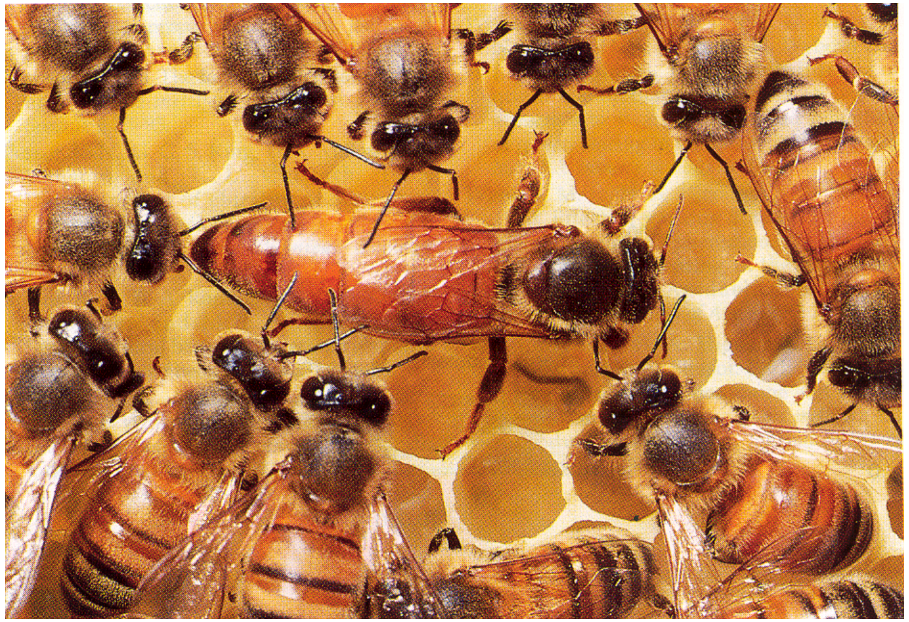
Natural selection can act on structures: e.g., hive fever and hornet defense in honey bees

Naturwissenschaften (2000) 87:229–231

SHORT COMMUNICATION

Philip T. Starks · Caroline A. Blackie
Thomas D. Seeley

Fever in honeybee colonies



Honeybees regulate temperature inside hive by:

- air circulation ("fanning")
- water evaporation
- Insulation
- generation of heat (wing muscle contractions)
- No single bee can regulate temperature alone
- Honeybee brood can be infected with a heat-sensitive pathogen
- A honeybee colony then increases its hive temperature (produces "hive fever")
- Natural selection can ACT ON colony property (fever), which SELECTS FOR genes that regulate fever responses

In the majority of cases, natural selection
ACTS ON individuals, but SELECTS FOR genes

Interesting cases:
Sometimes natural selection SELECTS FOR genes
against the interest of the individual

Sometimes natural selection ACTS ON organizational
structures above the level of the individual
(e.g., colony of some social insects)

But: MOST organizational structures above
the level of the individual are NOT
causally relevant to natural selection

**IT IS EASY TO BE DELUDED BY
FICTITIOUS "PROPERTIES" OF HIGHER LEVELS**

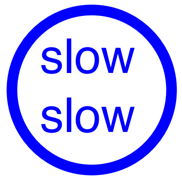
IT IS EASY TO BE DELUDED BY FICTITIOUS “PROPERTIES” OF HIGHER LEVELS

e.g. a fleet herd of deer   vs.   a herd of fleet deer

IT IS EASY TO BE DELUDED BY FICTITIOUS “PROPERTIES” OF HIGHER LEVELS

e.g. a fleet herd of deer   vs.   a herd of fleet deer

fleet deer

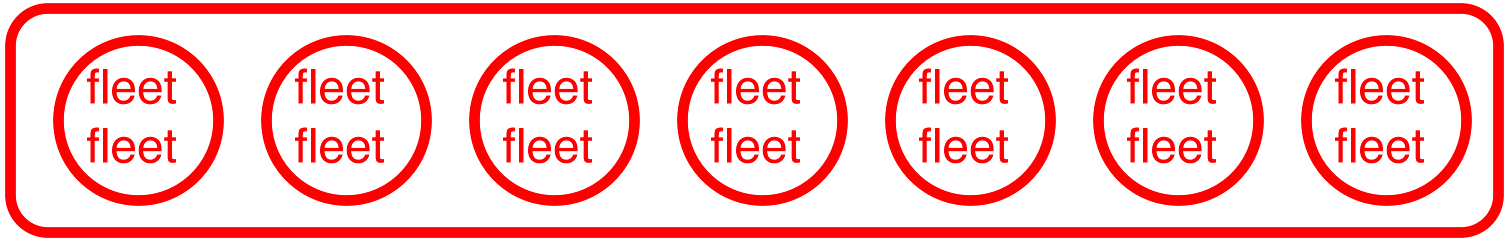


slow deer

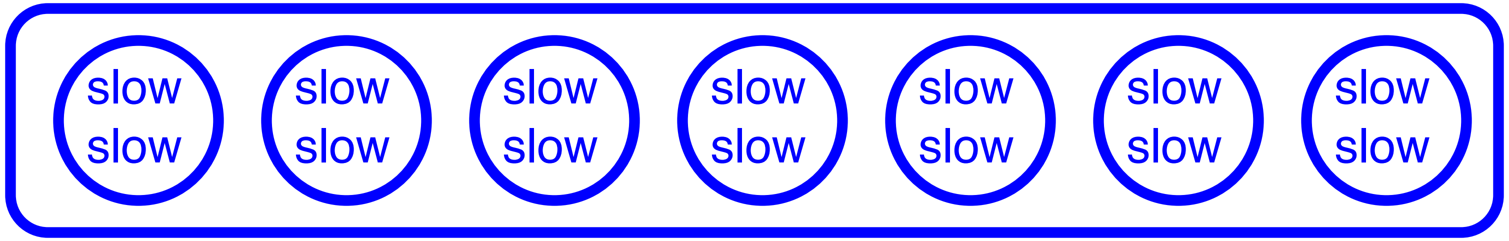
fleet = gene for fleetness
slow = gene for slowness

IT IS EASY TO BE DELUDED BY FICTITIOUS “PROPERTIES” OF HIGHER LEVELS

e.g. a fleet herd of deer vs. a herd of fleet deer



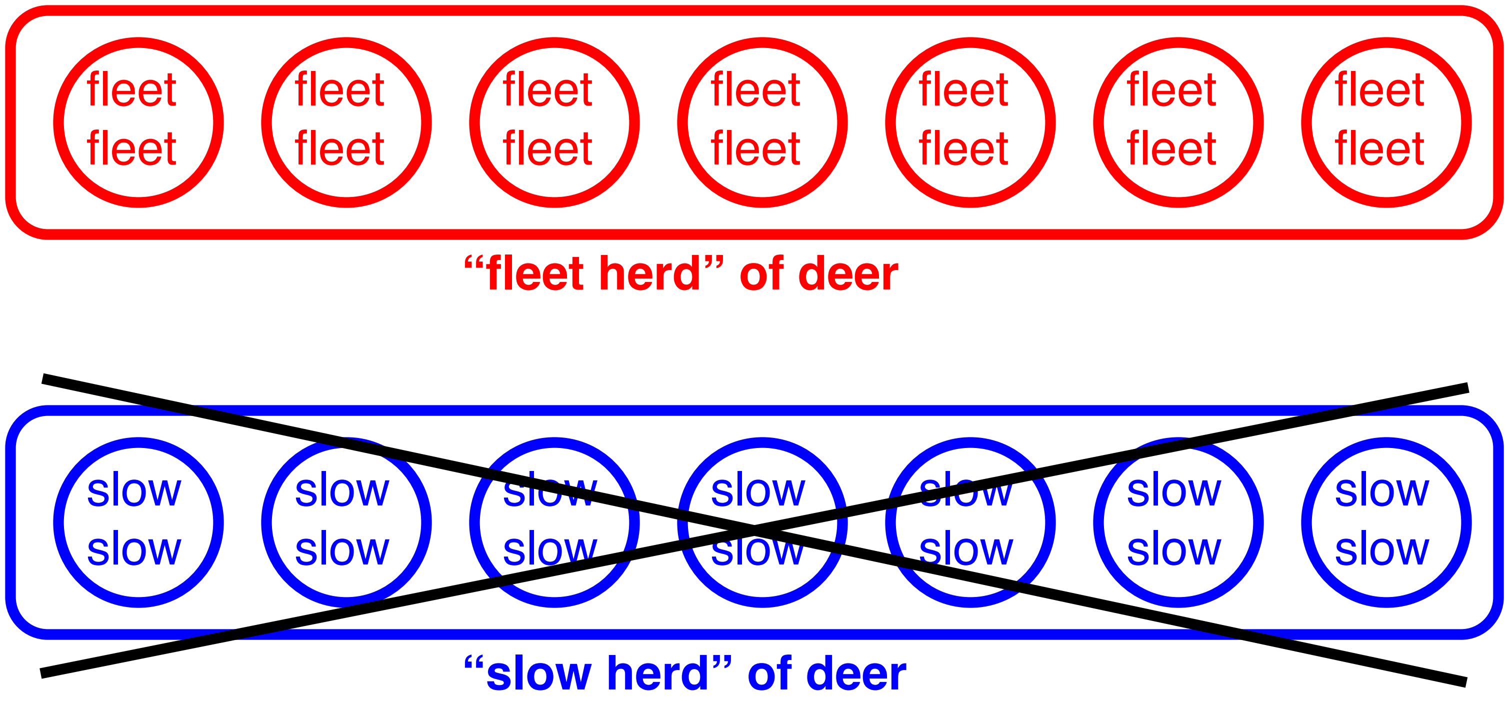
“fleet herd” of deer



“slow herd” of deer

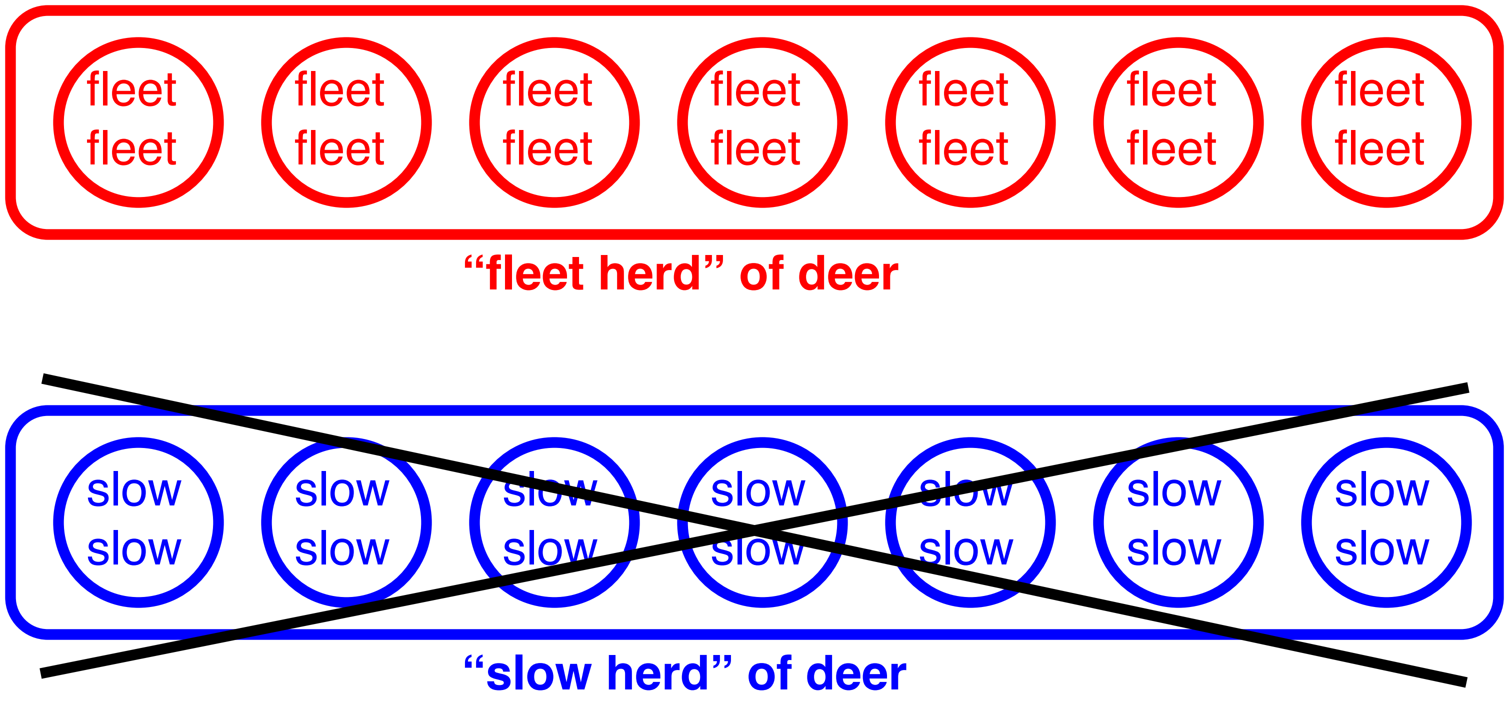
fleet = gene for fleetness
slow = gene for slowness

Differential predation may lead to the elimination of the “slow herd”



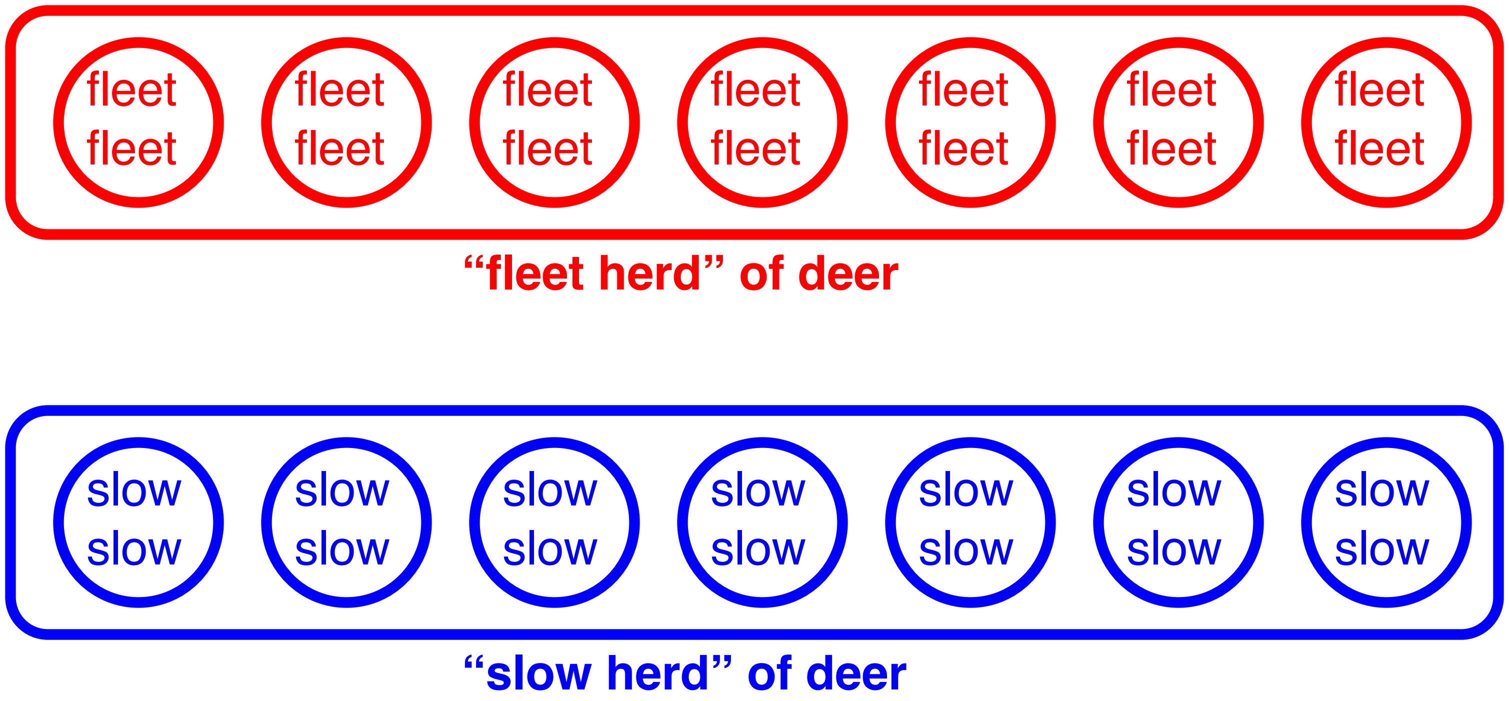
Differential predation may lead to the elimination of the "slow herd"

Does this mean selection ACTED ON the herd (= group)?



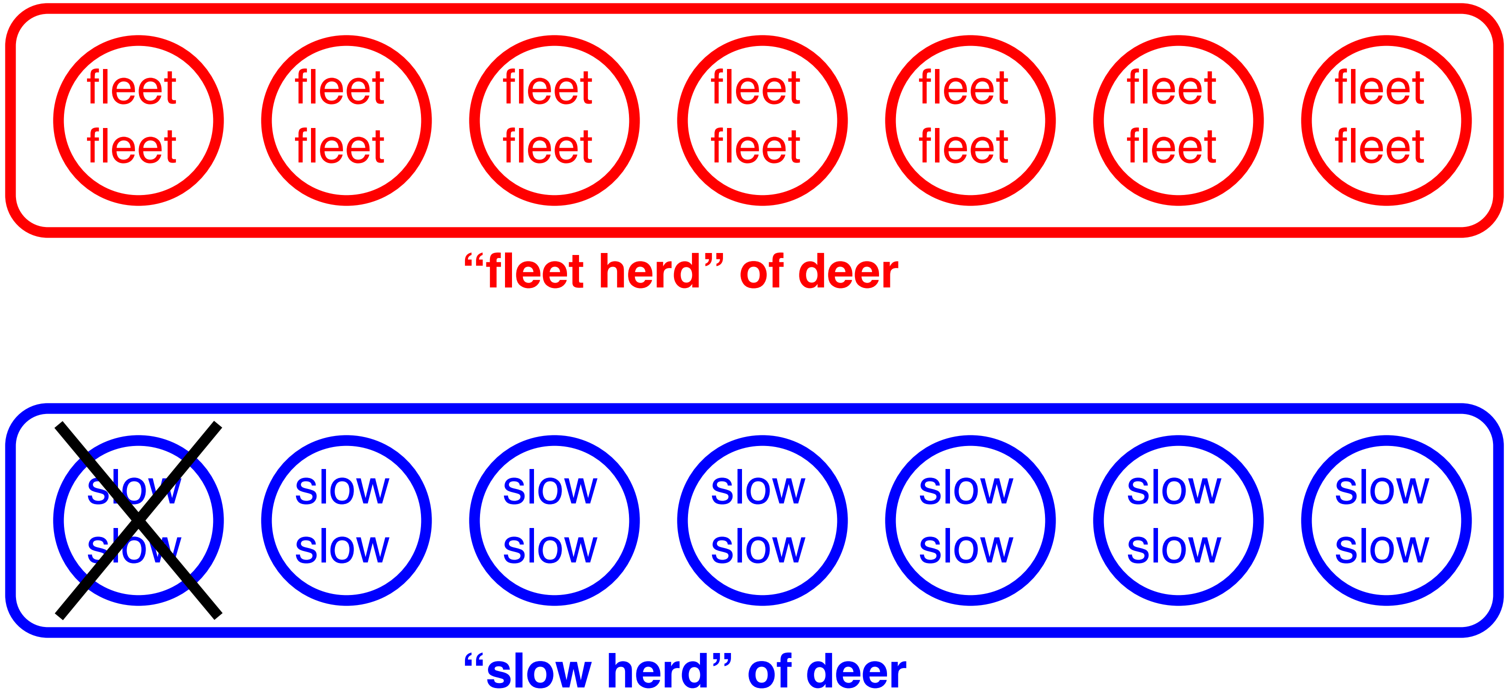
Differential predation may lead to the elimination of the "slow herd"

Does this mean selection ACTED ON the herd (= group)? NO!!!



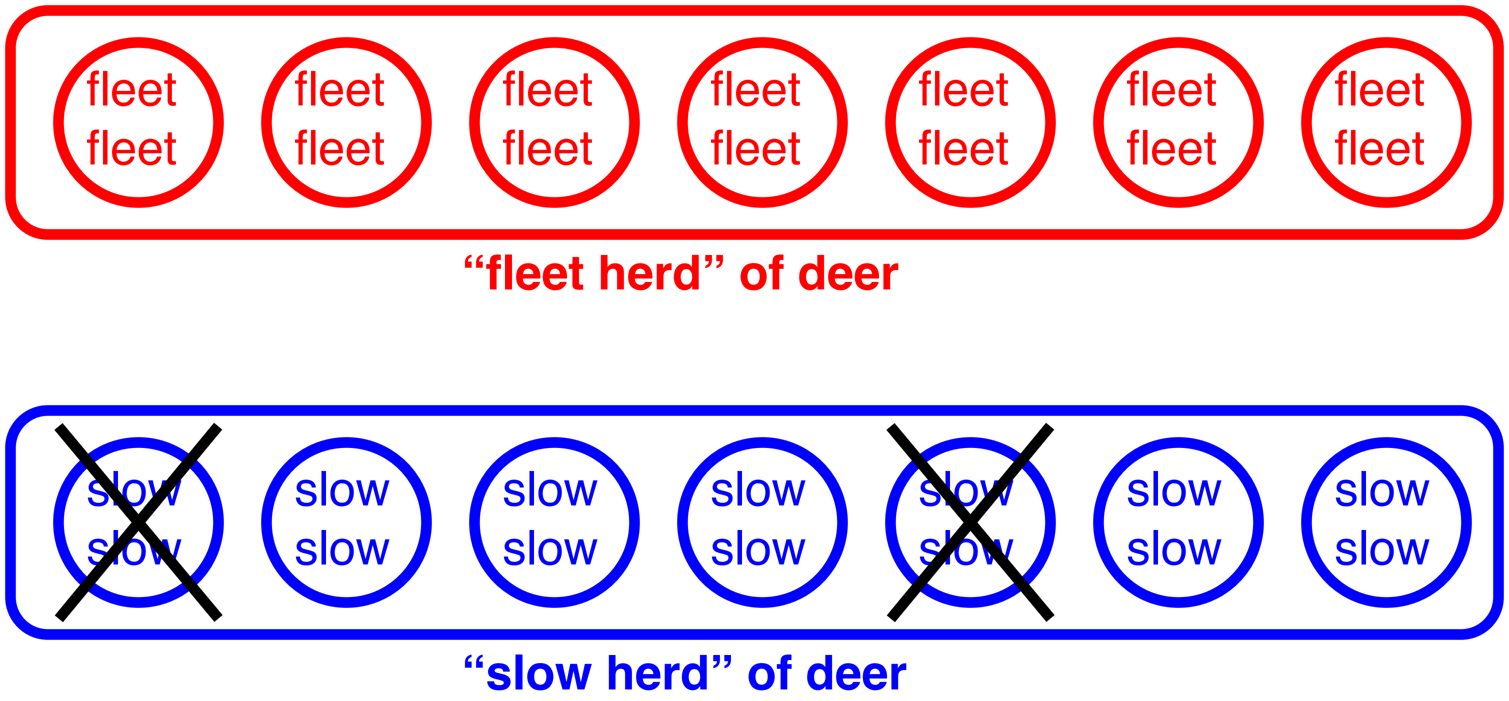
Differential predation may lead to the elimination of the "slow herd"

Does this mean selection ACTED ON the herd (= group)? NO!!!



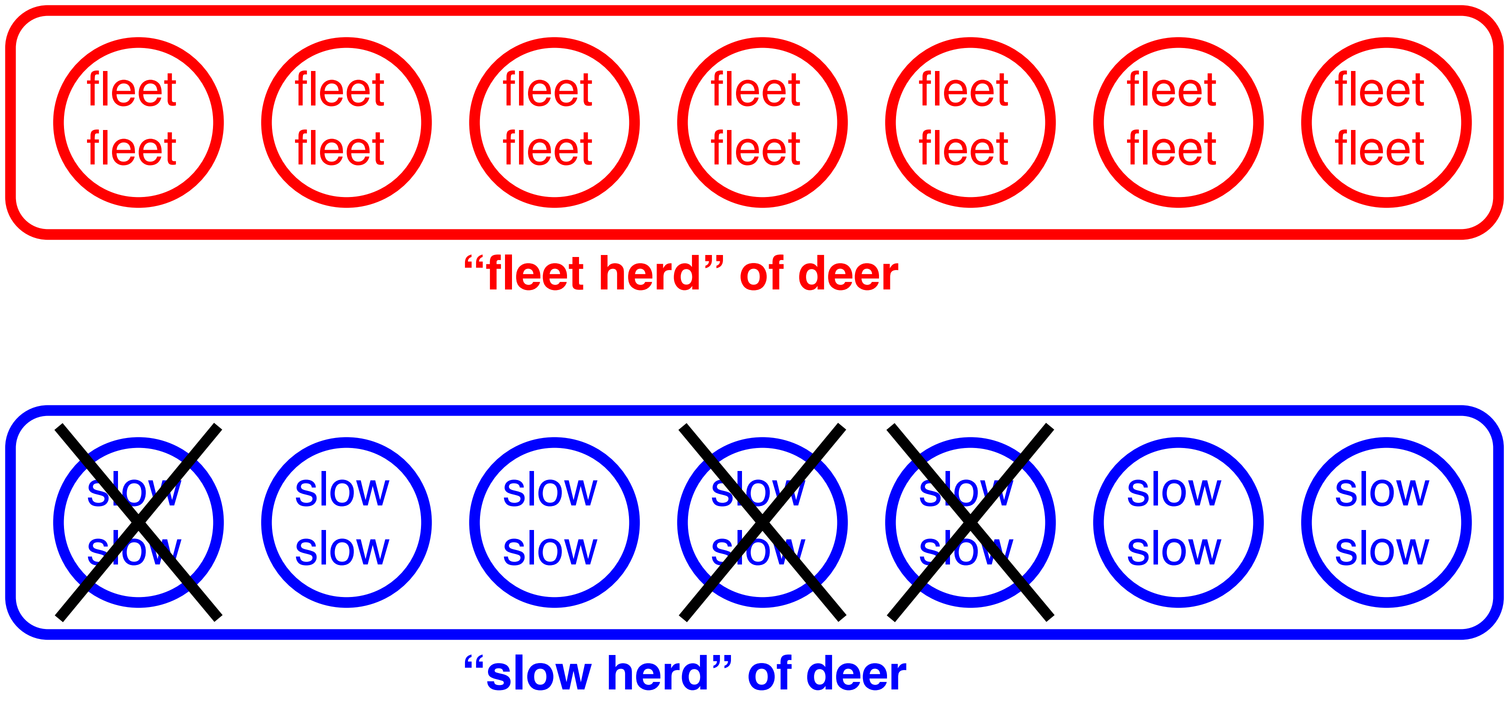
Differential predation may lead to the elimination of the "slow herd"

Does this mean selection ACTED ON the herd (= group)? NO!!!



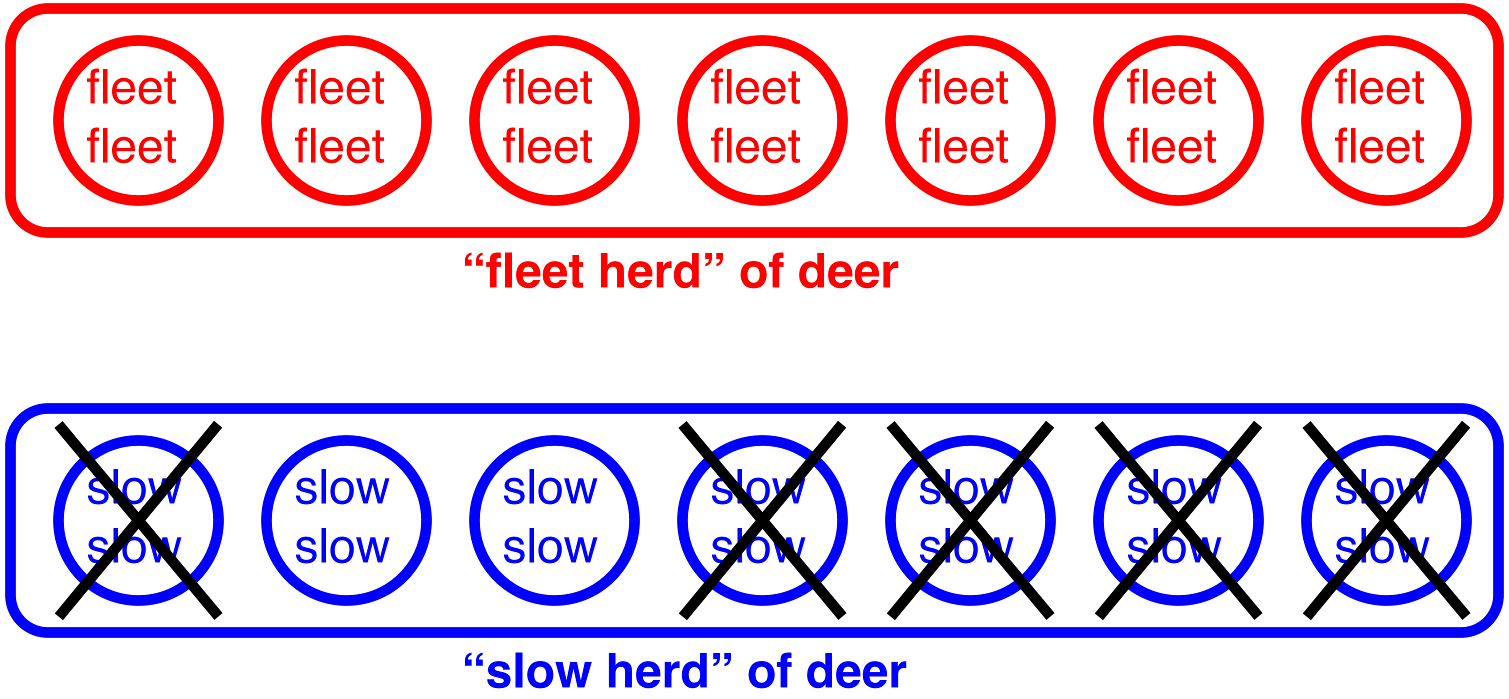
Differential predation may lead to the elimination of the "slow herd"

Does this mean selection ACTED ON the herd (= group)? NO!!!



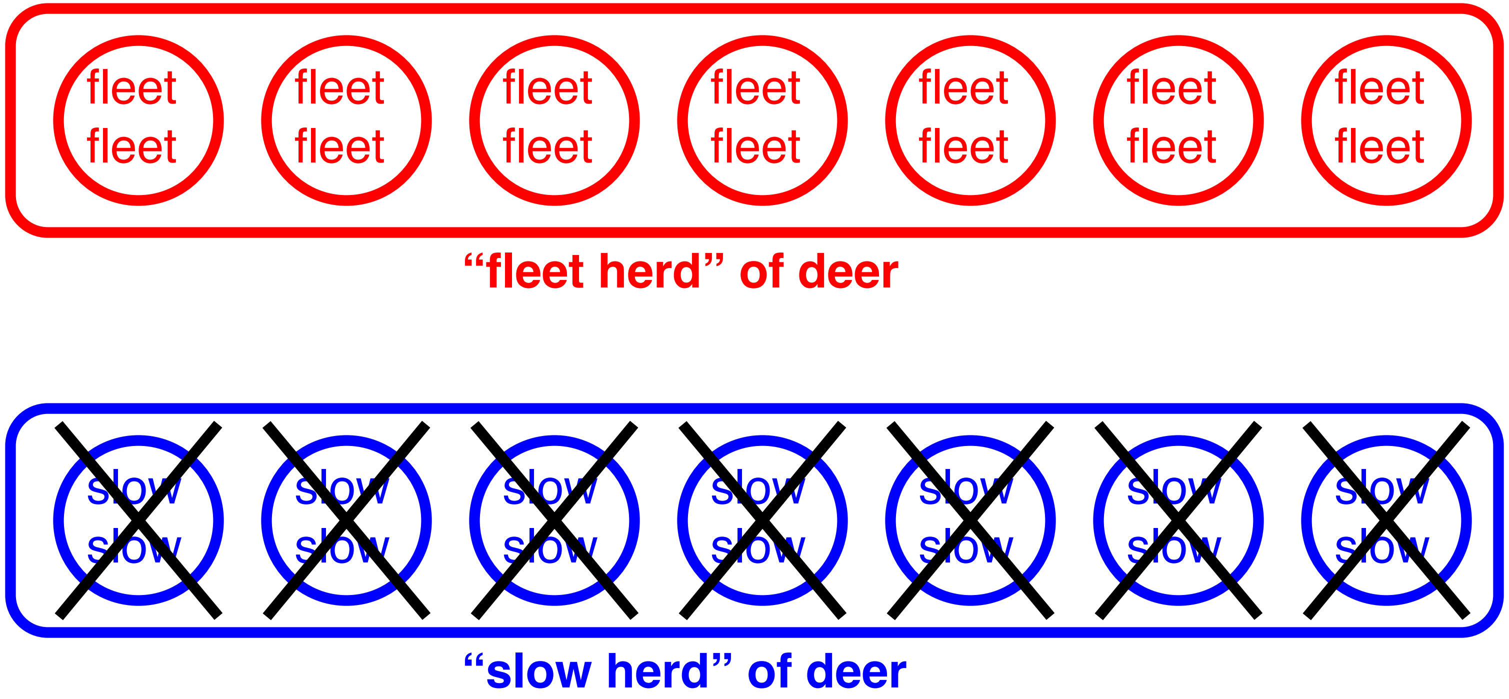
Differential predation may lead to the elimination of the "slow herd"

Does this mean selection ACTED ON the herd (= group)? NO!!!

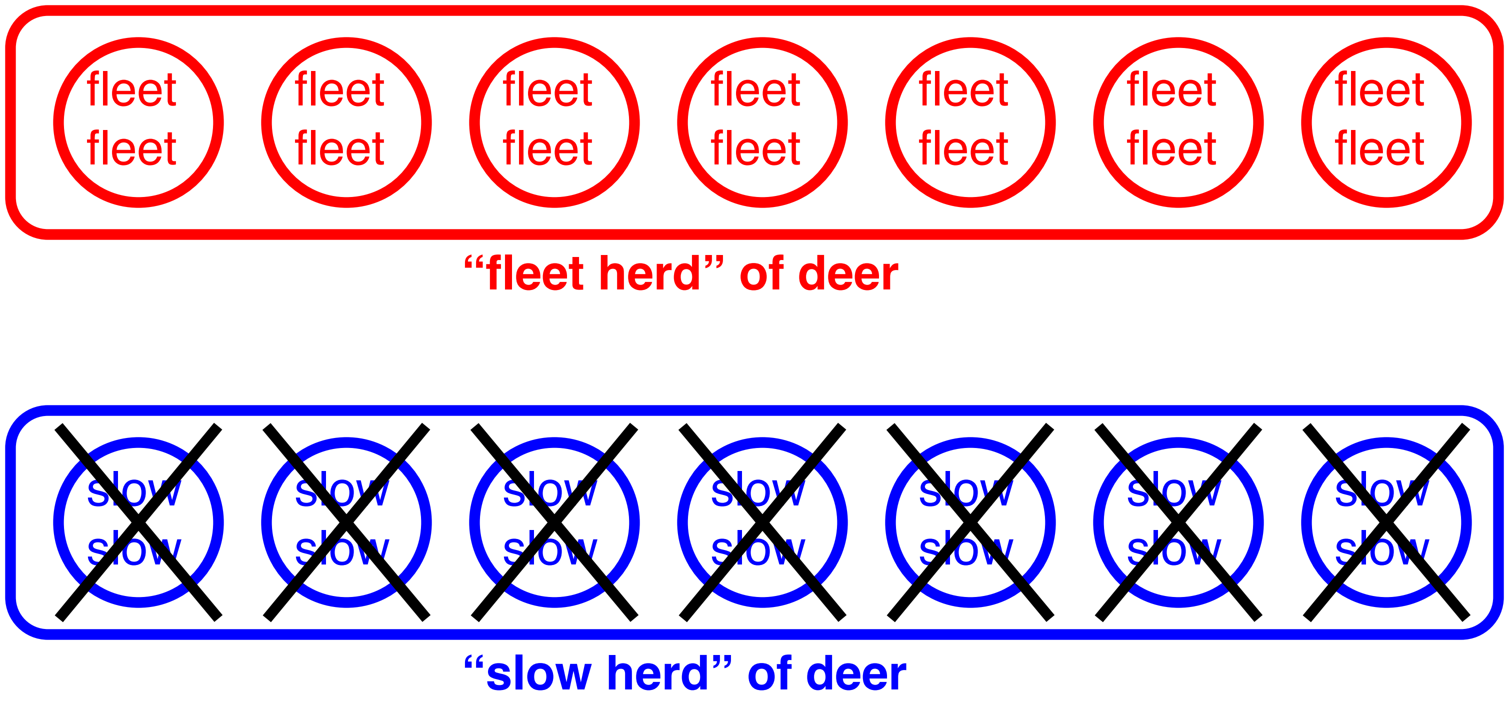


Differential predation may lead to the elimination of the "slow herd"

Does this mean selection ACTED ON the herd (= group)? NO!!!

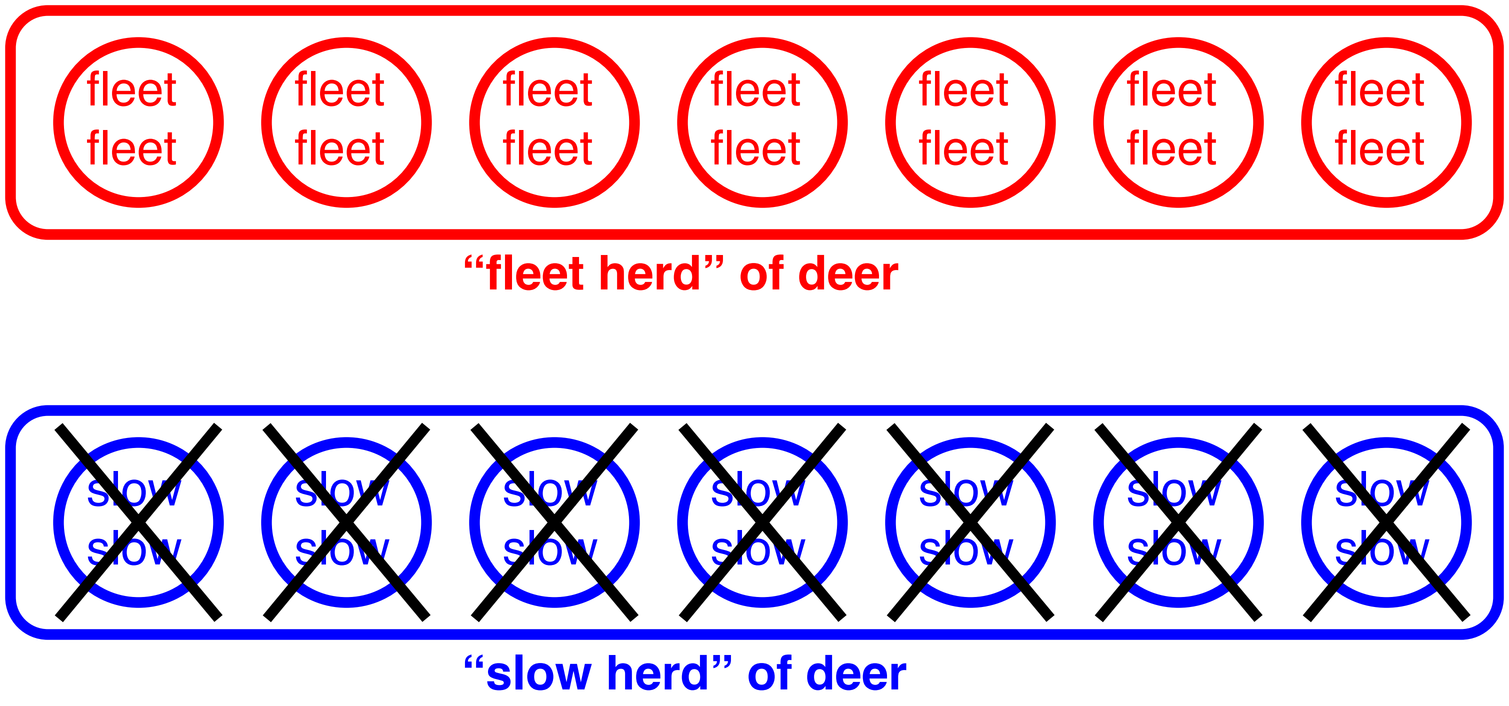


"Herd fleetness" is not a property that is causally engaged in the selective process, but individual fleetness is

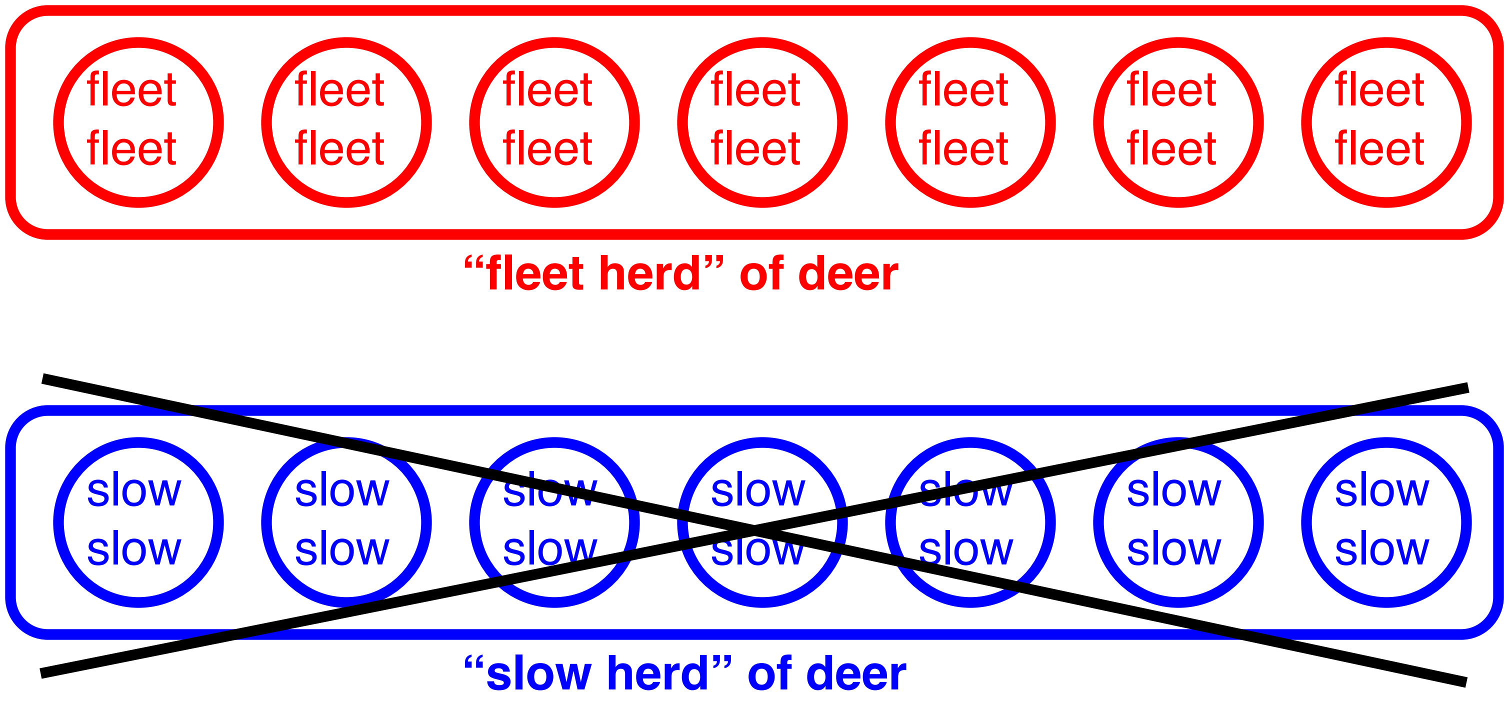


“Herd fleetness” is not a property that is causally engaged in the selective process, but individual fleetness is

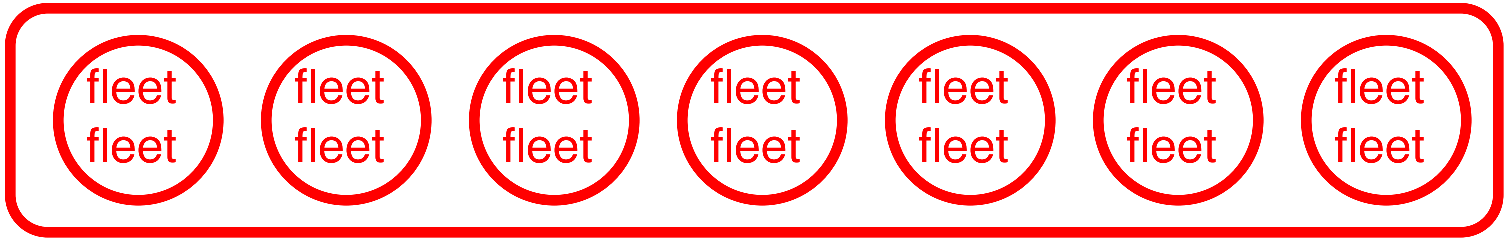
“Herd fleetness” is a statistical descriptor that we impose, but it is irrelevant to understanding selection for fleetness



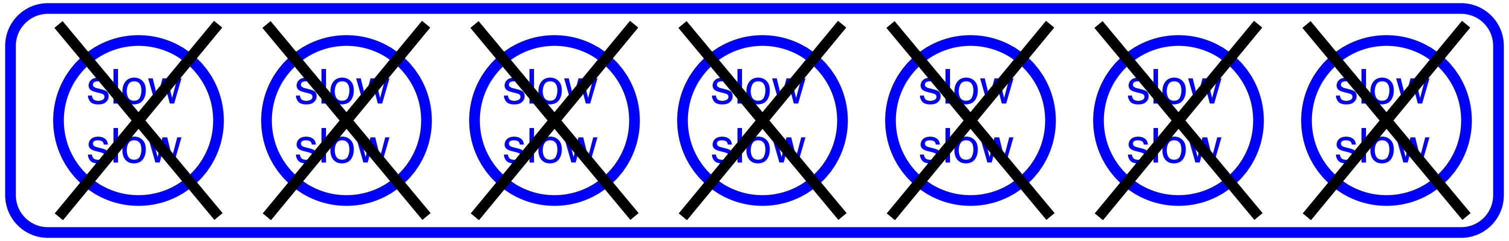
IT IS EASY TO BE DELUDED BY FICTITIOUS “PROPERTIES” OF HIGHER LEVELS AND FALSELY CONCLUDE THAT NATURAL OPERATES AT HIGHER LEVELS



<u>Take-home Message</u>:
NATURAL SELECTION NEEDS TO BE ANALYZED AT THE LEVEL WHERE NATURAL SELECTION *ACTS ON* AN ADAPTIVE TRAIT THAT IS CAUSALLY ENGAGED IN THE SELECTIVE PROCESS



"fleet herd" of deer



"slow herd" of deer

In the majority of cases, natural selection ACTS ON individuals, but SELECTS FOR genes

<u>Interesting cases</u>:

Sometimes natural selection SELECTS FOR genes against the interest of the individual

Sometimes natural selection ACTS ON organizational structures above the level of the individual (e.g., colony of some social insects)

But: MOST organizational structures above the level of the individual are NOT causally relevant to natural selection (i.e., in these cases, the causation underlying natural selection is not affected by features that we may recognize at higher levels)

Summary

Proper multilevel-selection analysis asks:

What does natural selection ACT ON?
What is SELECTED FOR?

Summary

Proper multilevel-selection analysis asks:

What does natural selection ACT ON?
What is SELECTED FOR?

Are higher levels of organization (e.g., group) ACTED ON by natural selection?

Summary

Proper multilevel-selection analysis asks:

What does natural selection ACT ON?
What is SELECTED FOR?

Are higher levels of organization (e.g., group) ACTED ON by natural selection?

do higher levels of organization have emergent properties that are causally engaged in the selective process? (-> *fever* of honeybee colony)

Summary

Proper multilevel-selection analysis asks:

What does natural selection ACT ON?
What is SELECTED FOR?

Are higher levels of organization (e.g., group) ACTED ON by natural selection?

- **do higher levels of organization have emergent properties that are causally engaged in the selective process? (-> *fever* of honeybee colony)**

- **or do “higher levels” have merely descriptive features that are not causally engaged in the selective process? (-> *fleet* herd of deer)**

Summary

Proper multilevel-selection analysis asks:

What does natural selection ACT ON?
What is SELECTED FOR?

Are higher levels of organization (e.g., group) ACTED ON by natural selection?

- **do higher levels of organization have emergent properties that are causally engaged in the selective process? (-> *fever* of honeybee colony)**

- **or do "higher levels" have merely descriptive features that are not causally engaged in the selective process? (-> *fleet* herd of deer)**

Does selection act on different levels at the same time and, if so, does selection at different levels conflict?

Biological databases

- NCBI
  - Achival database (Genbank)
  - Computer algorithm generated database (unigene)
  - Manually curated database (RefSeq)
- Swissprot
- GO
- KEGG
- Model system databases
  - YGD - Yeast
  - TAIR - Arabidopsis
  - FlyBase – fly
  - Wormbase - worm
  - MGD - Mouse