Polyphenic Insects

What makes for differences between individuals?

- genes
- environment

genotype X environment = phenotype

POLYPHENISM

- poly – many (more than one anyway)
- phen - form

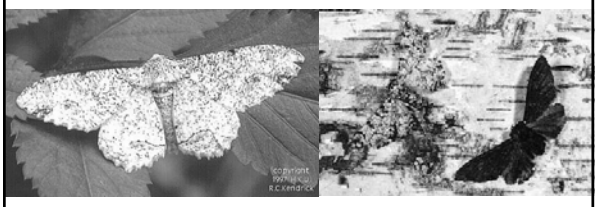
insects that are polyphenic have the natural potential to have more than one form at one or more stages of their lives

genetic polymorphism vs polyphenism

Polymorphism

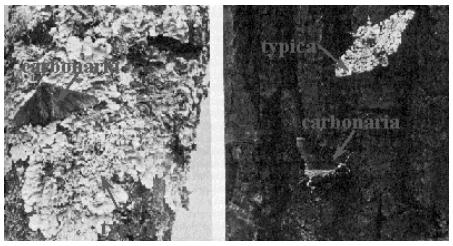
- insects that are polymorphic have the natural potential to be only one form but more than one form occurs in the population

the peppered moth



genotypes for dark or light moth

- light is favored on a light background
- dark is favored on a dark background



Genetic vs environmental control

- Genetic control - cannot adjust form in 1 generation
- Environmental control - can adjust form to current environment
- Selection for genetic vs environmental control can shift over evolutionary time
- Sometimes doesn't take a large genetic shift (not many genes) to make the difference

Polyphenism in insects

- Typically controlled by genes responsive to environmental variables that include nutrition and season
- In social insects, a large part of the environment is other individuals in their colonies

Environmental Signals

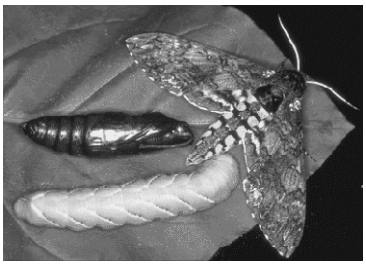
- Larval size
- Season (food type, day length)
- Food quality, crowding
- Other species (competitors, predators)
- Sloppy developmental practices
- Food quality
- Social cues

Polyphenism in insects can occur

- within a single individual over its life time (sequential)
- in successive generations (such as seasonally)
- in individuals in the same generation as in social insects, parasitic wasp larvae

a spectacular case of polyphenism within individuals

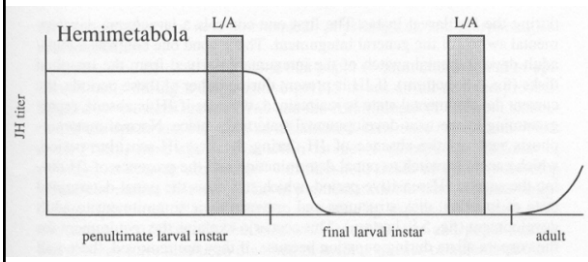
- larva
- pupa
- adult



what kind of individual will I become at the next molt

- L, P
- L, P
- L, P, or A
- P, or A
- L
- L
- P
- A

decision mediated by hormones (size, nutrition, growth…)



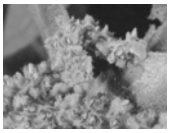
IMPORTANT CONCEPT: CRITICAL/SENSITIVE PERIOD

polyphenism in alternate forms for same life stage

- different generations - seasonal polyphenisms
- same generation - social insects

oak catkin caterpillar (Geometridae)

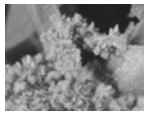
- spring - leaves are young, catkins in bloom



- fall - leaves are tough, no catkins

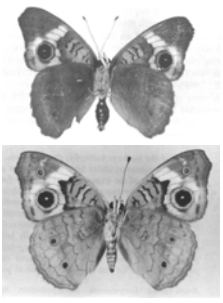
oak catkin caterpillar (Geometridae)

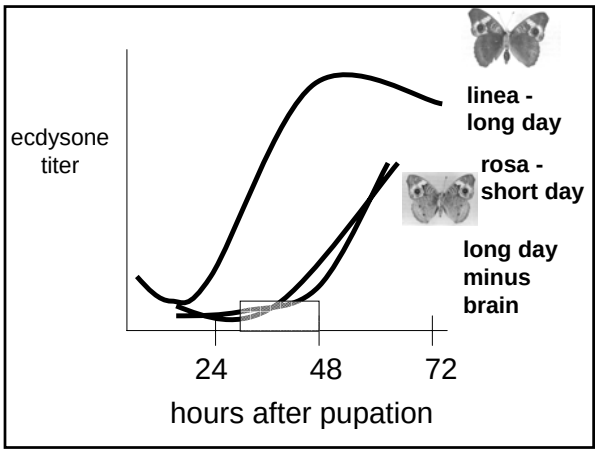
- diet induces the right form, regardless of light
- how?



buckeye butterfly (Nymphalidae)

- linea form in the summer
- rosa form in fall
- controlled by photoperiod



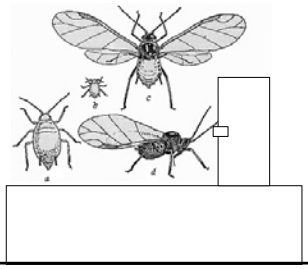


aphids

- the student of aphids should be cautioned never to generalize

aphid forms

- wings/wingless = alate/apterous



aphid forms

- parthenogenetic

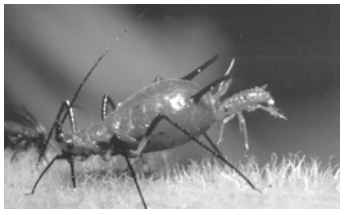
$$F \rightarrow F \rightarrow F$$

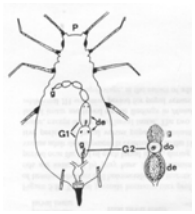
- sexual

$$F + M \rightarrow F,M$$

aphid forms

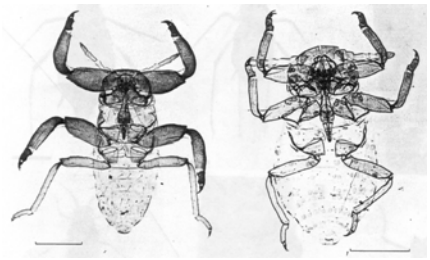
- eggs/live bearer

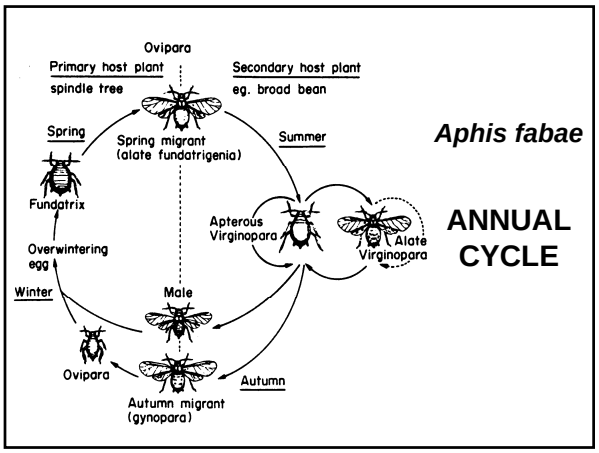




aphid forms

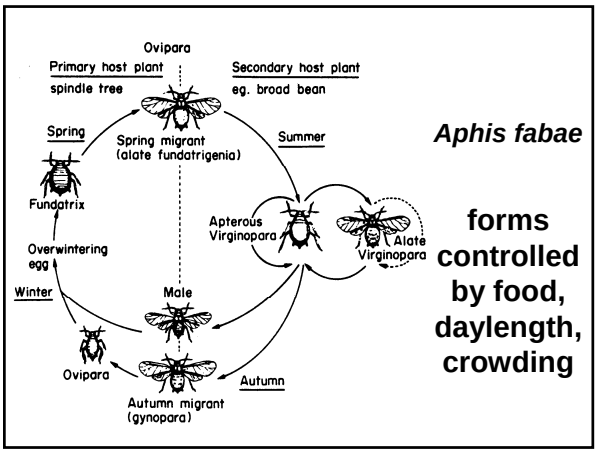
- soldier forms





Aphis fabae

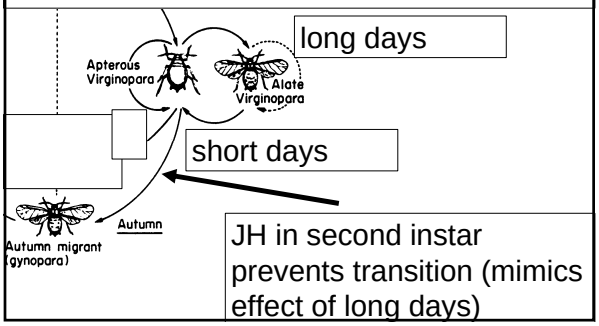
ANNUAL CYCLE



Aphis fabae

forms controlled by food, daylength, crowding

Short days causes aphids to develop as winged autumn gynopara

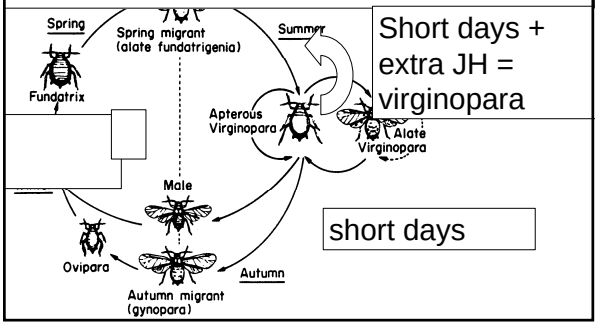


long days

short days

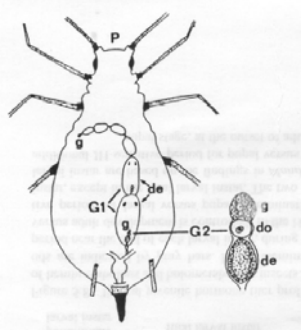
JH in second instar prevents transition (mimics effect of long days)

Short days causes aphids to develop as winged autumn gynopara

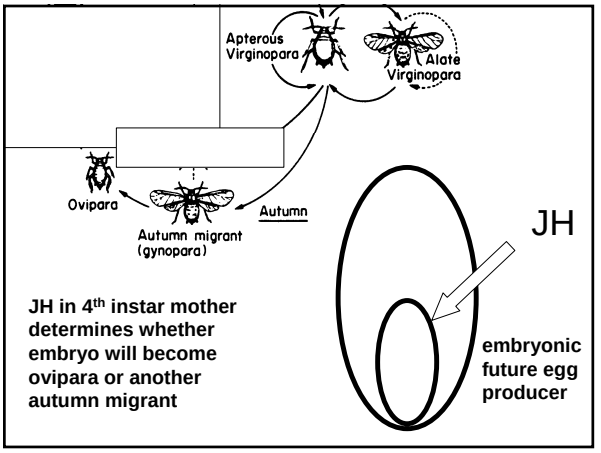


Short days + extra JH = virginopara

short days



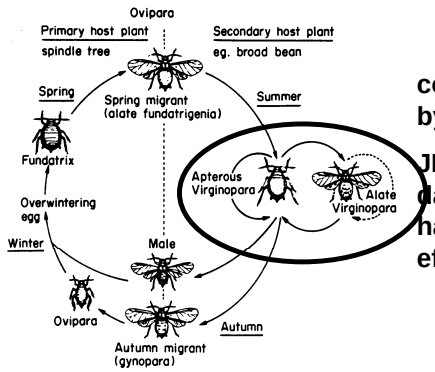
remember...



JH in 4th instar mother determines whether embryo will become ovipara or another autumn migrant

two forms responding to day length are determined by JH

- one sensitive period in larval stage
- another during embryogenesis



controlled by crowding

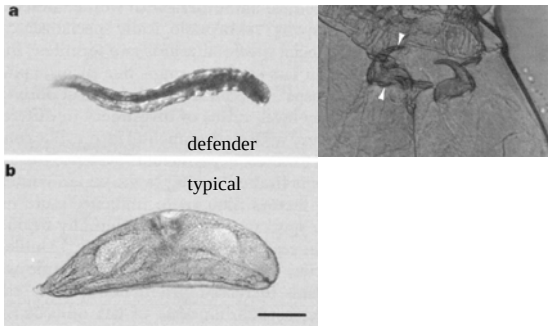
JH and daylength have no effect

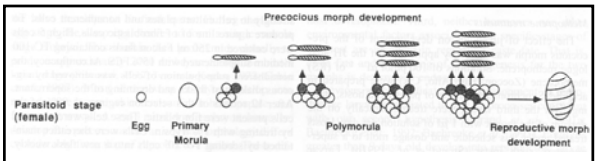
Copidosoma

- wasp
- parasitoid of Lepidoptera

Copidosoma

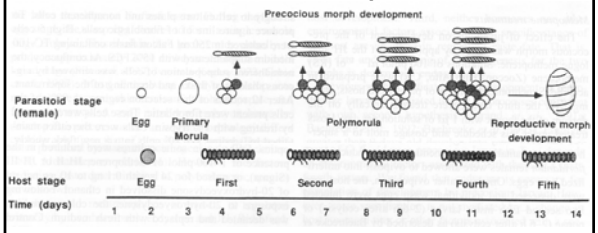
- egg-larval parasitoid
- lays its egg in egg of Lepidoptera
- produces two types of larvae FROM THE SAME EGG
- one is a soldier that doesn't complete development
- one is a normal larva that completes development





- egg divides without differentiating
- each daughter cell is capable of developing as an embryo
- polyembryony
- morula (blackberry)

what controls which type of larva develops?



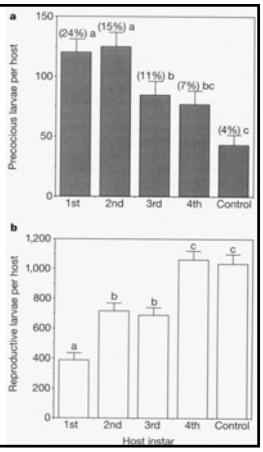
- same environment
- same genome
- no effect of extra hormones

Copidisoma's sometime problem

- competition from other parasitoids, like *Microplitis*
- = other wasps that lay eggs in either eggs or larvae of host
- does the presence of larval wasp of other species effect development of *Copidosoma* defenders?

EXPERIMENT

- *Copidosoma* allowed to lay eggs in host egg
- *Microplitis* allowed to lay eggs in larvae of different instars
- Does this affect the number of either defender or typical larvae per host?

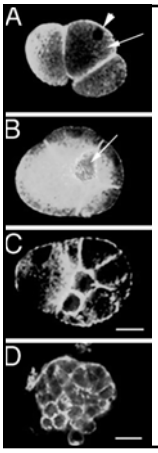


EXPERIMENT

- Yes, a larger percent of larvae become defenders when the host is parasitized by the second host, especially early
- But that doesn't get to the basic question

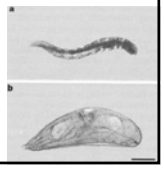
"reproductive" vs. soldier

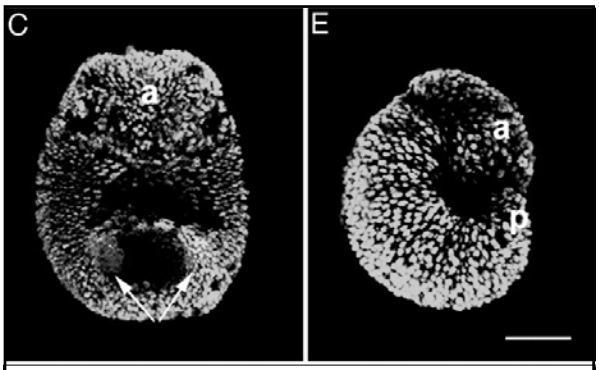
- Soldiers don't reproduce and don't have reproductive organs
- Do they lose them?



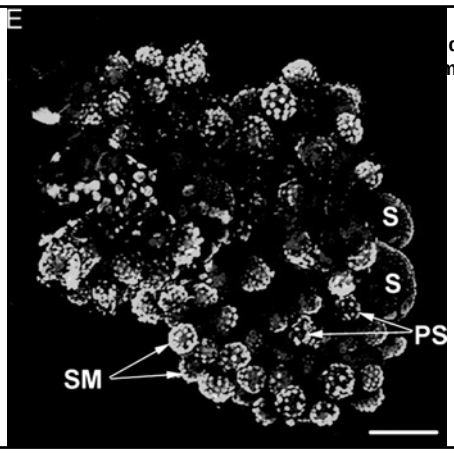
Expression of **vas gene**

- Indicator of germ cells
- By 4 cell stage, restricted to small blastomere
- Cells with expression are daughters, gdaughters, etc of blastomere 4

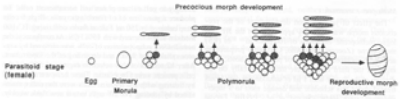




Reproductive larva | Soldier larva



what controls which type of larva develops?



- Not the usual hormones
- Random? loss of germ cell blastomere results in soldiers
- % becoming soldiers increased by presence of competitors

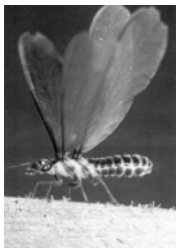
Macrotermes

Termites

- all are social
- hemimetabolous
- larvae serve as workers
- both sexes involved in social organization of colony

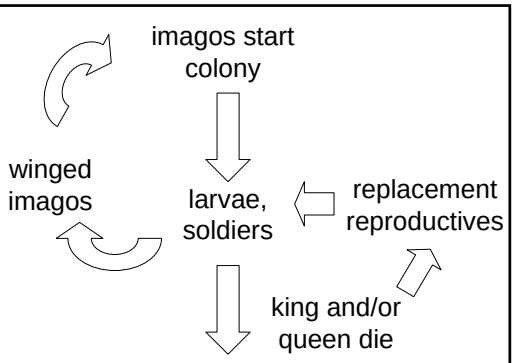
termite castes

- winged imagos (kings and queens)
- replacement reproductives - not so sclerotized, wingless



termite castes

- soldiers
- older larvae serve as workers (pseudergate)
- in some higher termites, special worker castes



how are the developmental switches regulated?

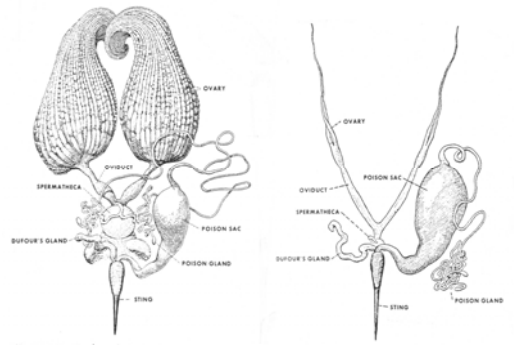
- strong inhibition by adult termites - sexuals and soldiers
- loss of sexuals or soldiers allows new ones to develop
- JH provokes soldier determination - the first discovery of the role of JH in caste determination in social insects!

Social Hymenoptera

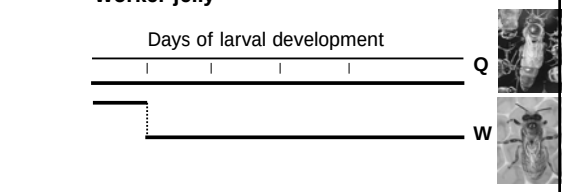
- ants, some bees, some wasps
- societies only females: queens and workers
- honey bees one of best studied

Many morphological differences between bee queens and worker

QUEEN	WORKER
less sensilla on antenna	more sensilla
smaller eyes	larger eyes
small mushroom bodies	larger mushroom bodies
vestigial food glands	large food glands
smooth curved sting	barbed sting
no pollen collectors on legs	pollen collectors on legs
short tongue	longer tongue



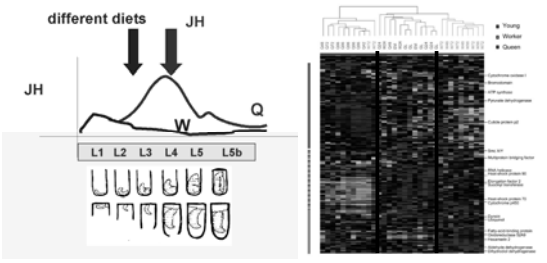
major difference in ovary, spermatheca development



- Diet determines caste, effect mimicked by JH

In bees, queens receive a more nutritious diet than workers

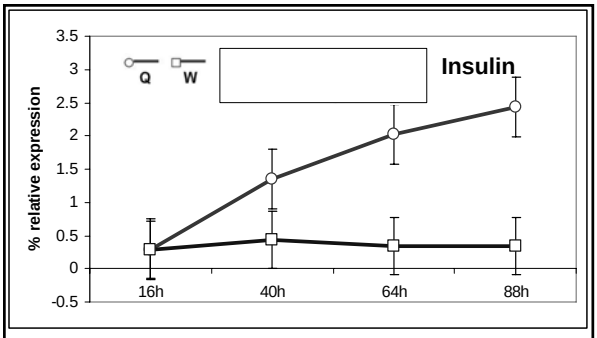
This difference is followed by higher levels of juvenile hormone in developing queens



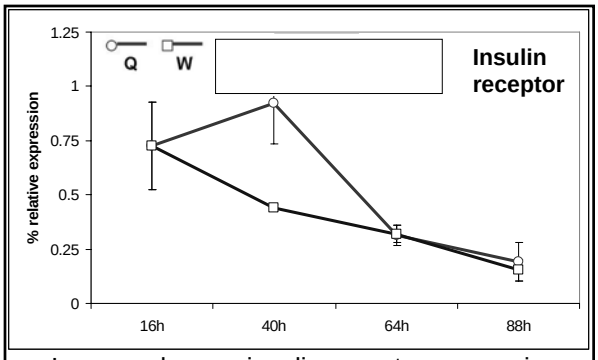
The hormonal difference is followed by major differences in gene expression

How does nutrition get translated into hormonal difference?

Nutrition → Insulin signaling pathway? → Juvenile hormone



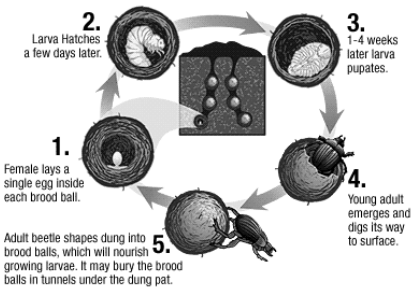
• Expression levels shifts to match those appropriate for food type.

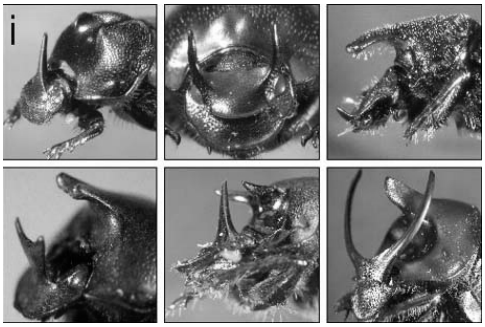


- In queen larvae, insulin receptor expression is at levels far above those of workers at 40h.

Summary: ILPs and IR

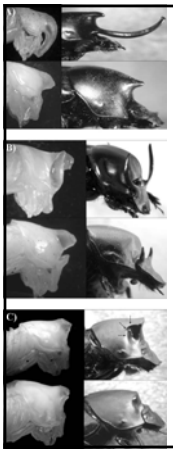
- Insulin pattern is consistent with response to improved diet quality in queen larvae
- Insulin receptor expression shows a maximum difference between castes on day 2
- So the insulin signaling system is probably the link between diet and JH levels





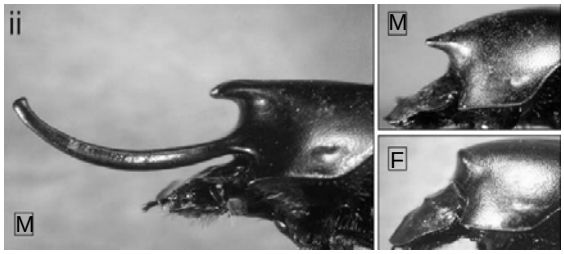
- Species of Onthophagus have a variety of horn types for males.

Why are there horns?

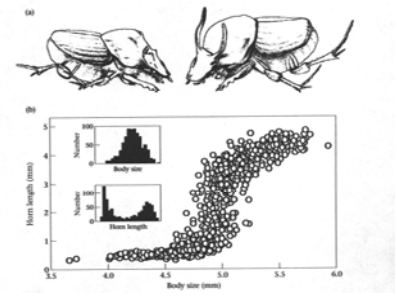


Three species

- males vary in size
- large males are horned
- small males are not



- Different sizes, different horn size
- Why (proximal)?

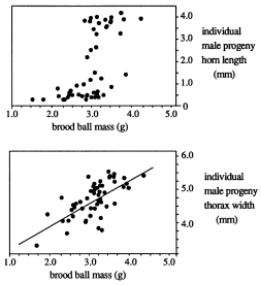


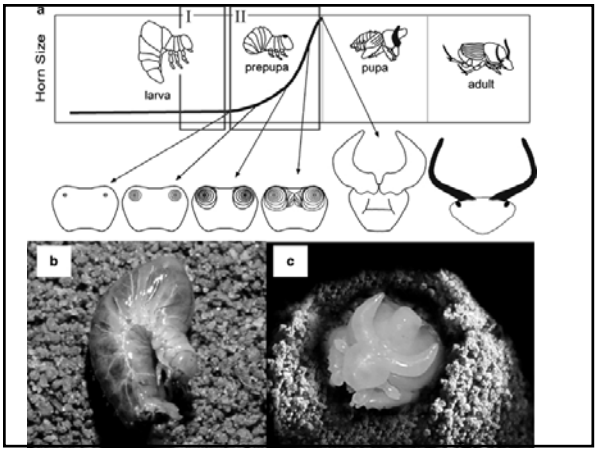
- Onthophagus taurus
- compare body size to horn size
- not many intermediates

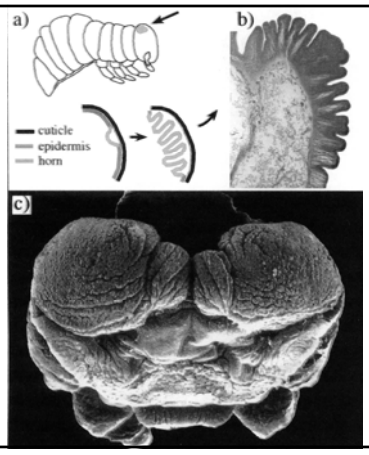
What is the cause of variation in size?

- dung quality varies with species
- supply of dung can vary with time
- larva gets only the amount of food in the dung ball (no refills)
- complete development with the resources available

larval food determines horn

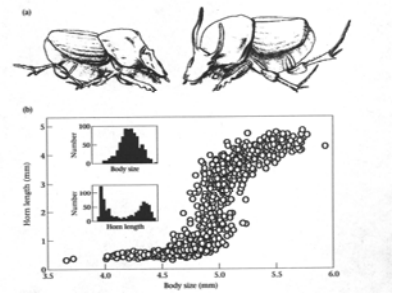






What signals that the larva has enough food/size to develop horns?

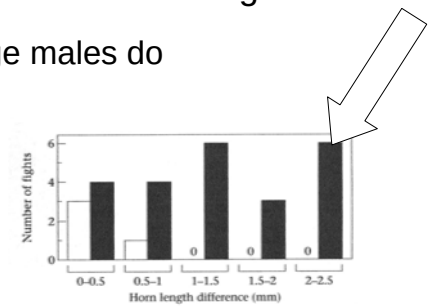
- Juvenile hormone



- are small males losers?

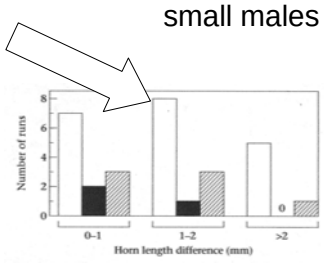
Who wins fights?

- large males do

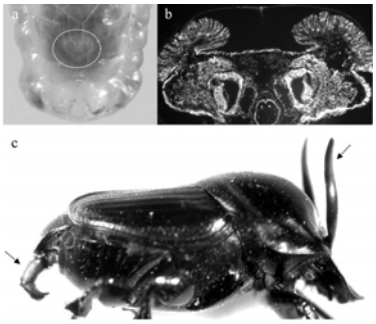


Who runs best in burrows?

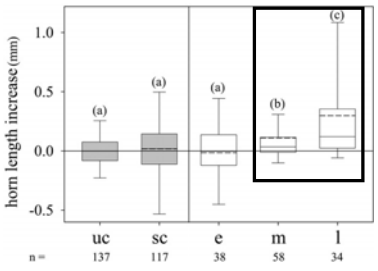
small males do

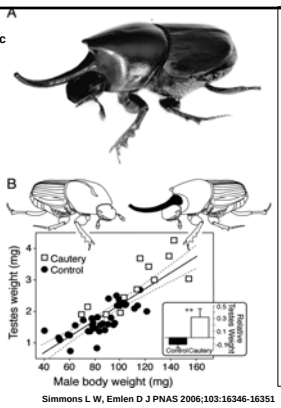


Horns vs. genitalia



Trade off





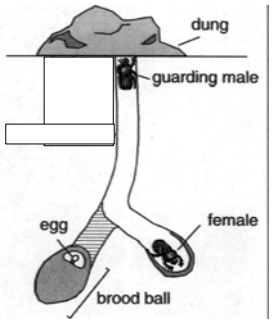
Simmons L W, Emlen D J PNAS 2006;103:16346-16351

PNAS

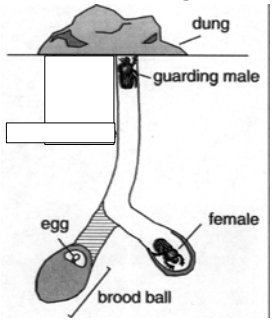
Other tissue tradeoffs

- testes
- wings
- antennae
- mouthparts

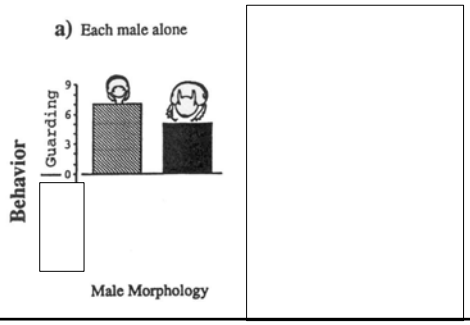
Mating strategies



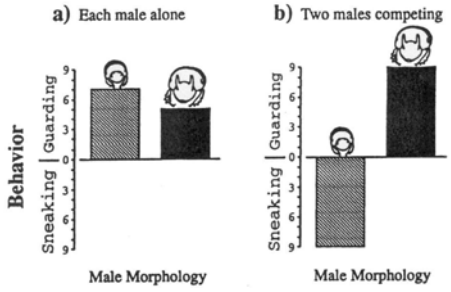
males compete (fight) for females, then guard them



Without competition, both types of male guard

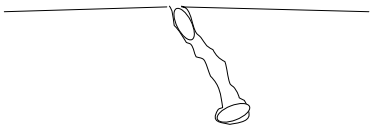


Small males have an alternative to fighting



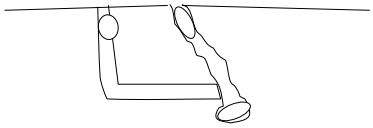
alternative male mating strategies

- larger size males with horns guards burrow that contains dung ball and female

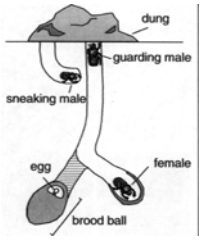


‘sneaking’ male mating strategies

- smaller males are hornless, move better in burrows and dig new burrow to sneak to female



alternative reproductive tactics



Small males can have <u>same success</u> as large, horned ones by switching to the sneaking strategy when forced into direction competition