Evolution of contest and display: Hawks & Doves

Possible behaviors:

  Display/threaten

  Fight (risks injury)

  Retreat if opponent threatens

Simple strategies:

  Hawk: fight until injured or opponent retreats

  Dove: retreat if anybody threatens (so keep if another dove, but surrender if hawk)

WHICH HAS HIGHER FITNESS?
IS THERE AN ESS?

1

Game theory intro: the rules for two kinds of players

Payoff matrix

Opponent:　Hawk　　Dove

Actor:　Hawk | $(V-C)/2$　V
Dove | 0　　V/2

V = value of resource being contested

C = cost of fighting due to injury

p = proportion of population made up of hawks
$W_H = W_o + 1/2(V-C)p + V(1-p)$
$W_D = W_o + 1/2V(1-p)$

2

The payoff matrix for encounters between the two types of players, with formulas for fitness consequences. 'p' is the frequency of hawk in the population – the proportion of the population playing hawk (so 1-p is frequency of dove). To understand calculation of fitness, think in terms of the average payoff over many random encounters among players

Pure ESS

Resource > cost; $V = 2$; $C = 1$

Opponent:	Hawk	Dove
Actor: Hawk	1/2	2
Dove	0	1

1/2 > 0, so Hawks resist invasion by doves
2 > 1, so Hawks can invade doves
ESS = all Hawks => pure ESS

$$W_H = W_o + 1/2(V\text{-}C)p + V(1\text{-}p)$$
$$W_D = W_o + 1/2V(1\text{-}p)$$

3

So, assigning actual numbers to the value of a resource 'packet' and to the average cost of losing a fignt, this is the numerical payoff matrix. No matter what p is, hawk has higher fitness; Hawk is not invasible by dove – it is an ESS. (Dove is invasible by hawk)

Mixed ESS

BUT WHAT IF Resource < cost; $V = 1$; $C = 2$

Opponent: Hawk   Dove

Actor:	Hawk	-1/2	1
	Dove	0	1/2

if $p = 1.0$, Doves can invade Hawks ($0 > -1/2$)
if $p-1 = 1.0$, Hawks can invade doves ($1 > 1/2$)
IMPLIES, some frequency of Hawks, p (and Doves, 1-p)
  where fitness function cross = MIXED ESS
to find stable p: set fitness of Hawks = fitness of Doves:
$W_H = W_o + 1/2(V-C)p + V(1-p) =$
$W_D = W_o + 1/2V(1-p)$ then substitute payoffs:
$(-1/2)p + (1-p) = (1/2)(1-p)$; $1 - 3p/2 = 1/2 - p/2$; $1/2 = p$
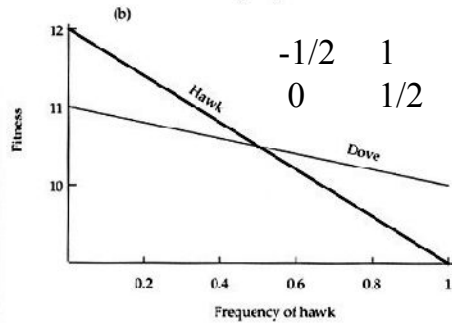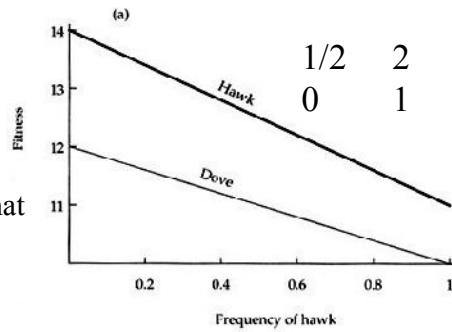
But what if the relative values of V and C are changed?

Frequency dependence

Frequency dependence means that fitness depends on strategy frequency.

IF V=2, C=1, not frequency dep

BUT, if V = 1, C=2
there's a MIXED ESS at p = 0.5

Fitness is *frequency-dependent; at any other value of p, the less common strategy has higher w!*

For first scenario, fitness of hawk goes down with increasing p – but it's always higher than fitness of dove. In second scenario, the fitness for the two cross – so are equal at that value of p. It's a stable equilibrium, because the less frequent type always has higher fitness (think about it).

Genetic polymorphism in ruff

16% light males, 84% dark males. Dark dominant and territorial.
Light males follow females.
Average mating success same at this frequency. 6

Uncorrelated asymmetry

Opponents differ, but not with regard to fighting ability

Example: hawk - dove - bourgeois

Bourgeois strategy: if owner, play hawk, if intruder play dove

If owner and intruder are equally frequent and get equal payoffs:

Opponent:	Hawk	Dove	Bourgeois
Actor: Hawk	$(V-C)/2$	V	$3V/4-C/4$
Dove	0	$V/2$	$V/4$
Bourgeois	$(V-C)/4$	$3V/4$	$V/2$

If $V > C$, then H is pure ESS; if $V < C$, then B is pure ESS
Therefore, arbitrary asymmetries offers ESS by resolving conflicts

Addition of further strategies adds complication, but can still be resolved if a pay-off matrix can be constructed.

Here, a third strategy essentially acts like a hawk IF it's already 'in possession' of a resource parcel; if it encounters another player already in possession of a parcel, it acts like a dove. (Thus 'bourgeois' – it's about ownership...). Bourgeois can be uninvasible if payoff matrix has right properties – so UNLIKE H or D, can be a simple ESS.

'Strategies' with situation-depended properties may be selected for...

An example of a real-world 'game' driven by conflicting fitness interests between sexes:

In polygynous systems involving male hierarchy or harem-keeping, male fitness may be much enhanced by mating with females as soon as possible after gaining status (because earlier production of offsrping by males is always fitness-enhancing, and because dominant individuals are likely to be displaced at some point, so fitness value of such early mating is enhanced). But females are not receptive/fertile when pregnant or lactating. So males may kill existing young – 'infanticidal male' would be one game strategy; 'non-infanticidal male' another.

Females may resist male infanticidal efforts (their young are CURRENT fitness for them, not for male) – but that has costs, too (vigilance, ill-will of dominant male...). SO females may acquiesce to infanticidal male. They may even spontaneously abort an existing pregnancy when a new dominant male takes over.

Think about fitness payoffs (costs, benefits) for female strategies (how much investment in protecting young from male 'pays off'? Does this depend on developmental state of young?) ALSO, are there ways of 'penalizing' males that would change the cost-benefit balance/payoff matrix for males?
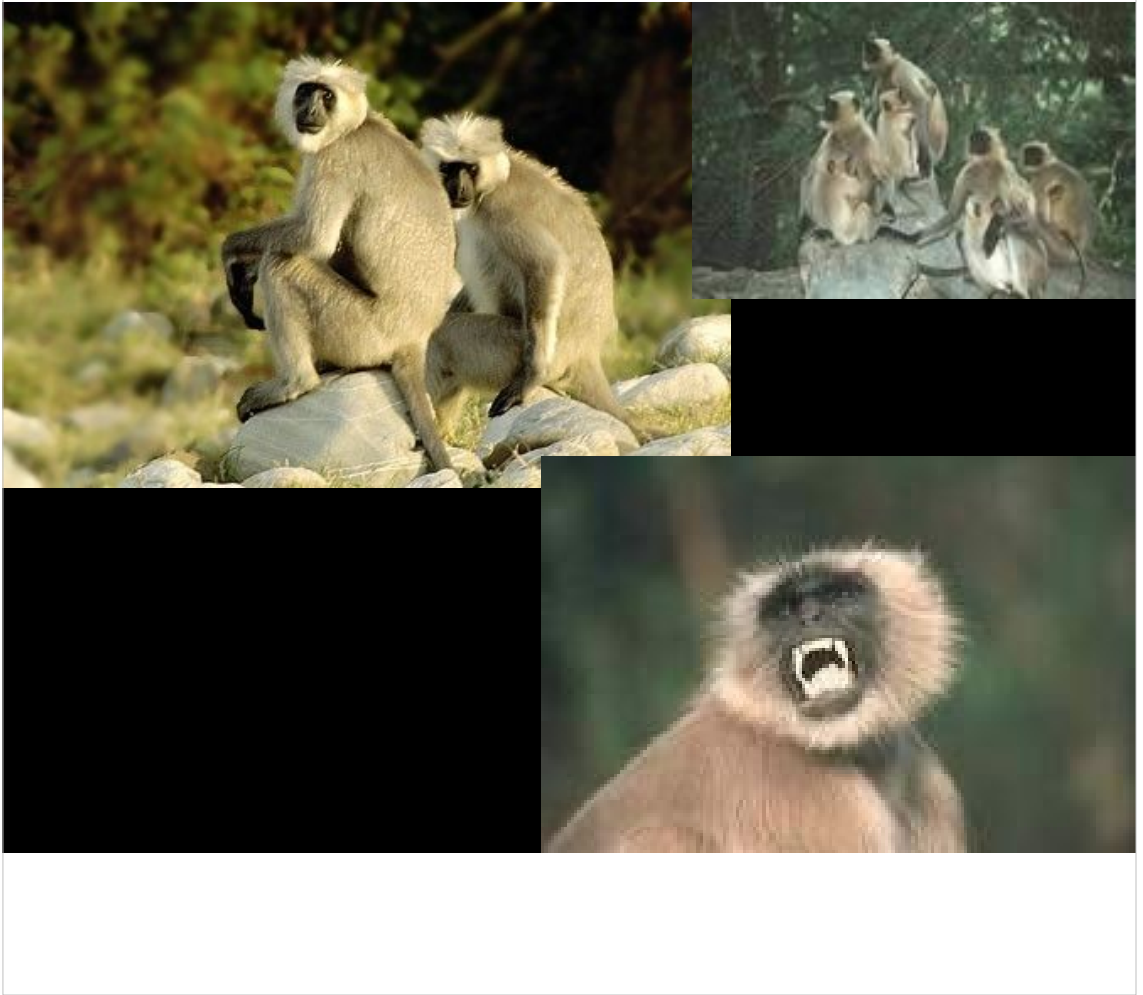
Classic study by Sarah Blaffer-Hrdy: male-dominance hierarchy polygyny in troupses of macaques in India. New dominant-males typically try to kill young offspring of females. Females may resist – may even band together – and apparently do 'penalize' males by delaying mating with infanticidal males.
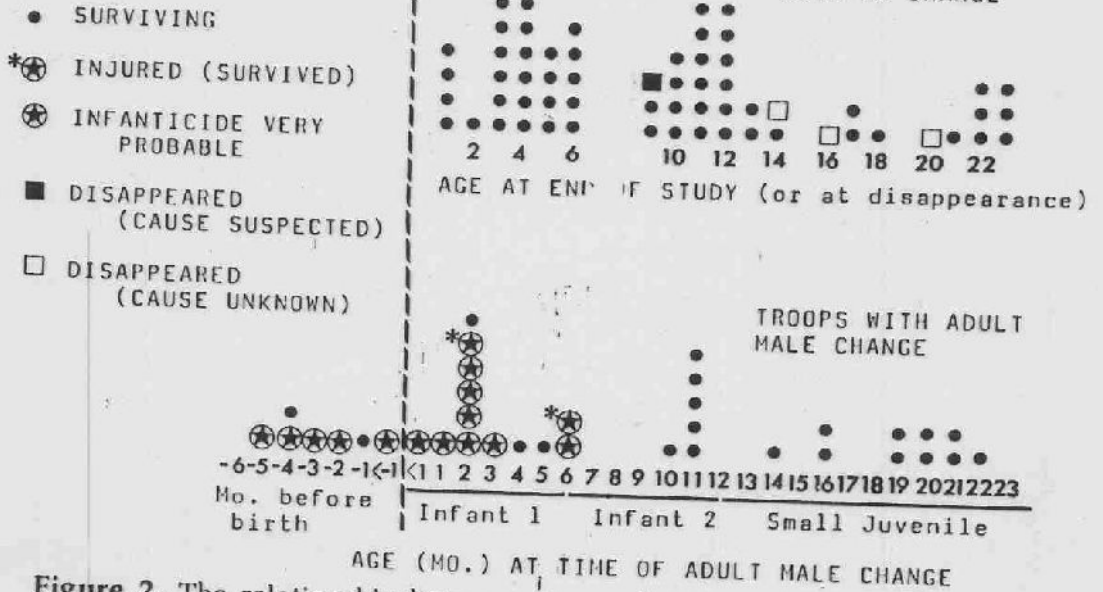
Figure 2. The relationship between age at the time of a male change and subsequent survival of infants and small juveniles. For comparison, the age at the end of the study period (February 1981) or at disappearance for individuals whose gestation and subsequent life up through 23 months were spent under stable conditions are presented (see text).
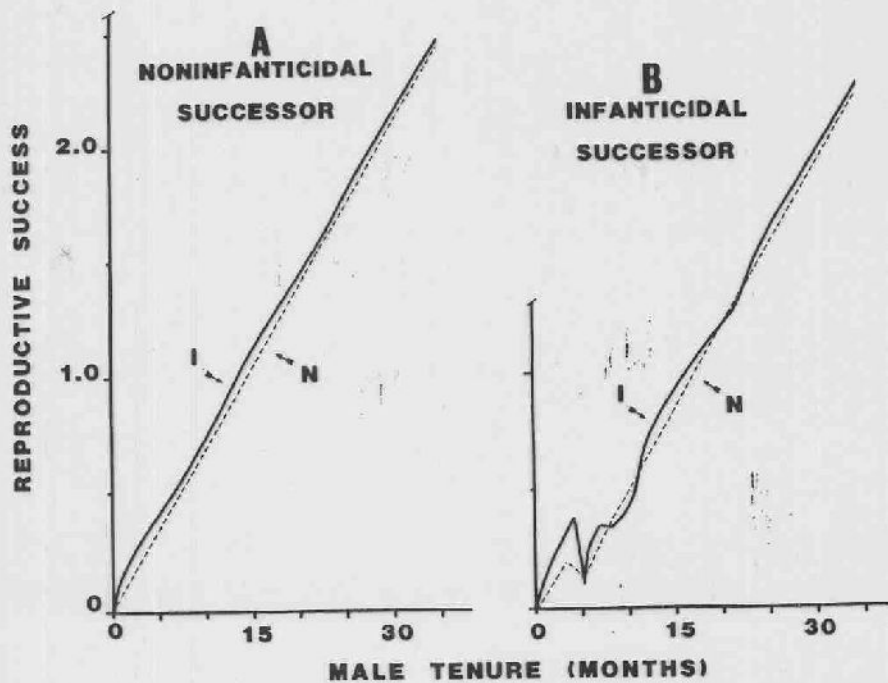
Figure 2. Expected reproductive success of infanticidal (solid line) and noninfanticidal (broken line) males under both replacement conditions as calculated from the Chapman–Hausfater model using reproductive parameter estimates based on longitudinal data from the langur population at Jodhpur, India. See Vogel and Loch (Chapter 12, this volume) for a complete discussion of the characteristics of this population and a description of the dataset from which these estimates were obtained.

Simulations by Hausfater and Blaffer Hrdy suggest show complex results in terms of fitness of infanticidal or non males. Relative fitness depends on tenure of male, nature of prior or subsequent male – AND female response to infanticide.

LIFE-HISTORY THEORY: Aside from mating strategy, fitness can be affected by how resources, once gained, are allocated. Fundamentally organisms must balance CURRENT reproduction against RESIDUAL REPRODUCTIVE VALUE (expectation of future reproduction).

Albatrosses are very long-lived (typically, high RRV), but resources are extremely dilute – require long-distance extended foraging – so CAN'T raise more than one chick at a time, and chick has long development time to be independent. Does selection favor longevity BECAUSE of this?

Beech trees are like albatrosses – long-lived, investing much in each 'offspring' (seed), but not reproducing at all until relatively old

Deer mice are anti-albatrosses; short-lived, reproduce early and often, often with large litters. RRV low (always a significant chance of dying before next opportunity to reproduce); current reproductive effort high.

DANDELION
Leontodon taraxacum L.
CHICORY FAMILY

Dandelions are to beech trees as deer mice are to albatrosses.

TABLE 8–1
Some of the reproductive and life-historical differences between r- and K-strategies

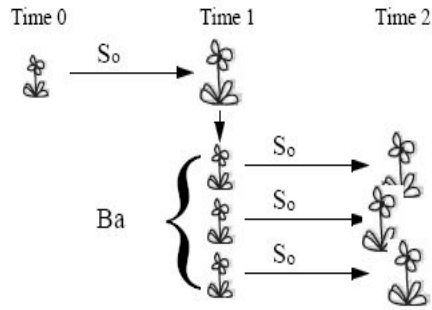| r-strategist	K-strategist
Many offspring	Fewer offspring
Low parental investment in each offspring	High parental investment in each offspring
High infant mortality (mitigated during population explosions)	Lower infant mortality
Short life	Long life
Rapid development	Slow development
Early reproduction	Delayed reproduction
Small body size	Large body size
Variability in numbers, so that population seldom approaches K	Relatively stable population size, at or near K
Recolonization of vacated areas and hence periodic local superabundance of resources	Consistent occupation of suitable habitat, so that resources more consistently exploited
Intraspecific competition often lax	Intraspecific competition generally keen
Mortality often catastrophic, relatively nonselective, and independent of population density	Mortality steadier, more selective, and dependent upon population density
High productivity (maximization of r)	High efficiency (maximization of K)

Source: From the *American Naturalist*, 104: 592–597 by E.R. Pianka by permission of The University of Chicago Press. Copyright © 1970 by The University of Chicago.

Different degrees of trade-off between increasing current reproduction (with low survival) and enhancing RRV (with less invested in current reprod) can be conceptualized along an axis between 'r-selected' organisms that 'maximize' current reproductive output (and so tend to have high population growth rates – r), and 'K-selected' organisms that are more 'optimized' for maintaining high RRV and individual competitiveness and survival (K is population biology name for 'carrying capacity' – where resource competition becomes severe).
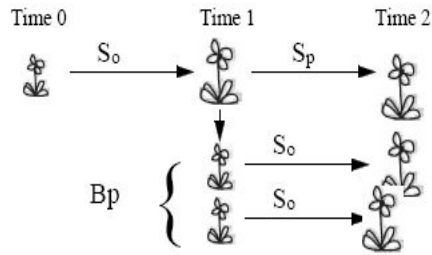
CONSIDER: are there *fundamental* fitness-based tradeoffs here? What aspects of selective environment are likely to shift organisms one direction or another?

Annual vs. Perennial

Annual Life History

Time 0 | Time 1 | Time 2

S_o

B_a {
S_o
S_o
S_o

Perennial Life History

Time 0 | Time 1 | Time 2

S_o → S_p →

B_p {
S_o
S_o

In the extreme, 'r-selection' can lead to putting ALL available resources into a 'current' reproductive event, leaving nothing for residual reproductive value (that is, dying). "Annual" plants do this, but so do some long-lived ones. In plants, species with a life-history of 'big-bang', one-time reproduction followed by death are called 'monocarpic'; those with at least likelihood of multiple reproductive events are polycarpic.
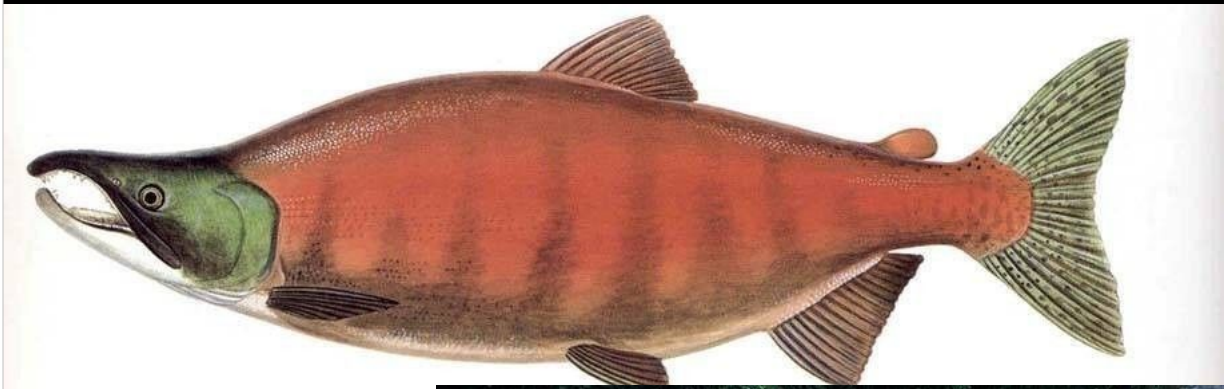
Equivalent in animals: big-bang-and-then-die life-history is called 'semelparous'

Humans, for example, are iteroparous

PACIFIC salmon are semelparous; Atlantic salmon CAN BE iteroparous.

Start with one female
in generation 1

10^3

she survives along with
1000 of her female offspring
she again produces 1000
surviving
females and each of her
offspring
produce 1000 females

1000 ♀   –1001 ♀

10^3 10^3

In generation 3 this female
is alive and has left 1,002,000
desendents

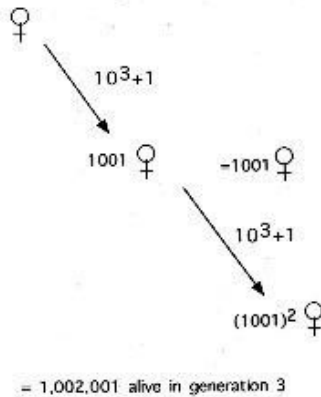♀ 1000 ♀ 1000 ♀ $(1000)^2$ ♀

= 1,002,001 alive in generation 3
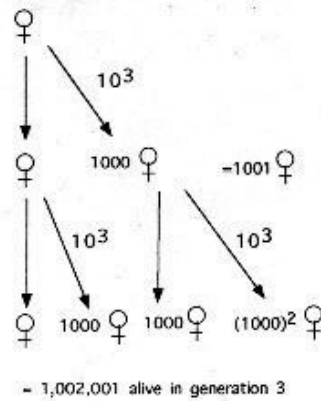
Cole's Paradox

Start with one female
in generation 1

♀

10^3+1

she dies, leaving
1000 of her female offspring
Each of her offspring
produce 1000 females

1001 ♀   –1001 ♀

10^3+1

In generation 3 this female
is has left 1,002,001
desendents

$(1001)^2$ ♀

= 1,002,001 alive in generation 3

Lamont Cole reasoned that, if one introduced to a population of immortal females who reproduced by some amount annually (say 1000 young each year), a mutant that produces 1001 offspring and then dies, it would have equal fitness. If it produced 1002 and then died, it would have higher fitness than original (would leave more descendants). He reasoned that, by abandoning all of the reserves necessary for personal survival, a female could surely add one or two eggs to clutch, seeds to crop, young to brood... SO, why aren't all organisms selected to be semelparous?

The answer probably lies in considering a simplifying assumption of Cole's model: it says all individuals – whether this year's offspring or the mother – have equal chance of suriving to next reproductive period. Is this reasonable? When is it more or less likely?
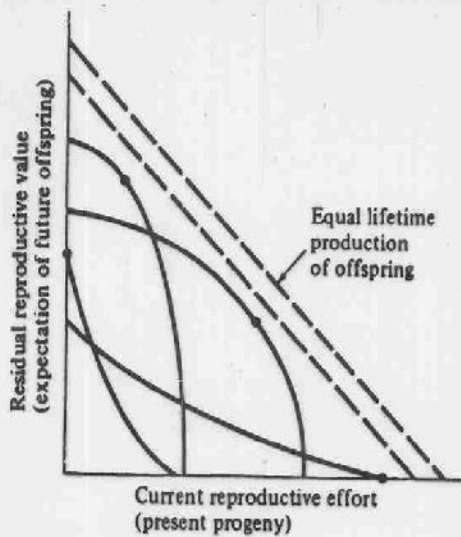
Equal lifetime
production
of offspring

Residual reproductive value
(expectation of future offspring)

Current reproductive effort
(present progeny)

ure 7.12. Trade-offs between current reproductive effort and
ectation of future offspring at any particular instant (or age).
ir curves relate costs in future progeny to profits in present
spring (and vice versa), with a dot marking the reproductive tac-
that maximizes total possible lifetime reproductive success.
ncave upward curves lead to all-or-none "big-bang" reproduc-
i, whereas convex upward curves result in repeated reproduction
roparity). Figures 7.13 and 7.14 depict these trade-offs through
litetime of a typical iteroparous and a semelparous organism,
ectively. [From Pianka (1976b).]

A graphic model of ways in which trade-offs between current and residual reprod values
might trade off. Selection should drive towards the point on the trade-off curve closest to
trhe diagonal line. IF the curve is concave upwards, selection will continually favor
increases in current reprod effort and – eventually – semelparity

If the curve is convex upwards varying degrees of 'K-selectedness' will be favored by
selection

Bamboos are long-lived, semelparous (monocarpic) plants; the usual reasons for this (low chance of adult survival to next reproductive event, for example) don't seem to apply. One argument is that, by producing vast quantities of seed at once – and *synchronizing* this production among individuals – seed-eaters might be overwhelmed so that many of the nutritious seeds will 'escape' being eaten. This is the 'predator satiation hypothesis' – but,selectively, it still focuses on the trade-offs between adult investment in reproduction and the chances of adulty *and offspring* survival...

Semelparity versus Iteroparity in Scarlet gilia
Paige and Whitman 1987

Ipomopsis aggregata in Arizona typically exhibits a semel-parous pattern, but is facultatively iteroparous, depending on the environmental conditions!
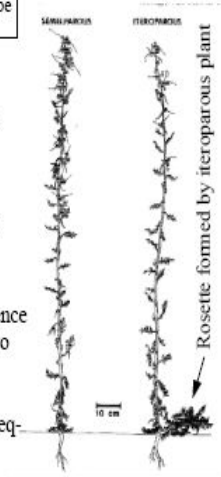
genotype----environment---->phenotype

Three Manipulations:
  1. Pollinator exclosures
  2. Flower chopping
  3. Herbivory simulation

Results:
  1 and 2 increased incidence of rosette production 5 to 7-fold
  3 did not increase the frequency of iteroparity.

Rosette formed by iteroparous plant

Scarlet gilia

There are various 'solutions' to the reproduce-now-and-shorten-life vs. wait-and live-longer trade-off. Some plants can respond to conditions by becoming either monocarpic or polycarpic

Some can change sex depending on resource availability (so can some animals). How is this related to the trade-off between reproductive and survival costs in their effects on fitness?

Bristlecone pine can live over 5000 years and may reproduce only every few centuries. Ultimate K-selection...

Figure 16-2   Trivers' model of the timing of parent-off-
spring conflict.
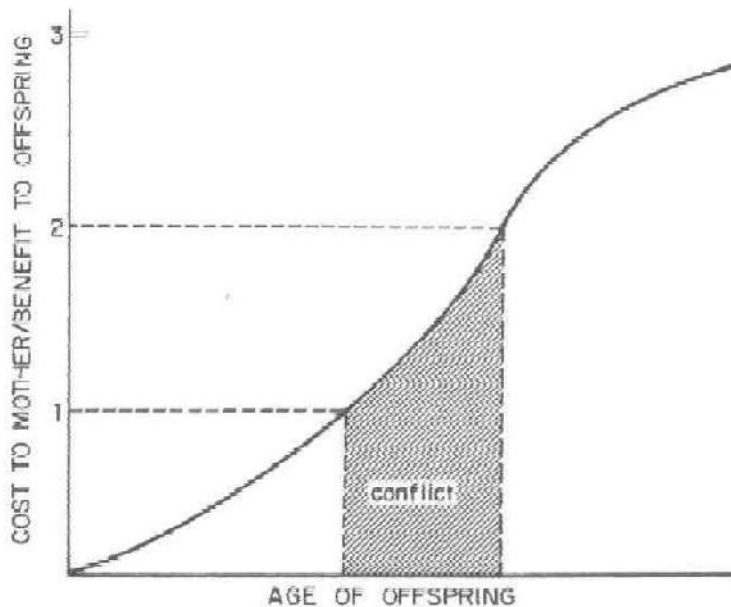
Resource allocation trade-offs can be seen as playing out through 'intragenomic' conflict; different traits (genes) in same organism may see 'fitness' maximized through different strategies; INDIVIDUAL fitness is the mediator.

There are also selective 'tensions' between closely related individuals, like parents and offspring. Even though they share 'fitness interests' – offspring are the coinage of fitness from parental 'perspective', and genes in offspring are likely to see copies of themselves in SIBLINGS, so offspring should be shaped by selection on their genes to favor parents investing not just in their own well-being but in producing siblings as well (a gene that allows parent to 'shift' attention to sibling eventually is likely to have higher fitness – see more copies in next generation – than one that's totally selfish...)

BUT from perspective of gene in a parent, ALL OFFSPRING are equally contributions to fitness; from perspective of gene in child, each sibling has only 50% chance of sharing any particular gene, so contributes less to child's fitness than 'self' does (half as much!).

SO, according to Robert Trivers, there should be a level of investment where parents fitness is optimized by shifting resources to next offspring – but child's fitness would be enhanced by retaining full parental commitment longer than that.

(*NOTE the shape of curve above; think about how value and cost change with age of child

max net RS for parent

max IF for offspring

B

C

1/2 C

B or C

p

y

PI
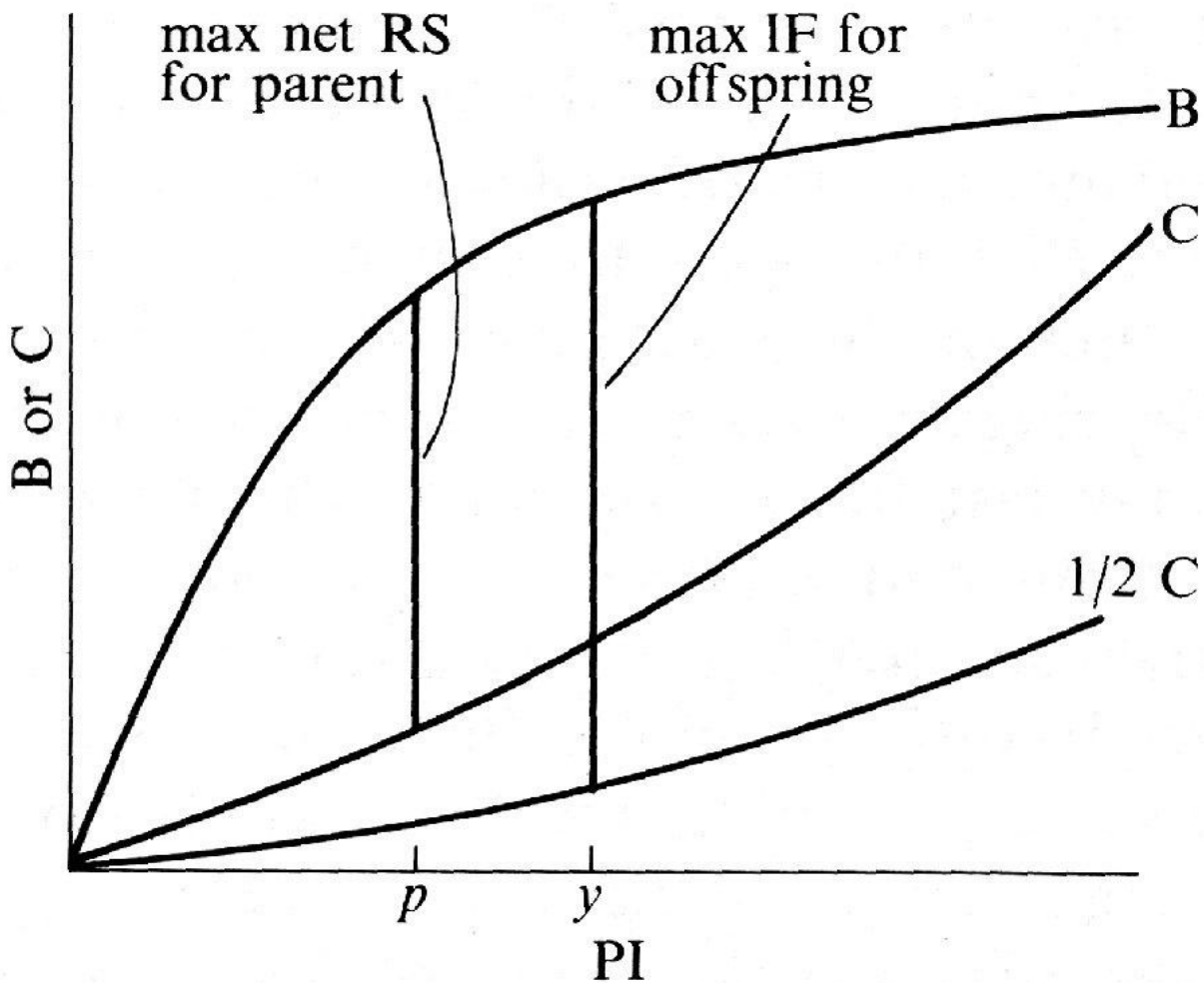
26

Trivers' graphical version of the model. "PI" is parental investment. B and C are benefit and cost. the curves are 'marginal' profit (fitness enhancement). IF benefits are 'saturating' (after a time, the gain in offspring's viability is less per each unit of investment), AND the cost (in terms of Residual Reprod Value of parent) increases with parental investment (it must, really), then there's a point of MAX 'return' where B-C is greatest. If the costs to the offspring are half the costs to the parent (because siblings only contribute half as much to your own fitness as you do yourself – while you're all equal to parents in fitness coinage), then that MAX is at a higher PI for offspring than for parent.

|	Mother's fitness	Offspring A's fitness	Offspring B's fitness
Offspring A gets 2 units of food	value of 2 units of food to offspring A * coefficient of relatedness between mother and offspring A = 7*0.5 = **3.5**	value of 2 units of food to offspring A * coefficient of relatedness between offspring A and recipient of food (offspring A) = 7*1 = **7** Best strategy for offspring A	value of 2 units of food to offspring A * coefficient of relatedness between offspring B and recipient of food (offspring A) = 7*0.5 = **3.5**
Offspring B gets 2 units of food	value of 2 units of food to offspring B * coefficient of relatedness between mother and offspring B = 7*0.5 = **3.5**	value of 2 units of food to offspring B * coefficient of relatedness between offspring A and recipient of food (offspring B) = 7*0.5 = **3.5**	value of 2 units of food to offspring B * coefficient of relatedness between offspring B and recipient of food (offspring B) = 7*1 = **7** Best strategy for offspring B
A and B each get 1 unit of food	value of 1 unit of food to offspring A * coefficient of relatedness between mother and offspring A + value of 1 unit of food to offspring B * coefficient of relatedness between mother and offspring B = (4*0.5) +(4*0.5) = 2+2 = **4** Best strategy for mother	value of 1 unit of food to offspring A * coefficient of relatedness between offspring A and recipient of food (offspring A) + value of 1 unit of food to offspring B * coefficient of relatedness between offspring A and recipient of food (offspring B) = (4*1)+(4*0.5) = 4+2 = **6**	value of 1 unit of food to offspring B * coefficient of relatedness between offspring B and recipient of food (offspring B) + value of 1 unit of food to offspring A * coefficient of relatedness between offspring B and recipient of food (offspring A) = (4*1)+(4*0.5) = 4+2 = **6**

Here's a working out of this model in terms of a simple scenario. Parent has two units of investment to allocate; the first unit given to an offspring enhances it's viability by 4 increments, but the second to same offspring only adds 3 via bility increments...
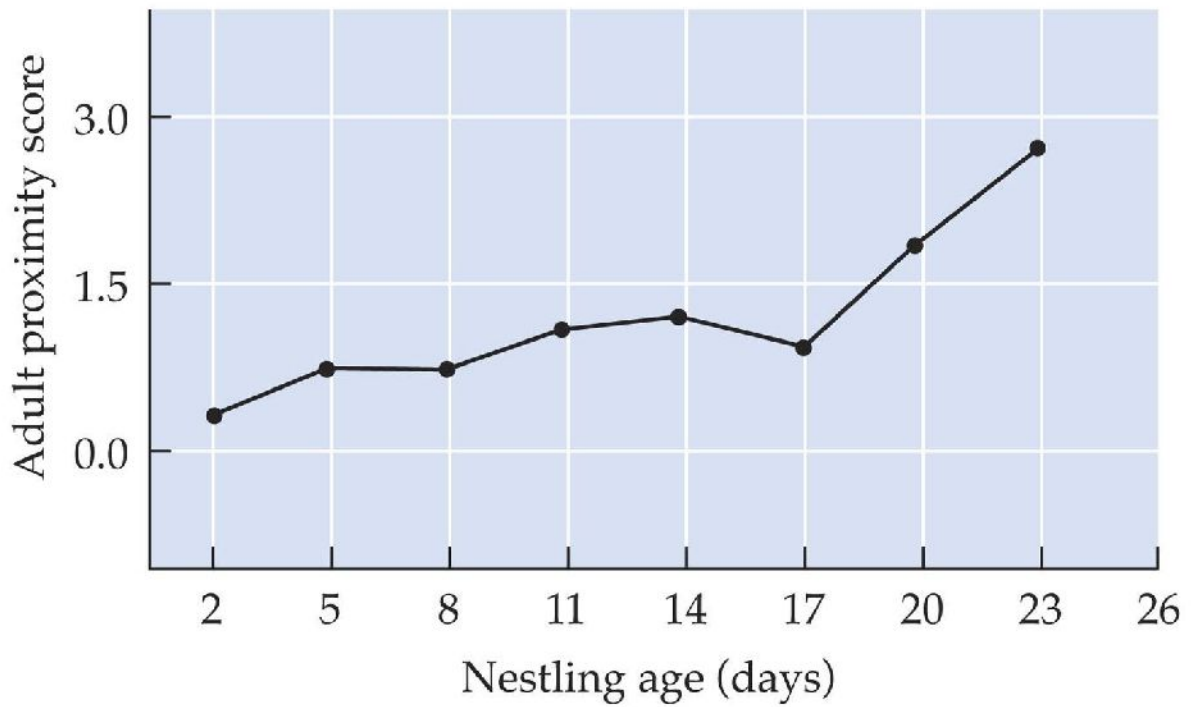
(A)

Chick survival probability

Nestling age (days)
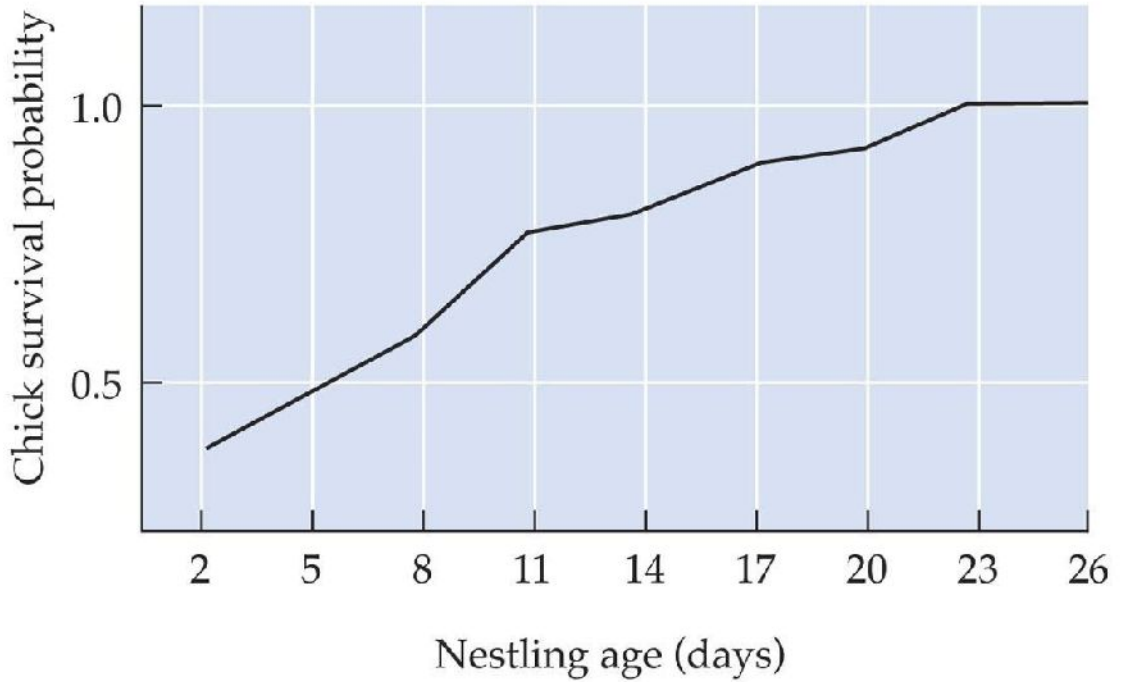
ANIMAL BEHAVIOR, Eighth Edition, Figure 12.27 (Part 1) © 2005 Sinauer Associates, Inc.

Viability of offspring does typically increase with age; once it plateaus, increase parental investment gains parent little

(B)

ANIMAL BEHAVIOR, Eighth Edition, Figure 12.27 (Part 2) © 2005 Sinauer Associates, Inc.

And parents tend to decrease presence in same time-frame (lower proximity score means more time at nest)

We developed the parent-offspring logic for full-sibling situation. What would the relationship be for half-siblings and parents? From sibling perspective? From parental?

A 'step-parent' has no direct fitness interest in continued investment in past offspring of other 'partner'. A large majority of human infanticide involves step-parents. Likewise in other animals. Behavioralists actually describe the 'evil-stepmother-syndrome...'

At a Brown Booby nest the older chick (under its parent) has driven its smaller sibling from The nest where it will die of exposure and starvation.

Sometimes such apparent conflicts aren't real conflicts. Brown Boobies can't actually raise more than one chick at a time, but typically lay two eggs. The older sibling commits siblicide and the parent does not resist. Why the second egg in the first place? (Bed-hedging...)

Simple perspective might suggest that parents have control in this conflict, so we should see resource investment maximizing parental fitness – offspring 'kicked out of nest' before they'd 'like' to be in own fitness interests.

BUT can offspring influence parental decisions? Think about cues parents respond to in feeding young. Think about the costs to parent of actually resisting importunities of young. (Noisy young might attract predators... Is the noisy young chick actually blackmailing parent?)

Altercation of generations: genetic conflicts of pregnancy.

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Abstract
Pregnancy is traditionally viewed as a harmonious collaboration between mother and fetus. From this perspective, viviparity poses a series of problems that maternal and fetal genes work together to solve and the many complications of pregnancy are interpreted as evidence of the malfunctioning of an evolved system or of the failure of natural selection to achieve an adaptive goal. This view fails to recognize aspects of genetic conflict that lie at the heart of gestation. At least three interrelated sources of conflict can be identified: (i) conflict between genes expressed in the mother and genes expressed in the fetus/placenta (parent-offspring conflict); (ii) conflict between maternally-derived and paternally-derived genes within the fetal genome (genomic imprinting); and (iii) conflict between maternal genes that recognize themselves in offspring and the rest of the maternal genome (gestational drive).

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In mammals, the physiological interaction of mother with young is particularly intimate. It may open the door for all kinds of mutual manipulation and turn parent offspring conflict into an arms race...

(1) hCG (human chorionic gonadotrophin)

A fetal tactic for controlling maintenance of pregnancy.

Pregnancy maintenance in most mammals is under maternal control: maternal pituitary's secretion of *luteinizing hormone* (LH) is necessary for stimulation of ovarian progesterone, which is essential for keeping the endometrium hospitable for conceptus.

In some species, including humans, the placenta (fetal tissue) eventually produces enough progesterone to maintain pregnancy even if the maternal ovary stops.

hCG gives the fetus another means for maintaining pregnancy, even before placental progesterone production is adequate:

hCG mimics hLH at maternal ovarian receptors, stimulating progesterone secretion

Evidence that hCG evolved as a fetal conflict tactic:

(1) Fetally produced hCG *selectively targets maternal tissues,* not fetal tissues.

(2) hCG evolved from hLH, and the evolutionary modifications have specifically diminished its affinity for certain other receptors that respond to hLH (especially TSH receptors) while retaining its impact at follicular hLH receptors

(3) It's a *"shouting"* signal : circulating levels of hCG are far higher than maximum maternal hLH levels - and yet hCG is inessential.

Thyroid disorders in pregnancy are apparently a costly vestige of this evolutionary conflict history.
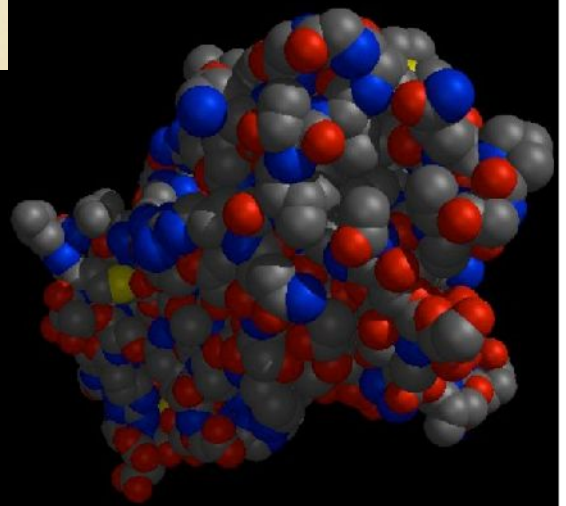
Deal in the womb: Fetal opiates, parent-offspring conflict, and the future of midwifery

Péter Apari [a], Lajos Rózsa [b,c,*]

Summary This paper argues that parent-offspring conflict is mediated by placental β-endorphins in placental mammals, i.e., foetuses make their mothers endorphin-dependent then manipulate them to increase nutrient allocation to the placenta. This hypothesis predicts that: (1) anatomic position of endorphin production should mirror its presumed role in fetal-maternal conflict; (2) endorphin levels should co-vary positively with nutrient carrying capacity of maternal blood system; (3) postpartum psychological symptoms (postpartum blues, depression and psychosis) in humans are side-effects of this mechanism that can be interpreted as endorphin-deprivation symptoms; (4) shortly after parturition, placentophagia could play an adaptive role in decreasing the negative side-effects of fetal manipulation; (5) later, breast-feeding induced endorphin excretion of the maternal pituitary saves mother from further deprivation symptoms. Finally, whatever the molecular mechanism of fetal manipulation is, widespread and intense medical care (such as caesarean section and use of antidepressants) affects the present and future evolution of mother-foetus conflict in the human species (and also in domestic animals) to increase 'fetal aggressiveness' and thus technology-dependency of reproduction.

The tripartite immune conflict in placentals and a hypothesis on fetal→maternal microchimerism

Péter Apari [a], Lajos Rózsa [b,c,*]

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There is a two-way traffic of immune cells through the placenta; and fetal immune cells are often present in the maternal body even long after giving birth. We present an adaptationist theory to interpret fetal→maternal microchimerism and the diverse set of concomitant medical phenomena. We handle fetal, maternal, and paternal adaptive interests separately and in interaction with one another. Fetuses may benefit from immunological information gathered by migrant cells in the maternal body, and also from improved maternal defence. However, they may be jeopardized by a selfish maternal usage of fetal→maternal microchimerism – i.e., some mothers get pregnant only to improve their immune system and then to abort. The use of microchimeric cells by the maternal immune system may contribute to the adaptive benefits of female choosiness and polyandry. While fathers may enjoy an indirect benefit from enhanced fetal and maternal health, they also face the risk of wasting sexual efforts due to selfish pregnancies of cheating females. Paternal alleles acting via clones of microchimeric cells in the maternal body could launch an immunological attack against the non-kin sperm in the female genitalia, or against the non-kin fetus in the womb. Furthermore, an intraspecific version of Zahavi's Mafia Hypothesis could explain a potential interaction between the abortion of fetuses and a subsequent rise of an autoimmune disease. We suggest that males may be capable to provoke microchimerism-induced autoimmune-like diseases in the mother in revenge of selfish pregnancies. This hypothetic paternal threat could increase the maternal costs associated to selfish pregnancies. From a medical point of view, we propose new interpretations for autoimmune-like diseases, infertility, miscarriage, and also for the prevailing connections among them. Specifically, we argue that miscarriages may cause autoimmune diseases, a reversed causality as compared to the currently accepted one.

A model of triploid endosperm evolution driven by parent-offspring conflict

Roger Härdling and Patric Nilsson
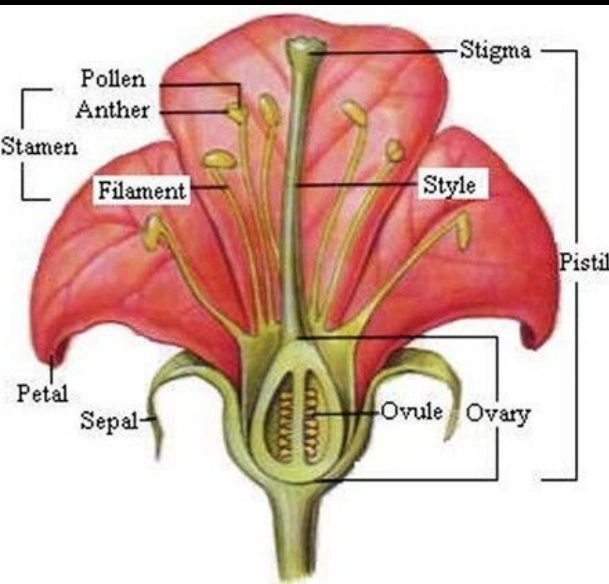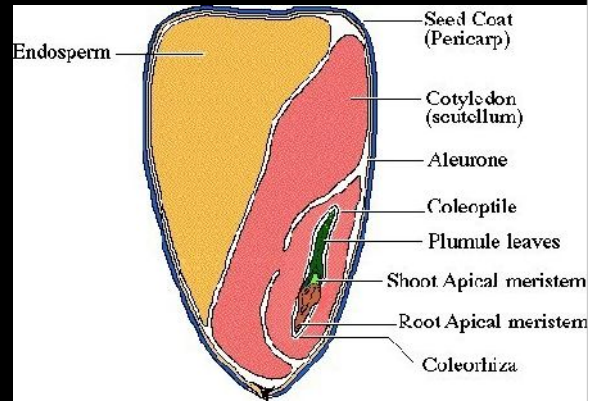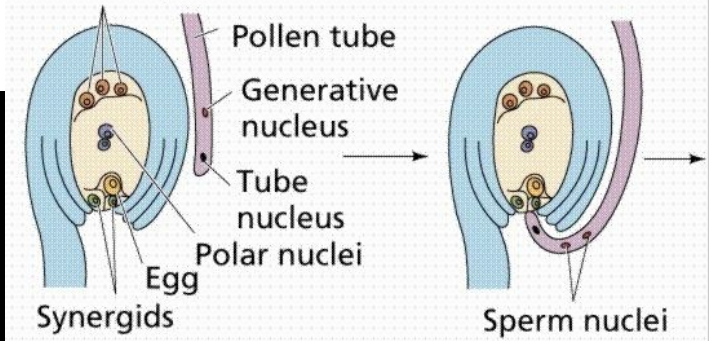
In many flowering plants, embryo in seed is provisioned by an 'endosperm' which is triploid tissue, 2 parts paternal, 1 part maternal genome. Is this an outcome of parent-offspring conflict for control of seed development? Of conflict between fitness interests of the two parents? Life gets complicated; still things to work out...