Mothers, Fathers and Children: the Evolutionary Origins of Conflict

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Outline

- Evolution
  - Natural selection
  - Sexual selection
  - Kin selection
  - Reciprocal Altruism
- Brainstorm: Examples of Conflict
- Conflict in the Animal World
  - Male-Female Conflict
  - Parent-Offspring Conflict
  - Sibling Conflict
- Humans

Adaptation

- Biological process
  - Organism becomes better suited to its environment
  - Fitness
- Shaped by natural selection
  - Occurs over geological time (hundreds to thousands of generations)

Fitness

- Capacity to produce lots of offspring relative to other individuals of the same species
  - Survive longer than other individuals (and consequently leave more offspring)

Natural Selection

- Heritable
  - Trait must be passed from parent to offspring
  - Genetics
- Variable
  - Within a species the trait must vary
  - Different individuals have different traits
- Differential fitness
  - The trait must be advantageous for some individuals
- Differential fitness is nonrandom
  - All individuals with displaying one form of a trait do better than individuals displaying an alternate form of the trait

Sexual Dimorphism

- Males and females differ in size, appearance and/or behavior

Ischnura damselflies

Male
Female

Orgia recens
Male
Female

Drosophila melanogaster
Male
Female

Chilocorus concavus
Male
Female

Doritis formosana
Male
Female
Parental investment (energy and time)

• Two questions:
  – How much does each sex invest in offspring?
  – Which sex is the limiting resource?

• Parental care is costly
• All models found in animals
  – No care
  – Mother only care
  – Father only care
  – Biparental care

Selection pressures for females

• Female reproductive success
  – Number of offspring
  – Offspring quality

Selection pressures for males

• Male reproductive success
  – Number of mates
    • Find a mate
    • Maintain a mate
  – Note: number of mates is a proxy for number of fertilizations (not necessarily 1:1).

Asymmetric selection pressures

Access to females will be a limiting resource for males, but access to mates will not be a limiting resource for females.
Behavioral Consequences of Asymmetric Selection on Males and Females

- For sex for which access to mates is limited:
  - Expect competition
  - **Intrasexual** selection
  - Usually males
- For the other sex:
  - Expect choosiness
  - **Intersexual** selection
  - Usually females
- Investment may be reversed:
  - Sex role reversal

Does mating *always* lead to fathering offspring?

- Many females mate multiply.

Kin Selection

When does it pay more to help your relatives than yourself?

Fitness

- **Fitness**
  - The extent to which an individual contributes genes to future generations
  - May be measured in terms of lifetime reproductive success
- **Inclusive fitness**
  - **Direct fitness**
    - Own progeny
  - **Indirect fitness**
    - Progeny of relatives

Evolutionary biologist J.B.S. Haldane, when asked if he would risk his life to save a drowning man answered, “No, but I would for two brothers or eight cousins.”
Hamilton’s Rule
altruistic behavior will spread if:

\[ Br > C \]

\( B = \) benefit to recipient
\( r = \) coefficient of relatedness
\( C = \) cost to the actor

Reciprocal Altruism

Reciprocal altruism—cooperation among non-kin

- Conditions: natural selection can favor altruistic acts
  - Cost to actor is smaller than benefit to recipient
  - Individuals that fail to reciprocate are punished
- Most likely to evolve when
  - Repeated interactions among individuals
  - Many opportunities for altruism
  - Individuals have good memories
  - Potential altruists interact in symmetrical situations

Scene from *A Beautiful Mind*

Conflict

Male-Female Conflict
Bateman’s Principle

Sexual selection—variation in mating success—will usually be a more potent force in the evolution of males than in the evolution of females.

Asymmetric limits on reproductive success in fruit flies

Bateman’s experiments (Drosophila melanogaster) the number of mates had a larger effect on the reproductive success of males than on the reproductive success females.

Male and female strategies for reproductive success can be fundamentally different

- How much parental care is required?
  - Lots: biparental care, little conflict
  - One parent: fundamentally different strategies, lots of conflict
    - Females invest equally in all offspring
    - Male fitness improves when female invests in his offspring only
Why do females mate multiply?

- Ensure all eggs fertilized
- Variation in progeny

How do males compete for fertilizations?

- **Sperm competition (SC)** - when the ejaculates of two or more males overlap in space and time within female reproductive tract
- Adaptations to reduce SC
  - Copulatory plugs, mate guarding, extremely large sperm
- Adaptations to increase SC
  - Larger ejaculates, more motile sperm

Adaptations to reduce SC

- Copulatory plugs
  - Spiders, Butterflies
- Mate guarding
  - Dung flies
- Sperm removal devices
  - Dragonflies
- Chemicals that induce female refractory period (reduce her interest in remating)
  - Drosophila
- and many more...

Sperm Morphology

- Largest sperm relative to body size: *Drosophila bifurca* (58 mm)

Alternative Reproductive Tactics (ARTs)

- In some species, if a male cannot compete directly, he may attempt matings through a different approach
- Note: not limited to males, but much more common in males
ARTs: yellow dung flies

- Large males fight over fresh pats of dung
  - Female comes to a pat
  - Males compete for her
- Small males look for females in the grass
- Female lays eggs immediately after mating, last male to mate fertilizes most of the eggs

ARTs in Dung Beetles

- Males differ in size and horns
- Sperm expenditure differs for the two morphs
- Residual testis mass of sneaks is higher than that of non-sneaks!

What do females gain by choosing among males?

- Direct benefits (resources)
- Indirect benefits (genes)

Direct benefit: nuptial gift

Sensory Bias—exploitation of other behaviors

Red Queen Hypothesis

Arms race, running to stay in place

Just at this moment, somehow or other, they began to run.

Alice never could quite make out, in thinking it over afterwards, how it was that they began: all she remembers is, that they were running hand in hand, and the Queen went so fast that it was all she could do to keep up with her; and still the Queen kept crying, ‘Faster! Faster!’ but Alice felt she could not go faster, thought she had not breath left to say so.

The most curious part of the thing was, that the trees and the other things round them never changed their places at all: however fast they went, they never seemed to pass anything. ‘I wonder if all the things move along with us?’ thought poor puzzled Alice. And the Queen seemed to guess her thoughts, for she cried, ‘Faster! Don’t try to talk!’ ….

‘Well, in our country,’ said Alice, still panting a little, ‘you’d generally get to somewhere else — if you ran very fast for a long time, as we’ve been doing.’

‘A slow sort of country!’ said the Queen. ‘Now, here, you see, it takes all the running you can do, to keep in the same place.

If you want to get somewhere else, you must run at least twice as fast as that!’
Sexually-antagonistic co-evolution

- Males and females are in an “arms race”
- As males evolve traits that manipulate females into mating with them… females evolve traits to resist the male manipulation!
- Then males evolve new traits that manipulate females, which is countered again by the females, etc.

Ducks: the effect of conflict on morphology

- Most birds have simple genitalia
  - Males lack external genitalia
  - Females have simple vaginas
- Many ducks have forced extra-pair copulations
  - Male phallus length and morphological elaborations positively correlated with frequency of forced extra-pair copulations
  - Females have evolved complex vaginal morphology

Infanticide

- Males can attain more matings by inducing female receptivity
- Female response
  - Defend young (rarely successful)
  - The older the young, the more they are defended
  - Spontaneous abortion of pregnancies in process
- Generally socially living animals with males that dominate a group of females
  - Lions
  - Common langurs
  - Baboons
  - Gorillas
  - Chimpanzees (but not bonobos)
  - Common bottlenose dolphins

Antagonistic sexual selection between male and female fruit flies

![Antagonistic sexual selection between male and female fruit flies](image)

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Flatworms
Dunnocks

Differential male/female interests reflected in kin selection through alarm calling

- Belding’s ground squirrels
  - Live in colonies
  - Call when predator spotted
  - Males disperse
  - Females in proximity are related

Parent-Child Conflict

Parent-offspring conflict

- Trade-off
  - Investment in current offspring weighed against future offspring
- Asymmetrical fitness interests
  - Parent to offspring: $r = 1/2$
    - Equally related to all offspring
    - Investment in current offspring may be at cost of future offspring
  - Offspring to self: $r = 1$
    - Relationship to siblings, max $r = 1/2$

Life History

Energy used for:
- Growth, metabolism, and repair
- Metabolism, repair, and reproduction

Energy source:
- Mother

Age (months): 0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20

1st litter (8 pups) 2nd litter (7 pups) Killed by predator
Sockeye salmon

How many offspring?

- Start with an assumption: all offspring are a fixed size.
- The more offspring parents attempt to raise at once: the less time and energy for each individual
  - Parent-offspring conflict

Lack’ s Hypothesis

- Selection will favor the clutch size that produces the most surviving offspring

Where did Lack go wrong?

- Assumption: no trade-off between parent’ s reproductive effort in one year and its survival or reproductive performance in the future.
  - Often this is the case
- Assumption: only effect of clutch size on offspring is in offspring survival
  - Offspring RS can be affected
  - Those from large clutches tend to have small clutches (and vice versa)

How big should offspring be?

- Relax previous assumption: size of offspring is fixed
- Trade-off:
  - many low quality offspring
  - few high quality offspring.
- Assumption 1: Trade-off between size and number.
- Assumption 2: Individual offspring will have a better chance of surviving if bigger.
  - Conflict between parents and offspring.
Evolution of egg size with reduced selection pressure

Weaning conflict

Full sibs

Half sibs

Helping conflict

• White fronted bee eater
• Fathers coerce sons into helping to raise sibs
• Harass sons trying to raise own
• Sons equally related to kids and sibs
• Parents more related to kids than grandkids

Kin selection:
Helpers-at-the-nest

• Florida scrub jay (*Aphelocoma coerulescens*)
  – Isolated population in c Florida
  – Studied since 1969
• Observations
  – Breeding pair may be helped by up to 6 others
  – Complete pedigree
• Experiment
  – In 1987 and 1988, helpers experimentally removed
  – Control: 21 untreated nests
  – Average number of helpers 1.8

Helping conflict

Kin selection:
Helpers-at-the-nest

Florida Scrub Jay Results

<table>
<thead>
<tr>
<th></th>
<th>Experimental group</th>
<th>Control group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial sample size</td>
<td>45</td>
<td>63</td>
</tr>
<tr>
<td>% survival egg to hatching</td>
<td>67</td>
<td>68</td>
</tr>
<tr>
<td>% survival hatching to fledging</td>
<td>30</td>
<td>63</td>
</tr>
<tr>
<td>% survival from fledging to day 60</td>
<td>33</td>
<td>81</td>
</tr>
<tr>
<td>% survival from egg to day 60</td>
<td>7</td>
<td>35</td>
</tr>
</tbody>
</table>

Sibling Conflict
Siblicide

- Masked booby
  - Two egg clutch, 2-10 days apart
  - One hatches before the other
  - Older pushes younger from nest
- Blue-footed booby
  - Short term low food, older reduces food intake (helps sib survive)
  - Long term: kill sibling

Siblicide: why are parents passive?

**Table 12.4** In boobies, the probability of siblicide varies with parent species and nestmate species

<table>
<thead>
<tr>
<th>Treatment</th>
<th>No siblicide</th>
<th>Siblicide</th>
</tr>
</thead>
<tbody>
<tr>
<td>Masked booby nestlings with masked booby parents</td>
<td>0</td>
<td>25</td>
</tr>
<tr>
<td>Blue-footed booby nestlings with masked booby parents</td>
<td>12</td>
<td>8</td>
</tr>
<tr>
<td>Masked booby nestlings with blue-footed booby parents</td>
<td>6</td>
<td>16</td>
</tr>
<tr>
<td>Blue-footed booby nestlings with blue-footed booby parents</td>
<td>17</td>
<td>0</td>
</tr>
</tbody>
</table>


Kin selection: Cannibalism

- Tiger salamanders (*Ambystoma tigrinum*)
- Spadefood toads (*Spea bomifrons*)
  - Two morphs of tadpoles
    - Omnivorous- mostly decaying plant matter
    - Large prey eating, including other tadpoles

Humans

Figure 1. Siblicide threshold in the hierarchy model. (a) The potential benefit, B, of each of four choices is a function of exponentially increasing food availability. (b) The slope of the graph of B increases with increasing food availability until a critical threshold value is reached (at which a chick is lost from the nest). (c) Values of the threshold in the hierarchy model with four siblings. The sloping broken line in the graph represents the inclusive fitness belonging to the non-victimal sibling. (d) Parental choice is the result of the benefit-calculation. (e) The graph of the benefit-calculation represents the potential maximization. (These three graphics were drawn using the same explicit equations and parameters, for a full explanation see Black & Parker 1987, reprinted with permission from Oxford University Press.)

Mock & Parker 1998
Male- Female Conflict
Beyond Mars and Venus

Differential Reproductive Success

- Most children born to a single man
  - Moulay Ismail Ibn Sharif, second ruler of the Moroccan Alaouite dynasty
    - 867 children
      - 525 sons
      - 342 daughters
- Most children born to a single woman
  - First wife of Feodor Vassilyev (1707-1782), Russian peasant
    - 69 (67 survived infancy)
      » 16 sets of twins (32)
      » 7 sets of triplets (21)
      » 4 sets of quadruplets (16)


Sexual selection in humans

- Men have higher variance in reproductive success
  - Bateman’s rule

Why do men have a higher variance in reproductive success?

- Male-male competition?
- Female choice?

Male-male competition

- Men (on average) are more violent
- More success in male-male combat leads to more offspring?
  - True for Yanomamö

Unokais = killers

Female choice

- Married men taller than single men (Poland)
- Taller men have more children than shorter men (West Point grads in 1950)
Unique qualities of humans (compared to chimps and gorillas)

- Less sexual dimorphism (had already diminished in Ardipithecus ramidus, 4.4 MYA)
- Loss of morphological adaptations for sperm competition
- Increased pair-bonding

Parent-Child Conflict

Fitness

But what is the natural human maternal instinct?

- Long childhood = long maternal care
- Pleistocene menarche later than today, pregnancy probably earliest late teens.
- Life expectancy in 30s?
- How many children did the average woman have?
- How much would women invest in each child?
- Attachment parenting is a very modern concept.
Investment in each sex

- How can a woman reject a daughter, her own sex?
- Male social control increases a mothers resources with birth of sons
- Men with resources have successful sons
- Low ranking women have success with daughters

Male reproductive performance more influenced by social status

Social status changes reproductive potential: Evidence from Late Medieval–Early Modern Portuguese Genealogies

Child abuse patterns consistent with evolutionary theory

Sibling Conflict

Reproductive performance of sons and mothers grouped by status (compared from Table 3.4)

Reproductive performance of sons and mothers grouped by status (compared from Table 3.4)
Portuguese genealogies: older siblings reduce probability of marriage (and thus children)

Table 5
Reproductive performance of men grouped by birth order.

<table>
<thead>
<tr>
<th>Birth order</th>
<th>N</th>
<th>nx</th>
<th>N</th>
<th>nx</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>504</td>
<td></td>
<td>1,561</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>366</td>
<td>843</td>
<td>223</td>
<td>785</td>
</tr>
<tr>
<td>3</td>
<td>240</td>
<td>447</td>
<td>111</td>
<td>422</td>
</tr>
<tr>
<td>4+</td>
<td>261</td>
<td>434</td>
<td>102</td>
<td>386</td>
</tr>
<tr>
<td>Total</td>
<td>1,371</td>
<td>3,285</td>
<td>812</td>
<td>3,140</td>
</tr>
</tbody>
</table>

Kruskal-Wallis (A) \( p < .000 \), (B) \( p < .09 \).

Figure 5
Proportion of ever-married men and women grouped by birth order.

Suggested Reading


Suggested Watching: PBS

- *Born wild: the first days of life*
- *What males want*
- *What females want*