Likelihood of paternal care depends on …

- Paternal certainty
  - Fertilization mode
- Degree to which male can contribute
  - State of embryos
- Availability of receptive females

As always, costs/benefits

External vs. Internal Fertilization

When male paternity is uncertain, the benefits of providing paternal care are substantially reduced.
Paternal care is especially common among fish.

The evolution of male-only care

- Birds and mammals have internal fertilization and determinate growth, while many fishes have external fertilization and indeterminate growth.
- Larger females can produce more eggs, so parental care is now more costly to females; providing care limits growth and future fecundity.
- External fertilization increases certainty of paternity for males: this lowers the cost of care.
- For fishes, the higher costs of care for females and lower costs of care for males can favor the evolution of male-only care.

Oviparity vs. Viviparity

- **Oviparity** (laying eggs)
  - Common in birds, fish & invertebrates
  - Early externalization of young permits extensive paternal care

- **Viviparity** (bearing live young)
  - Common only in mammals
  - Late externalization of young does not permit extensive paternal care

Altricial vs. Precocial
Inclusive Fitness
(individual’s collective genetic success)

• Direct + Indirect fitness
• Direct fitness = fitness gained through personal reproduction
• Indirect fitness = fitness gained by helping non-descendant kin survive

WD Hamilton
(1964, The genetical evolution of social behaviour, I, II)

Inclusive Fitness

- Not calculated by summing individual’s offspring and non-descendant kin
  Rather refers only to offspring and kin that owe their existence to the individual’s actions
- Not used to generate an absolute measure of an individual’s lifetime genetic contribution
  – Rather allows us to compare the evolutionary consequences of two alternative hereditary traits

Hamilton’s Rule

Evolution of altruism favored when:
\[
br > c
\]

Where:
- \( c \)= costs to actor in terms of his/her direct fitness
- \( b \)= benefit in fitness gained by recipient(s) of the altruistic act
- \( r \)= coefficient of relatedness

The probability that 2 individuals possess the same allele because they inherited it from a common ancestor
Proportion of the total genotype shared between individuals as a result of shared ancestry

(Hamilton 1964)
Coefficients of relatedness \( r \) between descendent (D) and non-descendant kin in diploid animals

<table>
<thead>
<tr>
<th>Relationship</th>
<th>Fraction of alleles shared</th>
<th>( r )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full siblings</td>
<td>1/2</td>
<td>0.5</td>
</tr>
<tr>
<td>Half siblings</td>
<td>1/4</td>
<td>0.25</td>
</tr>
<tr>
<td>Cousin-cousin</td>
<td>1/8</td>
<td>0.125</td>
</tr>
<tr>
<td>Parent-offspring (D)</td>
<td>1/4</td>
<td>0.25</td>
</tr>
<tr>
<td>Uncle/aunt-niece/nephew</td>
<td>1/4</td>
<td>0.25</td>
</tr>
<tr>
<td>Grandparent-grandchild (D)</td>
<td>1/4</td>
<td>0.25</td>
</tr>
</tbody>
</table>

JBS Haldane

“I’d lay down my life for 2 brothers or 8 cousins.”

- Myself: \( r = 1 \)
- Brothers: \( r = 0.5 \)
- First cousins: \( r = 0.125 \)

Parent-offspring conflict theory

- Parent-offspring conflict theory – parents and their dependent offspring are under different selection pressures:
  - Parents should maximize their lifetime reproductive success
  - Offspring should maximize the energy and protection they receive from parents to survive to reproductive age
- Parental investment
  - Any investment by parents in an offspring that increases offspring survival at the cost of the parent’s ability to invest in other offspring

**Red deer**

- Calf weight related to duration of suckling
- Heavier calves more likely to survive the next winter
- Expect calves to favor prolonged suckling

- BUT: mothers who suckle for a long time have reduced conception during next rut.
  SO: Mothers prefer shorter lactation

- Calves can therefore gain fitness at their mother’s expense

(Clutton-Brock et al. 1982)

**Human pregnancy**

- Placental tissue breaches maternal tissue and gains direct access to mother’s circulating blood
- Allows fetus to directly manipulate maternal physiology
- Conflict revealed after mother eats a meal:
  - In fetus’ interest to keep maternal blood sugar high: releases glucagon and other hormones to counter the activity of maternal insulin
  - Probable cause of gestational diabetes
- Long term costs to mother, including diabetes and possibly polycystic ovaries

(Haig 1993)

**Parental care trade-off in treehoppers**

- Research question: Within a species, why is there much variation in parental care such as egg guarding? (Zink 2003)
- Hypothesis: There is a trade-off between current and future reproduction
- Prediction 1: Egg guarding will increase egg survival (current reproduction)
- Prediction 2: Increased egg guarding will decrease future reproduction

**Parental care trade-off in treehoppers**

- Methods:
  - Tree hoppers (*Publilia concava*)
  - Marked individual females that had deposited an egg mass
  - Noted number of days they guarded the eggs
Parental care trade-off in treehoppers

• Results:
  – Egg hatching success was positively correlated with female egg-guarding duration

![Graph showing correlation between female guarding duration and hatching success](image)

• Conclusion:
  – Parental care (egg guarding) enhances current reproductive success but at a cost of future reproduction

Parental care trade-off in treehoppers

• Results:
  – Females that guarded a clutch for more than ten days had fewer and smaller future broods than females that spent less time egg guarding

![Bar charts showing number and size of future broods](image)

• Conclusion:
  – Parental care (egg guarding) enhances current reproductive success but at a cost of future reproduction

Sibling Rivalry

• As even full-sibs are not genetically identical, they can compete strongly for shares of finite parental investment
  – Can be between same-age or different-age siblings

![Diagram showing sexual and parent-offspring conflict](image)
Siblicide
(juvenile mortality caused by overt aggression among siblings)

- Occurs in some birds
  - Birds of prey
  - Herons
  - Egrets
  - Boobies

- Rare in mammals
  - Pigs
  - Spotted hyenas

5 traits common to siblicidal species
- Sibs compete for food
- Food delivered in monopolizable units
- Sibs have weapons
- Sibs differ in competitive ability
- Sibs confined in a small space

How can one benefit from killing a sibling?
- Facultative siblicide
  - Occurs in proportion to resource scarcity
- Obligate siblicide
  - Occurs regardless resource abundance
Why don’t parents intervene?

- Sometimes they do
- But when conditions are such that parents cannot rear all young successfully…
- Siblicide can save parents time & energy
- Extra egg(s) can provide insurance against loss of the first egg
  - predation
  - defective

Through asynchronous hatching, egret females set the stage for siblicide

- Not only does one chick hatch 1.5 days earlier, this first chick is also provided with additional androgens in its egg
- The extra androgens facilitate its being aggressive toward its smaller sibling

Siblicide can save parents time & energy

- Often conditions are such that parents can only rear one or two young successfully
  - When 2 booby chicks experimentally kept alive through siblicidal period, both chicks more likely to die
  - Therefore, may be adaptation to variable food supply

**TABLE 12.1** The effect of hatching asynchrony on parental efficiency in cattle egrets

<table>
<thead>
<tr>
<th>Brood Type</th>
<th>Mean survivors per nest</th>
<th>Food brought to nest (ml)</th>
<th>Parental efficiencya</th>
</tr>
</thead>
<tbody>
<tr>
<td>Synchronous brood</td>
<td>1.9</td>
<td>68.3</td>
<td>2.8</td>
</tr>
<tr>
<td>Normal asynchronous</td>
<td>2.3</td>
<td>53.1</td>
<td>4.4</td>
</tr>
<tr>
<td>brood</td>
<td>2.3</td>
<td>65.1</td>
<td>3.5</td>
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Source: Meek and Plager [134]

*aThe number of surviving chicks divided by the volume of food brought to the nest per day × 100

Evolution of Social Behavior

1. Costs & Benefits of Living in Groups
2. Evolution of Social Behavior
Society
a group of conspecifics in which there is some degree of cooperation and communication

The Sociality Continuum

Asocial
- Alone except when breeding
- Pairs
- Small, permeable groups
- Small, impermeable groups
- Large, permeable groups
- Large, impermeable groups
- Obligate gregariousness

Eusocial

Ecological conditions affect where a species falls on the sociality continuum

Under what circumstances is sociality likely to evolve?

- Asociality is favored when
  - Food is rare & widely dispersed
  - Predators are evaded by crypsis

Under what circumstances is sociality likely to evolve?

- Sociality is favored when
  - Food is rich & clumped
  - Predators are evaded through cooperative defense or dilution effects
Fitness costs of sociality

1. Increased competition within the group for key resources such as food, shelter and mates

For males, living in close proximity to others increases the likelihood of being cuckolded

2. Increased investment & risk of injury in establishing and maintaining dominance relationships

Subordinate ‘helper’ cichlid fish spend most of their time signaling submissive status to dominants
Fitness costs of sociality

3. Increased risk of disease & parasite transmission

From insecticide-treated nest

- The number of parasites/nestling increases with colony size

4. Increased risk conspecifics will kill your offspring

- Accidental death

- Infanticide

- Egg tossing

Fitness costs of sociality

5. Increased risk that conspecifics will exploit your parental care

- Egg dumping by female conspecifics increases incubation time and consequently energetic demands of raising a brood

- E.g. intraspecific brood parasitism in wood ducks

(Nielsen et al. 2006)
Fitness costs of sociality

6. Increased risk of mating with kin
   Inbreeding depression

Fitness benefits of sociality

1. Reduced predation risk
   a. Dilution effect
   b. ‘Many eyes’ for vigilance
   c. Cooperative defense
   d. Confuse predators
   e. Aid to injured individuals

Fitness Benefits of Sociality

2. Improved defense of limited resources such as food and space
Fitness benefits of sociality

3. Increase foraging efficiency
   a. Individuals can be less vigilant
   b. Facilitate capture of larger/more prey
   c. ‘Many eyes’ reduce food detection time
   d. ‘Many heads’ increase knowledge pool

Key to emperor penguin breeding success is huddling

- Breeds in Antarctic winter
- Males fast during mating (45 d) & incubation (65d)
- Ambient temp is –17 C
- Embryonic development requires 35 C
- Huddling represents 38% of time budget
- Inside huddles, ambient temp is 20-37 C

(Gilbert et al. 2006)

Fitness benefits of sociality

4. Improved shelter and/or maintenance of homeostasis

huddling

Fitness benefits of sociality

5. Decreased physiological costs of movement
Aerodynamic benefit: reduced cost of movement in pelicans

• Research question: Why do large birds fly in a V-formation? (Weimerskirch et al. 2001)
• Hypothesis: This formation reduces the cost of flying
• Birds in formation will have a lower wingbeat frequency and heart rate than solitary birds

Aerodynamic benefit: reduced cost of movement in pelicans

• Methods:
  – White pelicans (Pelecanus onocrotalus)
  – Placed heart rate monitors on trained birds
  – Videotaped flight formations and collected data on wingbeat frequency, noting location of each bird in formation

Aerodynamic benefit: reduced cost of movement in pelicans

• Results:
  – Birds in formation behind the leader had a slower wingbeat frequency and lower heart rate
• Conclusion:
  – Large birds have reduced flight costs by flying in formation

Fitness benefits of sociality

6. Division of Labor

Portuguese man-of-war is a colonial invertebrate made up of 4 different types of polyps.

Polyps specialized for:
  – Flotation
  – Feeding
  – Defense
  – Reproduction
Caste

a set of individuals of a particular morphological type and/or age group that performs specialized labor

worker & soldier ants

Fitness benefits of sociality

7. Improved reproductive output
   a. Close proximity of prospective mates
   b. Enhanced protection of young
   c. Increased provisioning (‘helpers’)
   d. Better education of young

Social interactions can have positive and negative effects on actors & recipients

Social interactions can have positive and negative effects on actors & recipients

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Mutualism (a.k.a. cooperation)

- By behaving cooperatively, both participants receive a fitness benefit
- Therefore, neither party tends to cheat

Heinrich’s crow juveniles cooperatively defend carcasses from territorial adults

Coalitions
alliances formed for joint aggressive action of benefit to all members

- Male lions form coalitions with non-related males. Without cooperation, none would have access to mates.
- Spotted hyenas frequently from coalitions against lower-ranking group-mates. This reinforces the social hierarchy.

Must mutualism be between conspecifics?

- Leaf-cutting ants & fungus
- Clown fish & sea anemone