Parental Care
Parental Investment

= any parental contribution to offspring that increases survival of the offspring and decreases the ability of the parent to have more offspring.

Direct
• Nursing
• Feeding
• Transporting
• Incubating

Indirect
• Maintaining a territory which is better for rearing
• Staying fit / dominant
• Caring for females
Factors in Providing Care

• If offspring are more likely to survive with care, then a mechanism exists for the evolution of parental care
  – but, parents must weigh costs/benefits to their own fitness

• In general, more “complex” animals require more development time: for primates parental care can be 25% of the offspring’s lifespan!
Potential parents must “decide” or be programmed as to the best strategy, but this depends on environmental factors:

Should I reproduce now or wait?

The answer depends on whether you engage in parental care, which adds greatly to the costs of reproduction.

**species with no parental care:**
- Energy costs
- Time costs
- Potential predator
- Vulnerability costs

**species with parental care:**
- Reproduction
- Energy costs
- Time costs
- Potential predator
- Vulnerability costs
  + Parental care
- Energy costs
- Time costs
- Potential predator
- Vulnerability costs
Decisions about parental investment should maximize *lifetime* reproductive success, not necessarily the success for a single bout of reproduction.

1. Resource allocation between self and offspring

2. Resource allocation amongst offspring

    Weighed against current vs. potential future offspring

Which must take into account age and condition of self!
Such decisions create conflicts between parents and offspring

-- which we will look at later in the lecture
Why does parental care evolve at all in K-selected organisms if costs are so high?

• Opportunity for strategic reproduction re: environment.

• Opportunity for strategic reproduction re: ageing.

• Need to control limiting resources when population at K.

• Opportunity for teaching
opportunity for strategic reproduction re: environment

K-selected organisms:

- larger body size
- slower development
- longer life span: live longer than environmental fluctuations

parental care

Strategically produced stability favors larger investment in fewer offspring.

Can wait for environment to be best suited for reproduction.

Minimize but can’t remove environmental fluctuations.
opportunity for strategic reproduction re: aging and reproductive plans

r-selection extreme: reproduce once, then die (semelparity)

Example: salmon

K-selection extreme: measured repeated reproduction (iteroparity)

Example: California Gulls...

Raise one or two chicks per year over 15 years. Older parents invest more care in offspring, and produce more offspring. Older parents have less chance of surviving to reproduce again, so reproductive effort increased at the expense of parent’s own health.
K-selected organisms are at carrying capacity of environment

Not opportunistic, i.e., we don’t breed only when unpredictable high levels of resources suddenly become available.

Can be great intraspecific competition for resources.

Offspring that take a long time to develop cannot compete with each other, so parents do it for them.

more parental care more parental investment

need to control limiting resources when population at K.
Opportunity for teaching

If resources scarce (at K), and competition for resources high, any advantage conferred to offspring increase your inclusive fitness.

Parental care → parental training of offspring

↓

Increase probability of genes being passed on
Who Provides Parental Care?

• Males
  – Common among fishes
• Females
  – Common in mammals
  – More likely across the entire animal kingdom
• Both sexes
  – Either equal or unequal (i.e. female provides most, with some help from the male)
  – 3% of mammals, 70% of birds!
• Siblings/others
  – Common in “altruistic”/social animals (honeybees, termites where all workers are related to each other; more on this in Chapter 13, The Evolution of Social Behavior)
So Who Should Care for Young?

Internal fertilization

1. “Certainty of Paternity” hypothesis: female is certain of parentage, male is uncertain
   - Known genetic relatedness leads to a higher likelihood of parental care

2. Gamete Order Hypothesis
   - Female stuck with offspring
   - Male #1 (1st to mate)
   - Male #2
   - Male #3 (last to mate and donate gametes)

Selection should favor abandonment (akin to brood parasitism)

Not displaced by subsequent males, ends up caring for offspring
3. Proximity hypothesis
   - Female is there during birth, so she will provide care
   - Statistically, males are not around, so will not provide care
External Fertilization

- If eggs are laid/fertilized in a male’s territory, then the male has equal or better certainty of paternity re: female.
- Females can desert, and often will!
- More commonly find male parental care

Values in the table are the number of fish families:

<table>
<thead>
<tr>
<th></th>
<th>internal fertilization</th>
<th>external fertilization</th>
</tr>
</thead>
<tbody>
<tr>
<td>male parental care</td>
<td>2</td>
<td>61</td>
</tr>
<tr>
<td>female parental care</td>
<td>14</td>
<td>24</td>
</tr>
<tr>
<td>no parental care</td>
<td>5</td>
<td>100</td>
</tr>
</tbody>
</table>

Note switch from female to male care with external fertilization
Can you show that certainty of paternity is a factor in parental care?

Male parental care (they build nests for this purpose)

3 kinds of males
1. “Parental”
2. “Young Sneakers”
3. “Female Impersonators”

Bluegill sunfish (Lepomis macrochirus)
Due to sneakers and female impersonators, the “parental” male may not be sure if the eggs he is caring for were fertilized by him.

When the eggs hatch, however, a chemical in the fry urine is detected by the male and it is genetically unique – so for fry male can tell his offspring from those fertilized by a different male.
What happens, relative to parental care, if paternal male sees sneaker males during spawning? (Expts: Stoltz & Neff 2006)

**Experiment 1**
Parental male at time of spawning
Sees this: a cage with 4 sneaker males

**Experiment 2**
Parental male at time of spawning
Sees this: a cage with no sneaker males (control)
The next day…

Do I defend my nest? How certain am I that the eggs were fertilized by me?

Predatory pumpkinseed sunfish introduced (in a cage)
Defense response of parental male when he sees predator:

Males are not as willing to defend eggs when they are less certain who the father is. They always know about the fry (due to chemical), so there is no difference shown for them!
From previous slide:

- **Males**
  - Common among fishes
- **Females**
  - Common in mammals
  - More likely across the entire animal kingdom
- **Both sexes**
  - Either equal or unequal (i.e. female provides most, with some help from the male)
  - 3% of mammals, 70% of birds!
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Recall from last slideset: male birds can contribute more to raising offspring (sit on eggs, feed young) than mammals. So parental care quite rare in mammals.
If there is parental care, then you should be able to recognize your offspring.

Although, as with the Oropendolas and Cow Birds, you may choose to ignore brood parasites if there are good reasons to do so.

In other cases, parasites become more and more deceptive and hosts more and more discriminating...
Another parasite is not so effective: its chicks are not vocal mimics and always rejected by wren adults.
The more colonial the swallow, the more distinctive are the calls.

Cliff swallows nest in large colonies, Barn swallows less so.

The implication is that more varied call structure makes individuals recognizable by parents.
Ring-billed Gulls: Nest in large colonies. Chick run about after hatching. Adults will care for any chick between hatching and five days old. At five days, adults learn to recognize their own chicks.

Kittiwake Gull: Nest on crags on vertical cliffs. Chicks stay put. Adults are incapable of recognizing their own vs foreign chicks!
Interestingly, the recognition system in gulls is not perfect, and some chicks will try to get other adults to adopt them. Sometimes it works.

Low-weight chicks either stay low-weight, or gain weight if they can get adopted.
Imperfect recognition is one aspect to how brood parasitism gets started…

Why incur costs of being a parent if someone else will do it for you?

Ancestral species:

- Small body size
- Small home range
- Non-migratory

some

Larger body size
Larger home range
migratory

some

Brood parasites

(All bird species that are brood parasites fall in this category)
How to be a better brood parasite…

Key is evolving a larger body size/weight

1. Within species target smaller individuals and lay your egg in their nest. The smaller individuals can’t fight you off as well.

2. Target smaller birds of a different species.

a) Since the target species is a smaller bird, you are guaranteed of being larger. This is not necessarily so within your species.

b) Your parasitic eggs are then larger, as are your chicks. They will be better able to demand more food from surrogate parents.

c) Your larger & heavier eggs are more difficult to remove.
Great tits are larger

Blue tit parent + Blue tit egg
Parents can get rid of parasite egg
Chicks don’t survive

Blue tit parent + Great tit egg
Parents can’t get rid of egg
Chicks survive

Great tits are smaller

- Nesting survival (percent)
Male waterbug with eggs. Females make large energetic investment in huge eggs, but males carry them around for aeration. Two pages devoted to this in Alcock, but no one knows what the advantage to male parental care is for this species!
**How Much Care?**

Care issues for parents… some programmed, some adaptive

<table>
<thead>
<tr>
<th>Offspring Produced per bout of reproduction</th>
<th>Short-lived (or at end of reproductive life), one or few bouts of reproduction</th>
<th>Long-lived, many bouts of reproduction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Many</td>
<td>Resource allocation among offspring</td>
<td>Resource allocation between parents &amp; offspring and between offspring</td>
</tr>
<tr>
<td>Few</td>
<td>Sacrifice Self for offspring</td>
<td>Resource allocation between parents and offspring (sacrifice offspring)</td>
</tr>
</tbody>
</table>

Sibling Rivalry!!!
Natural selection works differently on male parent, female parent, offspring.

Calculations for mother:

How much effort to put into offspring x in terms of promoting my genes relative to:

- other offspring.
- another round of reproduction.

Reject/ignore young when the benefit to conserving resources for another mating outweighs the advantage of continued care.
Calculations for offspring:

I share genes with future offspring from the same mother.

At some point, my mother’s continued reproduction puts more of my genes in the population even though I lose parental care.

That is, the extra fitness I achieve from parental care is counterbalanced by the inability of my mother to add more shared genes.
When cost:benefit ratio is 2 or more (assuming 50% shared genes mother-offspring), better for mother to put all energy into future reproduction.
Example – Sacrifice self for offspring

African spiders (*Stegodyphus mimosarum*):

After female broods eggs, hatchlings eat mother!
Example – Sacrifice offspring for self

- Wing clipping experiment on birds
  - Storm petrels (long-lived)
  - Starlings/flycatchers (short-lived)
- Mild wing-clipping requires parent bird to make much greater energetic investment in foraging.
- Measure: Collect shed feathers of adults and nestlings. Can determine...
  - From feather growth rate >
    - how soon parents molted-in replacement feathers
  - From feather biochemical analysis >
    - health/nutritional state of bird
Storm petrels go after planktonic crustaceans and go on foraging trips that can last for several days.

Clipping wings is a big energetic hit on the parents.

Starlings are short-lived in comparison with petrels, and make less parental investment. Clipping wings still costs them.
Example – Sacrifice offspring for self cont’d

<table>
<thead>
<tr>
<th>Bird</th>
<th>Adults</th>
<th>Nestlings</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control Parents</td>
<td>Wing-clipped Parents</td>
</tr>
<tr>
<td>Storm Petrel</td>
<td>No difference</td>
<td>No difference</td>
</tr>
<tr>
<td>Starling, etc</td>
<td>Healthy</td>
<td>Compromised</td>
</tr>
</tbody>
</table>

Short lived, sacrifice self
Long-lived, sacrifice brood
Programmed (but not genetic!) differences in parental care

Uterine position determines the amount of testosterone exposure:

“2F” males have 1/2X the amount of T

“2M” males have 2X the amount of T
Compared with 2F males, 2M males:

- 2X the amount of T
- Mounted females more rapidly
- Produced more offspring over time
- Spent more time searching for females
- Spent more energy searching for females
- Spent less effort relative to parental care

2M males → less time spent in contact with pups

2M males → castrated → spent more time with pups

2M males → castrated → T implants → spent less time with pups
Parental Favoritism/Sibling Rivalry

• Rarely is parental care given uniformly to all offspring
• Examples:
  – Birds will often allocate more resources to the first egg laid.
  – Asynchronous laying (also in birds) encourages sibicide.
• This leads to… sibling rivalry!
  – Examples: Pigs, Great Egrets
Sibling rivalry in piglets:

Mother often has more offspring than teats.

The larger piglets can secure one or two teats, but the smaller ones must compete with each other.

The first few days after birth are the most critical – catch-22 situation: The piglets expend critical energy that they can’t afford trying to displace other piglets. Also they have sharp teeth and can wound each other in fights!

Older piglets lose the sharp teeth – they seem to be solely for the purpose of sibling competition!
Sibicide in the Great Egret

(Note - sibicide is animals with no parental care is a type of cannibalism)

• Asynchronous laying/incubation of young
• One chick will therefore be bigger than the others
• Often, bigger chick will attack the younger chicks and kill them
• Parents are passive and do not intervene... WHY?
Why parental care does not extend to protect against sibicide?

Experimental manipulation of egrets -- add or subtract chicks to nests to make equal or unequal sibling sets in terms of age/size.

More synchronous broods (chicks all the same size)

- More fighting, poorer survival

Less synchronous broods (chicks different sizes)

- Less fighting, better survival
• More chicks at the same age means more simultaneous care load on parents.

• If parents must ration care, best to let offspring sort out the optimum brood size: less food overall leads to more fighting.

• With plenty of food all the chicks may make it.

• With less food, the first big healthy one(s) will prevail.

• Better to raise one superior chick than multiple scrawny ones.
Sibicide in the Great Egret

OK, but why lay more than one egg in the first place?

– Food is often scarce
– But, in times of plenty, both eggs can survive – maximize chances relative to unpredictable environment.
– Better to raise one fit chick than two less healthy ones
– The more fit chick will live and pass on genes – selection for sibling aggression
Differential Resource Allocation by Sex

Songlarks: Female parental care.

Males grow faster: By 20 days after hatching, they are double the BW of females.

Mothers give more and better quality captured food to sons than to daughters.

When **male** birds fledge, it is the largest of them who is most likely to get a territory and mates – they are polygynous. So mother is protecting her genetic investment in male offspring.
Surrogate parenting and helper parents

The Oldfield Mouse (*Peromyscus polionotus*) experiments (Susan Margulis).

Socially monogamous rodents with parental care.

In the wild, OMs live less than a year, but can make a new litter every month.
Due to fast production of litters
- can have a female who is nursing and pregnant.
- can have previous older brood still in nest when new pups born.

So some juvenile females may experience parental care (Observe or take part as helpers).

Does this make them better future parents?
Large colony of mice

Make 2 groups:

- Remove juvenile females from nest = “inexperienced”
  - Raise in an all-female group (so no matings, offspring)
    - Pair with inexperienced male
      - Poorer nest building
        - Lower probability of brood survival

- Leave juvenile females in nest = “experienced”
  - Raise with pregnant mother until the 2nd brood weaned.
    - Continue in an all-female group
      - Pair with inexperienced male
        - Better nest building
          - Higher probability of brood survival
parenting ability improves with maternal experience

Inexperienced: Higher proportion of females not building nest

Experienced: Lower proportion of females not building nest
ALLOPARENTAL CARE

...family group members other than the parents provide care.

In primates an extreme level of alloparental care found in the Callitrichidae family (Marmosets and Tamarins).
Why take care of offspring who are not related to you?

Well, maybe they are!
Marmosets & tamarins...

- Average family group size:
  - 8.7 members
    - 4.4 adults
    - 2.9 subadults
    - 1.4 juveniles

The reproductive pattern is most frequently:
1) twins (fraternal)
2) triplets
3) singletons
4) quadruplets
• The *Callitrichidae* family is unique among the primates in having a single chorionic cavity and single circulatory system shared by all its embryos, so...

• *Callitrichids* twins are chimeric in some tissues: *in utero* transfer of cells between siblings gives each twin a combination of its own tissue cell type and its sibling tissue cell type.

• Chimeric tissues typically include hematopoietic or diverse blood cells (placenta, blood, spleen, and liver) but may involve all somatic tissues types.

• Twins in the *Callitrichidae* family also display chimerism in their germ-line tissues.
Fig. 1. Vertical transmission of sibling alleles in C. kuhlii, shown for microsatellite locus CK2

The grandfather and grandmother (P) are individuals that had self alleles (198/216) and (218/240), respectively. They gave birth to male twins (F1) with self genotypes of (198/240) and (216/218). One male (216/218) was found to have sibling alleles (198/240) present in his heart, spleen, and lung samples, which represented 50% of cells in those tissues and were not present in the hair, skin, and brain samples. This male was paired with a female (220/232). The pair's twin infants (F2) were both heterozygous and nonchimeric; sibling 1 inherited one allele from the father (216) and one from the mother (232). Sibling 2 inherited 220 from the mother and the sibling allele (198) that the father had acquired from his twin through horizontal exchange [8].

Uncle A is more related to his brother’s offspring B than you would expect, so A will help raise B.


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Germ line chimerism may be pretty common.

Analysis of 36 twin sets for chimerism (that is first exchanged horizontally and then passed on vertically) within 15 family groups:

Twins in 5 of the family groups passed on alleles to their offspring that represented alleles exchanged from their siblings *in utero.*
Some alloparenting references


