

## **Mating: Primate females and males**

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- As we have seen before, the bottom line in evolution is reproductive success
  - **reproductive success**: measured as how many fertile adult offspring an individual produces in its lifetime
  - any trait that increases reproductive success becomes more common in the next generation
  - mating and parenting behavior must have a big effect on reproductive success
  - so mating and parenting behavior should be particularly easy to explain in terms of costs and benefits to reproductive success
  - but only those behavioral tendencies that are heritable
    - since learned behavior is not inherited by the offspring, explanations based on reproductive success don't apply
    - so this approach can only explain general, heritable, inborn tendencies
- Explanations in terms of “strategies”
  - **strategy**: a behavior that is viewed (or "explained") in terms of its results.
    - example: howler monkeys eat small amounts of many different leaves, rather than gorging on any one kind
      - effect: ensures that they get all their different needed nutrients, and reduces exposure to any particular plant toxin
      - this is a “strategy” of eating wide variety of foods
      - as if the howlers do in for the purpose of getting varied nutrients and avoiding toxins
    - This does NOT imply that animals make conscious choices based on reproductive success calculations!
      - the only implication is that these behaviors must have led to greater reproductive success, and hence became common
    - it does not matter what physiological or psychological mechanism causes the behavior
      - continuing with the howler monkey's “strategy”...
        - maybe their digestive system is such that they get uncomfortable if they eat very much in one sitting, so they tend to move and encounter some other kind of food
        - maybe their taste receptors respond less after they have been stimulated for a while by a given food, so any given food provides a positive sensation only for a short time, so they move on to something else
        - maybe howlers have a tendency to be skittish and nervous, so they rarely stay in one place long enough to eat much of a given kind of food
        - the exact mechanism could probably be figured out by careful observation or laboratory study, but for the purposes of evolutionary explanations, it does not matter
      - all that matters is that the “strategy” affects reproductive success
        - as in “it makes them healthier, so they have more offspring”
      - ideally, we would actually measure how much the strategy improves individuals' reproductive success, but this is hard to do in practice
        - so we often assume that if a behavior improves survival or health, it probably improves reproductive success

- Male and female reproductive strategies differ
  - Female strategies are fairly consistent across different species
    - females have to support the offspring during pregnancy and lactation
    - so females have to invest a lot in each infant
  - Male strategies vary a lot from one species to another
    - males can get away with doing nothing more than mating
    - or they can invest more in the offspring
      - defending the female and offspring's access to food or water
      - defending the offspring from predators or infanticidal males
      - carrying the offspring from one feeding or sleeping place to the next, etc.
- Summary of female mating strategy
  - a female can easily get a mate when necessary
    - since a female only needs to get pregnant a few times in her life
      - and it is to the benefit of any male around to be the father
    - so among females, there is not much variation in success at mating
    - so there is not much selection pressure for females to attract mates in general
  - a female may or may not be picky about choosing a mate (depends on species and possibly other factors)
    - if the offspring's success varies a lot depending on the father, then selection will favor female traits that help get the best mates
      - this apparently only happens in certain species... more on this later
  - what really affects female reproductive success is food
    - so female behavior emphasizes access to food
- Summary of male mating strategy
  - males can have almost unlimited numbers of offspring
    - since males are not forced to invest a lot in their offspring
    - so male reproductive success can vary over a much wider range than females' reproductive success
      - in a typical species, females might range from zero to five offspring
      - in the same species, males might range from zero to fifty offspring
  - the more a male mates, the more offspring he has
    - in most cases, spending effort on additional mating increases a male's reproductive success more than would spending that same effort on caring for any one offspring
    - (a few matings are likely to provide another whole offspring, while that much care for an existing offspring only improves its odds of survival very slightly)
  - so in mammals such as primates, selection usually favors traits in males that lead them to mate frequently
- Female reproductive strategy basics:
  - female mammals are obliged to invest a lot in each offspring
    - they have to pay the energetic costs of:
      - pregnancy
      - lactation (nursing)

- both require the female to find and consume more food than she would otherwise
  - she has to travel more to do so
  - while carrying the dependent suckling infant
  - because of all this, exposing herself to greater risk of malnourishment or predation
- because of the duration of gestation and lactation, females can only have a limited number of offspring in their lifetime
  - unlike males, who can have very large numbers of offspring
  - so each offspring is a big part of the female's total reproductive success
    - biology requires a female to "put all of her eggs in just a few baskets"
  - example:
    - say a typical female can have five offspring
    - then if just one dies, her reproductive success is reduced substantially (20%)
    - or if she can manage to have one more, it amounts to significantly more of her genes in the next generation
    - vs. a male, who could theoretically have hundreds of offspring
    - so the survival of one more or less doesn't make much difference
- so among females, selection should favor traits that improve the chances of each offspring surviving to reproductive age
- a female's reproductive success can vary a lot depending on her ability to get enough food (and possibly other resources, like safe sleeping places, etc.) for herself and her infant
  - females must be reasonably well nourished to be fertile (to be able to get pregnant)
  - they must get sufficient food to have a successful pregnancy and to produce enough milk
  - they must be sufficiently well nourished to watch, carry, and defend the infant
- field observations indicate that finding enough food does appear to be a real limiting factor in female reproductive success
  - evidence of the importance of food to female reproductive success:
    - in places where wild primates have been fed by people, populations shoot up
      - due to increased production of offspring (not just immigration of animals from other areas)
      - because better-fed females mature faster, live longer, and produce more offspring separated by shorter intervals
      - so food was the limiting factor in female r.s.
    - in one case, among baboons in Amboseli National park in Kenya, when environmental degradation reduced food supplies...
      - female birth rates and infant survival rates declined
      - so food was, again, the limiting factor in female r.s.
- So, natural selection must have favored female behavior that maximizes access to food
  - so there is often strong competition for resources between females of the same group
- Female competition
  - it often happens that two females will both want the same resource
    - a bit of food, a good spot for drinking water, a resting place, etc.
    - this is contest competition, in which one or the other gets the resource
    - if one individual consistently wins over the other, it is the more **dominant** of the two

- the other is the more **submissive** of the two
- in some species, dominance may be independently negotiated between pairs
  - in this case, there is no pattern of which individual is likely to be more dominant
- in other species, certain females may be dominant relative to many others
- if, so, there is a **dominance hierarchy**
  - in the most clear-cut cases, there is a single pecking order from least to most dominant
  - this is a **transitive** dominance hierarchy
  - if A beats B, and B beats C, then A will beat C;  $A > B > C$ .
  - in less "transitive" systems, this might not always hold true
- the degree of development of dominance hierarchies varies widely from species to species
  - in some species, these relationships are very long-lasting; in others they are readjusted more or less frequently as individuals age, get sick, etc.
- the most clearly defined, stable, transitive dominance hierarchies occur in primates in which there is the most within-group contest competition for food
  - the dominant individuals get more access to preferred foods
  - and in some cases have been shown to also have higher total reproductive success
    - as measured by things like age at first birth (younger is better, from an evolutionary point of view)
    - interbirth interval (shorter is better)
    - births per year (more is better)
    - infant survivorship (more survivors mean better success)
  - there are some species in which the dominant individuals do NOT have higher reproductive success, but these are rare cases
- Question: if the most dominant females have the highest reproductive success, why do any females ever behave submissively?
  - losing a dominance fight could be costly
    - possible injury
    - energy wasted
  - so selection should favor females that
    - strive to be dominant over others (to win in contest competition)
    - but are able to recognize when they can't win, and back down submissively with minimal cost
- female strategies involve a trade-off between the amount of time the female can invest in each infant and how many infants she can have
  - there must be an optimum somewhere between two extremes:
    - investing all her effort in just one offspring
    - having the maximum number of infants by abandoning each at birth and immediately conceiving another
  - female primates do observably regulate their investment in offspring
    - initially, they care for the infant a lot
      - stay in full-time contact with it, carry it around, etc.
    - as the infant matures, the mother starts to cut down her investment

- she is less cooperative when the infant wants to suckle
- does not always pick the infant up when it is time to move, or is less cooperative with carrying it
- this happens as the infant is getting bigger and heavier
  - so the cost of producing more milk for a bigger infant is rising
  - and the cost of carrying it is rising
  - at the same time, the infant is more able to care for itself
  - so the benefit of caring for it is getting less
- the mother has to wean the infant (stop nursing it) in order to have another
  - because lactation inhibits ovulation
  - although I wouldn't count on it if I were you...
- this produces an interesting conflict of interest between mothers and infants
  - it is in a mother's interest to give just enough investment to each infant to maximize her total reproductive success
    - the mother will want to wean the infant and cut back on carrying it around, watching it, etc.
  - it is in the infant's interest to get the maximum possible investment out of the mother, at the expense of previous and potential future offspring, its siblings
    - the infant would do better if the mother kept feeding and caring for it indefinitely
    - so selection will favor infants who use any possible method to get the mother to provide more care
      - whining, clinging, manipulating
      - including at the expense of other siblings
  - so there is an evolutionary reason for both mother-child conflict and sibling rivalry...
- This applies to humans, but be cautious
  - we definitely have some heritable, inborn behavioral tendencies
    - for example, most individuals seek sex
    - most females care for their children
  - these behaviors are
    - so universal that they must be at least partially genetic
    - and so obviously related to reproductive success that they must be strongly affected by natural selection
  - but our inborn tendencies are shaped by a lot of learned behavior and very complicated individual thinking
    - there is a raging debate about how far to take evolutionary explanations of behavior in humans... just keep that in mind

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