

## Basic primate ecology: Predators and living in groups

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- Predation
  - predators that kill primates include
    - pythons
    - raptorial birds
    - crocodiles
    - leopards, lions, tigers
    - people
    - even other primates, like chimps that hunt colobus monkeys
  - predation obviously affects reproductive success
  - so selection will presumably favor physical or behavioral traits that minimize the chance of getting killed
  - what those physical or behavioral traits are will depend on
    - how severe the risk is
    - the particular nature of the predators
- So, why are primates social (why do they live in groups)?
  - most mammals do not live in groups
  - this suggests that being social must have some costs to reproductive success
    - more competition for food, since members of the same group are always nearby
    - more vulnerable to infectious disease
  - but there must be some benefits to sociality for primates.
  - Two main suggestions of possible benefits of sociality:
    - **Resource defense theory of sociality**: being in a group improves access to resources compared to being alone
      - Note: this is a theory about sociality (forming groups), which is different from the similarly-named theory about resource-defense territoriality that we looked at earlier
      - being in a group improves the ability of females to defend resources against other competitors (usually their own species)
        - which they would not be able to do as well if they were alone with their infants
        - females are the focus because females' reproductive success is more strongly affected by access to food than is males' reproductive success
    - this is likely to be true if:
      - food is relatively scarce and high in value
        - that is, the benefit of controlling access to it is high
      - food sources are in patches *small* enough that they can be defended
      - food patches are *large* enough to support several individuals in a group
    - these conditions are often true of fruits, a common part of primate diets
    - evidence that suggests that the resource defense theory is correct in some cases:
      - where ranges overlap, larger groups generally can defeat smaller groups of the same species for access to food patches

- females in the larger groups tend to have higher reproductive success than those in the smaller groups of the same species
- so the tendency to live in larger groups would be selected for...
- evidence against the resource defense theory
  - true, larger groups get more access to food patches, but individuals within those groups face greater competition for food within the patches from their fellow group members
    - Charles Janson's study of brown capuchin monkeys showed that individuals within groups varied by 37% in the calories of food they ate, while the average calorie intake of entire groups only differed by 3%
      - that is, there is much more competition *within* groups than *between* them
      - which argues against the resource defense model
  - there is not as neat a correlation between sociality and resource patchiness as we might hope
    - many highly social primates are folivores, which eat leaves that are not very patchy in their distribution
    - frugivorous primates, which should be most strongly affected by the need for resource defense, span the whole range from social to solitary
- **Predation theory of sociality:** being in a group offers better protection from predators
  - for (at least) three reasons
    - detection
      - being with others makes it more likely that some member of the group will detect an approaching predator
      - each individual can expend less effort on vigilance
    - deterrence
      - some primate groups could threaten some predators, but this applies more to other kinds of animals
      - some predators may opt not to attack primates if they are in groups, preferring solitary targets as a more productive strategy
    - dilution
      - the larger the group, the less likely that any given member will be the victim when a predator does attack
- evidence that supports the predation theory
  - terrestrial primates tend to live in bigger groups than arboreal ones
    - presumably because there are more predatory threats on the ground
  - many of the primate species that are less social are large, more able to defend themselves
    - without needing to be in a group to deter predators
  - some primates adjust their sociality (group size) to the degree of predator threat
    - macaques on predator-free islands form smaller groups than those on the mainland, where predation is more of a threat
- weaknesses in the predation theory
  - predation events are rarely observed, so it is hard to assess the actual threat
  - there is no clear association of predation losses with group size

- that is, the predation theory suggests that the higher the predation risk, the larger the groups the primates should form
  - that is, where we see greater predations, we should see larger groups
  - but there is no evidence that primates that live in larger groups suffer higher predation losses
    - of course, this may be because sociality is effective at *preventing* predation losses
- both theories (resource defense and predation) probably have some role
  - they are not mutually exclusive
- Primates should form groups of a size that balances the benefits of living in a group with its costs
  - benefits of living in larger groups:
    - *larger* groups can better defend resource patches
    - *larger* groups can better resist predators
      - sure enough, a study of Old World Monkeys finds that species with the greatest risk of predation do live in the largest groups
  - costs of living in larger groups
    - members of *larger* groups suffer from more competition from others within their own group
    - members of *larger* groups are exposed to more communicable diseases
  - So, what do they actually do?
    - terrestrial primates tend to live in larger groups than arboreal ones
      - due to higher risk from predators on the ground?
    - frugivores tend to live in larger groups than folivores
      - due to greater importance of defending highly patchy fruit sources?
    - diurnal primates tend to live in larger groups than nocturnal ones
      - maybe due to daytime strategies of resisting predators or spotting them and running away, which work better with larger groups
      - vs. nighttime strategies of hiding from predators, which work better with smaller groups
- Both of the theorized benefits of sociality are greater for females than for males
  - the benefit of resource defense sociality is maximizing access to food
    - and females' reproductive success is more strongly affected by access to food than is males'
  - the benefit of predation defense sociality is minimizing risk of predation
    - which probably affects adult males and females about the same
    - but certainly affects juveniles and infants more than adults
    - and the loss of an offspring to a predator potentially affects a female parent more than a male parent
      - females can only have a limited number of offspring in their lives
        - females have to invest a lot of energy in each offspring
        - so losing one is a large hit to her reproductive success
      - while males can potentially have a large number of offspring in their lives
        - they may invest very little in each one

- so losing one offspring is not necessarily such a big blow to a males' reproductive success
- of course, not all males have a lot of offspring
- but the payoff in reproductive success is higher for strategies that maximize mating, compared to strategies that minimize loss to predators
- so these theories mostly explain why females form social groups
  - for ecological reasons
    - based on the distribution of food
    - and the nature of predation
- Boyd and Silk at this point discuss some arguments about why these groups of females tend to have two characteristics
  - **female philopatry**: females born into the group stay in the group
    - as opposed to males born into the group, who move out as they reach maturity
    - leading to a group composed mostly of related females, with any males being unrelated
  - **dominance hierarchies among females**
    - dominant females can take away a subordinate female's position for feeding, drinking, sleeping, etc.
    - the rigidity of these hierarchies varies depending on how much "contest competition" there is between females
      - **contest competition**: competition in which one individual or the other gets the resource
        - as in fighting over a piece of fruit
        - success is determined by the interaction of two or more competing individuals
      - **scramble competition**: competition in which individuals do better or worse compared to an absolute standard, not to each other
        - as in some being better at finding food than others
        - success is determined by the individual's ability to do the task, not by her interaction with others
    - the type of competition depends on the distribution of the resource
      - resources that are rare and concentrated in patches encourage contest competition
        - two females might fight over a rare, tasty fruit
      - resources that are common and dispersed lead to scramble competition
        - in a huge tree full of tasty leaves, the limit to each female's feeding is her own ability and hard work, not what others do
    - the more important contest competition is for a species, the stronger the dominance hierarchy
      - so the patchier and scarcer the preferred foods or other resources, the stronger the female dominance hierarchy is
  - males' reproductive success is most strongly affected by how many times they mate
    - so they simply go wherever the females are
      - this creates a chain of causes:
        - the ecology of the primate species,
          - especially the distribution of its food
          - and the risk from its predators, causes...

- a resulting distribution of females
  - in an optimum size of groups of females
  - and degree of female dominance hierarchy
  - which in turn causes...
- a corresponding distribution of males
  - including the number of males in each group of females
  - and male behavior when in a group of females or excluded from any group
- male reproductive success depends on
  - maximizing their own matings
  - minimizing matings by other males with the same females
- so for males, females are resources to be defended from other males of the same species
  - in small groups of females (up to five), one male can typically keep other males away from the females
    - forming a small multi-female, single-male group
  - in large groups of females (over ten), there are typically half a dozen or more males
    - often with a male dominance hierarchy
      - because males are in intense contest competition for access to the females
      - dominant males can keep subordinate males away from females
    - lots of challenges to the dominant male(s)
      - by lower-ranked males in the group
      - and outsider males who want access to the group
  - intermediate-sized groups of females may have from one to five or six males
- so ecology causes the females to form groups of some optimal size
  - and the need to maximize matings causes one or more males to join them
  - with the number determined roughly by the number of females, which in turn reflects the food and predation environment
- why don't more males join the group?
  - because the ones who are there drive them off, to maximize their own matings
  - so there are generally either lone males or groups of males trying to get access to the females
  - leads to lots of hostile encounters
- why don't males just stay in the groups they are born into?
  - because the reproductive success of individuals who mate with close relatives is reduced
  - the females gain a lot of access to food and/or security from predators (ultimately, reproductive success) by staying in the group they were born into
  - so the males gain more by leaving and finding a different group of females
- This all results in a range of group sizes and organizations
  - mostly determined by the behavior of females, which in turn is determined by their ecological circumstances
  - we can classify the various types of groups into a number of typical patterns, based on group composition – the number of females and number of males
  - Each type of group composition generally correlates with a particular combination of:
    - a certain kind of ranging behavior by females

- a certain kind of ranging behavior by males
- a certain mating system that results from the first two factors
  - we will look at these mating strategies later
- **solitary**
  - group composition: females associate with their infants and young offspring
  - older offspring and males associate with no other individuals except to mate or fight
  - ranging behavior by females: each female has her own home range or territory
  - ranging behavior by males: each male has a home range or territory that includes the home ranges of one or more females
  - the only anthropoids that are solitary are the orangutans
  - all the other solitary primates are prosimians
- **monogamy (or monogamous)**
  - group composition: one adult male, one adult female, immature offspring.
  - ranging behavior by females: each female has her own home range or territory
  - ranging behavior by males: each male has a home range or territory that is the same as that of one female
  - monogamous anthropoids include all the lesser apes (hylobatids: gibbons and siamangs) and some New World monkeys
  - some prosimians are monogamous
- **polyandry (or polyandrous)**
  - group composition: one adult female, several adult males, immature offspring
  - ranging behavior by females: each female has her own home range or territory
  - ranging behavior by males: several males share the home range or territory of each female
  - only found among some marmosets and tamarins (New World monkeys)
- **one-male polygyny (or one-male polygenous)**
  - group composition: multiple adult females, one lucky “resident” adult male, immature offspring.
    - the excess males form groups that occasionally try to drive off the resident male
  - ranging behavior by females: multiple adult females share a home range or territory
  - ranging behavior by males: one resident male shares the females' home range
    - the rest of the males use home ranges that overlap with the females' home ranges, but the resident male constantly tries to drive them out of it
  - one male, multifemale groups are found among some anthropoids
    - gorillas (some groups have one male, some have a few)
    - New World monkeys: howlers
    - Old World monkeys: geladas, langurs
- **multi-male polygyny (or multi-male polygenous)**
  - group composition: multiple adult females, multiple adult males, immature offspring ("multimale, multifemale groups")
    - usually female-bonded (female philopatric; females stay with their relatives in the group they are born into, but males disperse when they reach maturity)
  - ranging behavior by females: multiple adult females share a home range or territory
  - ranging behavior by males: multiple males share the female's home range or territory.

- common among many anthropoids other than the hominoids
  - especially among Old World monkeys
    - cercopithecines (baboons, macaques, vervets, etc.)
    - some colobines
  - and New World monkeys (squirrel monkeys, capuchin monkeys, etc.)
- of course, these are idealized descriptions
  - reality is more complex, individuals and groups differ
  - and some species have common "violations" of the rules, such as matings other than the ones prescribed by the general system
- what about the hominoids (apes and humans)?
  - all the hylobatids (lesser apes: gibbons and siamangs) are monogamous
    - living in monogamous pairs with their juvenile offspring
  - orangutans: solitary
    - females forage with their immature offspring
    - males maintain a territory that includes the home ranges of one or more females
    - but rarely encounter them except to mate
  - gorillas: variable, but mostly one-male polygyny
    - small multi-female groups with one or a few males
    - The dominant male may monopolize access to the females, but not in all cases
  - chimps and bonobos: have complex social organizations that do not fit the general schemes
    - Females and juveniles have their own home ranges and spend a lot of time on their own
    - Males form a group that jointly defends an area that includes the home ranges of various females.
  - humans: similar to some other primates in some ways, very different in others
    - moderate group size
    - but individuals often forage separately or in small sub-groups
    - tend to be territorial, but highly variable
    - mostly monogamous mating
      - long-term but not necessary permanent pairs
      - males typically invest a lot in offspring
    - unlike other monogamous primates, human breeding pairs do not live in isolation
      - instead, the pairs live within multifemale, multimale groups
      - this is unique among primates, if not among all mammals
    - we will look at why humans might have this strange social organization, and what effect it might have had on our evolution...