

Introduction to Biological Anthropology: Notes 11
Basic primate ecology: Food and territory

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- We want to understand the reasons behind
 - the lifestyles of our non-human primate relatives
 - their physical traits, both the ways they are similar to ours and how they are different
 - their behavior, both how it is similar to ours and how it is different
- that is, we want to understand the evolutionary pressures that led other primates to become the way they are
- if we understand how natural selection has shaped non-human primates, then
 - we will have good tools and analogies for understanding our own ancestors
 - who we cannot observe directly, since they are long gone
- Recap of a key concept: **reproductive success**
 - recall that evolution is only partially the result of differences in how well individuals survive
 - what really matters is how much they *reproduce*
 - the traits of the ones that leave the most offspring become more common
 - this is often expressed in terms of **reproductive success**
 - the number of offspring that an individual has that are fertile and survive to reproductive age
 - this is the net result of many factors, including
 - surviving
 - being healthy enough to be able to mate and have offspring
 - successfully competing for mates
 - caring for offspring so they make it to reproductive age
 - parental care is important in some species, and less so in others
 - plus anything else that affects the number of surviving offspring
 - we will try to explain physical and behavioral traits of primates in terms of how they contribute to maximizing reproductive success
 - a physical or behavioral trait would have been favored by natural selection if it helped in any way to increase the number of surviving, fertile offspring
 - improved the individual's chances of survival
 - overall health
 - success in mating, etc.
- In order to understand primates' physical and behavioral traits, and to realistically assess how the traits affect their reproductive success, we need to understand the ecology of primates
 - that is, how they fit into their environments
 - which includes both the physical surroundings
 - and other primates
- The ecology of primates (like other animals) depends on a number of variables
 - Boyd and Silk emphasize two main ones
 - finding, processing, eating, and digesting food

- avoiding predators
- Food requirements
 - food provides the energy (calories) required for an animal to survive and grow
 - how much food is needed? That depends on:
 - **Basal metabolic rate**
 - the rate an animal expends energy just to stay alive while at rest
 - can be measured in calories per hour
 - larger animals require more energy to maintain their bodies than smaller ones
 - so larger animals have a higher basal metabolic rate, and have to eat more total calories per day just to stay alive
 - but as we look at animals with larger and larger bodies, the metabolic rate (calories per hour) rises more slowly than the body weight
 - a larger animal needs fewer calories per pound of body weight than a smaller animal
 - so a smaller animal has to eat more relative to its body weight
 - so smaller animals generally have to concentrate on foods with a high caloric payoff per pound or per volume of food
 - like insects, gum, fruit
 - these are usually fairly scarce
 - think of hummingbirds, eating high-sugar flower nectar
 - all animals would be happy to subsist on such high-quality food
 - but there just is not enough of it around, or it is distributed in packages too small, to support a large-bodied animal
 - while larger animals can eat foods with lower caloric content per pound or per unit volume
 - like leaves, bark, etc.
 - think of elephants, which eat leaves, straw, woody plant parts
 - the elephant has to eat these in large quantities and digest them for a long time
 - these foods have fewer calories per pound of food
 - but are widely available, so a large animal with a lower requirement of calories per pound of body weight can find enough
 - but a small animal could not stuff enough of these foods into its body at one time to get the calories it needed
 - **activity** requires additional energy
 - so a typical animal might need to eat enough to provide twice its basal metabolic rate
 - thus a very active animal needs more food than one that moves slowly
 - **growing** requires additional energy
 - so infants and juveniles need to eat relatively more than their body weight and activity level would suggest
 - **reproducing** requires additional energy, primarily for females
 - **gestating** (being pregnant) requires additional energy
 - the additional calories required increase from almost none right after conception, to about 25% of the female's normal requirement as birth approaches
 - **lactating** (producing milk) requires even more than pregnancy

- lactation increases a female's caloric needs about 50%
- she is "eating for two" (or really "one and a half")
- these are crucial differences between male and female primates
 - females often need more food than males
 - females' reproductive success is *more* dependent on getting adequate food than is males'
 - even an undernourished male can sire an offspring
 - but an undernourished female may not bear a healthy infant, or may not be able to raise it to adulthood
 - this means that for females, access to food plays a greater role in natural selection than it does for males
- Food sources: different primates concentrate on many different foods
 - primates (and other animals) need two general categories of foods
 - some foods that provide carbohydrates (calories; energy)
 - other foods that provide protein (amino acids)
 - plus small amounts of minerals (sodium, iron, calcium, etc.)
 - and the diet should not have too much of any chemicals that are toxic or impede digestion
 - which means avoiding eating certain plants and animals
 - like most mammals, primates also need to drink water
 - most need water at least once a day
 - most primates eat many different foods, often 50 or more kinds
 - but each species emphasizes certain foods more than others
 - most prosimians get
 - carbohydrates from gum and fruit
 - protein from insects
 - most anthropoids get
 - carbohydrates from fruit
 - protein from insects or young leaves
 - most primates are fairly focussed on certain types of foods
 - Bushbabies (or galagos), a kind of prosimian, get 70% of their diet from insects, 20% from fruit, and 10% from gum
 - Spider monkeys get 80% of their diet from fruit, and 20% from leaves
 - Langurs get about 65% of their diet from leaves, 25% from fruit, and 10% from flowers
 - chimps eat mostly fruit, with smaller amounts of leaves, insects, very occasional meat, etc.
 - etc.
 - but while one type of food usually predominates, most primates do eat a variety of foods
 - unlike many other animals, they are not highly specialized on one particular kind of food
 - Types of diet by main emphasis:
 - **insectivore**: insect eater
 - insectivores are usually small
 - insects provide good quality, rapidly digestible food, but in small packages
 - larger animals would have trouble getting enough food if they depended on insects

- unless they had some highly efficient method of getting a lot of them, like the long, specialized tongue of an anteater
- while small animals have to depend on rapidly digestible food, because of their relatively higher metabolic rate
 - they simply can't hold enough low-quality food to get the calories they need
- insectivores typically have
 - high, pointy cusps on the teeth, including the molars, for breaking into the insect's tough exoskeletons
 - short, simple digestive tract
- **gummivore**: plant gum eater
 - gummivores are also usually small
 - same reasons as insectivores
 - gummivores typically have
 - sturdy incisors, and sometimes canines, that stick forward and are shaped for gouging into bark and scraping off gum
 - short, simple digestive tract
- **frugivore**: fruit eater
 - frugivores tend to be intermediate in size
 - fruits have fewer calories per pound than do insects and gum, but are still much better than leaves and other plant parts
 - fruit is typically more widely available, and in larger package sizes, than insects or gum
 - frugivores typically have
 - wide incisors for scraping out the meat of fruits from their rinds
 - low, rounded molar cusps for pulverizing fruit
 - often have large stomachs to hold the bulky leaves and other plant parts they eat along with the fruit
- **folivore**: leaf eater ("foliage")
 - folivores tend to be intermediate to large in size
 - leaves offer relatively few calories per pound, but are very plentiful
 - but an animal has to be relatively large to physically process enough leaves
 - and must have relatively lower caloric needs per pound of body weight, as larger-bodied animals do
 - folivores typically have
 - sharp, ridged molars for shearing leaves into small bits
 - long, more specialized digestive tract for processing a lot of leaves
 - often with a specialized section to house microorganisms that break down cellulose
 - often with a very large stomach to hold the large volumes of leaves required to get enough calories
- no primates are predominantly carnivore (unless you count insects as "meat")
 - some primates occasionally eat some other vertebrates, but it is not a predominant part of the diet
- human diet is unusual among primates
 - even more generalized (less specialized) than the rest

- we are too big to be insectivores or gummivores
 - and we lack specializations for catching lots of insects or scraping gum
- our teeth lack the specialized traits that would make them particularly effective for any one food
 - we don't have pointy canines for breaking into fruit, nor wide incisors for scraping pulp out of rinds
 - we don't have ridged molars that would help shear up foliage
- we have fairly long digestive tracts that can handle some foliage
 - but not the great length, large storage volume, or specialized cellulose-digesting sections that are needed for a committed foliage diet
- most humans (even in the distant past) apparently ate more meat than most, and probably all, other primates
 - but even so, typical pre-agricultural humans ate much more plant food than meat
 - we don't have dangerous canines, claws, or other physical features that would help us acquire and consume all this meat
 - bare-handed, a chimp is a much more formidable hunter than a human - yet chimps eat much less meat than humans
- humans can eat almost anything, but are not well adapted for any one kind of food in overwhelming amounts
- apparently our ability to acquire and pre-process food using our hands and tools have substituted for the physical adaptations that other primates have
- Food distribution
 - most primates live in tropical forests
 - where there are many different kinds of trees, but often individual trees of any given type are widely separated
 - we are used to forests of oaks, for example, where you find one oak tree after another, and acorns are all around
 - tropical forests are much more variable; once you finish with one fruit tree, finding another of the same type means searching and travelling a bit
 - that is, the resource distribution is "patchy"
 - preferred foods are usually available only in certain seasons
 - so the patchy distribution of resources such as fruits, specific types of young leaves, etc. is constantly changing throughout the year
 - at different times, different foods are available, at different locations
 - primates, like most animals, have a **home range**
 - an area that they consistently use, move around in, etc.
 - the size of an animal's home range (and its population density) depends on the distribution of its preferred foods
 - Folivores (leaf eaters)
 - leaves are widely distributed
 - many kinds of trees produce edible leaves
 - available most of the year
 - so folivores can get enough food in a fairly small home range

- Frugivores (fruit eaters)
 - fruits are concentrated in certain trees
 - many trees do not produce edible fruits
 - any given tree produces fruit only for a brief period each year
 - so frugivores typically need a larger home range in which to find enough food throughout the year
- Insectivores and gummivores
 - comparisons are not as sharp as the one between folivores and frugivores
 - but insects and gum are less dense in the forest than are leaves
 - so, like frugivores, insectivores and gummivores also tend to need larger home ranges than folivores
- Again, humans in the past were probably quite different
 - since humans could exploit a wider range of different foods, the distribution of humans' food resources would be more complex
 - humans might also be affected by the distribution of animals to hunt or carcasses to scavenge from
 - and also other, non-food resources like stone to make tools from
 - so non-human primates can show us the typical primate situation, and then we can look at how humans have varied from that baseline
- Activity patterns
 - What primates do
 - major activities that occupy most of a primate's time
 - eating
 - travelling
 - recap of locomotion terms
 - quadrupedal (usually implies palms down)
 - bipedal
 - quadrumanual
 - brachiation
 - vertical clinging and leaping
 - knuckle walking
 - resting, either alone or in social groups
 - minor activities that occupy only a small fraction of a primate's time, but may still be very important
 - grooming
 - playing (especially young)
 - fighting
 - mating
 - of course, the amount of time spent in each of these activities may vary according to the season, distribution of food at the time, etc.
- When they do it
 - **diurnal** - active during the day
 - almost all anthropoids are diurnal

- **nocturnal** - active during the night
 - more than half of the prosimians are nocturnal
 - typically smaller, less social, and more exclusively arboreal
- **catheemeral** – active intermittently both day and night
 - only a few primates follow this pattern
- the common ancestor of primates was probably nocturnal
 - because the majority of prosimians are nocturnal
 - and they appear to be the less derived branch of primates
- Where they do it
 - most primates sleep up in trees
 - most spend a lot of their waking time in the trees, too (arboreal)
 - but many also spend some time on the ground (terrestrial)
- Ranging behavior
 - almost all primate groups have a **home range**
 - the relatively well-defined area through which the group of animals moves while searching for food and places to rest or sleep
 - some primates defend the boundaries of their home ranges, excluding members of other groups
 - when a home range is exclusive and defended it is called a **territory**
 - territorial primates advertise the limits of their territories by vocalizing (howling, etc.)
 - and they often patrol the boundaries to drive off interlopers
 - so the ranges of territorial primates do not overlap
 - other primates do not defend the boundaries of their ranges
 - they are not territorial
 - so the ranges of non-territorial primates may overlap
 - so groups may encounter each other on the border or within overlapping ranges
 - responses to these encounters vary
 - they may fight
 - there may be a dominance relationship in which the lower-ranking group gives way to the higher-ranking group
 - such as letting the other group have access to water or food
 - or they may just mix together peacefully, although not many species do this
 - why are some primates territorial and others not?
 - why do the non-territorial ones vary in how they treat neighboring groups, from peaceful interaction to fighting?
- But first, a word about explaining behavior
 - the fact that many behaviors are typical of particular species tells us that they are to some degree genetic, that is, heritable
 - so we should be able to understand the evolution of behaviors in the same way as we understand the evolution of physical characteristics like beak depth
 - usually by looking at the relative cost and benefit of a given behavior
 - "cost" means how something reduces an individual's reproductive success
 - "benefit" means how something increases an individual's reproductive success

- if the benefits of a behavior outweigh the costs, the net effect is an increase in the individual's reproductive success
 - natural selection will automatically favor individuals who behave in that way
 - if there is a genetic component to the behavior, then it will become more common with each generation
 - so we can "explain" behaviors by figuring out how they create a net increase to the reproductive success of the individuals who do them
 - OK, so why are some primate groups territorial, and others not?
 - that depends on the evolutionary costs and benefits of being territorial
 - depending on the environment, territoriality may or may not be advantageous
 - territories probably have one or two kinds of benefits
 - better defense of resources (**resource-defense territoriality**)
 - from other primates who eat the same food, sleep in the same kind of tree, etc.
 - often means from others of the same species
 - benefit: better access to food, water, etc., leading to better health and survival, leading to more offspring
 - better defense of mates (**mate-defense territoriality**)
 - not from predators!
 - from competing males of the same species
 - benefit: male is more likely to father the offspring of the female(s) he is “defending”
 - note that defense against predators is really is not an issue for territoriality
 - it would be impossible for primates to exclude predators from an entire territory
 - costs of territoriality
 - requires vigilance (patrolling, listening, etc.)
 - advertising one's presence
 - active defense
 - these behaviors increase risks of injury and predation, and reduce time and energy available for foraging, eating, and mating
- so when do the benefits outweigh the costs?
 - depends on the distribution and quantity of food and mates
 - resource-defense territoriality probably provides more benefits than costs when
 - resources are scarce
 - so the benefit to monopolizing the resources is relatively high, since hunting for another patch would cost a lot of time and energy
 - resources are concentrated in patches
 - that are small enough to be defended
 - the cost of defending a small patch is not too high, but the cost of defending a large area *is* high
 - because a larger patch has a longer perimeter to control, and more area to keep watch over
 - but big enough to be worth defending
 - a patch is "big enough" if there is plenty of food for the group

- very small patches would lead to too much competition between the members of the same group
 - example: an environment with occasional trees full of fruit might encourage resource-defense territoriality
- mate-defense territoriality probably provides more benefits than costs under some circumstances
 - but hard to calculate the costs and benefits in real cases, so this explanation rests on indirect evidence
 - evidence: in some species, like gibbons and siamangs, only the males try to drive off neighboring groups
 - the reproductive success of both males and females is affected by their ability to get enough food
 - but the reproductive success of females is *more* dependent on getting enough food, because females need additional food for gestation and lactation
 - so if females don't mind intruders, it suggests that intruders do not significantly reduce their access to food
 - but only males' reproductive success is affected by the presence of other males
 - foreign groups will usually include males
 - and those foreign males could mate with the females
 - denying the original males that opportunity to have an offspring
 - but the females are equally reproductively successful regardless of whether they mate with a local male or a foreigner
 - the offspring is equally theirs in either case
 - so the fact that in some species only males act territorial suggests that competition for food is not the issue in these cases, but male-male competition for mates is.