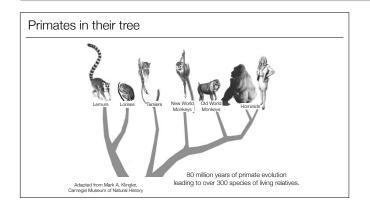
Primate Mating Systems

January 13, 2022

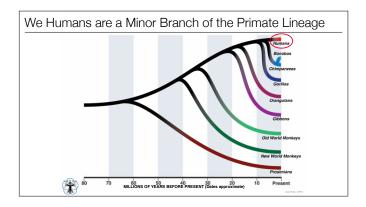
ANBI 116 Evolution of Sex

Pascal Gagneux

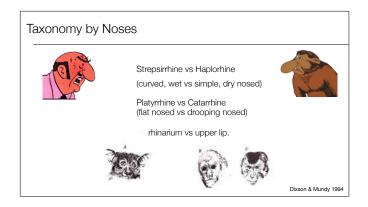


A Phylogeny, think of it as the grand summary of past mating behavior, at least those sexual encounters that led to successful reproduction and survival. Primates range from nocturnal and solitary to diurnal and highly social. R Sapolsky has reminded us that one of our specials as social primates seems to be to make each others lives miserable.

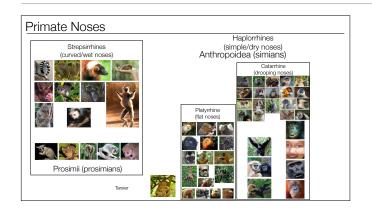
The precise number of primate species ranges from 300 to 600 species, depending on who's classification you accept.



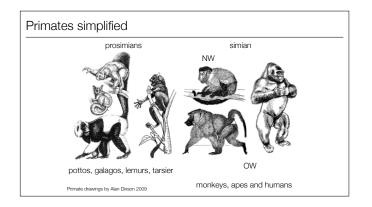
Time estimates for the divergence (branching) of the major primate lineages



Taxonomic names for primate groups are based on nose shapes and the morphology of the upper lip. in prosimians, the upper lip is still split and is part of the rhinarium typical of most mammals.



A few examples of each major group of primates. The name "primate" reflects human narcissism, considering ourselves among the "firsts".



Examples of prosimian primates. Left: (lower) The ruffed lemur (*Varecia variegata*); (middle) Lesser bushbaby (*Galago senegalensis*); (upper) The potto (*Perodicticus potto*). Right: A tarsier (*Tarsius spectrum*). After Schwartz(1987) and Clark (1962). Examples of anthropoid (simian) primates. Left: (lower) An Old World monkey, the baboon (*Papio sp.*); (upper) A South American capuchin (*Cebus sp.*); Right: A silverback male gorilla (*Gorilla gorilla*) beating its chest. After Clark (1962).

Modern Primatology: searching for the Origins of the Human Family?

Kinji Imanishi



Toshisada Nishida



Modern primatology started in Japan. Among the key question driving early Japanese primatologists was the question about eh origin of the family in humans.

Practice question: How come modern primatology started in Japan? Japan is one of the few countries that industrialized early and had large populations of local monkeys (Japanese Macaques).

Monogamy (sequential) Gibbons and Siamangs



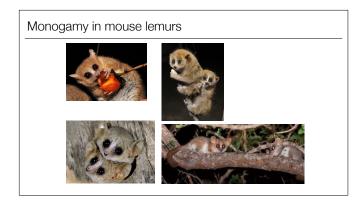
Serially monogamous apes gibbons and siamangs. These species of arboreal apes are known as the lesser apes. some have distinct coat colors in males and females of the same species. Brockelman and Reichard have observed male replacements in Khaoyai Natl Park, Thailand.

Monogamy (sequential) Aotus and Titi monkeys

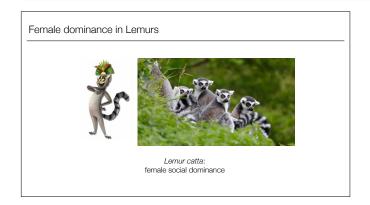


Several species of small South American monkeys live in very stable monogamous pairs: Aotus and *Callicebus* monkeys. Male replacements have also been observed in *Aotus azarai* in Northern Argentina. In these species, males carry infants most of the time and males and females look practically identical.

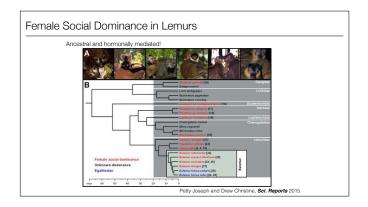
Practice question: which species of South American monkeys are monogamous? Owl monkeys and Titi monkeys.



Monogamy also exists in the tiny mouse lemurs of Madagascar, over 20 species of these little nocturnal primates have been described.



The famous ringtail (catta) lemurs are one of many larger lemur species with female social dominance. King Julien should really have been Queen Julienne.



In (A), male and female *Eulemur* (shown from left to right as *E. rubriventer*, *E. macaco flavifrons*, *E. coronatus*, *E. mongoz*, *E. fulvus collaris*, and *E. f. rufus*) are sexually dichromatic, but size monomorphic. In (B), FSD (depicted by species shown in red) is widespread across the strepsirrhine lineage (as is female genital masculinization), and appears to be diminished (depicted by species shown in purple) in only one of the most recently evolved clades of lemur, the Eulemur (identified by the box within Lemuridae). In the remaining species (depicted in black), social structure is either unknown or the species tends to be solitary.

- 1. Female and male genitalia in Eulemur species, females have larger scent glands and an elongated pendulous clitoris.
- 2. Eulemur species expressing female social dominance differ in their behavior from egalitarian Eulemur species: more female dominance (supplants), scent marking, aggression, but males in female dominant species still have much higher Testosterone.
- 3. Females in female socially dominant species are hormonally "masculinized" relative to Eulemur species with sexual co-dominance.

Female spider monkeys





no female social dominance

Spider monkeys (Ateles) in South America have "masculinized" genitalia, but no female social dominance.

Spider monkeys live in fission fusion social groups and females mate with a large number of males each cycle. High levels of "clandestine/hidden" copulations have been observed.

Sexual Mimicry in adolescent Gibbons

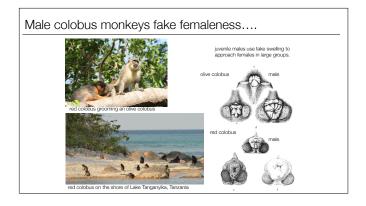




Nomascus leukogenis/gabriellae Mechanism to mitigate against femalefemale (mother daughter) competition?

White and yellow cheeked gibbons evolved transient sexual mimicry by young females. All infants are born buff colored, matching their mothers' coats. Adolescent males and females turn black, except for the light cheeks. Upon reaching sexual maturity, female turn back buff around the time they leave their parental territory.

The mimicry involves an elongated clitoris and fat pads under labia, looking like testes. It is good enough to have fooled many zoo veterinarians....



Colobus monkeys (so named because they lack thumbs, a feature independently evolved in South American spider monkeys) have male pseudo swellings.

These pseudo-swellings allow bachelor males to approach large single male groups and gain access to females.

Abduction of juvenile mates in Hamadryas baboons









falies abduct juvenile females and assemble a future "harem" Hans Kummer **Primate Societies: Group Techniques of** *Eco-logical Adaptation (1971)*

Hamadryas baboons abduct young immature females to build their exclusive access female groups. Males will also abduct females from other males and will risk injury to rescue such "stolen females".

During rescues, females who have been abducted a second time, will willingly return to their original abductor! This forced movement of females is the only instance of female exchanges between groups in baboons that usually have exclusive male dispersal.

Practice questions:

Which sex usually disperses to other social groups in most primates? Males.

Name four species of primates where females frequently disperse into other social groups: Chimpanzees, bonobos, Hamadryas baboons and humans.

Good fathers are sexy: Barbary Macaques





Macaca sylvanus: The only African Macaque species male parenting efforts rewarded by reproductive access to females

In Africa's only macaque, the barbary macaques, males woe females by demonstrating how well the bond and care for juveniles, especially male infants. Females appear to use capacity for paternal care as a read out for choosing their mates.

Practice question:

What type of male behavior could inform females on the fathering capacity of a potential mate?

His behavior towards youngsters in the group.

Female control in callitrichids (Marmosets & Tamarins)

tiny, territorial, and cooperatively polyandrous









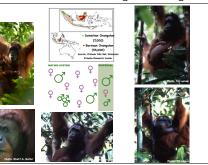
Cebuella, Callithrix, Saguinus, Callimico, Mico: dominant female suppresses reproduction in other group females, multiple males who provide paternal care

Many of the dwarf monkey species of South America known as Callitrichids live ion family unit with multiple males and a single reproductive female. The dominant female produces twins that are cared for by the males and the older sibs.In contrast to most other primates, lactation does not cause cessation of ovulation (lactational amenorrhea) but rather female callitrichids can get pregnant very soon after giving birth and while lactating.

Practice question: Which species of primate has dominant females that suppress reproduction of younger relatives?

Marmosets and other callitrichids.

Dispersed and alternative male strategies: Orangs

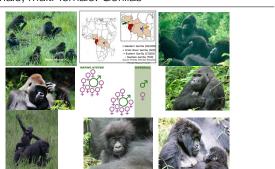


Alternative male strategies in orangutans: Orang utans have large flanged males who are mostly solitary and try to attract females with their songs.

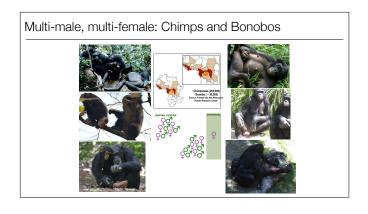
Smaller males reach sexual maturity without developing flanges, and gang up on females and force copulate females. Up to 50% of the offspring in Orangutans result from such forced copulations.

Male strategy is plastic as small males can start growing into flanged males if the social circumstances are right, i.e. they are the only male around such as in zoos after removal or death of the former large male.

Single male, multi-female: Gorillas



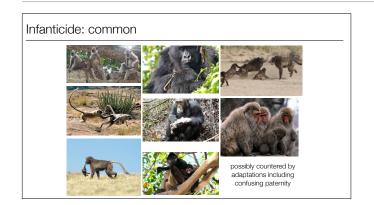
Gorillas form mostly single-male, multi -emale groups. There is intense male-male competition but almost entirely in the form of fighting for the role of silverback. Once established, a silverback and sometimes two brothers have exclusive reproductive access to the group's females.



Both of our closest living relatives, common chimpanzees and bonobos live in fission fusion, multi male multi female units. Each female will copulate with a large number of males in her group and sometimes even outside her group during each of her fertile cycles. Common chimpanzee are male dominated and bonobos are female dominated. Female bonobos control male aggression by physically punishing male dominance behavior.

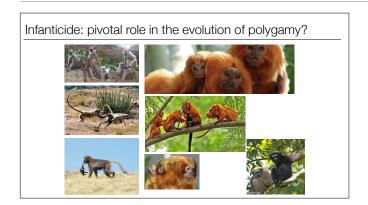
Common chimpanzees sometimes form "consortships" where a couple disappear for most of the female's ovulatory period. At sexual maturity it is the females that leave the social groups and join neighboring groups

Practice question: Do chimpanzees ever form temporary pair bonds? Yes, these are called consortships, and can result from female choice as well as involve male coercion....

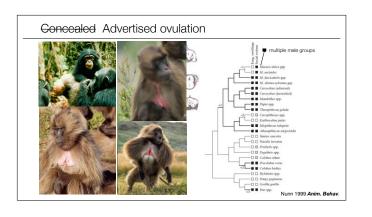


Infanticide among non-human primates is common. First clearly documented as normal part of primate behavior by primatologist Sarah Hrdy in Hanuman langurs in India. Males taking over another male's female group kill infants that are still suckling and by doing so, cause these females to resume ovulation.

Female primates can also kill offspring of other females, possibly as the result of female-female competition over resources.



The hypothesis that monogamy could have evolved to protect against infanticide is unlikely to explain all primate monogamy.



Advertising of ovulation is a derived trait in primates. There is a strong correlation between multi-male social organization and female sexual swellings, usually around the genitals but sometimes on the chest of females as in Gelada baboons, that also have male sexual skin display of the chest..giving them their name bleeding heart monkeys.... Practice Question: What do most species of primates that have conspicuous genital swelling in females have in common? The females of these species mate with several males of the group during each

Culture and Reproduction



Menstrual hut (Dogon country, Mali): ovulation.

Cultural convention forces honest signaling of ovulatory period.

Many human societies have menstrual taboos.

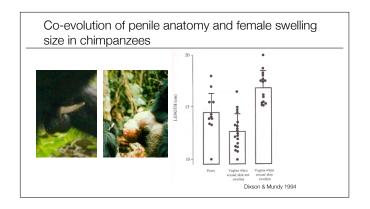
"Deconcealing" ovulation?

Human females have no overt signs of ovulation. Menstruation in human appears to be exceptionally strong and involves enough blood loss in many cases to contribute to anemia in many women around the world. Several cultures have evolved ritual menstruation huts, where menstruating women are expected to sequester during their periods. This represents a cultural way of forcing women to publicize that stage in their cycle.

Practice question: Human females do not advertise their ovulation status by any external signs. How doe certain cultures force females to divulge their ovulatory status? Many cultures have menstrual taboos and/or menstruation huts, this tells other members of the group that these females are not pregnant and will be resuming ovulation shortly.

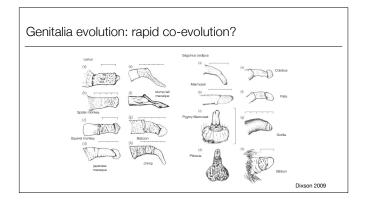


Chimpanzees about to mate in a tree in Gombe National Park, Tanzania. the "filiform penis" of the male has co-evolved with the female vagina that becomes elongated during each swelling.



Comparison of chimpanzee penis length variation with that of the vagina, both not swollen and swollen.

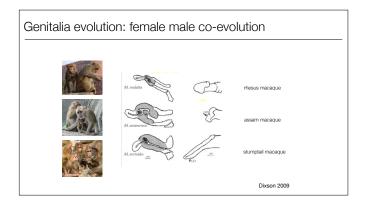
The swollen vagina is 80 % longer! Chimpanzees with longer penises can place their copulatory plug out of reach of males with shorter penises.



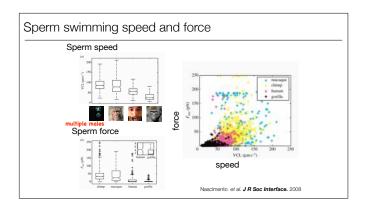
A sampling of non-human primate penises.

The barbed penises of lemurs actually trigger ovulation during mating. Simian primates are all spontaneous ovulators and have lost the penile barbs present in most prosimians.

Practice question: Which group of primates have large penile barbs? Prosimians including lemurs.



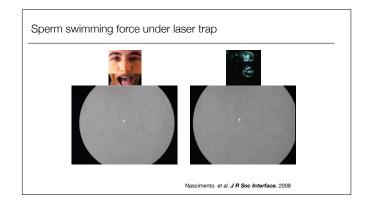
Co-evolution of vagina and penis morphology in macaques. Female non-human primate reproductive tracts have not been studied as well as male penises.....



Study of sperm swimming speed and force in four species of primates including humans. Using laser beams as "tweezers" individual live sperm can be captured by the light beam and by dialing down the force of the light, the swimming force of each sperm cells can be precisely measured. Chimpanzees and macaques have sperm that swim faster and with much more force, reflecting higher levels of sperm competition that gorillas and humans.

Practice question: Why are chimpanzees and macaques making sperm that swim faster and with more force than humans and chimpanzees?

Chimps and macaques have much more intense sperm competition.



Human and chimpanzee sperm held and escaping laser traps, at UC San Diego bioengineering lab (collaboration with Dr Mike Berns)



Collection of sperm from captive chimpanzees is relatively easy. Gorillas are much more difficult as masturbation in gorillas is much rarer.



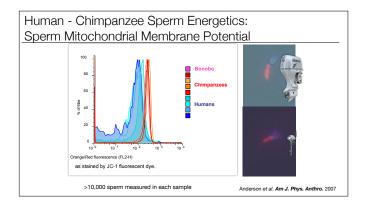
Collection of sperm from captive chimpanzees is relatively easy. read the story on in the Atlantic:

https://www.theatlantic.com/magazine/archive/2010/10/fertility-rites/308217/



A freshly collected chimpanzee ejaculate. The seminal fluid contains special proteins that cross-link and form a tough (gummy bear like) copulatory plug.

Mammals with much competition at the level of insemination often have males trying to "cork shut" females. The 3 billion plus sperm ejaculated by this male chimpanzee can be seen in the right most section and appear white. The sperm are not trapped in the plug but rather delivered just prior to the seminal fraction that from the plug. insert is a drawing of plug by Dixson.

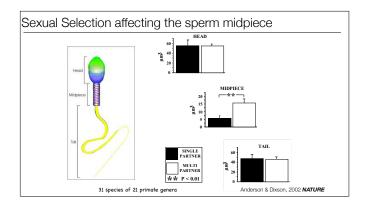


Measurement of energy production in the mid-piece of sperm from bonobos, chimpanzees and humans.

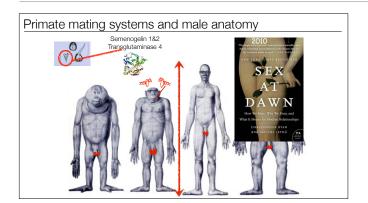
Compared to both apes species, humans have relatively low energy sperm. The red fluorescent dye reflects energy production by the mitochondria in the mid piece of the sperm.

Practice question: where are the mitochondria that provide much of the energy needed for sperm motion?

In the midpiece of the sperm.



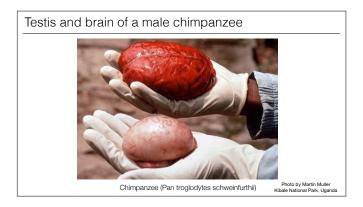
The volume of the sperm engine (midpiece housing the mitochondria) is larger in multi-male species

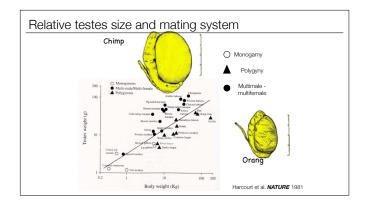


The paleofanatsy book such as "sex at dawn" on how we should all realize our inner bonobo are not really supported by biological evidence! Humans have: small testicles, small numbers of sperm, low energy, slow and weak sperm, and lack a copulatory plug!

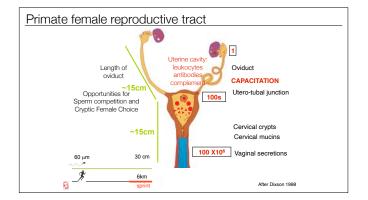
Practice question: What is some of the evidence arguing against humans having had a bonobo like mating system until recently?

Small testes, low sperm number, slow sperm, lack of copulatory plug.





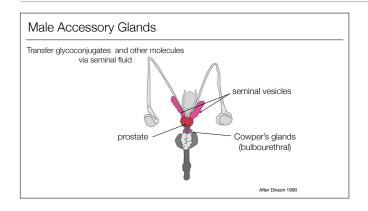
Relative testes size correlates with body size in primates, but deviations from expectations is indicative of prevailing mating system and levels of sperm competition. Most of the multi-male species are above the regression, with some exceptions such as spider monkeys.



Most sperm perish in the uterus at the hands of female immune cells. The arrival of sperm in the uterus after insemination triggers an outflow of immune cells (neutrophils and macrophages). In a large ape or human the tract measures approx. 30 cm from vagina to ampulla of the oviduct where fertilization occurs.

From the point of view of a sperm, which we all where at a point..... This amounts to a 5k run.

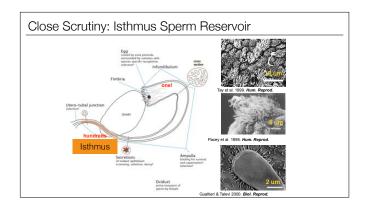
Practice question: at the scale of a sperm, how long is the journey through the female reproductive tract to the site of fertilization? approx 6km/3.5 miles.



Male mammals have evolved several accessory glands that produce large volumes of secretions (seminal fluid) packed with molecules that help sperm survival and function.

Practice question: What are male accessory glands?

The glands that produce much of the seminal fluid, prostate, seminal vesicles and Cowper's gland.

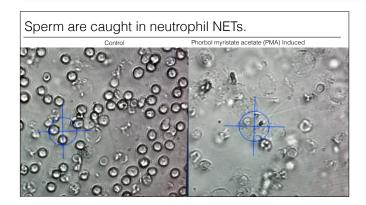


In the lower and narrow part of the oviduct (=fallopian tube=salpynx) female hold sperm in a tight and prolonged, hours to days, cellular embrace.

This allows further scrutiny of each sperm, prior to allowing each to dash off towards an ovulated egg.

Practice question: What is the isthmus sperm reservoir?

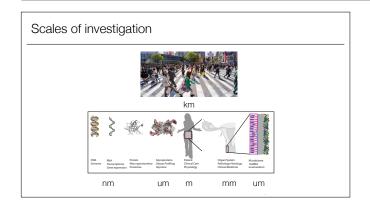
A location in the lower and narrower part of the oviduct (fallopian tubes) where sperm are held by the cells of the oviductal wall (epithelium).



Human sperm exposed to neutrophil immune cells in the lab. Once activated, the immune cells release their own chromatin (DNA spooled on histone proteins) as neutrophil extracellular nets (NETs) and literally net sperm. These sperm perish and get phagocytes by other immune cells (macrophages).

Practice question: Which type of immune cells are responsible for trapping sperm with NETs?

Neutrophils.



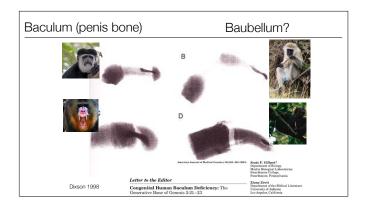
Practice Question: Walk me down by steps of 1000 times from the scale of societies until you reach the size of DNA:

:1000-> m a human body

:1000-> mm size of blood vessel

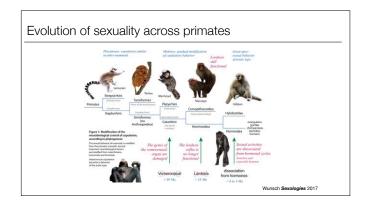
:1000-> micrometer (um) size of a cells

:1000-> nm size of a molecule

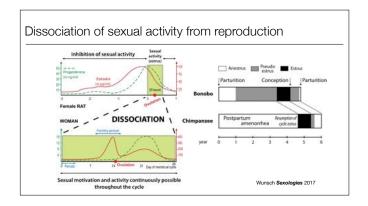


The baculum or penis bone is present in some primates but not others. Humans lack a baculum.

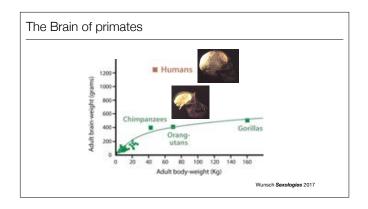
The baubellum or clitoral bone is even smaller but exists in the clitoris of many primates, not in humans.



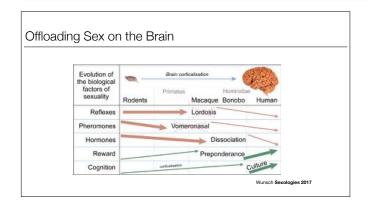
Studies, in biology, genetics and neurosciences, have shown that some of these factors have changed over the course of evolution. In primates, the olfactory circuits are impaired, sexual activities are dissociated from hormone cycles (reproduction and sexual behavior have become independent one from the other), the lordotic mating reflex is no longer functional and the cortex is highly developed in human beings. For these reasons, the analysis of available data suggests that: (1) the dynamics of sexual behavior has significantly evolved from the anthropoid primates; (2) the functional dynamic of heterosexual copulation is very probably disorganized; (3) the behavioral dynamics that emerge with the hominidae – from factors that still exist in heterosexual copulation – would seem to be based on a quest for erotic reward, by stimulation of the erogenous zones; and (4) in humans, due to the extensive cognitive development, sexuality is strongly structured by cultural representations.



In female rodents, sexual activity only takes place during the period in which hormone concentration is maximum and when ovulation takes place, while in female humans, activity can take place at any time in the cycle. Sexual activity gradually becomes independent of variations in hormone levels (Hormone graphs from Thibault and Levasseur, 2001). Shaded (or green), periods in the cycle when sexual activity is possible (in female rats, around 9 hours in a cycle lasting 4–5 days). Figure 3. Dissociation of sexual activity from reproduction in Pan. There appears to be a meaningful dissociation of sexual activity from hormone cycles in Pan paniscus (bonobo). The most noticeable difference is the long period of postpartum amenorrhoea in Pan troglodytes (common chimpanzee). Female chimpanzees are only receptive for on average 12.5 days in a cycle lasting 11.5 months, before 5 years of lack of ovulation after giving birth. Bonobos' receptiveness does not reduce during lactation (De Waal, 1988). Female bonobos are in receptive and exhibit partial or full swellings most of the time between births (Furuichi, 2011).



The human brain is three times larger than the next biggest primate brain.



Summary diagram: evolution of the main factors that govern sexual behavior in mammals. From Wunsch (2014).

Innate reflexes, scent and olfaction, as well as direct hormonal regulation have become less important. Reward and cognitive processing of desire and pleasure seeking have become much more important and subject to strong cultural influences.

Primate Sex

Social dimensions of sex in primates

e.g. 6000 copulations of a female chimp to produce 6 living offspring.

Much conflict and drama around primate sex.

Sex and dominance

Sex and violence

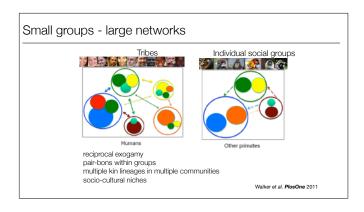
Sex and social harmony



rancesco Hayez

Practice question: How many times does a female chimpanzee that can have a maximum of six surviving offspring during her life copulate?

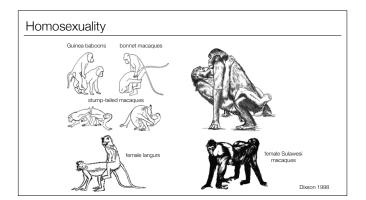
6000 times or more.



The evolved human social structure (left) of reciprocal exogamy including the exchange of mates, goods, and services (double-headed arrows), involves multiple kin lineages (filled circles) often existing in multiple residential communities (open circles). Extensive cooperation (overlap of filled circles) likely results in economies of scale within and across human communities. In contrast, in other primates (right) one or the other sex emigrates (dotted arrows). The lack of any reciprocal exogamy means that kin lineages are isolated to single communities and thus do not generate a meta-group social structure as found in humans. Kind lineages in humans are directly identified by language., essentially allowing the invention of "tribes".

Practice question: Explain the term reciprocal exogamy.

Repeated exchanges of mates, goods and services between different social groups.



Same sex sexual behavior is well documented across non-human species.

Male-male socio-sexual mounts and presentations in anthropoid primates.

guinea baboons (Papio papio)

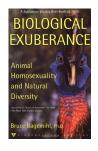
bonnet macaques (Macaca radiata).

stump-tail macaques (Macaca arctoides)

Female–female ventro-ventral mounting, with "G–G rubbing" in the bonobo (*Pan paniscus*).

Sulawesi macaque female embrace and genital inspection.

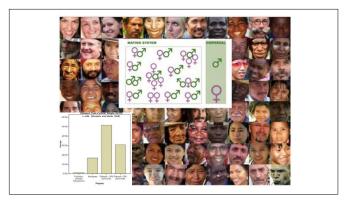
Naturalistic Fallacy in both directions?



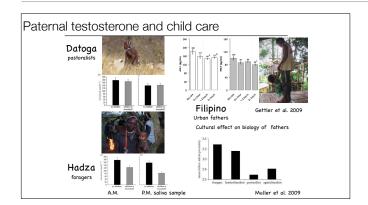




Books such as Biological Exuberance have collected thousands of examples of same sex behavior across animal species, amply documenting the many ways in which different species can engage in same sex sexual behavior. Compared to humans where a certain percentage of individuals self report exclusive attraction to the same sex, non-human primates have so far not really been shown to exclude heterosexual sex. Important to remember that we keep discovering novel aspects of non-human primate behavior in the wild and that absence of evidence is not evidence of absence. Even more important: what other species do has no relevance for justifying or condemning what humans do. Think about it, no other species has post offices or higher fighters.....not to mention stand up commedians.



Pair bonding is very common across human societies, irrespective of sexual orientation. The degrees of exclusivity vary strongly and are under very strong cultural, thus normative influence.

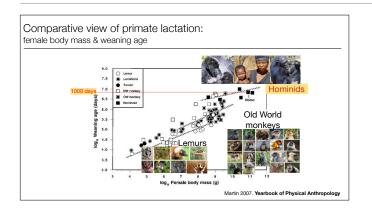


The exposure of new fathers to their babies appears to directly reduce circulating testosterone in the father. The effect is dependent on the amount of time spent in direct contact with the child.

Cultural traditions about paternal care can affect the biology of the fathers.

Practice question: What behavior can strongly affect the levels of testosterone in young males?

Spending time with their newborn infants.



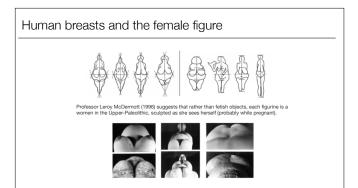
a few lactation times:

Tarsier lactation 2 months

Callithricids 90 days

spider monkey 330 days

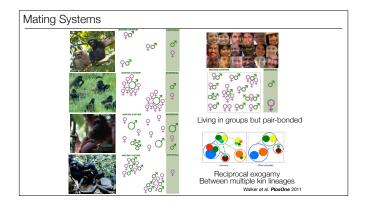
the investment of primate mothers in lactation is larger than that into making the baby for many of the larger primates.



Human breast: No counterpart in any other primate. What are the factors that led to the evolution of human breast?

Sexual selection via male preference? Natural selection as fat storage for costly pregnancy and lactation?

In biology, many things exist for more than just one reason.....



Contrasting Ape and human mating systems: We are the only primate that lives in groups but forms strong pair bonds. Combined with names and kinship terms, this allows the large social networks of tribes, even when the groups are small hunter gatherers. "species-typical" mating systems almost certainly are more plastic than strict classifications: chimpanzees can form temporary "pair bonds" (consortships) and orangutans can come together in multi-male, multi-female groups when food supplies allow, and there is no shortage of humans who seem not too interested in forming pair bonds, or at least not for very long.

Summary



80 million years of primate evolution resulted in over 300 species of living primates.

The diversity of matings systems and ways in which sexual selection has produced adaptations and side effects is staggering.

Families, monogamous units are extremely rare among non-human primates, but do exist in small numbers of species, including the lesser apes.

Sexual behavior in primates has become more cerebral, with the loss of primary roles of olfaction and loss of function of the vomero-nasal organ.

Homosexual behavior is common in many non-human primate species, but exclusive homosexuality has not been reported. It could represent a derived human phenomenon.

In humans, sexuality is immensely infused by cultural influences and meaning. It has become part of the human cultural niche.