

Primates, an Overview

Primates: 230+ species

- Most are frugivorous or folivorous; few are carnivores.
- Most are arboreal. A few are terrestrial, Some groups have special locomotory adaptations.
- Most are diurnal and tropical.

Synapomorphy: a reminder

- Definition: a character that is *shared* for a group of organisms, and *derived* relative to a primitive state.
- Remember that synapomorphies diagnose the group, but this doesn't mean that all members have the character as described, either due to secondary loss, or further evolution.

Some primate synapomorphies

Morphological

- Opposable thumb and big toe, along with generally grasping hands. Functions:
 - assist in grasping and manipulation behaviors
 - adaptation to arboreal lifestyle
- Flat nails rather than claws (at least on big toe), and pads on fingers & toes (produce fingerprints).
- Hindlimb-dominated locomotion
- Loss of vibrissae (e.g. cat whiskers. General definition of vibrissae: Any of the long, stiff, bristlelike hairs that project from the snout or brow of most mammals. often serve as tactile organs, especially in nocturnal and marine mammals.
- Reduced number of teeth (maximum of 2 incisors, 1 canine, 3 premolars, 3 molars in each jaw quadrant)
- Relative reduction in olfactory sensory system, compared to other mammals. Evidence:
 - smaller snouts,
 - olfactory lobe primarily taken over by “higher-order functions” in primates. Basal primates scent-mark, but more derived forms have lost this.
- Increased reliance on vision. Evidence: eyes are
 - large relative to skull (large orbits), and
 - have a high degree of “frontation” (placement toward the front of the face), which allows for higher degree of binocular vision.
- Large braincase : body size ratio (compared to other mammals)

Behavioral and/or reproductive

- Long gestation relative to maternal body size
- small litter size
- slow post-natal growth
- long period of maternal investment and care
- late sexual development
- long life span
- Diet: highly variable

Primates in two broad groupings:

	Strepsirrhines	Haplorrhines
Membership	"prosimians" minus tarsiers	"Anthropoids" + tarsiers
Noses	Wet	dry
Dental combs (tightly clustered incisors/canines for grooming)	Present (except aye-aye)	Absent
Nocturnal / diurnal	75% nocturnal, with tapetums	>90% diurnal
Reliance on olfaction	Relatively high	Relatively low
Brain : body size ratio	Low	High
Reproductive activity	Breeding season	Individual cycles
Other reproductive parameters	Have litters; multiple sets of nipples	Have singletons or twins; one pair of nipples

Lemuroids

- Most speciose group of Strepsirrhines.
- Restricted to Madagascar and the Seychelles.
- Most are arboreal, either pair-bonded or live in social groups, and have female dominance.
- Five families, including the "true lemurs," family Lemuridae, which includes ringtails, as well as the ubiquitous, voracious, and occasionally vicious brown lemurs.

Cheirogalidae: mouse & dwarf lemurs

- Includes the world's smallest primate.
- Thought to be solitary; anecdotal evidence suggests pair-bonding.
- Nocturnal.

Daubentonidae: The aye-aye

- Fills the woodpecker niche.
- In some regions, it is *fady* (taboo) to "mock, deride, kill or eat" the aye-aye. In others, it is considered bad luck not to kill one if you see it, otherwise someone in your village will die.

Indriidae: Sifakas & Indris

- All indriids locomote with "vertical grasping and leaping." When forests are cut, and there are no vertical stems left to grasp, they try terrestrial locomotion, which they are not equipped to do with any grace.
- The indri is the largest extant lemur (10 kg). Pair-bonded individuals call at dawn and dusk, their songs echoing off the hilltops.
- *Babakoto*, Betsimisaraka for indri, means "ancestor of man."

Within Haplorrhines: Platyrrhines (NWM) and Catarrhines (OWM, plus apes and hominids)

Platyrrhines (cebids + callitrichids): new world monkeys (NWM)

- Platyrrhines are named for their nostril placement: far apart and pointing sideways.
- Many cebids have prehensile tails.

Callitrichidae: marmosets & tamarins

- Small, arboreal monkeys with claws on most phalanges; thumb and big toe not opposable. Restricted to South America.
- 5 genera, 26 named species.
- Live in family groups; mating system is monogamy or polyandry (both rare in primates, and in mammals generally).
- Total neonatal mass is large relative to maternal bodyweight. Twins are common. In such species, males carry the young (an important job for delicious, arboreal animals), and polyandry is common.

Catarrhines: old world monkeys (OWM) & apes

- Nostrils close together, pointed downward
- No scent marking
- Tail sometimes absent, never prehensile.

Cercopithecines

- Includes baboons, mangabeys, mandrills, guenons, vervets (6 *spp.*), patas monkeys, and macaques, all of which are limited to Africa, except macaques, which are also in Asia and Gibraltar (Spain).
- Many are semi-terrestrial, sleeping in trees or on cliff-faces, foraging by day in large groups on grasslands.
- Highly sexually dimorphic
- Two morphological synapomorphies:
 - Ischial callosities: leathery, hairless, butt pads, on which they sit.
 - Cheek pouches: cheeks that expand like those of hamsters to allow the secure temporary storage of food.

Baboons

- Most geographically widespread of all primate species, except one.
- Traditionally considered five mostly allopatric species, all in the genus *Papio* (Okavango baboons are chacma baboons: *Papio hamadryas ursinus*). Their ability to interbreed with one another when they come into contact has prompted some to argue that they are a single species, with five subspecies. Other researchers think there are seven species.

Ape synapomorphies:

- Ability to **brachiate**: vertical hanging and swinging using forelimbs. Thus, apes have highly mobile shoulder joints and arms; flatter ribcages; and shorter, less mobile spines than OWMs. Brachiation requires increased range of movement around shoulder joint.
- No tails

Lesser apes: Gibbons and the siamang. Distribution: SE Asian rainforests.

- Long term pair bonding (in some *spp.*, pairs duet at dawn and dusk)
- Territorial defense through vocalizations (individuals in some species may use their hands to modulate vocalizations)

Great apes: orangutan, gorilla, chimp, bonobo

- orangs: solitary (depending on resources), folivorous (sometimes frugivorous)
- gorillas: polygynous, folivorous, alpha male excludes other males
- chimps: polygynous, omnivorous (including monkey meat), first non-humans known to use tools and wage war
- bonobos: promiscuous, omnivorous, sex-for-food trades and group care-giving

In-class Workshop

Article on which the following questions are based: Mennill *et al* 2002 (*Female Eavesdropping on Male Song Contests in Songbirds*, Science 296:873, as cited in Cheney and Seyfarth 2007:141).

Summary of article: Females listen to their mate when he sings competitively with other males. When a female's mate is in competition with a novel intruder who is aggressive to him, but submissive to a known male who is less dominant, he is far more likely to be cuckolded by her: some of the eggs in their shared nest aren't his. Competitions with intruders who are submissive to the mate, and aggressive to other known males, do not prompt a change in female behavior. When she has a high-ranking mate, the eggs tend to be all his. When she has a low-ranking mate, there's a high rate of extra-pair copulation regardless.

- Review graphs, statistics.
- Break into groups of 4-5. Read the paper (p5 of this handout).
- Answer the following questions in your small group.
- Go over answers as a class.

Workshop Questions

1. What are the two distinctions between the "submissive" playback and the "aggressive" playback? Why are these likely to be accurate representations of submissive and aggressive encounters between males? Under what circumstances might you find one or the other of these in a situation between males that was not competitive?
2. What is the value in having two different "control"s?
3. Why does the female care so much about who wins a song competition? Identify as many evolutionary and ecological parameters as possible.
4. What are the ramifications of this research beyond paternity?
5. If the female cares so much about who is winning the singing contest, why aren't all of the offspring in her nest fathered by the guy who sings best and/or most dominantly?

ECOLOGY

Female Eavesdropping on Male Song Contests in Songbirds

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Male song reflects the quality of the singer in many animals and plays a role in female choice of social and copulation partners. Eavesdropping on male-male vocal interactions is a means by which females can compare different males' singing behavior directly and make immediate comparisons between potential partners on the basis of their relative vocal performance (1, 2). Using an interactive playback experiment followed by microsatellite paternity analysis, we investigated whether female black-capped chickadees (*Parus atricapilla*) base their reproductive decisions on information gained through eavesdropping.

Black-capped chickadees are socially monogamous songbirds that follow a mixed reproductive strategy in which one-third of broods include young that are not related to their social father (3). From 1999 to 2001, we assessed dominance ranks in a free-living population of chickadees at Queen's University Biological Station, Canada, to predict which males were likely to be sought for extrapair copulations (high-ranking males) and which males were likely to lose paternity within their nests (low-ranking males) (3, 4).

At the start of the breeding season, when male-male song contests are common and females actively solicit copulations, we used interactive song playback to engage territorial male chickadees in countersinging interactions with a simulated intruder (5). We performed 6.0-min playback trials to dyads of neighboring high-ranking and low-ranking males from the same winter flock. In control treatments, we mimicked natural territorial encounters; we simulated an intruder that sang submissively (Fig. 1A) with the high-ranking playback subject and sang aggressively (Fig. 1B) with the low-ranking neighbor. In experimental treatments, we attempted to alter eavesdropping females' perceptions of their social mates; we simulated an intruder that sang aggressively with the high-ranking playback subject and sang submissively with the low-ranking neighbor. To test whether interactive playback altered the normal pattern of paternity in the nests of subject males, we conducted paternity analysis on blood samples collected from offspring (6).

High-ranking males that lost song contests

with a simulated intruder lost paternity in their nests (Fig. 1C); high-ranking males that received playback simulating an aggressive intruder showed a significantly greater level of paternity loss than high-ranking males that received playback simulating a submissive intruder (control I; Fisher's exact test, $P = 0.05$) and a significantly greater level than a control group of high-ranking males that received no playback (control II; $P = 0.05$). As predicted (3, 4), we observed little

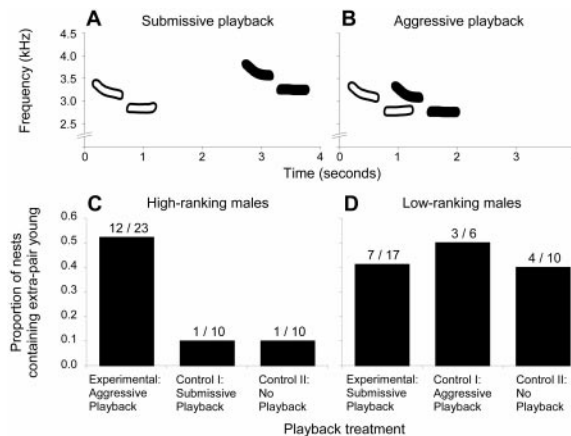


Fig. 1. Sound spectrograms of vocal interactions recorded during (A) submissive playback trials in which the simulated submissive intruder (black) avoided matching the pitch and overlapping the songs of the subject (white) and (B) aggressive playback trials in which the simulated aggressive intruder (black) matched the pitch and overlapped the songs of the subject (white). (C) High-ranking males who received aggressive playback treatment lost paternity significantly more often than high-ranking males who received control treatments. (D) Low-ranking males who received submissive playback treatment did not lose paternity significantly less often than low-ranking males who received control treatments.

extrapair paternity in the nests of high-ranking males that received submissive playback and high-ranking males that received no playback. Thus, females paired to high-ranking playback subjects adopted a mixed reproductive strategy after hearing brief song contests in which their mate fared poorly. This change in female reproductive decisions after short playback sessions suggests that information available through eavesdropping plays an important role in female assessment of male quality.

Playback mimicking a submissive intruder did not reduce the level of extrapair paternity in the nests of low-ranking males (Fig. 1D); paternity loss by low-ranking males that received playback simulating a submissive intruder was not significantly different than for low-ranking males that received playback simulating an ag-

gressive intruder (control I; $P = 1.0$) or low-ranking males that received no playback (control II; $P = 1.0$). The females paired with low-ranking males that received submissive playback may have engaged in extrapair copulations before playback sessions or may have heard natural male-male song contests in which their partner revealed his low-ranking status. Whereas females paired to low-ranking males normally overhear their mate win some song contests and lose others, females paired to high-ranking males are only accustomed to hearing their mates win. As such, two short playback sessions were sufficient to alter high-ranking, but not low-ranking, females' perceptions of their partners' status.

We tested the alternative explanation that unusual patterns of extrapair paternity could have arisen from females reacting to changes in their partners' postplayback behavior, rather than from eavesdropping per se. We detected no significant changes in male behavior after playback (5), further suggesting that changes in female reproductive decisions arose through female eavesdropping on male song contests.

Our results support the idea that information may be transferred between individuals in a communication network rather than simply within a dyadic context (2) and provide a conceptual link between the attractive and repellent properties of male song where mate attraction and territory defense may be simultaneous functions of a common signal. Finally, our results show that short playback sessions can have long-lasting and far-reaching effects on individual fitness.

References and Notes

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2. P. K. McGregor, T. Peake, *Acta Ethol.* **2**, 71 (2000).
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4. S. M. Smith, *Behaviour* **107**, 15 (1988).
5. See supplemental information available on Science Online at www.sciencemag.org/cgi/content/full/296/5569/873/DC1.
6. Paternity was analyzed by polymerase chain reaction amplification of two highly variable microsatellite loci. Offspring were considered extrapair young if they had one ($n = 44$) or two ($n = 22$) allelic mismatches with their social father. The combined exclusionary power was 0.91 given one known parent.
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