Two Big Questions on Primate Sociality

(1) Why are primates social (‘gregarious’) at all?

(2) What ecological variables account for variance in social relationships?
Sociality

- AKA “gregariousness”
- Lots of communication
- Spatial and temporal proximity
- Members of a group carry out daily activities together
- Group persists over time
These two questions are closely related. Most “groups” are a bunch of females who have relationships with each other: female-bonded with dominance hierarchies, cooperation, relatively stable relationships.
Wrangham’s Model: The Resource Defense Hypothesis

• Female RS limited by access to food
• Male RS limited by access to females
• Most primates are female-bonded
• Why don’t low-ranking females leave?
• Because to get access to patchy food, you HAVE to be in a group; the costs of group feeding are less than the costs of solitary feeding because groups out-compete individuals in fighting over food patches; better to be in a group and get a little of the patch than be alone and get none
Wrangham’s Model: The Resource Defense Hypothesis

• In a group, there are benefits with regard to between-group competition for food
• There is, however, a cost of within-group feeding competition
• This model assumes that intragroup feeding competition will always be less than intergroup feeding competition
• Why female bondedness?
• Because if you have to form a group, it’s best to do it with relatives; if you’re not in the same group as relatives, you’d be in intergroup feeding competition with them, and that’s bad because *intragroup feeding competition will always be less than intergroup feeding competition*
Wrangham’s Model:
The Resource Defense Hypothesis

- The patches being defended must be large enough to satisfy all group members, otherwise the lowest rankers would just leave.
- When there are fluctuations in food availability (due to, e.g., seasonality), in order to accommodate for food scarcity, diets must be switched to ones that are lower-quality and higher in abundance.
- Growth Diet: when times are good, eat a high-quality diet (e.g., fruits and nuts).
- Subsistence Diet: when times are bad, eat a low-quality diet of abundant foods (e.g., leaves and grass).
- In female-bonded species, there is a Growth Diet when times are good and a Subsistence Diet when times are bad.
- Non-female-bonded species are not characterized by these two diet types.
Wrangham’s Model: The Resource Defense Hypothesis

- **Evidence**
  - There is a lot of intergroup feeding competition, and females are very active in the aggressive confrontations
  - Territoriality
  - Intergroup dominance hierarchies

- **Consequence**
  - Once females are forced into groups for purposes of intergroup competition, the intragroups feeding competition leads to a dominance hierarchy within the group

- **Example**
  - In capuchins, females in large groups have more food, higher reproductive rates, and after intergroup confrontations, the losing group has to travel further to get food, and is more food-stressed
Wrangham’s Model: The Resource Defense Hypothesis

• Non-female bonded groups: chimps, gorillas, hamadryas; why do they not conform to the model (i.e., perhaps, “the excuses”?)
• Reasons:
  – Chimps are always on a growth diet, and when times are bad they spend more time foraging rather than switching to a low-quality diet (chimps can’t eat many leaves)
  – Gorillas are solely folivorous
  – Hamadryas don’t have fleshy fruits around
  – For all 3 species, intergroup competition is only male-male or is absent
Males?

- They go where the females do, and fight among themselves to get to mate with the females
- How many males? (OMU vs. multimale)
- Females don’t want males eating their food, and they don’t want to be harassed by a bunch of males hanging around
- Males don’t want other males around
- BUT males can help in between-group feeding competition
- Lots of tradeoffs
- Pattern
  - in territorial FB groups, UNImale
  - In nonterritorial FB groups, MULTImale
Wrangham’s Challenger: van Schaik

• Carel van Schaik: Dutch primatologist
• Said that intragroup feeding competition is MORE than intergroup feeding competition
• Notice that predation is a big problem for primates…
Predation
Predation

• We don’t always see it (that’s precisely how most predators work)
• Even a small amount of predation can be a significant selective agent
• How to solve the problem?
  – Be cryptic and solitary (prosimians)
  – Be gregarious
Van Schäik’s Predator Defense Hypothesis

• There is a lot of within-group feeding competition, but animals group in order to thwart predators
• Why?
Predation

• Why gregarious?
  – Defensive mobbing of predators
  – Improved early detection of predators
  – Grouping clumps individuals, so a randomly-searching predator would be less likely to come across prey (modeled)
  – ‘Selfish herd’ (modeled): aggregation reduces individual risk of being taken by a predator (but assumes aggregation does not increase conspicuousness)
  – Startle/Confusion/Flash displays (e.g., stotting by gazelles) function better in a group context
Van Schaik’s Predator Defense Hypothesis

• Evidence: geladas
  – Wrangham says they group when food is patchy
  – Van Schaik says they do so where there are more predators
  – Van Schaik won
  – Another example: Long-tailed macaques in the presence or absence of big cats; when big cats are around, females group more (within-species variation)
Wrangham vs. van Schaik

• Wrangham says if you look in a group, females in larger groups get more food and have higher RS; but if the group gets too big, RS goes down.

• Van Schaik says group-living lowers RS because of food competition, but the predation defense means a longer lifespan, so greater RS; with a large group, reproductive RATE is lower, but lifetime reproduction is higher.

• The data fit vanSchaik’s model.
Sociality: Two Big Questions
Question 2:

What ecological variables account for cross-species variance in primate sociality?
Primate social systems vary widely
Primate social systems vary widely

Above diagonal: Members of *at least* one sex mate exclusively with their Partner in the group

Below diagonal: mateships are transient; they are short-lived and temporary within the group

Rodseth et al. 1991
Within-species variability: Gorillas

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<thead>
<tr>
<th>MALE RELATIONSHIPS</th>
<th>MALES ABSENT</th>
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<tr>
<td>With nonkin only</td>
<td>22</td>
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<td>With no other male</td>
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<td>With male kin</td>
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<td>All-male groups</td>
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<td>Lone males</td>
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## Within-species variability: Humans

### Male Relationships

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<td>Matrifocal families (w/ extreme promiscuity)</td>
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**Note:**
- Autonomous polygynous families?
- Autonomous monogamous families?
- Conjugal families in communities (w/ extreme patriarchy)
- Conjugal families in communities
- Remote monasteries
- Hermits
What evolutionary principles explain this variability in primate social systems?
The following principles explain some, but not all, of the variability:

- Females: fitness most constrained by access to resources
- Males: fitness most constrained by access to mates

Socioecological model

Food quality and distribution

LARGE DISTANCES BETWEEN LIKE TREES
Trees bearing a favored food are often distributed patchily

HIGH FIBER CONTENT
Cell walls of plant parts, especially mature leaves, can contain much fiber (inset), which is resistant to digestion

LIMITED AVAILABILITY
Many favored items are available only part of the year, some for only hours

INCOMPLETE NUTRITION
Few plant foods are both high in energy (calories) and high in critically needed protein, vitamins and minerals

CHEMICAL DEFENSES
Potential foods often contain chemicals that are ill tasting or poisonous or that interfere with digestion of other foods

Milton 1993
Resource monopolizability

- Low-value, dispersed, non-monopolizable
- Valuable, clumped, monopolizable
A folivore and a frugivore/insectivore

Red Colobus

Capuchin
The socioecological model
Resource competition affects within-group female relationships

• ‘Contest’ food competition
  – Food is valuable, clumped, and monopolizable
  – Individuals benefit from ‘displacing’ their competitors
  – Displacement and agonistic rates high
  – Dominance hierarchies, coalitions
  – Female philopatry

• ‘Scramble’ food competition
  – Food is low-value, dispersed, abundant, and thus nonmonopolizable
  – No benefits to ‘displacing’ competitors
  – Displacement and agonistic rates low
  – No need to maintain dominance or coalitions
  – No need to stick around with female kin

Vervets: Female coalitions important
Female coalition

Social carnivores (the model fits nonprimates too:
Lionesses defend territory against other prides and cubs from infanticidal males
(Grinnell & McComb 1996)
Female primates fight, & they fight together!

Gelada baboons
End of lecture