



Feeding Ecology in Apes and other Primates

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Conference Abstracts



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Primate foraging: foods, functions, and fitness

Stuart A. Altmann

*Department of Ecology & Evolutionary Biology; Princeton University; 118 Eno Hall;
Princeton NJ 08544; U.S.A.*

Research on primate foraging is now at a transition point. For a growing number of primate species, field studies have richly documented the animals' basic natural history, including many aspects of their feeding ecology. For many of these species, plausible explanations have been proposed for the adaptive significance of the specific ways in which they make a living. The problem that we now face is this: How do we make the transition from such post hoc explanations to testable hypotheses about foraging behavior?

Underlying virtually all proposed explanations for the adaptive significance of behavior is the following question: Under given conditions, how would a well-adapted animal of this species behave? If the answer to this question can be given explicitly, then for any given pair of individuals, we would know which one has behavior that is better adapted to the circumstances. This leads us to a very powerful two-step technique: First, relate individual differences in behavior within a species to differences in their functional consequences. Second, relate these functional differences to individual differences in life history components, which, in turn, alter biological fitness—the raw material of natural selection.

For example, for the members of a primate group, we can ask whether those individuals whose foraging behavior yielded better diets were the ones that bred at an earlier age, had shorter inter-birth intervals, lived longer, or had other life history traits that led to higher fitness. This is exactly what we did in a study of foraging behavior in the yearling baboons of one group of yellow baboons in the Amboseli region of Kenya (Altmann 1998). The foraging behavior of those females that, as yearlings, yielded greater protein surpluses, relative to their requirements, or came closer to their energy-maximizing diets (their "energy shortfalls") are the ones that, as adults, produced more infants and had more infants that survived their first year of life.

Energy shortfall appears to be the major dietary factor that affected the baboons' fitness. It accounted for 96% of the variance in females' fecundity (number of live-born infants) and 81% of their reproductive success (number of surviving juveniles). Energy apparently brought about these effects through effects on survival: differences in energy shortfall were sufficient to predict which individuals survived to adulthood and to account for 92% of the variance in females' subsequent survival; that is, in the duration of their reproductive life span. The number of infants and yearlings that a female baboon produced in her lifetime was closely correlated with the length of her reproductive period: those that lived longer produced more offspring. That is a consequence of an age-constant birth rate.

Relating individual differences in foraging behavior, its function, and its fitness consequences in populations of wild primates is laborious, but it is feasible under the very conditions that make some primate populations particularly suitable for long-term study. Basically, three types of field samples are required: samples of food-specific feeding bout rates and of food intake rates during bouts, and representative samples of the foods that are eaten, for subsequent chemical analysis of nutrients, toxins, and other components. In addition, the basic census data on dates of births and deaths are required.

Chimpanzee food choice: availability or cultural differences

Christophe Boesch¹, Zoro Bertin Gone Bi¹, Dean Anderson², Daniel Stahl¹

¹ *Max Planck Institute for Evolutionary Anthropology; Deutscher Platz 6;
04103 Leipzig; Germany*

² *University of Wisconsin Madison; Zoology; 430 Lincoln Drive; Madison WI 53706; USA*

How do individuals select their food? How different can such decisions be with varying availabilities? How much of such choices are cultural? These are the questions we want to address with data collected with chimpanzees living in Taï National Park, Côte d'Ivoire. The particularities of the Taï chimpanzee project has been in the last year that we have been able to follow three different neighboring communities of chimpanzees, which have been habituated to human observers. At the same behavioral observations were collected on each of these communities, the food distribution and production has been documented in the home ranges of the same three communities. Comparing food selection and amount consumed with availability between the three communities will allow us to gain insight in food choice and test how decisions are made.

Similarities and differences in the caloric intake by primates as exposed by seasonality

Nancy Lou Conklin-Brittain, Cheryl D. Knott, Richard W. Wrangham

Anthropology Department; Peabody Museum; Harvard University; Cambridge; MA 02138; USA

Traditional optimal foraging theory (OFT) is predicated on the hypothesis that an optimal forager will maximize net caloric intake. Usually the assumption is that in the wild it is so difficult to procure enough energy that the possibility of over-consumption of energy rarely needs to be considered. Similarly, if a high energy food source is available and not associated with prohibitive costs, the assumption is that it will be eaten.

In 1974, Westoby explained why the OFT's use of calories needed to be modified when applied to herbivores. This modification of considering the individual nutrients and antifeedants instead of total calories, was applied by McKey et al. (1981) to primates and since that time has been the standard in primatology. From a comparative study of sympatric chimpanzees and monkeys at the Kanyawara site within Kibale National Forest, Uganda and a study of orangutans at Gunung Palung, Borneo, Indonesia, we will initially evaluate this traditional focus on individual chemical fractions, using multiple regression. We have already shown that the non-colobine cercopithecines and chimpanzees, over a span of 12 months, focus on consuming foods high in easily digestible carbohydrates and sugars while their focus on fat is less consistent and protein does not seem to factor into their selection process (Conklin-Brittain et al. in prep). Here we will include the orangutan data and examine selectivity on a seasonal basis rather than an annual basis, to determine whether the nutrient selectivity changes with season. Season is based on relative fruit availability during a year, rather than rainfall.

Subsequent to the chemically based evaluation, we will return to the original OFT use of calories (joules) and evaluate, regardless of how selectivity might change based on nutrients, does caloric intake significantly vary seasonally and similarly among all 5 species of primates. Knott (1998, 1999) has shown that during a mast year, orangutan caloric intake varied dramatically with fruit availability. Here we will include the African data as well as a non-mast year for the orangutans. We will then discuss how to reconcile the nutrient data with the caloric data - is it a question simply of increased intake or is there an increased intake specifically of more calorically dense foods, or both?

Behavioral chains and the sensory ecology of primate food selection

Nathaniel J. Dominy

*Department of Ecology and Evolution, University of Chicago; 1101 East 57th Street
Chicago IL 60637; USA*

Primate feeding tends to involve a series of behavioral elements during which an individual responds to successive stimuli of different modalities. When the outcome of a sensory evaluation is to reject a food item, primates frequently select another, similar item and repeat the evaluation process. The sequential nature of such behavioral elements is called a behavioral chain. Although modification of behavior can be observed as faster decision making or as changes in preference, the sequence is typically constant. A chain of primate behavior can be divided into two consecutive phases during food selection: (1) searching and (2) contact-testing. The searching phase ends by establishing contact with a food item. Once a food is contacted, different forms of haptic behavior are exhibited, which involve repeated contact with the digits, lips, or incisors. The contact-testing phase ends with food acceptance (deglutition). At this point mechanical and gustatory information have become available in the oral cavity in addition to olfactory information. The final decision to accept or reject a food item is based not only on the sensory properties of the food itself, but also on the primate's physiological state (satiety, reproductive status) and information from previous experiences. All these factors are integrated in the central nervous system and in concert determine food acceptance and preference. The existence of primate behavioral chains implies that diffuse, widespread correlations exist in the physicochemical attributes of foods. Here I attempt to define these relationships and discuss their impact on the evolution of primate sensory systems. Attention is focused on the traits of fruits that may attract primates during searching (color and ethanol content) and the traits that may provide information during contact-testing (texture, sugar concentration, and ethanol content).

Back-Calculation of the diet based on stable isotope data: a critical review

Ulfert Focken, Klaus Becker

*Department of Aquaculture Systems and Animal Nutrition in the Tropics and Subtropics;
University of Hohenheim (480B); Fruwirthstr. 12; 70593 Stuttgart; Germany*

Back-calculation of the diet of an animal based on the comparison of $\delta^{13}\text{C}$ - and/or $\delta^{15}\text{N}$ -values of the body with those of potential food items is one of the most frequent applications of stable isotope analysis in animal ecology. The concept is based on DeNiro & Epstein's (1976, 1978, 1981) classical studies on the relationship of isotopic ratios ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) "You are what you eat – plus a few per mill", which can be inverted to "What you eat is what you are – minus a few per mill". However, several assumptions have to be made for this approach: The first one is that the difference in isotopic ratios between an animal and its diet (trophic shift) is constant for all diets, the second that mixtures between two (or more) diet components behave exactly the same as the pure components, another one that there are no influences due to feeding level or other physiological conditions of the animal. Even more assumptions have to be made in case of archeological or paleontological studies, when not the whole body but only certain morphological and chemical fractions such as teeth or collagen from bones can be analyzed (Schwarcz 1991). Boutton *et al.* (1984) investigated the carbon isotopic ratios of collagen extracted from human remains from Missouri and Arkansas. The remains were dated from 3200 BC to 1880 AD. Samples dated before 1000 AD had relatively constant $\delta^{13}\text{C}$ values of about -21‰ , in later samples, $\delta^{13}\text{C}$ gradually increased to values between -13.5‰ and -10.5‰ . Assuming a constant difference between diet and collagen of $\sim 6\text{‰}$, they concluded that before 1000 AD, the diet was entirely derived from C3-plants ($\delta^{13}\text{C} - 27\text{‰}$), while later corn ($\delta^{13}\text{C} - 12.5\text{‰}$) became an important food source, making up 35-70% of the total diet.

Gannes *et al.* (1997) concluded that the use of unverified assumptions is a major obstacle to the application of stable isotope studies. There is increasing evidence that the trophic shift is not constant, but influenced e.g. by the type of diet (Tieszen *et al.* 1983, Webb *et al.* 1998), interaction between C3- and C4-plant material in the gut of animals (Bruckenthal *et al.* 1985), effects of ration size and feed quality (Focken 2001, Gaye-Siessegger *et al.* 2003). Relatively small changes in the value assumed for the trophic shift may have strong effects on the composition of the diet in back-calculation (Gaye-Siessegger *et al.* 2004), thus the uncertainty in the value of the trophic shift due to the unknown feeding level and individual metabolic disposition of the animal investigated may produce such a large range for the backcalculated composition of the diet that the result becomes meaningless. Focken (2004) fed diets with different wheat/corn ratios to fish, and observed an overestimation of corn in the backcalculated diets.

In view of the more recent studies mentioned above, the contribution of corn may have been overestimated due to differences in the digestion and assimilation of nutrients from C3- and C4-plants, the interaction between those or the nutritional status may have improved in the same time scale and thus the difference in $\delta^{13}\text{C}$ between diet and collagen changed.

Chemical characteristics of food eaten by primates from different radiations: how important is protein?

Jörg Ganzhorn¹, C. Stark, A. Arrigo-Nelson, S. Atsalis, A. Bollen, C. Borries², V. Carrai, G. Donati, J. Fietz, A. Koenig², M. Kowalewski, P. Lahann, D. Schwab, P. Stephenson, C. Tan, E. Vogel²

¹ *Zoologisches Institut und Zoologisches Museum; Universität Hamburg; Martin-Luther-King-Platz 3; 21073 Hamburg; Germany*

² *Department of Anthropology; Stony Brook University; Stony Brook; NY 11794-4364; USA*

The present assignment of primates to dietary guilds is based on the assumption that protein is a key limiting factor. Large species should satisfy their protein requirements with leaves. Small species should rely on animal matter as the main source of protein. Yet, many studies have failed to demonstrate clear relationships between primate food selection and protein concentrations if estimates of protein availabilities were based on the concentrations of nitrogen. Over the last few years we compiled data on the chemical composition of leaves and fruit eaten by primates from different radiations (lemurs, langurs, neotropical primates). All samples have been analyzed with the same equipment and methodology. Using this dataset we will investigate whether the nitrogen concentrations in the food of different primate species match the predictions derived from metabolic considerations and niche separation due to the reliance on different sources of protein.

Feeding ecology of bonobos and common chimpanzees: a comparative study of the quality of plant foods

Gottfried Hohmann¹, Andrew Fowler², Sylvia Ortmann³

¹ *Max Planck Institute for Evolutionary Anthropology; Deutscher Platz 6; 04103 Leipzig; Germany*

² *Anthropology Dept. University College London; Gower Street; London WC1E 6BT; UK*

³ *Institute for Zoo- and Wildlife Research; Alfred-Kowalke-Str. 17; 10315 Berlin; Germany*

Recent approaches explaining variation of social systems in non-human primates in an adaptive way are based on the socio-ecological paradigm that implies female relations to be set by ecological conditions while male relations are linked to mating opportunities. Females of both Pan species emigrate and so, are not closely related with each other. One would therefore predict that close social ties are absent in females and that they are relatively asocial. While female chimpanzees of most populations behave in the predicted way, bonobos do not. Distribution of bonobos is restricted to the lowland rainforest of the central Congo basin south of the Congo river. Chimpanzees occur in various geographical zones north of the river. Although chimpanzees have successfully occupied a wide range of habitats, many populations live in primary forests. Both species are omnivorous with a clear preference for ripe fruit. In spite of these similarities, both species show remarkable differences in grouping patterns, female gregariousness, and dominance relations. Conventional hypotheses suggested that the discrepancy in social relations has derived from differences in the distribution of food sources, size of food patches or seasonal variation of forest productivity. Comparison of data from single disjunct populations of bonobos and chimpanzees provided some support for the hypotheses, but data from rainforest chimpanzees did not fit into the model. Previous studies focussed on quantitative parameters of food sources. In our study, we investigated various parameters of the quality of plant foods. Observations on gregariousness and samples of food plants and non-foodplants were collected for 12 months simultaneously at two sites, Lui Kotal, (bonobos) and Gashaka Gumti (chimpanzees) using the same protocol for data collection and storage of samples. Here we will report on annual variation of macro-nutrients and anti-feedants in plant foods consumed by the two Pan populations. The results will be related to site-specific patterns of seasonal variation of climate, forest composition and forest productivity.

Estimating the effects of gut constraints on primate social ecology

Charles Janson, Erin Vogel

Department of Ecology and Evolution, State Univ. of New York, Stony Brook, NY 11790/USA

Most theories and empirical analyses of food competition or foraging behavior in primates assume that all foragers of a given primate group will obtain the same fitness gain from using a particular food item at a given time (the benefit of a food item may vary over time as the availability of other food types changes). However, many analyses of behavior in birds have successfully incorporated the 'state' of the bird (usually assessed as fat storage) into models of dynamic programming to predict time-varying preferences for food types and predator risk aversion. We feel that it is high time to expand primate foraging and competition studies to explicitly incorporate dynamic state variables. An obvious variable to focus on in primates is 'hunger', which will often vary dramatically during the course of a day and from individual to individual within a group, depending on their short- and long-term foraging success. First, we present two examples (one from foraging and one from food competition) in which knowledge of hunger can greatly affect theoretical predictions. Second, we discuss one possible way to operationalize the concept of hunger, as the fractional occupancy of the forager's gut. Simply put, when the forager is full, additional food has zero marginal fitness value to the forager. We present a simple input-output model that should allow the fractional gut occupancy to be estimated from detailed field data on feeding histories. Finally, we present an empirical analysis of rates of aggression at food trees, in which average fractional gut occupancy was estimated for white-faced capuchin monkeys. We test whether, in this case, fractional gut occupancy helps to explain variation in rates of aggression across different feeding trees.

The predictive power of socio-ecological models: a reconsideration of resource distribution, group cohesion, and female dominance hierarchies

Andreas Koenig, Carola Borries

Department of Anthropology, Stony Brook University, Stony Brook, NY 11794-4364, USA

Over the past two decades various attempts have been made predicting competitive regimes and female social relationships based on resource distribution, predation pressure, and male coercion. Particularly resource distribution has been invoked as primary force molding female social relationships and dispersal patterns. Although partly successful the predictive power of the models has been repeatedly criticized. Here we reconsider the role of resource distribution and its link to energy gain as well as aggression rates and linearity of hierarchies. Resource distribution has previously been categorized according to food types or analyzed via ecological methods lacking an animal-centered view. Such approaches neglect early assumptions of the importance of resource size and densities as well as group size on energy gain. Moreover, theoretical considerations and recent results show that resource quality and group spread may strongly modify a potential skew in energy gain. Furthermore, accounting for group cohesion, group size, and resource characteristics aggression rates might be highly variable even if energy gain is similar. In consequence, aggression over food might be a good indicator of how individuals gain and monopolize resources, but a weak predictor of the overall effect of competition on an individual's energy gain. Finally, considering dominance hierarchies, it can be shown that observed linearity or "strength" of hierarchies is largely a function of observation time, interaction rates, and group size, thus, reducing the usefulness of such concepts. Instead relationship consistency (unidirectionality) and relationship stability provide a more promising alternative.

In summary, resource characteristics may predict asymmetry in energy gain, but additional factors such as group cohesion and size need to be incorporated as well. Considering social structure, however, the predictive power of current models seems to be weak. Future efforts are needed to identify links between feeding competition and its presumed social consequences.

Tannin-herbivore interactions, their effects on nutritional ecology of mammalian herbivores and methods for assessing biological activity of tannins

Harinder P.S. Makkar¹, Klaus Becker²

¹ *Animal Production and Health Section; Joint FAO/IAEA Division; International Atomic Energy Agency; Vienna; Austria*

² *Institute for Animal Production in the Tropics and Subtropics (480); University of Hohenheim; D-70599 Stuttgart; Germany*

Tannins are a distinct group of phenolic polymers. Their presence in the Plant Kingdom is widespread and they are involved in defense against herbivores (e.g., animals, insects, and birds) and pathogenic microorganisms. Tannins are broadly categorized into two major categories: condensed tannins, CT (syn. proanthocyanidins) and hydrolysable tannins (HT).

The CT affect digestibility and uptake of nutrients, especially of proteins. These also affect intake and palatability. The HT, at higher levels of intake, in addition to causing aforesaid biological effects could produce toxicity and death of animals – yellow wood (*Terminalia oblongata*) and oak (*Quercus incana*) poisoning in animals being the examples. Environmental conditions such as availability of water and ambient temperature influence tannin content and activity, affecting nutritional ecology of both domestic and wild animals. Wild animals seem to be affected adversely to a lesser degree than the domestic animals, however limited information is available on the mechanisms of adaptation to tannins by animals. Rats, mice, monkeys, humans, koala bears, hares, rabbits, deer, pigs secrete proline-rich protein (PRP) in saliva, which have affinity for tannins and form complexes rendering them inactive in the digestive tract and thus providing a natural defense mechanism in these animals. Other animals that do not secrete salivary PRP are more prone to the effects of tannins or need other defense mechanisms. The use of surfactants and elevated pH and protein turnover in gut to minimize the complexation of tannins and proteins may be the adaptive mechanisms used by animals to ameliorate tannin effects will be highlighted. The paper will also present methods for determination of content and biological activity of tannins in herbivore diets, predicting their effects on herbivores.

Causes and consequences of central place foraging among Hadza hunter-gatherers

Frank W. Marlowe

Department of Anthropology; Harvard University; Peabody Museum 26; 11 Divinity Avenue; Cambridge; MA 02138

Most human hunter-gatherers are central place foragers, a trait shared by some birds and carnivores but not primates. While the significance of this fact is often noted, there has been surprisingly little empirical investigation into its causes and consequences. Here, I begin by showing the Hadza pattern of daily foraging for both sexes across all ages. Then, I look at how food taken varies with foraging party size and composition. The amounts and types of food consumed away from camp and in camp are analyzed by age, sex, and marital status. I consider the influence of the spatio-temporal distribution of foods, the sexual division of labor and provisioning of a spouse, provisioning of children who cannot go foraging, and the processing, cooking, or storing of food at a central place. Some of the consequences of central place foraging explored include patterns of food-sharing, age at weaning, and challenges of mate-guarding.

How does food constrain the density and demographic composition of agile gibbon populations in habitats of varying quality?

Andrew Marshall

Harvard University; Dept of Anthropology; Peabody Museum 26; 11 Divinity Avenue; Cambridge; MA 02138

My talk will focus on testing hypotheses about the role of resources in regulating primate density and demographic structure across heterogeneous landscapes. Most studies that examine the role of food resources in constraining primate habitat utilization are based on unspecified models and assumptions (usually implicit and untested) about the way spatial and temporal fluctuations in food availability affect primate populations. A more explicit examination of these ecological models and their underlying assumptions is required if we are to further our understanding of the role of ecological factors in shaping primate population dynamics. I will briefly review existing models and use them to generate testable alternative hypotheses. I will then present data demonstrating differences in agile gibbon density and group composition in 7 distinct habitats in Gunung Palung National Park, West Kalimantan, Indonesia. Long term data will be utilized to conduct a preference analysis of gibbon foods so that tree and liana genera can be characterized as preferred or fallback foods. Data from 5.0 ha of botanical plots in each habitat will be used to estimate habitat-specific availability of both classes of foods. These data will be used to test competing hypotheses about which aspects of food availability constrain gibbon populations at Gunung Palung. Comparable data from other primates at Gunung Palung will be used to examine whether the gibbon models can be applied more widely.

The possible application of marker methods for estimating dietary intake and nutritive value in primates

Robert W. Mayes

Macaulay Land Use Research Institute; Craigiebuckler; Aberdeen; AB15 8QH; UK

The physical examination of primate faeces for residues of different food items has served as a useful complement to direct observation in dietary studies with free-ranging animals. There is potential for gaining further quantitative information on dietary composition, intake and digestion through the use of chemical markers in the faeces, originating either from materials naturally present in the diet, or artificially administered. Such markers should ideally be physiologically inert, completely recoverable in faeces and their analysis should be straightforward yet accurate and precise. Over the last 20 years there has been considerable interest in the use of plant-wax hydrocarbons (especially n-alkanes) for carrying out dietary studies in grazing ruminants within the agricultural sector. These compounds are analysed as discrete compounds and are close to 'ideal markers' in other respects. The digestibility of the whole diet can be estimated from the relative concentrations of plant-wax alkanes in the diet and faeces. Through the dilution of known amounts of an artificial n-alkane (of similar carbon chain length to dietary alkanes) administered to animals, faecal output can be determined. Concurrent digestibility and faecal output measurements allow alkanes to be used to estimate dietary intake. Because n-alkanes are present in plant waxes as mixtures, which tend to differ in composition between plant species and plant parts, the patterns found in faeces can be used to determine the botanical composition of the diet. Other plant-wax compounds, including branched-chain alkanes, alkenes and long-chain fatty acids and alcohols are also recoverable in faeces and allow more complex dietary mixtures to be quantified. These methodologies have been applied to wild ruminants (red deer and moose), and have been validated in non-ruminant mammals and birds. Furthermore, the approach is not restricted to plant components of the diet; the cuticular waxes of insects and spiders contain complex mixtures of branched-chain alkanes, which have been shown to be recoverable in the faeces of insectivorous birds and bats.

The compounds present in the cuticular wax of plants and insects have the potential to be used as faecal markers to quantify the intake, composition and quality of the diet of free-living primates. However, in many circumstances, the wide range of food items selected and large temporal variation in diet composition presents big challenges to the use of these marker techniques. Evaluation of such methodologies for use in primate feeding studies may require a degree of controlled testing with captive animals. It may also be necessary to search for new markers in order to accommodate dietary items which are unlikely to contain plant-wax compounds.

Diet composition and nutrient intake in free ranging animals – a methodological approach

Sylvia Ortmann

Institute for Zoo and Wildlife Research; Alfred-Kowalke-Str. 17; 10315 Berlin; Germany

Feeding is a fundamental interaction between an animal and its environment and several aspects of wildlife ecology are related to nutrition, e.g. population dynamics and regulation, habitat use, animal behaviour, predator-prey interactions. Nutrients and particularly energy can provide limits in which animals and populations must operate and most animal species from various habitats have to cope with seasonal changes in forage nutrient supply, composition, and spatial distribution. A couple of methods and techniques are meanwhile developed to get an estimate of forage quality in natural habitats, the amount and pattern of dietary intake and assimilation. Here I briefly introduce and discuss the application of some selected methods providing an insight into qualitative and quantitative aspects of wildlife nutrition. Chemical and structural analysis of forage and faeces, for example, is a non invasive technique which does not require treatment of the animal itself but allow an estimate of digestibility and composition of the diet. Faecal markers (Cr, n-alkanes) provide sufficient information on digestibility, passage rate and botanical composition of herbivorous diet. Stable isotope analysis of tissues from living organisms (hair, blood, urine) is useful for estimating an animals field metabolic rate, but also its trophic level in a food web and its diet because the isotopic composition of animals is linked to that of its diet due to biosynthetic processes. The advantage of these methods is that they are relatively cheap and easily applicable in comparative and systematic studies and thus they will significantly contribute to enhance our knowledge about the feeding ecology of apes and other primates.

Feeding and ranging ecology of chimpanzees in an open environment at Fongoli, Senegal

Jill D. Pruetz

Department of Anthropology; 324 Curtiss Hall; Iowa State University; Ames; Iowa 50011; USA.

The Fongoli community of chimpanzees in southeastern Senegal has been continuously studied since April 2001. The community's range is on the margin of chimpanzee habitat in Africa, in a semi-arid, open environment. The study site is dominated by woodland and wooded grassland interspersed with areas of bamboo woodland, plateau, and thicket. Small areas of gallery forest (1% of study area) provide important foods and shelter (i.e., caves, evergreen nesting trees), but much of chimpanzee feeding occurs in open habitat. Based on preliminary observational data on this small community (25 known individuals), Fongoli chimpanzees use areas seasonally (e.g., ~12 km² during a two-month period at the beginning of the rainy season) but are estimated to have a much larger annual community range of at least 50 km², as indicated by nesting patterns and estimated ranges of identified individuals. Based on data from >500 fecal samples and from numerous observations of chimpanzees, diet at Fongoli includes 27 fruit species; bark feeding on 3 species; leaf feeding on 5 species, including 2 terrestrial herbaceous species; geophagy; whole leaf swallowing, as indicative of medicinal plant use; feeding on honey; insectivory on termites, weaver and driver ants; and meat eating of *Galago* sp., as well as other mammalian prey. Patterns of food availability indicate that Fongoli chimpanzees could be expected to occur in smaller, more dispersed parties than chimpanzees elsewhere. However, small chimpanzee communities are typically characterized by social cohesiveness. Such issues will be examined in light of the available data.

Variability of the feeding ecology of Eastern gorillas

Martha M. Robbins

Max Planck Institute for Evolutionary Anthropology; Deutscher Platz 6; 04103 Leipzig; Germany

Ecological conditions are predicted to have an impact on a multitude of behaviors and life history characteristics exhibited by a species, including diet, ranging patterns, reproduction, and social behavior, which all ultimately result in the species' social system. A useful way to test current models of socioecology is to make intraspecific comparisons of populations occurring in differing ecological conditions. Gorillas are an appealing species to consider for within-species comparative studies because they occur in widely varying habitats across Africa. In particular, eastern gorillas (*Gorilla beringei*) occupy a large altitudinal range with correspondingly extensive variation in habitat types and food availability. The first aim of this presentation is to present new results on the diet, ranging patterns, and social behavior the mountain gorillas in Bwindi Impenetrable National Park, Uganda. It is now apparent that findings from the well-studied Karisoke mountain gorillas, which live in one extreme of gorilla habitats, cannot be extrapolated to other eastern gorilla populations. Secondly, comparisons will be made using the information available for diet, ranging behavior, and social behavior among the gorillas of Virunga Volcanoes, Kahuzi-Biega, and Bwindi to test aspects of the socioecological model. Finally, future research necessary to expand our knowledge of the variability of gorilla feeding ecology and social system will be discussed.

Does ecological home range quality influence the development of social polyandry in white-handed gibbons?

Tommaso Savini^{1,2}, Ulrich H. Reichard²

¹ *Université de Liege, Department of Science; Quai van Beneden 16; B-4020 Liege; Belgium*

² *Max Planck Institute for Evolutionary Anthropology, Department of Primatology; Deutscher Platz 6; D-04103 Leipzig; Germany*

Most mammals live in polygynous groups because given mammalian females' reproductive physiology, polygyny often maximises individual fitness. This is advantageous to males, because they can increase their reproductive output with the number of mating partners and to females, because food competition may be reduced, unless a male is needed to provide a service that can not be shared among females. Thus, social polyandry may evolve where females live apart from each other as a result of strong feeding competition and when more individuals than the parents are needed to successfully raise offspring. It is predominantly found in species where other group members or an additional male are necessary to feed, carry or warm young or indirectly help by, e.g., defending a territory.

Long-term observations of a well-known white-handed gibbon population at Khao Yai National Park, Thailand, have shown that about 10 % of social units are polyandrous. Because reasons for social polyandry in gibbons are not yet understood, we have begun to investigate if the observed group structure flexibility, and particularly the occurrence of social polyandry, is caused by ecological pressures. Our working hypothesis is that social polyandry may result from a need of more than one adult male to secure sufficient resources for successful reproduction and offspring development, because a preliminary analysis suggested a link between large range size, low food production and social polyandry. White-handed gibbons are well known for their territorial behaviour. When a home range increases in size, it may become increasingly difficult for a single male to maintain its boundaries and to defend the largest ranges two males may come to live with one female. Home range size varies at our site between c. 15 – 30 ha (n = 6). The need for a large home range in turn could be a consequence of inhabiting a relatively poor area.

To test our working hypothesis we have started to compare the food plant productivity of home ranges inhabited by socially monogamous and socially polyandrous groups. So far we collected ecological data on five socially monogamous and one socially polyandrous group. Another two socially polyandrous groups are under investigation. We have collected data on the spatio-temporal distribution of food sources of 20% of the groups' home ranges along botanical belt transects to measure food abundance. More than 20000 trees have been measured (DBH) and classified and data on the phenology of important fig (24 species) and non-fig (27 species) food tree as well as six non-fig climber species are available for monthly calculations of productivity. Productivity is measured as food abundance index, which links data on gibbon food tree densities (stems/ha) with mean basal area of trunks (cm²/ha) and relative fruit presence (phenology). In addition to estimating home range productivity behavioural observations are presently conducted on three socially polyandrous groups to quantify the males' participation in inter-group encounters, within-group duet singing and sexual interactions and allow direct comparison with socially monogamous males.

Sex differences in foraging and tool use in wild orangutans

Carel P. van Schaik

Anthropologisches Institut und Museum; Universität Zürich-Irchel; Winterthurerstr. 190; CH-8057 Zürich

Unique among primates, human foragers show a persistent pattern of foraging and sharing, known as the sexual division of labor, involving pronounced sex differences in foraging, with men most hunting and women most gathering, delayed consumption, tool-assisted food procurement and processing and mutual sharing (or at least one-way provisioning). This combination of elements is uniquely derived, shown by no other primate.

Why did this suite of characters evolve? It is reasonable to assume that ecological sex differences and a tendency toward food sharing are a necessary precondition for the sexual division of labor. Hence, we should explore sex differences in feeding and foraging and patterns in food sharing among nonhuman primates. In this study, we examined sex differences in a population of Sumatran orangutans with both meat eating and routine tool use, thus providing us with a parallel to chimpanzees. We distinguish between adult females and two classes of sexually mature males: flanged and unflanged. We found that meat eating is perhaps biased toward females. If combined with data from nearby Ketambe, the pattern shows a clear female bias. If only flanged males are compared with females, females spend proportionately more feeding time on insects and more on fruit. However, differences with unflanged males may be more like sex differences in chimpanzees, and the pattern is reversed if females are compared with them. Tool use is not female-biased. Food sharing outside the mother-infant context is not uncommon, but the most common direction is from female to female and occasionally from female to male.

The patterns in orangutans are therefore different from those in chimpanzees. Explanations based on differences in intrinsic nutritional needs, based on body size and reproduction, are therefore unlikely to hold, a conclusion confirmed by a recent study of sex differences among Gombe chimpanzees (Pandolfi 2003). We examine the alternative hypothesis that sex differences in socio-ecological strategies are more likely to explain the ecological sex differences, and generally find it supported. The basis of the sexual division of labor must be sought in aspects of human social organization, especially the need for males to maintain alliances, rather than in ecology.

The influence of crop-raiding on the feeding ecology and ranging behaviour of *Papio anubis*

Ymke Warren, Caroline Ross

University of Surrey Roehampton; School of Life Sciences; West Hill; London SW15 3SN; U.K.

The focus of this paper will be the results of field observations made of baboons (*Papio anubis*) in Gashaka Gumti National Park, Nigeria. An outline of the feeding ecology of two groups, one crop-raiding maize fields near the village of Gashaka on the south-western park boundary (CR group) and the second a forest-living group that does not raid crops (NR group) is given. A detailed analysis of their ranging behaviour involving several analytical techniques, including GIS, is used to compare the two groups and to examine crop-raiding in the context of the feeding ecology and patterns of habitat utilization. GGNP study baboons ate 211 different food items, concentrating the majority of their foraging time on fruits and beans/seeds from trees but also including a wide variety of other foods from various plant and animal sources. Differences between the two groups in feeding ecology occur because of differences in both presence and availability of food items (food plants might be present but not productive for various reasons). There also appeared to be a more stable food base within NR group's range as they foraged on three monthly staple foods for seven or more months of the study whereas CR group had only one monthly staple food that they consumed during six months of the study. The carrying of foods in the cheek pouches, mouth or hands away from the source was observed in GGNP study groups. The food item most often consumed from cheek pouches was oil palm fruits and this is explained by the intra-individual competition that could occur when foraging on this fruit. For CR group the second highest ranking identified food item carried away from source to be fed on was maize and this is explained by the need to avoid the hazards found in agricultural areas. Although previous studies suggest that crop-raiding may lead to a reduction in home range size, the two groups had similar home range sizes; this is explained by the relative proportions and quality of different habitat types in each group's home range. Both study groups exhibited preferences for use of certain habitats used primarily for feeding or resting, but water availability and sleep sites did not appear to strongly influence the study group's ranging patterns. The study groups also appeared to use their habitat in accordance with potential predator threats, including the threat of human predation. We conclude by comparing our findings to those of previous studies, and discussing whether this study helps us to understand the reasons why animals raid crops.

Sumatran orangutan sociality, reproduction and fruit availability

Serge Wich¹, T. Mitra Setia, M. L. Geurts, S. S. Utami

¹ Utrecht University; Behavioural Biology; PO Box 80086; 3508 TB; Utrecht; The Netherlands

Previous studies have suggested that orangutan sociality depends on the availability of fruit and that therefore larger parties are found in periods of high fruit availability. It has also been suggested that a lack of fruit can cause negative energy balances and that therefore conceptions and mating are to be expected in periods of high fruit availability, such as mast fruiting periods. We investigated these questions for an orangutan population (*Pongo abelii*) on Sumatra on which long-term data are available. We found no correlation between fruit availability and overall orangutan party size or for each age-sex class separately. We further report that mating frequency and conceptions are not more likely to occur in periods of high fruit availability and that in addition conceptions were also not more common during mast fruiting periods or less common during periods of very low fruit availability. The results indicate that at least orangutan sociality and reproduction at Ketambe are not in any obvious manner related to overall fruit availability, but are more likely to be related to locally available large fig trees for females and to the availability of reproductive females for both flanged and unflanged males. The results might be in contrast to certain orangutan populations on Kalimantan where negative effects of low fruit availability seem to be more pronounced on both sociality and reproduction. These results indicate that caution should be taken not to generalise Sumatran and Bornean orangutans and to be cautious with results from short-term studies.

Habitat utilization by sympatric populations of gorillas and chimpanzees

Juichi YAMAGIWA

*Laboratory of Human Evolution Studies; Faculty of Science; Kyoto University;
Sakyo; Kyoto 606-8502; Japan*

Based on 9-years data on diet and ranging of gorillas and chimpanzees in Kahuzi-Biega National Park, Democratic Republic of Congo, foraging strategies and factors influencing them are analyzed in relation to fruit availability. Fruit phenology was monitored monthly by both transect census and fruit trail methods. Gorillas showing opportunistic frugivorous diet preferred the fruit species that were available for the prolonged periods, while chimpanzees showing persistent frugivorous diet relied on the fruit species whose availability fluctuated monthly and annually. Fruit species preferred only by chimpanzees showed a distinct intra-specific synchrony in fruiting, while fruit species preferred by gorillas and chimpanzees did not. These differences in fruiting patterns may influence the foraging patterns of gorillas and chimpanzees. Gorillas tended to travel widely in a cohesive group and to increase their consumption of fruits in the primary forest during the dry season. By contrast, chimpanzees tended to continuously visit particular fruiting trees individually in a small home range throughout the entire year. Gorillas increased day journey length when they showed frugivorous diets, and chimpanzees tended to expand monthly range during the period of fruit scarcity. Their different responses to the changes in fruit availability may support their sympatry and may have promoted different sociality from each other based on female dispersal. Due to large body weight and poor digestibility of unripe fruit and mature leaves, ecological constraints may have forced them to find behavioral and social flexibility coping with diets. Lack of territoriality and site fidelity provide gorillas the opportunity of inter-unit interactions at which females transfer. Fission-fusion grouping patterns enable chimpanzees to survive at low density, ranging widely with rare inter-group interactions. Habitat utilization by gorillas and chimpanzees in the montane forest of Kahuzi may show a good example of inter- and intra-specific feeding competition shaping sociality of great apes at a lean fruit habitat.