

**Abstracts
of
Talks and Posters**

Male and Female Life Histories and Behavior

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A primary goal for evolutionary biologists is understanding how phenotypic traits influence fitness. One approach is to identify traits that impact short-term mating success or conception success. However, relying solely on these correlates of short-term fecundity may result in inaccurate estimates of the relative importance of traits. For instance, in the neotropical bird species *Chiroxiphia linearis*, the long-tailed manakin, male fitness is vastly more sensitive to changes in survival than it is to changes of the same relative magnitude in fecundity. This result is somewhat counterintuitive for a lekking species with extreme reproductive skew among males. In contrast, fitness of prairie warblers, a monogamous species, is relatively insensitive to changes in survival and is more sensitive to changes in fecundity. Measuring the potential strength of selection on phenotypic traits depends on correctly identifying those life-history stages to which fitness is most sensitive. This, in turn, depends on an understanding of the whole life history. Here we present life history analyses of male and female baboons to identify critical stages in the life history of each sex. We employ demographic matrix methods, which are long familiar to demographers and population ecologists but less used by behavioral ecologists. We complement this approach with path analyses, which enable us to identify in more detail the behavioral traits in each sex that influence the most critical life history stages.

Is There a Primate Way of Aging?

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Compared with other mammals, many primate species are characterized by large brains, complex social systems, and a "slow" life history (delayed maturity, low reproductive rate, and decelerated rate of physiological decay). It has been hypothesized that these three characteristics are causally inter-related. That is large brains facilitated the evolution of complex social systems, complex social systems then lead to the dual effects of favoring further elaboration of cognitive abilities as well as decreasing extrinsic environmental hazards thereby facilitating the evolution of retarded aging. A comparative analysis among primates and other mammalian orders will be used to critically evaluate this hypothesis, particularly with respect to reproductive and cognitive patterns of aging.

Primate Brains and Life Histories

Robert Barton (Department of Anthropology, University of Durham, UK)
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There is a widespread assumption that life histories and brain size evolution are fundamentally connected. A number of different suggestions have been made about the nature of this postulated connection. For example, it has been suggested that slowly-developing and long-lived species encounter greater cognitive challenges and therefore need larger brains. Alternatively, large brains may simply take longer to develop, so that selection on brain size affects life histories indirectly, or life histories may act as a constraint on a species' brain size. We analyze the logic of, and empirical evidence for these theories. An important empirical issue is the problem that correlations between brain size and life history variables may be overestimated when each variable is first "corrected" using error-prone estimates of body size, and we both test for such an artifact and control for it in our analyses. We also evaluate the view that the conservatism of the developmental program of the brain may limit the role of selection on specific neural systems, and find no compelling evidence for it. Instead, comparative evidence supports the idea that socio-ecological factors selected for specific information-processing capacities.

Comparison of the Life History Patterns of Three Squirrel Monkey Species: Ecological Bases and Phylogenetic Constraints

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Squirrel monkeys (*Saimiri* spp.) probably present the most extensive genetically-based geographic variation in social organization of any primate. Throughout their range in Costa Rica, *S. oerstedii* exhibit the least aggressive social behavior of any large multi-female, multi-male primate social organization. Neither males nor females can be described as the dominant sex. Female *S. boliviensis* in Peru are dominant to males and have strong female-female bonds. Both sexes form a single linear dominance hierarchy among *S. sciureus* in Suriname, with all or most males dominant to all females. The extent of social divergence among these species is surprising as the morphology and diet of squirrel monkeys are relatively homogeneous throughout their distribution in Central and South America. Here I extend this interspecific comparison to the life history patterns of the three squirrel monkey species. As with social organization, the extent of species divergence in life history patterns is great. Maternal age at first birth, interbirth interval, infant age at independent locomotion and weaning, extent of birth synchrony, age-specific susceptibility to predation, prevalence of 'aunting' behavior, and the existence of all-male troops are only some of the life history parameters for which field studies now document marked species differences. Preliminary analyses suggest that geographic variation

in the amplitude of seasonal fluctuations in food abundance, competitive regimes for fruit resources, and susceptibility to predation underlie much of the observed life history. On the other hand, juxtaposition of life history patterns on a newly available molecular phylogeny for the genus *Saimiri* indicates that phylogenetic constraints on these parameters have been relatively weak.

Early Life Histories of Male and Female Rhesus Macaques: Harassment of Infants by Other Group Members

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Male macaques are reported to experience higher mortality rates than females during early infancy, possibly as a result of being larger at birth and more vulnerable to nutritional stress than female infants. In contrast, female macaques are reported to experience higher mortality rates than males during the juvenile period. The greater mortality rate of juvenile females may result from competition for food with larger male peers, but has also been suggested to be influenced by harassment from unrelated adult females in the group, who may benefit from reducing the size and strength of competing matriline. We have used data on the interactions of infant rhesus macaques during their first six months of life in order to investigate whether harassment from other group members occurs at an early age, and whether more harassment is directed towards female, than male, infants. We also investigated how mothers react to aggression shown to their infants and whether this reaction may be influenced by the mother's social rank. The study was carried out on 19 infants and mothers living in small, captive social groups. The data suggest that female infants did receive more harassment than male infants and that how mothers reacted to this harassment depended upon social rank. Following an aggressive encounter, high/medium-ranking mothers appeared to intervene and re-establish contact with their daughters, but move away soon afterwards, while low-ranking mothers appeared to pre-empt further harassment by allowing their daughters to remain in physical contact. Body weight data collected on these infants suggest that early growth is also related to the sex of the infant and the rank of the mother.

Cooperative and Communal Breeding in Mammals

Timothy H. Clutton-Brock (Department of Zoology, University of Cambridge, UK)

Studies of cooperative breeding in birds have focused on three main questions:

- Why do subordinate adults remain in their natal group?
- Why do they not breed?
- Why do they help?

The paper examines the distribution of communal and cooperative breeding in mammals and assesses current answers to these three questions.

Determination of Maternal Style and its Influence on the Development of Social Behavior of Infant Bonobos (*Pan paniscus*)

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Mothers play a primary role in the emotional and social development and the learning of the species' social organization and traditions. Variation in maternal behavior is reflected in maternal styles. The interactions of mothers and infants are complexly intertwined and the behavior of one necessarily affects the behavior of the other. Next to the mother, siblings are the most frequent social partners for many primates. The presence of siblings may facilitate infant independence and social development. This study compares four mother-infant pairs living in two semi free-ranging social groups at the animal parks Planckendael and Apenheul. The bonobo infants were observed at the age of 6, 7 and 10 months for a total of more than 200 observation hours. We scored the frequencies of rejection and restriction of the mothers, corrected for the actions of the infant itself. The maternal style may vary from extremely rejective to very protective. Infants of more rejective mothers were expected to spend more time in social play than infants of more protective mothers. The presence of siblings was expected to increase the infants' opportunities for social interaction by having a readily available social partner. The results indicate that the maternal style influences the behavior of the infants more than the presence or absence of siblings. If siblings are present however, they are the next most important play partners.

Dominance Relationships and Competition among Captive Female Hamadryas Baboons

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Dominance relationships among female primates are associated with competition for food and safety. In our study group of hamadryas baboons at Antwerp Zoo, a linear and stable hierarchy was found among the females during the last seven years. We investigated if this linear hierarchy could be associated with contest competition for food and/or safety. Female rank is based on spontaneous submission during non-food conditions. Since hamadryas males are thought to be the females' main protector, we used proximity to the alpha-male as a measure of competition for safety. Spatial scans were made both day and night. Feeding time and feeding bout length were used as a measure of feeding competition. Video-recordings were made during feeding sessions with clumped food, which is a normal feeding condition at Antwerp Zoo. No correlation could be found between female rank and proximity to the alpha-male in any of the one-male units (OMU). In addition, no correlation could be found between female rank and feeding time or feeding bout length. However, the

alpha female of each OMU had better access to food in the first five minutes. Our study revealed that there is no contest competition for safety between the females, probably because of the "safer" environment in captivity, but that contest competition for preferred food does occur. However, this contest competition is reduced between females of different OMU's due to the spatial separation between these OMU's, that is controlled by their leaders. In addition, only the most dominant female within a OMU benefits from her dominance status. For the lower-ranking females other factors, such as friendship with the alpha female, can mask the influence of rank.

Demography of *Lemur catta* at Berenty Reserve, Madagascar, 1972-1997: Effects of Density, Troop Size, and Climate

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Margaret Solberg (Department of Zoology, University of Texas, USA)

Valerie Perel (John Hopkins Medical School, Baltimore, USA)

The social structure of ringtailed lemurs has been studied intermittently at Berenty Reserve, Madagascar since 1972, with almost continuous annual records for the past ten years. Population density in the 1 km² main study area grades from 100/km² in the natural spiny desert and scrub habitat, to 200/km² in natural gallery forest, to 400/km² in the tourist zone, where the diet is supplemented by introduced tree species and by tourist provisioning. Troops in the tourist area are larger than those in the gallery forest, and these, in turn, larger than those in scrub. Larger troops have overall lower birth rate than smaller troops. However, residuals from non-linear regressions of troop size effects indicate birth rate in the Tourist Front significantly above the regression line, Gallery Troop birth rate significantly below, and Scrub Troops about on the line. One-year survival was above the regression line in Tourist Front and Gallery, but far below in Scrub. Tourist Front birth rate was buffered against adverse year effects, while the natural forest troops birth rate dropped in bad years. We conclude by discussing the implications of these results for the persistence and conservation of ring-tailed lemur populations.

Brain Size Evolution in Primates

Robin I. M. Dunbar (Population Biology Research Group, School of Biological Sciences, University of Liverpool, UK)

Primates are characterized by unusually large brains relative to other mammals, mainly because there has been a disproportional expansion of the neocortex in the primates. Comparative analyses of brain part volumes in the primates suggests that increases in neocortex volume within the primate lineage correlate with social

rather than ecological variables. Indeed, although total brain volume correlates with the usual life history parameters (e.g. gestation length, body size) in primates, relative neocortex size correlates with the length of the juvenile period (i.e. the period of socialization and intense social learning). I shall suggest that increases in brain size among primates have been driven largely by the need to evolve social strategies that require considerable information-processing abilities in order to be able to support large closely bonded social groups. More importantly, comparisons between brain components suggest that, once brain size reaches a certain absolute size, the decreasing marginal gains in visual processing power meant that increasingly large volumes of neural matter that would normally be devoted to the visual system in smaller primates could now be devoted to higher social cognitive functions.

Living in a Neotropical Forest: Arboreal Rodents, Primates, and Marsupials

John Eisenberg (School of Forest Resources and Conservation, University of Florida, USA)

In the broad sense whatever major mammalian taxon we study, we may observe certain generalizations. Forest-adapted tropical forms, in particular specialized arboreal forms, tend to exhibit life history traits suggestive of "K" selection. That is to say that within a lineage the arboreal specialist taxa, when body size factors are eliminated, exhibit a greater longevity, smaller annual reproductive potential, and a delayed age at first reproduction. Often a relative increase in cranial capacity is demonstrated. The peculiar faunal history of South America lends itself to several analytical approaches yielding hypotheses which in turn can be tested by establishing comparable trends in the mammalian faunas of the Australasian Region and the Palaeotropics. The unique features of the primate life history patterns are readily apparent, but such broad taxonomic comparisons as examined in this paper may shed some light on the early evolution of life history traits shared by ancestral primate lineages.

Modeling the Reproductive Life History Characteristics of Primates

Timothy B. Gage (University at Albany, State University of New York, USA)

The objective of this paper is to compare three methods of fitting reproductive distributions and estimating life history parameters at the population level. The organisms examined include several marmoset, rhesus and chimpanzee populations, as well as several human populations, Przewalski's horse, and Asian elephants. The methods compared are all taken from the human demographic literature and include the gamma (four parameters), the Hadwiger (inverse Gaussian, four parameters) and the Brass polynomial (three parameters). All of the methods are fitted us-

ing a standard non-linear fitting routine. The results indicate that the Brass polynomial, while the simplest method, fits as well or better than the gamma or the Hadwiger distributions. In addition the Brass polynomial provides direct statistical estimates of the length of the pre-reproductive period, the length of the reproductive period, the maximum age at reproduction, and the level of fertility. Thus this method appears to be ideal for studying life histories of a variety of species including a wide range of primates. A particularly interesting ancillary finding is that the length of the reproductive period for chimpanzees (40.5 years, *Pan troglodytes*) appears to be significantly longer than that for the human populations examined (32.8 to 35.9 years).

Primate Nutritional Ecology and Metabolic Strategies

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Many hypotheses concerning carrying capacities, the evolution of primate social behavior and life history characteristics imply that primate populations are limited by food availability and that individuals compete for food within and between species. Effects of the assumed food limitations are treated as being applicable similarly to all individuals and all species. However, different primate species have different mechanisms to manage energy resources by either saving energy during lean times or by storage of energy during times of high food abundance. Optimization of these traits are subject to different constraints and so are the species involved. Different phenomena and life history traits associated with these different constraints in primates will be compared with non-primate taxa for which more data are available.

Singing Behavior of the Silvery Gibbon (*Hylobates moloch*) in Central Java, Indonesia

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All gibbon species are known to produce loud, long and well patterned morning songs. In virtually all species, mated males spend at least as much time singing as mated females. The only previous study on the singing behavior of the silvery gibbon (*Hylobates moloch*) was carried out in Western Java and revealed that territorial males of *H. moloch* do not appear to sing (only 2 male songs were heard during 130 full days of listening). We carried out a short study on the singing behavior of the silvery gibbon in Linggo Asri in Central Java. Gibbon singing activity was monitored

on a daily basis during 19 consecutive days in October 1998. We heard a total of 125 song bouts of at least 11 groups. Most groups could be individually identified by individual-specific song characteristics. No duet songs were heard. Most of the song bouts (n=108, 86%) were female solo songs, but we also heard at least 13 male solo song bouts. Most male songs (62%) started between 04:20-04:40, when it was still dark. All female songs, in contrast, started after 05:00 and female singing activity peaked around 06:00. Conclusions: (1.) Silvery gibbons are unusual among gibbons in that duet songs do not occur and most song bouts are female solo songs (86%). (2.) In contrast to an earlier study in western Java, males in Central Java also produced songs, albeit less frequently than females (13 vs. 108 song bouts). (3.) Males prefer to sing before dawn, whereas females sing later in the day. (4.) Similarly separated periods of male and female solo songs were also observed in Kloss gibbons (*H. klossii*) on the Mentawai Islands. This may represent a derived characteristic shared by *H. moloch* and *H. Klossii*.

Dental Development and Primate Life Histories

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Karen E. Samonds & William L. Jungers (Department of Anatomical Sciences, State University of New York at Stony Brook, USA)

Across the Order Primates, the timing and sequence of dental eruption vary both on absolute and relative scales (i.e., vis-à-vis particular ages and particular life history landmarks such as age at weaning or age at sexual maturation). Whereas much has been written about the absolute timing of dental eruption in relation to body and brain size, the complexity of the variation in the relative timing of dental and life history landmarks, as well as the heterochronic decoupling of aspects of dental and overall somatic growth and development, remain poorly understood. Despite tight overall integration of dental eruption patterns, there are important differences in the timing of dental eruption among species of primates that are surprisingly uninformed by variation in body or brain size. Attempts to understand why dental eruption is relatively precocious in some clades and delayed in others must grapple with the influence of factors such as diet and phylogeny. This presentation focuses on that complexity. Diet might be presumed to influence dental development in a variety of ways (relating to resource distribution and intraspecific competition for food resources, the mechanical properties of foods, protein content, etc.). Strepsirrhines might differ from anthropoids in ways that relate to differences in their reproductive biology or in their patterns of prenatal vs. postnatal growth and development. For over 40 species of primates at selected absolute ages (four months, one year) and life history stages (weaning, female sexual maturation), we examine dental endowment (cheek teeth occlusal area) and precocity (number of postcanine teeth erupted) as percentages of species' mean adult values. This allows us to directly test alternative hypotheses regarding the influence of dietary and phylogenetic factors, as well as adult body and brain size, on dental developmental schedules. Certain patterns

emerge. We show, for example, that when compared to their more frugivorous, like-sized relatives, folivorous strepsirrhines resemble folivorous anthropoids in exhibiting accelerated dental development on an absolute scale, relative to craniofacial growth, and relative to particular life history landmarks. Nevertheless, there are important ways in which, even within the Strepsirrhini or the Anthropoidea, alternative developmental strategies among like-sized species with similar diets are manifested.

The Evolution of Human Life Histories: Lines of Evidence to Explain Human Uniqueness

Kristen Hawkes (Department of Anthropology, University of Utah, USA)

Human life histories differ from those of other primates in several striking ways, including our patterns of growth, age at maturity, long adult life spans, and mid-life menopause. Plausible explanatory hypotheses have linked these features to various other distinctive features of our species. Since modern humans are the solitary living representative of the radiation of genus *Homo*, no direct tests can be made with appropriate phylogenetic comparisons. But recent work on life history variation among living primates still provides a key line of evidence for causal links among life history variables and socioecology in human evolution. I illustrate this with an evaluation of the grandmother hypothesis.

Ecological and social determinants of birth intervals in baboons

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Birth rates in primates have long been proposed to result from an interaction between ecological and social factors. Here we analyse a variety of social and environmental variables to determine which best explain the observed variation in interbirth intervals across 14 baboon populations. Both the number of females in the group and mean annual temperature are found to be important, and a multivariate equation containing the quadratic components of both these variables accounts for almost all the observed variance in interbirth intervals. The quadratic relationship with temperature is explained in terms of the energetic costs of maintaining a stable body temperature at both low and high temperatures. The quadratic relationship with number of females on the other hand results from relationships with both food availability and the costs of increasing intragroup competition as group size increases. While females may be able to exert a certain degree of choice in their reproductive scheduling decisions, they are ultimately constrained by limits imposed upon them by the complex interactions between their ecological and demographic environment.

Molecular DNA Analysis for the Reconstruction of Kinship and Reproductive Success of Primates

Uta-Dorothee Immel (Institut für Anthropologie, Universität Göttingen, Germany)

Molecular genetic techniques provide immense opportunities for population genetics, assigning biological relationships and genotyping in primates by the analysis of DNA. DNA profiling is used for genetic management and conservation genetics of endangered free-ranging primates, zoo populations and livestock breeding. It also has great implications for ethological field workers who are interested in reproduction strategies to clarify social structures in the organization of societies of primates. The genetic affinity of 99% between human and orangutans (*Pongo pygmaeus* ssp.) should allow the usage of human short tandem repeat loci (STR). Therefore it is expected that, due to this high degree of relatedness, most of the microsatellite markers used in humans to determine kinship and identification can also be employed to set up DNA-profiles of non-human primates. To test whether the mode of inheritance of the alleles enables us to reconstruct genealogies as it does in humans, the initial investigations were carried out on family groups. In this study, chromosomal DNA from orangutans (*Pongo pygmaeus*ssp.) were extracted from excrements. Feces samples were screened for up to nine microsatellite markers in a multiplex-PCR approach from zoo populations of orangutans. Their kinship is known and documented in the "International Studbook of the Orangutan". I was able to show that five of the nine human autosomal STRs in question amplified in orangutans. Fragment length determination enabled me to reconstruct kinship in the documented family structures. Furthermore, I show that orangutans reveal polymorphisms comparable to humans in these systems. This means genotyping for each individual enabled us to reconstruct biological kinships. At the moment, further studies involving the STR-loci that initially did not show results during the multiplex approach are carried out. It is the objective of these experiments to examine whether the loci in question simply do not exist in orangutans at all or if they are not detectable during the multiplex-PCR.

Predation, Life Histories, and the Evolution of Sociality

Charles H. Janson (Department of Ecology & Evolution, State University of New York at Stony Brook, USA)

In this contribution, I explore how predation risk affects two aspects of primate biology: life history and social organization. These two aspects must be considered together, because both act as mechanisms to cope with high predation risk, and both affect an individual's foraging ecology. Evidence from other life-history studies overwhelmingly argues that body size is an overarching constraint on life-history parameters within broad taxonomic groups. Thus, I model fitness as a function of two variables: body size (S) and risky foraging behavior (R). Following Peter Abrams work, I

use R as a proxy for a suite of social and ecological behaviors, all of which increase food intake and fecundity at the expense of increased predation risk. Examples of such behaviors include: smaller, less cohesive groups; lower vigilance; use of habitats with more predators but higher food densities. As body size increases, predation rate decreases, but so does the ability to translate food intake into offspring (as suggested by James Brown). Net food intake (after deducting metabolic costs) may increase or decrease with S . I use the results of the theoretical analysis to interpret previously published analyses of the covariation seen between primate body size, estimated predation rate, group size, and fecundity.

Dynamic Models of Alternative Male Reproductive Strategies

James Holland Jones (Department of Anthropology, Harvard University, USA)

Alternative male reproductive strategies are a common feature of primate social systems. Adopting any particular strategy often involves an irreversible somatic commitment, as in the development of large size and epigamic traits in orangutans (*Pongo pygmaeus*). Somatic commitment means that choice of strategy becomes an ontogenetic, life-history decision. The best strategy a male can employ is a function of (1) his current state, (2) his future behavior, and (3) both the density of competing males and the strategies they employ. The evolutionarily stable life history is the state-dependent lifetime sequence of strategies that maximizes some measure of fitness. I analyzed alternative reproductive strategies for an orangutan-like animal as a state-dependent stochastic dynamic game. The model posits two strategies: (1) attractive but dangerous (large), and (2) unattractive but safe (small). Large males enjoy high mating success but draw the agonistic attention of other males, whereas small males avoid intrasexual agonism but have reduced mating opportunities. A male's state changes as a function of the strategy adopted and age. I took parameter values from the orangutan literature, and used a variety of functional forms for state dynamics. The ESS life history depends on the specific model parameterization. However, certain general results emerge. To achieve the ratio of male morphs reported from field studies (~1:2), either the costs of the large strategy or the benefits of the small strategy must be quite high. Paradoxically, the best life history for a male in poor condition is to grow large quickly, whereas the best strategy for a male in good condition is to delay maturation. While inspired by orangutan socioecology, the results I describe are quite general. Modeling exercises such as this help formulate precise hypotheses which can be tested with field data.

Life History Inference Based on Age at First Molar Emergence in Fossil Apes

Jay Kelley (College of Dentistry, University of Illinois, USA)

I have hypothesized that life history may have been a principal adaptive factor in the divergence of Old World monkeys and apes, and that this might be reflected in

Miocene representatives of the two groups (Kelley, 1997). Across a wide spectrum of extant primates, mean age at first molar (M1) emergence is correlated with a number of individual life history traits relating to rate of maturation. Age at M1 emergence can therefore serve as a substitute for approximating overall rates of maturation in comparative contexts. Here I report estimates of age at M1 emergence in individuals of early Miocene *Afropithecus turkanensis* (17 Mya), and late Miocene *Sivapithecus parvada* (10 Mya), the latter widely considered to belong to the Pongo lineage. Both individuals died while the M1 was in the process of erupting. Both also have incisors that preserve perikymata, periodic growth lines on the surface of the teeth that record the duration of growth. Perikymata counts were combined with data on dental growth in extant anthropoids, and in early Miocene Proconsul species (Beynon et al., 1998), to calculate estimated ages at death and, therefore, ages at first molar emergence in the two fossil individuals. Age at M1 emergence for the *Sivapithecus* juvenile was estimated at between 38 and 42 months. This is essentially identical to the average value of approximately 39 months for *Pan troglodytes*. Age at M1 emergence for the *Afropithecus* juvenile was estimated at approximately 30 months. This is within the range of *Pan troglodytes*, but well outside the ranges of all extant cercopithecoid monkeys for which there are data. These results suggest that a shift toward prolonged maturation occurred early in the history of the hominoid lineage, and that the very prolonged maturation characteristic of extant great apes was fully established early in the history of this group.

Life History and Social Behavior in the Long-lived Bechstein's Bats (*Myotis bechsteinii*)

Gerald Kerth (Zoologisches Institut, Universität Zürich, Switzerland)

Myotis bechsteinii is a medium-sized, non-migratory and forest dwelling bat. Females rear their pups in maternity colonies that usually consist of 20-40 adult females; males are solitary. Since 1993 I have been studying the social behavior and the genetic population structure of Bechstein's bats in Germany (since 1998 additionally in Switzerland), to analyze the adaptive value of female social behavior. Using mitochondrial as well as genomic markers I estimated gene flow, relatedness within social groups and population structure among 17 maternity colonies living in close geographic range. I found that colonies consist of maternally closely related bats which indicates that females are strongly philopatric and almost never leave their natal social groups. During several summers I further observed the females' behavior, survival and reproductive success in five colonies, in which all bats were individually marked. Individual females did not give birth every year (on average, each female weaned 0.6 young per year), and colonies generally comprised reproductive as well as nonreproductive bats. However, the proportion of reproducing females per colony varied strongly among years, ranging from 0 to 100 % (with a mean of about 60 %). The low annual individual reproductive success was balanced by a high survival rate of about 80% per year for adult females, which can reach an age of 20 years. The social organization of Bechstein's bat colonies suggest that the long-lived

females need familiar and perhaps related cooperation partners for raising their young. Several cooperative behaviors have been described for bats. Some, like information transfer are principally not restricted to the reproductive status of colony members, others like allo-mothering might preferentially or exclusively occur among lactating females. I discuss the influence of age, reproductive status and genetic relatedness on the social behavior of female Bechstein's bats.

Phenotypic Plasticity of Primate Life Histories

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Life history 'invariants' now appear to be firmly embedded as concepts relating to phylogeny, mass-specific traits and selection. However, such a perspective necessarily ignores key traits of plasticity and variability, without which no selection could occur. Primates, representing a large monophyletic group of species, containing an array of radiations of different time depths and occupying a range of niches, make an interesting starting point for an exploration of phenotypic plasticity. The key questions we ask are (1) what is the extent of intra-specific variation in life history traits; and (2) what are the correlates, if any, with the observed level of variation (mass, local ecology and sociality). We explore variance in age at first reproduction, age at weaning and growth rate for both strepsirrhine and haplorhine primates. We have not used phylogenetic subtraction methodologies, since we are explicitly examining the effect of phylogeny on these traits. Sub-family, genera and species are separately considered through variance measures, and the effect of captivity is used to illustrate the potential for variance. We can thus attempt to make conclusions about life history traits that are constrained in their potential for variance, which may be those deeply embedded in the phylogenetic history of a lineage, and those that are labile and respond facultatively to local ecological and social conditions.

"Killer-mentality" in Captive Hamadryas Baboons (*Papio hamadryas hamadryas*): An Existing Phenomenon

Iris Leinfelder, Rebekka Deleu & Mark Nelissen (Department of Behavioural Biology, University of Antwerp, Belgium)

At least since 1993 the hamadryas baboon (*Papio hamadryas hamadryas*) colony at the Antwerp Zoo suffered from a high degree of infant mortality. Since infanticide is considered as one of the important causes of infant mortality in hamadryas baboons, we started a detailed investigation to the circumstances under which infants died. Possible causes of death were hypothesized, varying from decreased infant via-

bility due to inbreeding, to infanticides by group members. All possible killers and their motives -with respect to sociobiological hypotheses- were postulated. Four directly witnessed and four video-recorded cases of infanticide together with similarities to 19 other cases of infant mortality indicate one of the harem leaders as the most important cause of infant death. This is in agreement with earlier findings in other groups in captivity. Although directly observed incidents of infant killing in other hamadryas groups are limited, infanticide seems to be a common event. It has been suggested that uncertainty of the leader position can lead to infanticides by the male. None of the observed infanticides in our study occurred during periods of stag-gering leadership, but the infanticidal male was one of the three males who competed in 1991 to establish a harem. This led to a period of social instability, coinciding with infant abuse and infanticides. It can be argued that a behavior which can be adaptive in such circumstances has evolved to a "killer-mentality", without apparent advantage.

Comparative Socioecology of *Macaca thibetana* and *Macaca sylvanus*

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Despite significant geographic, taxonomic, and genetic distinctions, *M. thibetana* and *M. sylvanus* are among the 20 species of *Macaca* that share remarkable similarities in many aspects of their social structure. This study aims to compare the socioecology of *M. thibetana* and *M. sylvanus*. A comparison of published results on *M. sylvanus* and my long-term study (1987-1998) on *M. thibetana* in Huangshan, China, revealed the following similarities in the social organization of these two macaques: (1) they are the two largest macaques, (2) they live in groups with the highest male to female ratios and a large proportion of natal adult males, (3) males do not emigrate from their natal groups until reaching adulthood, (4) they have extensive male-infant caretaking and bridging behavior, (5) the social hierarchy among males is egalitarian, and (6) males both compete and cooperate. Ecologically, *M. thibetana* resembles *M. sylvanus* in that (1) they live in montane habitats near the subtropical/temperate boundary, (2) they experience low predator pressure in their habitats, and (3) they rely heavily on foliage and structural plant parts. However, the differences of life history strategies between the two species are obvious. For example, female Barbary monkeys in estrus form short-term consortship (average 17.3 min) and mate with nearly all adult males each day, but female Tibetan monkeys engage in long-term consortship (average 2.7 days) and can be relatively monopolized by their consorts. These results confirm that ecological variables indeed influence their social organization, yet the life history strategies of individuals may modify its process.

The Puzzle of Primate Juvenility

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Life history theory illuminates how growth, maintenance, and reproduction are adaptively modulated in relation to age and size across lifespans. Research on life histories therefore must focus substantially on pre-reproductive phases. In species exhibiting determinate growth, including virtually all primates, individuals achieve most growth before initiating reproductive careers. To understand primate life histories, then, detailed growth data are needed for diverse taxa. A variety of logistical difficulties has prevented accumulation of much data, including the large sizes and long lives of many primates. Complicating matters further is that regulatory plasticity is a direct target of selection and life histories essentially express reaction norms, where ontogenetic trajectories respond constantly to individual perceptions of variable environments. Consequently, understanding of individual taxa will require data on behavior, physiology, and morphology from wide ranges of conditions. We review what is known about somatic growth trajectories in prosimian and anthropoid primates and suggest foci for future research. Because animal juvenility generally functions to maximize opportunity for growth, understanding the suppressed growth rates characteristic of most juvenile primates is a primary goal. Group living has been suggested simultaneously to permit and require slow growth for primates. Indeed, if primate gregariousness is best explained as predator protection, it is also best interpreted as parental investment, as the vulnerability of no class approaches that of primates' slow-growing offspring. Immatures' inevitable difficulties in feeding competition may require that they grow slowly to minimize instantaneous risks of malnourishment. Effects of predation and foraging competition both predict that non-gregarious and small-group primates exhibit faster juvenile growth than taxa that characteristically form large social groups. Other risks engaged by immatures are social and the two sexes encounter divergent challenges in this domain. We review physical and behavioral patterns of primate development in relation to predictions from current understanding of male and female socioecology. Future research, within and across species, should approach primate development from the reaction norm perspective. Correlated suites of traits and adjustments should be sought among patterns of foraging, growth, maturation, dominance acquisition, social play, social bonding, and dispersal.

Primate Life Histories and Phylogeny

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This contribution starts with a brief review of two recent comprehensive models of mammalian life history evolution, both of which aim to explain the well-known

patterns of trait covariation among species as inevitable results of simple trade-offs. We examine the ability of these models to explain primates' unusually slow life histories and their allometric grade shifts. The second section is a phylogenetic analysis of life history variation within the order. We estimate the rate of life history evolution, and make comparisons among traits (and with non-life-history traits) and among clades. A comparison with carnivores shows that primate litter size evolves peculiarly slowly. Implications of this finding are discussed. We end by turning the usual phylogenetic comparative approach around, with a life history analysis of phylogeny variation. It has long been appreciated that some parts of the tree of life are very bushy (e.g. Cercopithecidae) whereas others are extremely sparse (e.g. Tarsiidae); this observation leads naturally to a search for a possible cause. We review hypotheses that link these diversity differences to life history variation among clades. A methodological digression shows how such hypotheses can be tested rigorously, and highlights flaws in some previous work. Finally, we present preliminary results from our analyses.

Do Male Mouse Lemurs (*Microcebus murinus*) Face a Trade Off Between Survival and Reproduction During the Dry Season?

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Gray mouse lemurs are unusual among mammals in that adult females hibernate for several months during the cool dry season, whereas adult males are apparently active year-round. However, male activity has not yet been studied in detail, and why males may forgo hibernation is also not known. Because food availability is reduced and predation risk increased during the dry season, this male behavior may reduce their probability of survival. This potential cost may be compensated by improved reproductive success because mating begins soon after female emergence and active males may have a competitive advantage. The goal of my study, therefore, was to quantify male activity during the dry season to determine several unknown behavioral aspects of this sex difference. To this end, I observed 6 male and 6 female *M. murinus* between April and September 1999 at the Kirindy forest research station. These individuals were radio-collared and subjected to regular focal animal observations. I found that no male entered hibernation, but that all of them were regularly inactive. Periods of inactivity lasted from one night to about a week, interspersed by one or several nights of activity. Time devoted to feeding, moving and resting during nights of activity did not change over the course of the dry season. Males also maintained their body mass between April and September. These results indicate that all males are regularly active throughout the dry season. The costs of activity may not be as high as previously thought. However, the potential benefits of this strategy, as well as potential ecological or social constraints, remain to be determined for a complete understanding of this unique mammalian sex difference.

Radar Imagery as a Tool in Pre-classification of Primate Habitats in the Tai National Park, Ivory Coast

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The Tai National Park protects the largest remaining area (4540 km²) of tropical rainforest in Westafrica. The park was established in 1972 and suffered from illegal logging activities in the past. The influence of illegal hunting on primates was studied. The importance of primates as seed dispersers and the consequences of hunting primates on the recruitment of tree communities and vegetation composition were analyzed. For habitat pre-classification, radar imagery was used to separate riparian forest from dense rain forest. In a first step, the radar image was rectified and geocoded using ground reference points with known geographic location. A gamma map filter was applied to reduce image speckle. Geographical display was improved by contrast stretching. In the image the densely forested Tai National Park appears in green colors. Within the forest the riparian vegetation can be traced as bright zones. L-Band RADAR is sensitive to structural properties of vegetation and separates riparian forest from dense rain forest.

Food Preferences and Habitat Utilization of Java Gibbon (*Hylobates moloch*) in Ujung Kulon National Park, West Java, Indonesia

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The Javan Gibbon (*Hylobates moloch* AUDEBERT) is considered the most threatened endemic species on the island of Java. Research was conducted at two different areas in Ujung Kulon NP, in the Cicanolong and in Curug Cikacang areas, and 52 effective days were spent in the field. Observations on the distribution of Javan gibbon groups in these sites were carried out by Triangle or Call Count Method (for indirect observation) and the Concentration Count Method (for direct observation). The results showed that in the Cicanolong area the density of Javan gibbon is 2,3 groups per sq. km and 10,73 individuals per sq. km (n = 6 groups). In the Curug Cikacang area, density was found 1,87 groups per sq. km and 8,21 individuals per sq. km (n = 5 groups). The home range of the observed 11 groups varied from 7,5 to 9,6 ha with an average of 8,82 ha in Cicanolong and from 5,1 to 10,1 ha with an average of 8,53 ha in the Curug Cikacang area. There are 27 species of food plants used by Javan gibbon. The ten most preferred food plants are *Ficus callophylla*, *Spondias pinnata*, *Diospyros hermaphrodita*, *Pometia pinnata*, *Artocarpus elastica*, *Paratocarpus venerosa*, *Eugenia polyantha*, *Baccaurea javanica*, *Dillenia excelsa*. Within vegetation sample plots, it was recognized that 21 species (35%) of seedlings, 11 species (42%) of saplings, 7 species (88%) of poles, and 22 species (54%) of trees stages in the Cicanolong areas, and 29 species (33%) of seedlings, 22 species (40%) of saplings, 8 species (32%)

of poles, and 21 species (38%) of trees stages in the Curug Cikacang area are food plants of Javan gibbon. Based on the preferred proportion of food plants species in sample plots and on birthing success in both research sites, Ujung Kulon National Park is the most suitable habitat for Javan gibbon.

Life History, Infant Care Strategies and Brain Size in Primates

Caroline Ross (School of Life Sciences, Roehampton Institute London, UK)

Primate development is characterized by having a relatively long period of infant dependence followed by a relatively long period between weaning and reproduction. Species which breed relatively late in life tend to be those in which infants are carried and where brain size is relatively large. Both infant carrying and the evolution of large brain size have been linked to the evolution of social living and it is therefore expected that late age at maturity will be found in more social primate species. In this paper I use comparative analyses to explore the links between the evolution of large brain size, sociality and infant care patterns. Infant carrying may have some energetic costs (species that carry their infants travel shorter distances and maintain smaller home ranges than do non-carriers of the same body size) and reproductive costs (carriers mature relatively later than do non-carriers). However, its repeated evolution in the primate order suggests that it also has some benefits, the most likely being a reduced mortality risk for carried infants. One way in which mothers may off-set the costs of carrying infants is to allow others to help with infant care, something that is only possible for group-living species. Mothers of carrying species who have help with infant care from other individuals, do have higher birth rates than those species without non-maternal care. Brain size may also influence reproductive rates- as primates with relatively brain sizes mature relatively late when compared to other species. Although a number of theories have been proposed to explain the link between brain size and age at maturity, the data presented here suggest that the energetic constraints imposed by growing and maintaining a large brain prevent species with relatively large brains from growing rapidly to maturity. If this is the case one might expect that mothers who are caring for large-brained infants might be particularly strongly selected to solicit non-maternal care thus saving energy that they can then divert to growing their 'costly' infants. The links between the evolution of large brain size, social behavior and life-history strategies are discussed with reference to infant care strategies in haplorhine and strepsirhine primates, as compared with other mammalian taxa.

Male Home Ranges in a Promiscuous Primate (*Microcebus murinus*) during Consecutive Breeding Seasons in North-West Madagascar

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In dispersed, promiscuous species the spatial distribution of receptive females is an important factor influencing male mating strategies. Therefore, home range size

can be decisive for male mating success. In one captive colony, males of *Microcebus murinus* form weight-based hierarchies with only the dominant male having access to oestrous females. In another captive colony, dominant males mate more frequently than subdominant males but dominance cannot be derived from body weight. In order to examine the relevance of these findings in wild *M. murinus* males, data from our study site in north-west Madagascar based on triangulation and mark-recapture procedures were analyzed for three successive breeding seasons (1996-1998). Home ranges were telemetrically determined for 10 males in 1998 including 3 males with known home ranges from previous years. At the beginning of the breeding season in September 1998 home range sizes increased significantly. Average percentage overlap between the individuals increased from 23.7% (24 pairs without overlap) in August to 38.8% (2 pairs without overlap) in September. Spatial exclusion could not be observed. A positive correlation between home range size and body weight could be detected in September. Throughout the years, 2 of the 3 focal males were heavier than the average of all males captured at the study site. The weight of the third male remained always below the mean. For these 3 males, the relationship between body weight and home range size could not be established throughout the study years, indicating that long-term home range size is not necessarily related to body weight. The percentage overlap of intra-individual range areas over consecutive years varied, on average, from 52% to 72%, showing that males form spatially stable long-term home ranges. We assume that individual and variable Behavioural strategies rather than single morphological factors determine home range sizes in the gray mouse lemur.

Social Influences on the Life History of Male Mandrills

Joanna M. Setchell & Alan F. Dixson (Sub-Department of Animal Behavior, University of Cambridge, UK and Centre for the Reproduction of Endangered Species, Zoological Society of San Diego, USA)

Male mandrills are remarkable for their large size and the magnificence of their secondary sexual characteristics (red and blue 'sexual skin' on the face and rump, large canines and impressive pelage). Not all males develop these traits equally and the question arises as to how social and other environmental factors might affect development during adolescence. Behavioural, morphological and endocrinological data were collected over a 2 year period for 31 male mandrills living in two semi-free ranging breeding groups in naturally rain-forested enclosures in Gabon. During adolescence (beginning at 5 years) males increased in body size, testicular volume and sexual skin coloration, the sternal gland developed and the canine teeth erupted. Adolescent males peripheralised or emigrated from their social groups. Individual differences in the timing of these events correlated with dominance rank, whereas maternal rank had no measurable effect. Higher ranking males developed faster and emigrated earlier. Emigration was an active process rather than a response to aggression from adult males. It is unknown how long males remain solitary in the wild but in the enclosures several males rejoined social groups and in these cases a

marked increase in sexual skin coloration occurred. Adolescent males were sexually active during the annual breeding season, but achieved less mating success than top-ranking adult males. Increased pubertal development occurred during the mating season and during periods of social unrest (overthrow of alpha males). Previous work on semi-free ranging mandrills indicated that adult males occur as either well developed, group associated individuals, or peripheral/solitary males with muted secondary sexual development. These studies reveal a more complex spectrum of developmental changes, influenced by physical (mating season) and social cues (adolescent rank, presence/absence of adult males, perturbations in the adult male dominance hierarchy). The long-term effects of these differences upon ultimate life-time reproductive success remain to be established.

Evolution of the Menopause

Daryl P. Shanley & Thomas B. L. Kirkwood (Biological Gerontology Group, University of Manchester, UK)

The rapid reproductive senescence associated with the menopause in human females occurs well in advance of general somatic senescence and poses an interesting evolutionary problem. In the course of human evolution increasing encephalisation and the constraints of bipedal locomotion has led to a trade-off of infant cranial size at birth and size of the pelvic canal. Consequently, human reproduction is characterized by particularly dangerous births and long periods of care for altricially born offspring. A hypothesis for the evolution of the menopause is that in view of the danger of giving birth, at some point in the life history it is worth more in terms of inclusive fitness to redirect the effort from individual reproduction to gain fitness benefits from existing offspring. The life table of a traditional living population is analyzed to determine whether the level of influence that an older female has on her kin is sufficient to offset the declining value of her continued reproduction. Daughters may potentially benefit from the presence of their mother by a reduction in mortality and/or an enhancement in fertility. This assistance may also extend to granddaughters. The mother is assumed to provide assistance only if she has no dependent young children. Post-reproductive females are therefore more likely to be available to provide help. The relative costs and benefits of providing and receiving assistance are constrained by the data and are calculated with different assumptions concerning intergenerational interaction. The age of menopause is approximately 50 years in the observed population. Using the same costs and benefits but assuming a lower or higher age of menopause, hypothetical populations are created. By contrasting the hypothetical populations with the observed one, the limiting conditions for menopause to be evolutionarily adaptive are identified. It is found that menopause is beneficial even if only small increases in fecundity of adult daughters and in survival of grandchildren result from the assistance provided by a post-reproductive female.

Life History and Genetic Variation in *Hypogeomys antimena*, a Monogamous Malagasy Rodent

Simone Sommer (Zoologisches Institut, Universität Hamburg, Germany)

The Malagasy giant jumping rat (*Hypogeomys antimena*) is one of the most endangered mammal species due to recent restrictions of its geographic range to less than 20 x 40 km of dry deciduous forest on the western coast of Madagascar. The first continuous long-term investigations of different life history and ecological aspects of this largest endemic rodent started in 1992. This research indicates that *Hypogeomys* is monogamous. Pairbonds apparently last until one mate dies. Pairs defend an exclusive territory throughout the year. The reproductive rate is very low, each couple has only 1-2 offspring per year. Male offspring leave the parental burrow and territory at the age of about one year (before the next reproductive period starts), while female offspring show a delayed dispersal and stay with their parents for one more reproductive period even after the next generation is born. *H. antimena* is predated upon by only two top predator species. An annual age- and sex specific predation peak has been documented. Declines in geographic range and, therefore, population size, as well as constraints by the mating system are often reflected in the reduction of genetic variability of a population. Sequence variation at a MHC class II gene was examined by direct sequencing and SSCP (single stranded conformation polymorphism). Objectives were: (1) to investigate levels of polymorphism in the MHC-complex of this highly endangered species that experienced a severe reduction in population size and (2) to investigate the genetic mating system by assessing the frequency of extra pair paternity (EPP) as EPP might have important consequences for increase gene flow, and thus genetic variability within a population. The amplified gene segment had a very low variability (only two alleles) in *H. antimena* compared with other mammalian species. The alleles segregated consistently with Mendelian expectations in families. No case of EPP was found. The present data suggest no difference between the social and the genetic mating system.

Major Concepts and Questions in Life History Evolution

Stephen Stearns (Zoologisches Institut, Universität Basel, Switzerland)

The essential concepts of bet-hedging will be reviewed - spreading of risk to reduce variance in fitness, variance discounting, and the conditions that lead to risk-prone and risk-averse strategies. These concepts were developed in a long-term dialogue between economics and biology. The history of that dialogue reveals who knew what when, and what difference it has made. In addition, I will discuss adaptive dynamics and invasion models, which are robust enough to make predictions in stochastic and chaotic populations.

Life History and Infant Rearing Strategies of Three *Hapalemur* Species

Chia L. Tan (Doctoral Program in Anthropological Sciences, State University of New York at Stony Brook, USA)

This paper presents an interspecific comparison of the life history and infant care patterns of *Hapalemur griseus* (0.9 kg), *H. aureus* (1.5 kg) and *H. simus* (2.4 kg). I studied the three species in Ranomafana National Park, Madagascar, beginning in 1996. Supplementary data were culled from captive records. In the southeastern rain forests, *H. griseus* and *H. simus* mate in May/June and *H. aureus* in July/August. Following gestation lengths of 137 days (n=5) and 149 days (n=2) for *H. griseus* and *H. simus*, respectively, they give birth during the transitional time between the dry and wet seasons. *H. aureus* gestates for 138 days (n=12) and births coincide with the onset of rainy seasons. *H. griseus* has an extended birth season; parturition may occur between September and April/May in Madagascar. All three species produce singletons, though twinning in *H. griseus* has been observed. *H. griseus* infants are weaned after 4 months old, compared to 6 and 8 months in *H. aureus* and *H. simus*, respectively. Interbirth intervals for *H. aureus* (n=13) and *H. simus* (n=4) are one year but slightly longer for *H. griseus* (1.3 years, n=33). The dispersal age of a male *H. griseus* is approximately three years. A female *H. aureus* emigrated from her natal group at three years of age. In *H. simus*, male offspring disperse between 3 and 4 years old. The age of first reproduction in female *H. griseus* is 3.1 years (n=8). In captivity, a female *H. griseus* reached longevity of 23 years. Unlike *H. griseus* and *H. aureus*, *H. simus* does not practice infant parking and oral transport. Additionally, *H. aureus* mothers choose secluded areas to 'nest' their altricial neonates for the first 10 to 14 days, a behavior that is absent in the other two congeners. In depth analyses of the life history variations and infant rearing strategies of the three *Hapalemur* species may reflect interplay of factors such as body size, social organization, activity pattern, and ecology.

Life History and the Social Behavior of Primates

Carel P. van Schaik (Department of Biological Anthropology and Anatomy, Duke University, USA)

Traditionally, studies of social evolution in vertebrates have focused on the selective impact of ecological factors such as food, predation and parasitism on social organization (spatial distribution, composition and stability of social units) and social structure (patterning of social interactions and relationships). However, as shown by major social differences between taxa in similar ecological conditions, other factors must play a major role as well. In this presentation, I will examine the role of life history. Among the life history variables most likely to affect social behavior in mammals, lifespan, litter size and state of infant development at birth are thought to have the strongest impact. After briefly reviewing the impacts of lifespan and litter size, the rest of this talk focuses on one consequence of altriciality (and sometimes

litter size), namely the length of lactation relative to gestation. Where lactation is relatively long, the loss of her dependent offspring advances the female's subsequent reproduction. It is shown that post-partum mating and conception are very rare in these species. As a result, infanticide by males is concentrated in these same species. The risk of infanticide by males has selected for a variety of counterstrategies by females and likely sires, many of which involve social behavior. Among primates, year-round male-female association, multi-maleness in groups, male bonding in fission-fusion species, dispersal tactics, female polyandrous mating, sexual swellings, female mating calls and abortion in response to male immigration have all been thought to be responses to infanticide risk. A review and a comparative test of these claims, especially in primates, indicates that a seemingly trivial aspect of life history has had major implications for social behavior in primates and several other mammals.

The Meaning of Kinship among Female Rhesus Macaques: Familiarity or Degree of Relatedness?

Anja Widdig (Institut für Medizinische Genetik, Charité, Humboldt-Universität zu Berlin, Germany)

Rhesus macaques live in a female-philopatric system where females remaining with their kin while males migrate from their natal group around puberty. Few males monopolize all fertile females during a mating season, so infants born in the same cohort tend to be paternal siblings. According to kin selection theory, individuals increase their indirect fitness when co-operating with their kin more than with non-kin, therefore, selection should favor kin recognition in both maternal and paternal kin. Familiarity mediated by the mother seems to be the mechanism of maternal kin recognition. When females mate with more than one male, paternal kin recognition may be more difficult. However, familiarity due to age proximity might be a possible mechanism of paternal kin recognition, as a given age cohort is likely to represent a group of paternal siblings. Here I evaluate whether the degree of relatedness or familiarity favors kin-biased behavior. Data were collected on female rhesus macaques on Cayo Santiago, Puerto Rico (group R). Paternity was determined using microsatellites and DNA-fingerprinting. The prediction that kin-biased behavior increase as a function of the degree of relatedness was not confirmed by the data as neither rates for proximity, grooming nor support increased with the degree of relatedness. Data on paternal siblings laid in between of those from maternal siblings and non-kin. To test whether age proximity favors familiarity, females born in the same year (peers) were compared with females born in different cohorts (non-peers). Here peers shown higher rates for proximity, grooming and support than non-peers. The results suggest that familiarity is more relevant for kin-biased behavior than the degree of relatedness.

Brain and Body Energetics in Weanling Primates: Implications for Life Histories

Helen T. Wood (Department of Anthropology, University College London, UK)

Two features that distinguish primates from most other non-primate taxa are 1) the relatively large primate brain and 2) their extensive investment in offspring growth and development. The process of weaning is an important aspect of this investment as it encompasses both the allocation of maternal resources and the metabolic and Behavioural competence of the juvenile. Lee et al. (*J. Zool., Lond.* 225: 99-114, 1991) suggest that body mass at weaning reflects a threshold above which the infant can no longer rely on the maternal milk yield to supply its energetic needs, but beyond which it is able to support its own maintenance requirements. The study presented here investigates the hypothesis that brain size at weaning also has important energetic implications. The demands of brain growth, and more importantly of brain maintenance, place a high energetic burden on the infant. This may be especially appropriate in the case of the primates, where the sub-adult brain consumes more than twice the energy of that of a similarly sized non-primate mammal. This study examines the relationship between body weight, brain weight and weaning weight in various primate species for which data is available from the literature. Ontogenetic trajectories for both brain and body mass are reconstructed, and integrated with weaning data. The results shows that, contrary to previous assumptions, brain growth can continue well after birth in primate species, and that the cessation of this postnatal brain growth occurs just prior to weaning. The energetic demands of brain and body growth over the infancy period are modeled, taking into account the mother's contribution to energy intake via lactation, in order to investigate infant and maternal weaning strategies. The results are discussed in the context of evolutionary change in primate life histories, especially for the large-brained cebids and hominids.