

Abstracts
of
Talks and Posters

Queuing and queue jumping: long term patterns of dominance rank and mating success in male savannah baboons

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Variance in reproductive success among individuals is a central variable in both sexual selection theory and reproductive skew theory. In many species, variance in male fighting ability is a major source of variance in reproductive success. However, in some species of mammals, primates in particular, studies have varied greatly in the extent to which they detect a relationship between male fighting ability (or dominance rank) and male mating success. Some studies report that male dominance rank is a perfect predictor of mating success, while others have reported no effect, or even a negative relationship between rank and mating success. This has led to heated debate over the importance of fighting ability for male mating success in these species. Here we present an analysis of the relationship between dominance rank and male mating success over 32 group-years in a single population of wild savannah baboons (*Papio cynocephalus*). When data were pooled over the entire period, higher ranking males had greater access to fertile females. However, when we examined successive six-month blocks of time rather than pooling the data, we found variance in the extent to which rank predicted mating success. This resulted from the fact that, in some periods, the dominance hierarchy functioned as a queue in which males waited for mating opportunities, so that rank predicted mating success extremely well. In other periods, the queuing system broke down, and dominance rank failed to predict mating success. This happened when the number of adult males in the group was large, when males differed greatly in age (and hence in fighting ability), and when the highest ranking male maintained his rank for only short periods.

The variance within this single population is similar to the variance observed between populations. Our long-term results indicate that this variance is not an artifact of methodological differences between short-term studies, but is due to true variance in the extent to which high ranking males are able to monopolize access to females. The processes that contribute to this variance - density-dependence of the ability to monopolize, age-dependence of fighting ability, and individual differences in the ability to maintain high dominance rank - are not species-specific but probably general to many social systems. Hence, our results probably apply to a wide range of primate and nonprimate species, and indicate that variance in male fighting ability is indeed an important source of variance in reproductive success over the long term for these species. However, other sources of variance, in particular demographic contexts and alternative mating strategies, shape patterns of mating success as well.

The evolution of sexual displays in primates

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Inter-specific variation in the flamboyance of visual sexual signals is usually assumed to reflect variation in the intensity of inter-sexual selection. In primates, the

picture is complicated by the use of different modes of signaling in nocturnal species (amongst which signaling is predominantly pheromonal) and diurnal species (amongst which visual signaling, including colorful ornaments, predominates). Phylogenetic comparative analysis reveals an inverse relationship between the development of the vomeronasal organ and accessory olfactory bulb (involved in processing pheromones) on the one hand, and flamboyant visual signaling and an expanded visual cortex on the other hand. I suggest that pheromonal and visual signals convey similar information about mate quality, and were to a large extent evolutionary alternatives associated with nocturnal and diurnal lifestyles, respectively. However, activity patterns do not appear to have been the only constraint (in diurnal New World monkeys, for example, pheromonal signaling is more important than in Old World monkeys). Within diurnal clades, the intensity of inter-sexual selection can be invoked to explain variation in visual flamboyance. Variation in olfactory signaling in relation to sexual selection is much less well documented, but merits investigation. Finally, given the importance of mate choice for fitness, sexual selection should be seriously considered as an important factor in primate brain evolution.

Post-copulatory sexual selection in birds

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The mating system of most (ca. 90 %) bird species is social monogamy; a pair of birds working together to rear offspring. Polygyny also occurs, and more rarely polyandry, and a few species appear to have a promiscuous mating system. Behavioral observations and molecular analyses of parentage reveal that in all mating systems some females copulate with more than one male during a single breeding cycle. Strict genetic monogamy is relatively rare and occurs predominantly in species with long-term pair bonds, such as seabirds. The adaptive significance of extra-pair copulations for males is clear since this behavior increases the number of offspring they father; the advantages to females of copulating with multiple males are less clear, although some studies suggest that extra-pair offspring are of higher quality than within-pair offspring, but there is no consensus about this. Numerous adaptations to sperm competition exist, most notably, larger relative testes mass in species with high levels of sperm competition. In addition, males perform a number of paternity guards, notably following of their female partner during the days on which she is fertile. Copulation with multiple partners by females results in sperm competition and provides the opportunity for cryptic female choice. The mechanisms of sperm competition reveal that a range of factors affects the outcome of sperm competition, notably, sperm numbers and sperm quality. Individual variation exists in both these traits and in addition, some species can also facultatively adjust the number of sperm they transfer during copulation, but sperm quality appears to be constant throughout life. Cryptic female choice can occur in many different ways, before, during or after insemination and fertilization. Some forms of cryptic female choice are difficult to detect and distinguish from male effects, and there few unambiguous examples. We found no evidence that female fowl could preferentially utilize the sperm

of particular males when mixtures of sperm artificially inseminated and females had no phenotypic cues on which to base their choice. On the other hand, in natural matings females preferentially retained the sperm of attractive males.

Behavioral correlates of reproductive success in wild chimpanzees

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Behavioral estimates of reproductive success, such as measures of the length of time or manner of male-female association as well as copulation frequency, have commonly been used to infer male reproductive success in species with polygynous mating systems. Genetic determination of paternity allows the testing of the assumptions and predictions of such behavioral estimates. We use the information from the genetic determination of paternity for 31 infants living in two neighboring chimpanzee communities within the Taï National Park, Côte d'Ivoire, to investigate the predictive value of three behavioral measures of male reproductive success: mating frequency with the estrous female, consortship time and association patterns. In addition, we investigated the most relevant factors determining male reproductive success. Comparison with results from other studies of chimpanzee and primate populations will be included.

Assessing male reproductive success in wild mountain gorillas using DNA analysis

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Mountain gorillas (*Gorilla gorilla beringei*) are traditionally described as having a one-male mating system in which a single dominant silverback fathers most, if not all, of the group offspring born during his tenure. However, approximately 40 % of mountain gorilla groups have more than one adult male, and subordinate males have been observed copulating with group females. This has led researchers to question the degree to which dominant males monopolize reproduction in gorilla groups, an issue that can only be addressed through DNA-based analyses of paternity. To determine the extent to which socially dominant male gorillas monopolize reproduction by group females, we are analyzing nuclear DNA from fecal samples collected from some 90 individually recognized gorillas at Karisoke Research Center, Rwanda. These gorillas comprise 4 groups, including 46 mother-offspring pairs, spanning multiple generations. Genotyping of group members at 10 polymorphic microsatellite loci reveals a sufficient amount of genetic variability for significant assignments of paternity (paternity exclusion probabilities always >0.95). The results of this genetic study, integrated with data on male dominance rank and group composi-

tion, show that although there is a high degree of reproductive skew among gorilla males, it is unlikely to be based on dominance alone, as subordinate males also sire offspring.

Sexual selection and acoustic communication in small nocturnal Malagasy primates, the mouse lemurs (*Microcebus* spp.)

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According to standard view in evolutionary ecology, selection should favor the diversification of signaling and recognition systems in coexisting sibling species to guarantee the recognition of conspecifics and assortative mating. To date, empirical evidence in support of this hypothesis is scarce for primates. Acoustic communication in two nocturnal, sympatrically living and genetically distinct sibling species of comparable body size, the gray and the golden brown mouse lemur, *Microcebus murinus* and *M. ravelobensis*, was compared to identify the degree of interspecific acoustic variation. The response to conspecific and heterospecific calls was studied by playback experiments in order to gain insight into respective recognition mechanisms. Both species are promiscuous and live in a complex, dispersed, multi-male, multi-female system. Vocalizations used for distance communication showed a different level of interspecific distinctiveness. Calls given during rallying group members and during mating showed species-specificity with regard to syntax (syllable form and structure), whereas calls used at activity onset and during alarm were statistically similar. In playback experiments, gray mouse lemurs did not differentiate between the heterospecific, statistically indiscriminate calls, but exhibited significantly stronger reactions towards conspecific calls differing in syntax. Results suggest that sexual selection affects the sound generating and perception system of nocturnal primates differently. The evolution of species-specificity in a communication system in an area of sympatry might reduce reproductive costs of hybridization by acting as a premating isolation mechanism.

What psychopathology can tell about human mating strategies

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The potential of psychopathology to contribute to the understanding of evolved psychological capacities, mechanisms, and strategies – and *vice versa* – has largely been underestimated. From an evolutionary perspective, psychopathology deals with dysfunctions, costs and trade-offs of such capacities, and with their representation and organization in the human brain. Evolutionary psychology has revealed in many cross-cultural studies how sexual selection has shaped human mate preferences and mating tactics. According to Parental Investment Theory, women are predicted to prefer, on a relative time scale, long-term mates who are capable of provid-

ing sufficient resources. Men, by contrast, are more likely to prefer partners with high fertility. As men's reproductive success is constrained by the number of potential partners, they benefit more from short-term mating relative to women, from having multiple mates (polygyny), or perhaps in some cases from circumvention of female choice by sexual coercion. Although relatively rare in clinical settings, some distinct psychotic syndromes may be interpreted as reflections of such evolved sexual strategies and counter-strategies, respectively. This hypothesis is exemplified by case demonstrations of delusional jealousy, erotomania, and erotic paranoia, the latter possibly representing the fear of male sexual coercion. Evolutionary psychopathology may buttress the study of the nature of evolved psychological mechanisms in several ways: The reduction of "cortical control" may unveil evolved mechanisms in "purer" form. Specific hypotheses may be added from a psychopathological perspective and empirically tested in healthy and clinical populations. The "hard-wiring" of evolved mechanisms in the CNS may be clarified through psychopathology. In reverse, evolutionary psychology provides a powerful framework for psychopathological research.

Sexual selection in primates

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Sexual selection is commonly used to denote different evolutionary processes by different workers. Instead of contrasting sexual and natural selection, it is usually more useful to examine contrasts in the intensity, medium, and target of selection between the sexes. Drawing on long-term research from other vertebrates, I speculate on the operation of selection on males and females in polygynous primates.

Male coercion in hamadryas baboons (*Papio hamadryas*): intra-sexual competition and female choice

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The mating system of the hamadryas baboon involves harem defense polygyny and sequential polyandry. The harem male's reproductive success is thought to be positively related to the number (and reproductive value) of females that he owns and to the length of his tenure as harem holder. On the other hand, the harem females' reproductive rate is thought to be related to their ability both to access food resources and to avoid reproductive suppression due to female competition (and aggressive coercion by males). Thus, although it may pay females to associate with powerful, protective males, because they provide them two major fitness-related services: access to food and protection against harassment from other females and males, intersexual conflict should be expected to arise because (a) females in small

harems and (b) subordinate females in large harems face social constraints that may seriously limit their reproductive success. In addition to sexual, affiliative and cooperative interactions, the social relationships between the harem males and their females in the one-male/multi-female social systems of some species of nonhuman primates also involve the use of coercion or punishment by males. This male "herding" behavior may serve two general functions: to exclude rival males (intrasexual competition) and to prevent female desertion (intersexual conflict and female choice). In this paper we present a preliminary analysis of herding interactions from a close study of the social relationships between 14 adult males (11 harem leaders and 3 followers) and 36 adult females, members of the multi-level colony of hamadryas baboons housed at the Madrid Zoo, in order to explore the role of intrasexual competition (hypothesis 1) and female choice (hypothesis 2) in the rate at which males coerce the females. Predictions from both hypotheses are tested using a sample of about 1200 herding interactions in which we analyze the effect of subject-related variables (e.g., male age, male reproductive status, female reproductive condition), relationships-related variables (e.g., affiliation, cooperation), and demography-related variables (e.g., sociogenic sex ratio of the colony, harem size, number of females in estrus). Our results suggest that both processes do have a role in the occurrence of male coercion, although the weight of each is hard to establish and remains to be elucidated.

Male and female mating strategies in gray mouse lemurs (*Microcebus murinus*): who decides?

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Because of their higher potential reproductive rates, males are expected to compete among themselves over access to fertile females. Females, in turn, are expected to choose one or several high quality males. The mating system of the solitary gray mouse lemur (*Microcebus murinus*) is characterized by seasonally, but asynchronously, receptive females, seasonally fluctuating sexual dimorphism in body mass, relatively large testes and a high degree of home range overlap between and within the sexes. These observations suggested the existence of scramble competition polygyny. To obtain a more detailed knowledge of male and female mating strategies, we radiotracked 36 females during preestrus and 19 of them during their single night of receptivity. Males regularly encountered preestrous females and up to 12 males were observed in the vicinity of receptive females, which mated with 1-7 males up to 11 times without exhibiting any obvious mate choice. After a mating, however, females either escaped in the vegetation or into a tree hole. Females staying less time in hiding mated with several different males. Females in tree holes were guarded by 1-7 males for between 1 and 11h. Guarding males were regularly harassed by other males and either aggressively chased rivals successfully or were displaced by them. Thus, the mating system of this species is indeed characterized by scramble competition polygyny, but males are able to aggressively monopolize access to females. Male monopolization potential, however, largely depends on female be-

havior, but it is not known why females chose different strategies. Additional long-term observations in combination with genetic analyses will be used to determine male and female reproductive success and thus the pay-offs of these different strategies.

Do male long-tailed macaques (*Macaca fascicularis*) know when females are most likely to conceive?

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The evidence for infanticide being an adaptive male reproductive strategy in primates is increasing. Females could reduce the risk of infanticide by male group members through mating polyandrously during the ovarian cycle and thereby confusing paternity. On the other hand, sexual selection should drive females to concentrate matings to a preferred potential father during time of highest fertility. The latter would contravene paternity confusion if other males could still determine the female's time of ovulation and thus deduce their own paternity chances. Using a playback experiment, the aim of this study was to investigate whether male long-tailed macaques are able to recognize the time of highest fertility if they do not have access to the female. The study was carried out on a group of macaques living in the nature reserve and recreation park of Pangandaran, West-Java. A female copulation call was recorded at the beginning of estrus and was then played back to male group members once every second day until the end of estrus. During playbacks, the female and higher-ranking males were out of sight of the experimental male and the speaker was positioned away from the group so that male reactions could clearly be identified as response to the stimulus. Male response (within a 1 minute test-period) was classified according to the promptness with which males approached the speaker, which was taken as an indication of the male's interest in the female as a potential mating partner. Ten males were tested using the calls of 5 different female group members. In total, 15 male/female pairs were tested. All females engaged in continuous consortships with the alpha male and mated exclusively with him for several days during their cycle. When the call of a female was played at the beginning of her estrus, only 4 of the males approached the speaker within the test period. In 10 cases, promptness of approaching the speaker increased with progression of the female's estrus, with lowest latencies occurring within the period of consortship with the alpha-male (25 s up to less than 1 s). Thereafter, reaction times abruptly decreased again and males did not approach the speaker following the end of estrus. Assuming that the period of highest fertility occurs during the time the female concentrates matings to the alpha-male, the present results provide evidence that male long-tailed macaques can recognize a female's time of highest fertility, providing themselves with the potential ability to estimate their likelihood of paternity. The behavioral data will now be compared with faecal steroid profiles in order to determine the time of ovulation during the experimental phase. (Supported by DFG grant no. Ni186/14-1 and the Lucie-Burgers Stichting, Arnhem, NL).

Baboon loud calls: indicators of male quality?

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Sexual selection has favored the evolution of exaggerated male traits in numerous species. This also applies to the vocal domain, where males of some species produce calls that are much more conspicuous than those of females. An example is the loud call ('wahoo') given by free-ranging male baboons (*Papio cynocephalus ursinus*). We examined the acoustic structure of calls given during male contests and those given in response to predators in order to test a set of predictions concerning the relationship between acoustic structure and physical traits of the caller. To do so, we inspected the acoustic structure of male wahoos for variation in relation to age, and examined the difference between male and female calls. The analysis revealed a number of significant differences between alarm and contest wahoos. Contest wahoos are distinguished from alarm wahoos in that they are given at a much higher rate, exhibit lower frequency characteristics, have a longer 'hoo' duration, and a relatively louder 'hoo' portion. Adult males exhibit lower frequency characteristics than younger males, and their 'hoo' portion is relatively louder and longer. Adult males also exhibit significantly lower frequency characteristics and a longer call duration than females. We argue that some of the acoustic features are simply related to changes in body size and can thus be viewed as examples of 'cheap' honest signalling. Other features, however, appear to be exaggerated and costly to produce. These may possibly function to indicate male stamina and endurance.

Special design, female multiple mating, and genetic benefits: changes in women's preferences and sexuality across the menstrual cycle

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Since the publication of Trivers's seminal article on parental investment and sexual selection, theorists have put forward a number of reasons why females might seek multiple matings, even in circumstances in which multiple mating could not lead to additional conceptions. In addition to a variety of material benefits, females can potentially garner genetic benefits for offspring through multiple mating: good genes associated with viability, compatible genes that complement their own, and genes that increase the genetic diversity of their offspring. Selection for adaptations that lead females to engage in extra-pair sex to obtain genetic benefits, should they exist, can be detected through the telltale signs of special design: Arrangements of phenotypic features that perform the function of obtaining genetic benefits, and not readily explained by any alternative evolutionary account. This talk will describe features in women that may have evolved as adaptations that function to obtain good genes through multiple mating: changes in female preferences across the menstrual cycle. If ancestral females could have obtained genetic benefits from ex-

tra-pair partners, but at some cost, their sexual attraction to men who possess indicators of good genes (at least ancestrally) may have been shaped to be maximal when they are in the fertile phase of their cycle—i.e., when sex with such men could have yielded genetic benefits—and attenuated when outside of the fertile phase. Research shows that: a) normally ovulating women prefer the scent of symmetrical men selectively during the fertile phase of their cycle; b) the faces that women prefer when fertile are more masculine than those they prefer outside the fertile period; c) women's assessment of men's behavioral displays changes across the cycle; d) women report greater sexual attraction to men other than a primary partner during the fertile phase; e) women are more likely to have extra-pair sex during the fertile phase. In addition, men appear to be more likely to spend time with and be vigilant about a mate's whereabouts during the fertile phase, particularly when the female mate appears to be attracted to other men. Alternative explanations and benefits associated with this pattern of preferences and attraction will be discussed.

Sexual selection and sexual dichromatism in primates

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Color differences between the sexes have been investigated in a variety of animal taxa, such as birds, yet relatively little attention has been directed toward primate sexual dichromatism. Systems under the operation of sexual selection can give rise to signals, which allow individuals to assess the signaler's phenotype. Recent experimental evidence, which demonstrates that variation in the blue and aquamarine scrotal color exhibited by vervet monkeys (*Cercopithecus aethiops sabaues*), is both predictive of dominance status and the potential for aggressive exchanges, within pairs of unfamiliar, size-matched males. The finding that males attend to color differences between males would imply that intrasexual selection can promote signals, conveying aggressiveness or competitive ability. While males may pay close attention to dominance signals, these visual signals are simultaneously broadcast to others and may be used, for example, in female mate choice. Based on these findings, I examine primate scrotal color in a phylogenetic context to gain insight into how the evolution of sexual dichromatism in sexual skin may differ from the evolution of all-body sexual dichromatism.

Mate choice differences according to sex and age: an analysis of personal advertisements in the Spanish population

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Evolutionary theorists have posited that men and women may differ in their mate preferences. Many studies sampled in Anglo-American populations have con-

firmed this prediction. The cross-cultural study of mate preferences by Buss (1989) suggested that the Spanish population differs from the evolutionary predictions in some trait preferences. We used 7415 advertisements published in Spanish newspapers to analyze traits sought and offered by men and women of different age groups. Some results supported evolutionary predictions: Spanish men sought younger, physically attractive women, and offered their socioeconomic status. Spanish women sought older men with status/resources, and in turn offered their physical attractiveness. However, some results are contrary to evolutionary predictions and seem specific for the Spanish population: Women seek more physical attractiveness and fidelity than men. Traits sought and offered by advertisers may be conditioned by the personal situation of the advertiser, as is the case for age, children from previous relationships, socioeconomic status and physical attractiveness. Mean age of advertisers (around 40), and Spain's social indicators (world's lowest birth rate; age of mothers at parturition, age of marriage) suggest that the majority of advertisers are people that have been unsuccessful in the mating arena at the conventional age, and are looking for company more than for a reproduction partner.

Sexual selection, sexual conflict, and variation in offspring viability

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Despite thirty years of remarkable head-way in understanding the ultimate causes of social organization and behavior in sexual species, much about within-population variation in individual behavior remains opaque. Is unexplained variation just noise? Have models of sexual selection left out crucial variables? In my talk, I will review how Darwinian and post-Darwinian models of sexual selection might change if variation among females was routinely a part of these models. New models of social behavior stress how reproductive competition among females could account for much remaining previously unexplained variation in the behavior of individual females *and males*, life-history variation, and fitness. I will stress novel, testable predictions of a new sexual selection theory and the implications for future investigations of social behavior evolution.

Males are males, indeed: positive correlation of perceived visual and olfactory masculinity

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According to parental investment theory, females are under high selection pressure for proper evaluation of a sexual partner. In humans, visual and olfactory cues seem to be most prominent in this context. Previous research has shown that male body odor attractiveness relates to visual attractiveness or low fluctuating asymmetry.

Thus, a body odor is considered as an honest signal of male quality. In this study we tested whether there is any concordance in perceiving masculinity by senses of smell and vision. Eighteen female subjects rated 3 to 8 T-shirts (worn by males for three consecutive nights) and photography portraits of the same males for their pleasantness, attractiveness and masculinity. Target sample consisted of 24 men. A within-subject, double-blind experimental design was used. Data were adjusted by the General Linear Models Procedure for unbalanced ANOVA (SAS) with factors: both raters and target's identity, menstrual cycle phase (both while rating T-shirts and photographs) and contraceptive use by the female subjects. Residual correlation coefficients were computed between visual and olfactory cues in pleasantness, attractiveness and masculinity. Only the correlation between perceived visual and olfactory masculinity appeared significant ($r = 0.36$, $n = 98$, $P < 0.001$). These results suggest that masculinity, which may indicate the male's quality, is perceived consistently by at least two sensory channels.

Scent marking and sexual selection in neotropical primates

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I examine the role of sexual selection for the patterning of scent marking in neotropical monkeys (Platyrrhini). Sexual selection theory predicts that intrasexual competition between females and male choice of females occurs when paternal investment in offspring is essential for female reproductive success. Here the hypothesis is tested that patterns of scent-marking in platyrrhines are related to intrasexual competition for mates and thus are ultimately shaped by sexual selection. More specifically, I test the hypothesis that female competition for paternal care is responsible for female-biased rates of scent-marking. Data from the literature and from own studies on scent marking and infant care are used for the test. It is shown that female-biased rates of scent marking exist in platyrrhine taxa where male contribution to infant care exceeds female contribution, whereas male-biased rates are found in species without or with negligible paternal care. Differences in scent-gland size support this finding. These results provide preliminary evidence for a role of sexual selection in shaping patterns of olfactory communication in platyrrhines.

Pair-living and stable territoriality in red-tailed sportive lemurs (*Lepilemur ruficaudatus*)

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Red-tailed sportive lemurs (*Lepilemur ruficaudatus*) are the smallest folivorous primates and are presumed to live in pairs within small stable territories. Pairliving

among mammals is puzzling in itself, and territory defense by the pair is equally unexpected in a folivorous species. The aim of this ongoing study is to investigate causes and consequences of the social and mating system in this small folivorous primate with special focus on habitat use, territory stability and mechanisms that maintain the pair bond. Beginning in October 2000 a total of 29 animals were captured and 19 of them were radio-collared in Kirindy forest in Western Madagascar. Analysis of morphometric data revealed no sexual size dimorphism. We could identify 6 adjacent pairs, which occupied exclusive territories of about 1 ha in size. Pair members often used sleeping trees within their territories. In 2001, we were able to recapture 6 individuals already marked in a previous study in 1996. This allowed us to compare home range size and stability over a 5-year period. All of the 6 animals were recaptured within the territory they already occupied in 1996, suggesting that pairs of *L. ruficaudatus* maintain stable territories for several years. Stability and exclusivity of territories and the evolution of pair-living are often discussed in terms of resource defense, female defense, mate guarding and infanticide avoidance. The relative importance of each of these factors will be examined in up-coming field seasons.

Female sexual advertisement reflects resource availability in 20th century UK society

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According to evolutionary theory, men and women differ with regard to the characteristics they value in potential mates. In general, men show a general preference for physical attractiveness, while females seek cues that relate to resources and future earning potential. Here we suggest that if women pursue marriage as an economic strategy, female sexual advertisement should increase during periods of economic hardship, when the number of high quality male partners becomes a limited resource. In order to assess this possibility, measures were taken of both the tightness of clothing and of the degree of skin display from models portrayed in UK Vogue magazine, from 1916 to 1999. These estimates of sexual advertisement were then analyzed in relation to indices of economic prosperity. Preliminary analyses indicate that the findings differ according to clothing style. For day wear, female sexual advertisement apparently increases in periods of economic hardship, while for evening wear the converse appears true, with sexual advertisement decreasing in periods of economic hardship. No significant results were found for the data set as a whole, and these findings are discussed within an evolutionary framework to suggest possible explanations for these differences.

Models of reproductive competition

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Animal societies vary markedly in the extent to which reproduction is monopolized by dominant individuals. In recent years, many different models have been developed to explain this variation. I review these models, distinguishing between two basic types: transactional models focus on group stability and the constraints this places on the division of reproduction, while compromise models ignore issues of group stability and view the division of reproduction as the outcome of a conflict in which each group member has a limited or partial ability to enforce its own optimum. I argue that the two kinds of analysis are better seen as special cases of a general underlying theory, rather than alternative paradigms, and illustrate the possibilities and problems of empirically testing this unified theory, and the prospects for future theoretical advances.

Sexual activity and sexual swellings in females: a comparison of three colobus species

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In several primate species females develop large sexual swellings, which they maintain for a relatively long period. This strong and costly female signal of receptivity is usually accompanied by increased sexual activity but it is not always restricted to peri-ovulatory periods. The evolutionary pressures that shaped female swellings and the current functions of the swellings are still debated. In this study I compare female sexual activity in red (*Procolobus badius*), olive (*Procolobus verus*) and black-and-white colobus (*Colobus polykomos*) living in the Taï National Park in Ivory Coast. Only females of the first two species develop long-lasting sexual swellings. The red colobus groups contain 10-18 adult males and 15-25 reproducing females. The olive colobus groups contain 1-3 adult males and 1-6 reproducing females. The black-and-white colobus groups contain 1-2 adult males and 4-6 reproducing females. Observational techniques such as focal animal, scan and *ad libitum* sampling were used to obtain data on sexual behavior and reproductive cycles of individually recognized females in the wild. Data were gathered over a period of two (red colobus), five (olive colobus) or six (black-and-white colobus) years on one to three groups per species. The red and olive colobus females were sexually active for longer periods per menstrual cycle than the black-and-white colobus females. Mating was more seasonal in the red colobus than in the other two species. I argue that the long-lasting sexual swellings of the red and the olive colobus ensure high male/female ratios in groups. In the red colobus I suggest that this increases male protection each female and her offspring receive against predation. In the olive colobus I argue this increases the male protection against inter-specific harassment and the paternal care that each female and her offspring receive.

Do chimpanzees in the Taï forest (Côte d'Ivoire) exhibit sex-specific ranging patterns?

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Sex differences in ranging patterns are suggested to be the outcome of a sexual conflict. While males seek to maximize access to potential mates, females should maximize feeding efficiency. Thus, studying sex differences in ranging behavior may help to understand differences in foraging strategies and association patterns in group-living animals. For chimpanzees, it has been reported that females have smaller home ranges (HR) and more distinct core areas than males. In Taï, however, this has not been observed. Sex differences in ranging are small. In this study we analyze long-term ranging patterns over a period of 10 years (total HR) and 4 years (individual ranging), respectively. During this time the total number of chimpanzees decreased from 51 individuals to 23, providing the opportunity to analyze the effects of community size on ranging patterns under identical ecological conditions. We found a general decrease in HR size with decreasing community size, although total HR increased in recent years despite a further decrease in community size. Individual HRs overlapped by more than 80%, however, and males used a slightly larger part of the total HR than females. Daily travel distances were slightly higher for males compared to females. Additionally, individual core areas were found to overlap by more than 70%, and individual centers of activity were within the same 500 x 500m range (males and females). Thus, sex differences in individual ranging patterns are not pronounced in this group of chimpanzees. However, with increasing total HR size in recent years, individual differences and sex differences emerge, indicating that the lack of sex differences might be related to a relatively small HR rather than to absolute community size.

Abortions in Hanuman langurs (*Semnopithecus entellus*): a female reproductive strategy?

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In several rodent, ungulate, and primate species a high incidence of pregnancy terminations was documented following introduction or immigration of an unfamiliar male. This was explained as (i) a non-adaptive consequence of a high level of stress, (ii) forced abortions resulting from male's goal-directed attacks, or (iii) termination of investment in fetus by female herself, supposing that the infant would be at a risk of infanticide anyway. We present a quantitative test of the last hypothesis based on data from Hanuman langurs (*Semnopithecus entellus*) published for the well-studied Jodhpur population and on data collected in our own field study in Bhangar, NW India. We performed the survival analysis of the length of the period a pregnant female experienced between troop takeover by a new male and the birth of

her first surviving offspring. This analysis revealed that females indeed decrease their reproductive rate by supposedly preventive abortion (hazard ratio 0.28, $p < 0.001$, controlled for age of the fetus). In concordance, logistic regression did not show any optimization of pregnancy terminations above the co-incidence with infanticidal takeovers. Rate of infanticide in time of (expected) infant's birth is not a good predictor of incidence of abortion ($\chi^2_{(11)} = 12.63$, $p > 0.05$). We conclude that abortions are not among females' strategies to avoid infanticide in Hanuman langurs. However, no abortions occurred during non-infanticidal takeovers. Infanticidal males were often observed harassing females not accompanied by small infants and there are anecdotal observations of harsh attacks followed by abortions. Thus, we expect these abortions to be induced by infanticidal males, as a part of their sexually selected reproductive strategy, at the expense of females.

Sexually antagonistic selection on primate size

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Male intrasexual selection in haplorhine primates increases male size and to a lesser degree also female size (Lindenfors and Tullberg 1998 *Biological Journal of the Linnean Society* 64: 413-447). Two questions surrounding this pattern are analyzed here: (1) why female size increases when selection is on males, and (2) why female size does not increase to the same extent as that of males. Intragroup competition, a selection force possibly working in concert with sexual selection, does not select for larger female size. Nor are females found to increase in size because of a need to bear larger male offspring. Instead, the potential for indirect selection on female size through a genetic correlation concerning size-controlling genes is discussed. Independent contrast analyses show that large size has negative effects on female reproductive rate across the primate order. Consequentially, matched-pairs analyses on haplorhines, where sister groups are matched according to mating system, reveal that females of species in more polygynous clades have lower reproductive rates than females of species in less polygynous clades. This is also true, however, when the effects of size are removed. A possible explanation of this pattern is the fact that the age at weaning is also found to be significantly greater in sexually selected species even when the effects of size are removed. These results, both when correcting for size and when not, suggest that sexual selection has shifted female size from one favoring female fecundity to another favoring male success in competition. This depicts antagonistic selection pressures on female size and a trade-off for females between the ecologically optimal size of their foremothers and the larger size that made their forefathers successful.

Nonfecundable matings as a test of male "quality" in primates

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Although empirically linked, and often conflated in writings about female primate sexual behavior, mating during nonfecundable periods and mating with multiple males are logically distinct phenomena. In this paper, a hypothesis accounting for the former phenomenon is proposed and subject to preliminary tests: females mate during nonfecundable periods to test male "quality" while the costs of copulating with a low-quality male are relatively low. Courtship rituals, copulation itself, and third parties' reactions to witnessing copulations could provide females with reliable information about a male's health, strength, physical coordination, willingness to incur costs to benefit a particular female, and willingness to incur risks in the form of aggression by rival males. Females could compare males to each other, and/or compare the same male's courtship and copulatory performance at different times. This hypothesis leads to the predictions that mating during nonfecundable periods will characterize species and situations in which (1) females encounter a large number of prospective mating partners, (2) rates of turnover in male group membership are high, (3) rates of male dominance rank changes are high, (4) females can reliably incite male-male competition by initiating matings, whereas male-male competition is rare in other contexts and (5) mating behavior is more elaborate (e.g. long courtship sequences, complex courtship-specific behaviors, multi-mount copulations, and/or long copulatory bouts), thereby providing females with a lot of information. Unlike hypothesis for nonfecundable matings that emphasize infanticide avoidance (and that also lead to some of the above predictions), the "testing male quality" hypothesis predicts that females will sometimes copulate repeatedly, during infecundable periods, with the same male, even in monogamous or "harem" polygynous groups. These predictions are evaluated using published data, and new directions for research are proposed.

Homosexuals seeking partners: a test of the sexual selection hypothesis

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The relative parental investment of the two sexes in offspring has controlled the evolution and operation of primate sexual selection; females, who invest heavily in reproduction, are choosier in selecting a mate than males, who seek quantity over quality. Thus, human females seek mates who will bring resources and permanence to the relationship, whereas men seek traits signaling reproductive potential, e.g., beauty (health) and youth. Analyses of personal ads placed by heterosexual men and women seeking companions have confirmed this gender bias, i.e. women seek resources and sincerity; men seek physical attributes. An interesting question arises with respect to the traits sought in the selection of partners by homosexuals, for most of whom reproduction is not the primary goal. Here we test the null hypothesis that

male and female (lesbian) homosexuals do not differ with respect to the traits sought in, or offered to, potential partners. The data were drawn from 800 homosexual personal advertisements (400 men, 400 lesbians) that appeared in a weekly newspaper. Traits sought and/or offered by the advertiser were coded into the categories of resources, sincerity, age, physical attractiveness and body shape (including height and weight). Intergender differences were tested for significance ($p < 0.05$) by Chi-square. The genders did not differ in their mention of resources or sincerity, although both traits were important, being mentioned by about one-quarter of each group. Males tended to seek younger partners; lesbians, older. Of those mentioning physical attractiveness and/or body shape, significantly more male homosexuals offered attractiveness (44 %) and body shape (81 %) than did lesbians (32 % and 46 %, respectively). The genders did not differ in the percent seeking physical attractiveness (21 %), but more males sought body shape (34 % males vs. 20 % lesbians). The hypothesis is rejected, viz., homosexuals differed by gender in the traits sought and offered in partner selection.

Examining the function of female copulation calls in captive long-tailed macaques (*Macaca fascicularis*)

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Similar to other female primates, long-tail macaques often vocalize during copulation. Hypotheses about the function of the calls include prompting: a) male contest b) sperm competition c) male ejaculation. Data on the timing of the call with respect to the onset of the male's ejaculation and post-copulatory behavior allow discrimination between these hypotheses. If the female calls before ejaculation it may attract higher ranked males to interrupt the copulation and thus, promote contest. To trigger male ejaculation, the call must precede it, and mating disruptions should be rare. In contrast, calling after the onset of ejaculation would ensure the sperm of one male in the female's reproductive tract and may attract other males to mate with her, promoting sperm competition. Copulations of captive long-tailed macaques were videotaped opportunistically. The female was continuously recorded for up to 10 minutes after mating. Copulation calls were uttered more frequently after the onset of ejaculation. Disruptions were rare. Following a call, females mated with the same male more frequently than with a different male. Mate guarding by the male did not account for this last finding. Thus, the data do not support hypotheses that copulation calls incite male contest, sperm competition or trigger ejaculation in long-tailed macaques. Other functions remain to be investigated.

Sexual selection, behavior and sexually transmitted disease

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Sexual selection occurs when individuals vary in their opportunities for successful reproduction through mate choice and intra-sexual competition. By altering the

contact structure of reproductive encounters, sexual selection can modify the distribution of disease, especially sexually transmitted diseases (STDs), within social groups and populations. Intuitively, individuals that are more successful in mating should have greater risk for STDs, although recent theoretical models provide more fine-grained predictions for the distribution of STDs within and across species. Through its influence on the risk of STDs, sexual selection also may influence the evolution of behavioral counter-strategies that reduce the risk of infection, but little is known about these behavioral counter-strategies in primates and other mammals.

In this talk, I will explore the ecological and evolutionary relationships among sexual selection, behavior and STDs. First, I will review briefly recent theoretical models that examine how the risk of STDs varies among individuals in relation to the intensity of sexual selection. Using a comparative database on the parasites of primates, I will test the prediction that prevalence of STDs in females increases with increasing polygyny, as measured by the adult sex ratio and body mass dimorphism. Second, I will examine behavioral counter-strategies to STDs, as these behaviors operate in conjunction with the immune system to defend the body from parasites. If female choice is effective in mammals, it might seem that females could avoid STDs by inspecting genitalia of prospective partners prior to copulation and thus avoid infected males. However, a recent theoretical model shows that identification and evasion of STD-infected males selects for more cryptic infections because in this case, concealment increases the reproductive success of both infected hosts and their parasites. Other behavioral counter-strategies may be effective, however, including monogamy, post-copulatory genital grooming (effective in male rats), and post-copulatory urination (a putative counterstrategy to STDs in some human cultures). Using phylogenetic comparative methods, I will explore the distribution of these and other behaviors, including genital inspection, in relation to the intensity of sexual selection, partner number and life history variables. Initial results suggest that behavioral counter-strategies to STDs are rare in primates, leaving the immune system as the primary defense against STDs. An important conclusion of this talk is that dual consideration of sexual selection and STDs leads to new insights to the dynamics of individual interactions in mammalian mating systems. These results serve to test theoretical models while highlighting the need for additional data on parasite avoidance strategies.

Unusual sex ratio and male life-histories in redfronted lemur groups

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Lemur groups are comprised of on average even number of adult males and females. In the majority of primate species, however, group size is female-biased due to male-male competition. In redfronted lemurs (*Eulemur fulvus rufus*) this apparent lack of mate competition has been attributed to a social system of multiple pairs with mating privileges between pair-partners. During our study, however, we found no evidence for pair-bonds but could identify a central dominant male in each group monopolizing access to females, which leaves the even sex ratio unexplained. Therefore, we investigated factors leading to a high number of males. Demographic data on a

population of redfronted lemurs living in Kirindy forest, Madagascar have been collected since 1996. We analyzed their sex ratio on the population and group level. Birth sex ratio was even (13F:13M), while adult sex ratio on the population (1:1.55), as well as the group level (1:1.40), was male-biased. Differences between population and group level are mainly due to solitary animals. Adult mortality was slightly male biased (3F:6M) considering the skewed sex ratio. Hence, neither birth sex ratio nor differential mortality by sex can explain the high number of males. Proximally, group composition is primarily modified by male migration. We observed 5 cases of migration by a single male and 9 cases of joint migration involving a total of 24 males. In 5 cases, where we observed joint incursions in detail, all resident males left the group. Groups with more males were less likely to experience incursion. Therefore, large male group size pays for resident central males and at the same time for natal males who can form alliances before dispersal. Indeed, in 24 group years, sexually mature natal males delayed dispersal for a total of 13 years. Waiting for allies is only possible in animals with relatively fast life histories, such as redfronted lemurs, who need less than three years to reach sexual maturity. Hence, male life-history may be partly responsible for the unusual sex ratio in redfronted lemur groups.

Dominance and sexual behavior in Barbary macaques (*Macaca sylvanus*)

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This study was carried out on the Barbary macaques in the national park of Djurdjura (Algeria). We show that sexual interactions in this population are neither influenced by the dominance hierarchy nor do they occur randomly. During the mating season, four methods of observation were used: focal animal sampling, instantaneous and scan sampling, sequence sampling and all occurrences sampling of specific behaviors. Our analyses revealed significant differences in sexual behavior among males. Some low-ranking males were observed to copulate more often than some high-ranking males. Analyses of the sexual behaviors received by females also revealed individual variation. As among males, some low-ranking females were observed to mate more often than some high-ranking females. Closer examination of sexual interactions initiated by males revealed that the majority of males, including high-ranking ones, did not interact sexually with all females. In addition, study of the sexual behaviors received by females revealed that, except the lowest-ranking females, they had sexual interactions with all the males. Thus, individual preferences among certain male-female dyads appears to exist. We therefore conclude that: (1) sexual interactions occur independent of the dominance hierarchy, (2) certain individuals did not engage in sexual interactions with all individuals of the opposite sex and (3) the monkeys show a tendency to express more sexual behaviors with certain partners than with others.

Sexual selection of vocal folds and vocal tract in humans

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Sexual dimorphism is strongly evident in human vocal anatomy, for example with males showing both greater overall supralaryngeal vocal tract length (VTL) and vocal-fold length than females. However, while VTL is roughly proportionate to body-size both within and across sexes, male vocal-fold length is much greater than expected based on overall body-size dimorphism and only weakly related to individual size. It is furthermore not clear why this "excess" dimorphism occurs. On the one hand, the fundamental frequency (F_0) of vocal-fold vibration is directly related to overall length of the folds, and contributes strongly to listener perceptions that lower-pitched voices are associated with larger body-sizes and higher social dominance. On the other hand, this feature is not a reliable indicator of body-size. One recent account therefore argues that VTL cues provided by vocal-tract resonances provide honest cues to vocalizer size, whereas dimorphism in F_0 evolved as a dishonest signal. Here, this proposal was tested by analyzing voices from male and female athletes recorded in televised interviews. Unexpectedly, neither F_0 nor resonances were found to predict talker height or weight. This outcome suggests both that VTL has not been specifically selected, and that dishonest body-size cueing is not responsible for human vocal-fold dimorphism. Instead, the important factor may be that lowered F_0 contributes to individual vocal distinctiveness, which in turn is more important for males than females. A series of perceptual experiments requisitely showed that listeners hearing brief vowel stimuli could better discriminate individual identity in male than in female voices. This difference disappeared when listeners were instructed to attend to vowel quality rather than the talkers involved. As vocal-production anatomy and perceptual processing are fundamentally similar in humans and species like macaques and baboons, this alternative to the "body-size" view may have important implications for a variety of large-bodied primates.

Queens and consorts vs. democrats and kings: the sexual politics of reproductive skew

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Egalitarianism in females provides incentives for male despotism: if females breed at similar rates, males can gain significant reproductive benefits from monopolizing as many females as possible. Thus it is not surprising that comparative studies have found broad correlations between breeding system (as defined by the number of males and females in the same group) and the degree of sexual dimorphism in primates, ungulates and pinnipeds — taxa in which females generally reproduce at the same rate. However, female despotism prevents males from monopolizing more than one or two breeding females and thus stifles the potential for significant dimorphism. Female despotism is widespread in carnivores and not only is sex-

ual dimorphism minimal to non-existent in most species, but some carnivores are characterized by female dominance over males. We will focus on the contrast between the highly dimorphic African lion, where the females are egalitarian and the highly decorated males are despotic, and the spotted hyena, where the females are so despotic that they dominate the undecorated males.

Cross-cultural differences in attractiveness judgments of male faces: results from rural Jamaican and urban UK samples

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Human facial attractiveness has received much attention as a possible biological signal in "good genes" models of sexual selection. Women's preferences for male faces are complex: in men's faces, putative cues to 'good genes' (e.g. exaggerated sexually dimorphic facial features perceived as "masculinity") carry the cost of a perceived decrease in probable paternal investment (masculine faces receive negative personality attributions). Women's preferences for male faces appear to represent a trade-off between cues to good genes and cues to paternal investment which varies as a result of hormonal status, relationship context, and mate value. The research reported here compares female preferences for male faces in rural Jamaica and urban UK. Using photorealistic computer generated stimuli with manipulated levels of sexual dimorphism, women's preferences for masculinity were assessed. Jamaican women appear to value facial masculinity in potential partners more than their UK counterparts. The differences in preferences between the two populations may reflect differing pathogen loads in the two environments (Jamaica's higher pathogen load may increase the value of cues to 'good genes'), or a response to a cultural contingency: in this case, the expectation of low paternal investment in Jamaica (rendering cues to paternal investment in faces less informative).

Intrasexual selection and dimorphism in primates

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Sexual dimorphism in primates is widely viewed as a function of sexual selection through the mechanism of male-male competition for access to mates. Recent studies, however, provide evidence that dimorphism in canine tooth size and body size reflect different selection pressures on males and females. Comparative analyses suggest that male and female intrasexual competition are correlated with male and female canine tooth size, suggesting in turn that competition over either mates or resources affects the expression of dimorphism. Recent studies suggest that selection on patterns of male and female growth effects size dimorphism. Less often considered are the effects of female choice and female mating strategies on the evolution of dimorphism. Here I review evidence for a variety of hypotheses about the effect of

male and female reproductive strategies on the evolution of dimorphism in canine size, body size, pelage, and sex skins. Patterns of dimorphism in these features, as well as differential patterns of male and female growth, are clearly consistent with the classic male-male competition hypothesis, but also suggest that female choice, female mating strategies to counter infanticide, natural selection affecting female growth, and female intrasexual competition effect the expression of dimorphism in primates. Teasing apart all of these hypotheses through comparative analyses is very strongly impacted by the fact that we must use behavioral surrogates as estimates of various selective pressures. Hence, tests of hypotheses are contingent on the interpretation of the relation between behavioral patterns and selective processes. A great deal more work is necessary to test these hypotheses, but there is great promise in working to understand the interaction between behavior, ecology and morphology in primates.

Sexual selection, multiple mating and paternity in captive grey mouse le-murs (*Microcebus murinus*)

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Sexual selection theory predicts that the importance of dominance between males for access to females depends on the potential to monopolize estrous females. We examined the relationship between male dominance, mating behavior and reproductive success in a promiscuous nocturnal primate species, the grey mouse lemur (*Microcebus murinus*) in captivity in order to test predictions derived for different competitive regimes between males. Moreover, the relationship between male age, relatedness between the mates and reproductive success was investigated. Dominance relationships were investigated in five groups, each consisting of 4 (2 males, 2 females) individuals. Paternity was analyzed for 19 infants belonging to 10 litters born in seven different groups by employing 13 nuclear microsatellite markers that have recently been developed. Dominance could be established in the majority of study groups and dominant males mated more frequently than subdominant males. Dominant males, however, fathered only half of the infants born in the study groups, although the captive conditions principally allowed the monopolization of mates. Multiple mating was observed or deduced from the paternity data in the majority of groups. For the first time in primates we detected one definite case of multiple paternity. Younger males sired more than half of the offspring and fathers were less related to the mother than their competitors in two out of three cases. We conclude that contest competition between males is unlikely to be the primary factor predicting the reproductive outcome whereas female choice and sperm competition are likely to be effective within this seasonal breeder.

Male-male competition, sexual coercion and female choice in multimale mountain gorilla groups

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Behavioral aspects of sexual selection in mountain gorillas (*Gorilla beringei beringei*) traditionally were considered to occur mainly during intergroup interactions because of the predominantly one-male social system. However, approximately 40 % of gorilla groups in the Virunga Volcanoes are multi-male. Therefore it is important to examine sexual selected behaviors within multi-male groups to better understand the strategies used by individuals to achieve reproductive success and the species' variable social system. Two multi-male mountain gorilla groups were studied at the Karisoke Research Center, Rwanda to examine male-male competition, sexual coercion, and female choice in relation to observed mating behavior. All agonistic, affiliative, and sexual interactions observed amongst males and females were recorded and comparisons of behavioral patterns during estrus and non-estrus periods were made. While the dominant males participated in the majority of the copulations, subordinate males actively pursued and participated in a significant number of matings. On days that females were in estrus, male-male competition increased, male coercion of females increased, and most females mated with more than one male even at the probable time of conception. These results from the Virunga Volcanoes also will be compared to preliminary results of an ongoing study of mountain gorillas in Bwindi Impenetrable National Park, Uganda, specifically the behavioral changes associated with the transition of a group from one-male to multi-male structure. This study emphasizes that individuals exhibit behavioral flexibility in their reproductive strategies and that the three behavioral components of sexual selection considered are important factors in the evolution of the variable social system observed in mountain gorillas.

Sexual selection and multilevel animal societies: Exploring why core breeding groups form herds in zebras and other species

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Animal societies derive from the social relationships that exist among its members. Behavioral ecologists have traditionally focused on the core relationships defining a mating system as a means towards understanding the role of ecology in the evolution of sociality. However, emphasis on mating systems has tended to marginalize the importance of interactions and relationships that extend beyond the basic breeding unit. In true multilevel primate societies, such as those exhibited by Gelada and Hamadryas baboons, the association between breeding units into larger social groupings seems to arise because these groups fulfill specific functions that breeding units alone do not. For Gelada, protection against predation appears to be enhanced by forming higher level societies, whereas improved resource defense

seems to be the benefit provided by larger groupings of *Hamadryas* baboons. But does higher-level sociality evolve simply to solve ecological problems that core breeding groups can not? Or, is there a role for sexual selection? Comparisons with different taxa that share similar needs and life-styles but with different body plans often provide insights that help elucidate general patterns, or rules.

In our recent studies of the Plains zebras of Kenya, 'top-down' forces associated with avoiding predators and 'bottom-up' forces of vegetation distribution and abundance are important in determining the characteristics of herds. Both herd size and composition, as measured by the extent to which herds are composed of both family groups and bachelor groups, are influenced more by vegetation than by anti-predator considerations. But what appears to matter most is the risk of stallions being cuckolded. Pressure from neighboring bachelor males—those that are reproductively competent, but not bonded to any females—to mate with harem females is best reduced by harem stallions joining together. When coalitions form, female contact by bachelors is significantly reduced. And although female foraging success remains high regardless of the presence or absence of bachelors or whether a harem is with, or without, other harems, a stallion's foraging plummets unless he can join other stallions to amortize the costs of reproductive protection. And for the bachelor males the lure of contacting large numbers of females forces them to form larger groups and then to join herds. Thus in Plains zebras the forces of sexual selection and the feedbacks that the different age, sex and reproductive classes impose on each other appear to be responsible for the evolution of higher levels of sociality. In this anti-cuckolding situation no conflicts of interest arise among stallions and their females because cost-benefit considerations show females to be 'indifferent' to the social options that males are moving among. But this need not always be the case and situations where females, or even bachelor males, themselves compete need to be explored to determine how conflicts at one level are settled that then allow sociality to develop at another.

Infant carrying as a male sexual strategy of cotton-top tamarin (*Saguinus oedipus*)

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Captive studies have explored the role of fathers of cotton-top tamarin in infant carrying as a strategy to have sexual access to breeding females. However, in captivity, in absence of any other reproductive opportunity, male helpers might be interested in showing mothers their abilities in infant carrying. In this study, we explore the willingness of fathers and helpers to help mothers in infant carrying across the pre-, peri-, and post-ovulatory post-partum periods. If carrying is used by male helpers as a sexual strategy, it could be expected to show mothers a larger willingness to help her during the peri-ovulatory period. We have considered "solicitation of infants transfer" as an accurate measure of the willingness to help by the taker. We observed four large ($N > 5$) groups nine weeks after the birth of infants. All-occurrences of in-

fant-transfers were recorded continuously during 30-minute observation sessions 6-7 days a week. During the peri-ovulatory period male helpers demanded infants from their mother more frequently than fathers (ANOVA-Friedman's-test, $n=4$, $df=8$, $p<0.05$; $q_T=4.387$, $p<0.05$). Fathers demanded infants more frequently while these were carried by male helpers than by mothers (ANOVA-Friedman's-test, $n=4$, $df=2$, $p<0.05$; $q_T=3.5$, $p<0.05$). Frequently we observed fathers acting as "bridges", demanding infants from helpers and immediately transferring them to mothers. Male helpers might be interested in carrying in order to increase their chances to be selected by breeding females. However, during the peri-ovulatory-period infants are still totally dependent on mothers' milk and an extreme demand on infant carrying could cause infant's death. Father's involvement might be more related with a regulatory role in carrying, at least in captivity where fathers must have certainty on their paternity.

Sexual selection, male mating strategies and reproductive success in a promiscuous, nocturnal Malagasy primate, the grey mouse lemur (*Microcebus murinus*)

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Sexual selection theory predicts that males show a high intrasexual variation in reproductive success which may depend on age, body mass, rank or social experience. Grey mouse lemurs are small, seasonal breeders living in a complex and dispersed multi-male, multi-female system in the dry deciduous forest of western Madagascar. In our study population in northwestern Madagascar, females are philopatric whereas males migrate, most likely during their first year of life. The population showed a high turn-over rate during a period of 5 years which might be due to predation and migration. 33 % of the offspring reached sexual maturity close to their birth site. In order to investigate how males compete for mates and in how far male strategies are related to reproductive success, a population of 255 individuals (154 males, 101 females) were genotyped by 7 polymorphic microsatellite markers. Mating strategies of 10 males (5 non-resident males captured first time, 5 resident males captured at least once in two different years) were determined radiotelemetrically. Home range size increased significantly during the breeding season, with large home range overlaps between males indicating scramble and contest competition. Resident males had significantly larger home ranges than non-residents. Home range size and access to females (as determined by female capture sites within male home ranges) showed a significant positive correlation. No correlation between body weight and home range size was found. 20 % of the possible offspring ($N=204$) could be assigned to 24 % of the potential fathers ($N=132$) by the CERVUS2.0 program. 16 % ($N=18$) of the non-resident males ($N1=110$) reproduced successfully, whereas 31-33 % of the resident males sired offspring in their second to fourth year of residence ($N2=35$, $N3=13$, $N4=3$). Results suggest that male reproductive success in this

species is independent of body mass, but dependent on residency and most likely social experience.

The potential for sexual selection in a pair-living nocturnal primate

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Studies on sexual selection concentrate on polygynous species with pronounced sexual adornments. Pair-living primates have been shown to be less dimorphic and exhibit smaller testis size than closely related polygynous taxa. These findings may lead to the conclusion that sexual selection is weak or absent in these species. Competition over mates and female choice occur if the adult sex ratio is biased towards one sex, mates vary in quality, or genetic monogamy is not strict. In this paper we investigate the potential for sexual selection in a pair-living nocturnal lemur, the fork-marked lemur (*Phaner furcifer*). Data were collected 1999-2001 on 8 pairs living in Kirindy forest, Madagascar and DNA-microsatellite analyses (6 loci) were performed for paternity exclusion. Sex ratio among territory owners was slightly male-biased, because, besides pairs with offspring, we found one 2-male, 1-female unit. Competition over breeding positions was even more pronounced because full-grown sexually mature offspring lived in several families and these individuals probably compete with non-parental territory owners. Mate quality in fork-marked lemurs is potentially advertised by extensive vocal displays that are perceptible over more than two territory diameters. Calling is energetically expensive and therefore a good candidate for an honest signal of mate quality. Male fork-marked lemurs use a sexually dimorphic throat-gland to mark food resources, sleeping sites and mates, which may advertise the quality of a male, as well. Finally, sexual selection occurs where monogamy is not perfect. We found cases where the social father at the time of birth was excluded as the genetic father, suggesting the occurrence of EPCs in *Phaner*. We conclude that despite the absence of sexual dimorphism in body and canine size and relatively small testis size, the life history and socio-ecology of fork-marked lemurs provides ample opportunity for sexual selection.

Secondary sexual characteristics in male mandrills (*Mandrillus sphinx*)

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Male mandrills have spectacular secondary sexual adornments (SSAs). These include red and blue sexual skin on the face, rump, and genitalia; a sternal scent marking gland; and a "fatted" rump. Previous research has shown that the degree of secondary sexual development differs between adult males. In order to investigate the influence of male social rank on the development and maintenance of SSAs I examined the morphology, endocrinology and behavior of 23 male mandrills aged 5-15 yrs,

living in two semifree-ranging groups in Gabon. Male SSAs began to develop at the age of 6 yrs, and males attained adult size and secondary sexual development at an average age of 9 yrs. There was marked variation between adolescent males in the timing of development. Dominant males had higher T levels and more developed SSAs for their age. Amongst adult males, alpha males had the highest T, and the most developed SSAs. Subordinate adult males had lower T and less developed SSAs. Gaining alpha rank resulted in increased T levels and development of SSAs, whilst males that lost alpha status showed decreased development of SSAs. These findings demonstrate that the display of SSAs in male mandrills is influenced by the outcome of male-male competition. SSAs respond to changes in social status and thus are an indication of an individual male's current state rather than his genetic quality. Extravagant SSAs may serve to advertise the quality of males to one another, and therefore to reduce the probability of escalated agonistic interactions between males; and in addition may serve to attract females.

Sex ratios and sexual selection in primate groups

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In nearly all mammalian species, sex ratios are evenly balanced within populations, even though the ratio of males to females within social groups varies widely. When males outnumber females in social groups, opportunities for intrasexual competition arise among males, generating selective pressures that shape male morphology, mating tactics, and social relationships. The selective forces shaping sex ratios within populations differ from the selective pressures that influence the ratio of males to females in social groups. While overall sex ratios are generally expected to be balanced, under certain situations individuals may bias the sex ratio of their own progeny. Primatologists have given considerable thought to the possibility that females facultatively adjust the sex ratio of their progeny in response to variation in their sons' and daughters' reproductive prospects. The reproductive prospects of males and females may be influenced by their mothers' condition or social rank. In this paper, I briefly review the selective forces that shape the evolution of sex ratios. Then, I consider the empirical record which includes multiple, but often contradictory, reports of seemingly adaptive adjustments of progeny sex ratios. Finally, I consider how the distribution of males and females in social groups shapes behavioral strategies.

Sexual selection and communication

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Scientific documentation that a trait is sexually selected requires: (1) Finding a trait that is sexually dimorphic (2) Demonstrating variation on that trait within a

population (3) Determining preferences by the opposite sex for one part of the distribution over others (4) Showing that expressed preferences actually result in differential mating (5) Verifying that the outcome of differential mating leads to differential reproductive success in terms of increased numbers, survival or quality of offspring. Although there are many striking examples of sexually dimorphic signals (distinctive visual features, long or loud calls) in males of polygynous or multi-male, multi-female breeding groups, few studies have gone beyond describing dimorphism to documenting variation in signals that leads to differential preferences. Documenting differential preferences and mating will probably require experimental studies on captive primates.

In socially monogamous or cooperatively breeding species where males contribute extensively to infant care, male selection of females is at least as important as female choice of males. Scent marks produced by females display variation within a population as well as over a reproductive cycle and males respond preferentially to marks from the peri-ovulatory period and to marks from reproductively active versus reproductively non-functional females. Recent functional magnetic resonance imaging studies of neural activity of awake common marmosets in brain areas associated with copulation (anterior hypothalamus and preoptic area) show differential activation to different quality scent marks, suggesting a neural mechanism for differential mating in response to scent marks.

However, in human and nonhuman primates signals derived through sexual selection are probably not sufficient to explain mate choice. Some primates respond to novel, arbitrary signals with increased preferences over natural signals. Through social reinforcement primates learn to respond to multiple aspects of a potential mate. Specific mating preferences can then be maintained in the presence of degraded or absent signals thought to result from sexual selection.

Sex ratios at Chester Zoo chimpanzee (*Pan troglodytes*) breeding centre: implications for developing social behaviour in young chimpanzees

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Chester Zoo Chimpanzee Breeding Centre (CBC) houses a single colony of 29 chimpanzees. This group has been the focus of many behavioral studies as it is one of the few captive colonies that approaches the size of natural wild groups. One of the most notable features of the group's demography is the heavily skewed sex ratio seen across all age classes. In the light of these demographic parameters, this paper examines how the demographic profile of the CBC group might affect the behavioral development of juvenile and adolescent females (n=8, aged 3-12 years old). The heavily female-biased sex ratio could potentially have both positive and negative effects. For instance, the high proportion of mothers with infants in the population has led to a high infant handling frequency. We have recorded a mean percentage of frequency-bout to be 2.98 % (SD=2.30 %) for the youngest females (n=4) of the group throughout 8 months of observations. This might confer a benefit to the young fe-

males as by learning these skills, they will increase their future infants' survival and therefore inclusive fitness. However, the quasi-lack of peers of the opposite sex might affect the development of their sexual behavior and its performance in the near future. The relationship between the development of socio-sexual behavior and the sex ratios in the Chester Zoo colony will be examined in the context of those of other captive chimpanzee colonies and of wild communities. This study aims to contribute to the literature investigating the influence between sex ratio(s) and social organization in primate populations.

Sex differences in reproductive skew: an effect of differences in reproductive potential

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Trivers (1972) pointed out that sex differences in parental investment determine male and female sexual strategies. Because males usually invest less in their offspring than females, the reproductive potential of males is usually higher than that of females. In this paper, I will argue that this difference between the sexes also affects differences in the nature of reproductive skew among males and females in group-living animals. Three different models describe the relationship between reproductive skew and relatedness among same-sexed individuals living in a group: complete control models; incomplete control models; and socioecological nepotism models. Which model applies depends on the relationship between the shareability of limiting resources and reproductive success. The most important factor shaping this relationship is reproductive potential: when this is high, monopolization of limiting resources will result in proportional returns, when the reproductive potential is low it will result in diminishing returns. The reproductive potential depends on both the reproductive rate of a species and the nature of the limiting resources. As males usually invest less and have a higher reproductive potential than females, males will usually have a proportional relationship between the monopolization of limiting resources and reproductive success. Consequently, the behavior of males typically conforms to complete or incomplete control models. In contrast, each of the three models may apply to females. This is documented by comparisons among primate and among carnivore species.

Sexual strategies in *Pan paniscus*: implications of female dominance

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Bonobo society is unique among great apes because of the fact that females can occupy high social positions. Based on analysis of agonistic interactions in three captive study groups, we found a significantly linear dominance hierarchy (Apenheul: 3

adult males, 5 adult females, 493 hrs, $h' = 0.87$, $p < 0.05$; Wuppertal: 4 adult males, 2 adult females, 203 hrs, $h' = 1.0$, $p < 0.05$; Planckendael: 3 adult males: 4 adult females, 190 hrs, $h' = 0.85$, $p < 0.05$). Although females occupied the highest position in all three study groups, some males still had high-ranking positions. In the elaboration of their sexual strategies, males not only have to take into account competing males, but also higher ranking females. The latter are theoretically expected to freely exert mate choice and to counter male attempts towards monopolisation of copulations. We present data of male mating success in the study groups and investigated to what extent the males of the study groups were able to monopolise females sexually. In contradiction with expectations of Altmann's priority of access model, males did not monopolise copulations, even if only one female was in oestrus at a time. Male competition was not completely absent, however, because males interfered in copulations of other males and low ranking males copulated sneakily. Sexual coercion by males was never observed. Apparently high dominance rank frees females to exert mate choice and to interfere competitively with the behaviour of lower ranking individuals. The alpha females of two groups aggressively intervened with copulations. Elsewhere we suggested that females can use several strategies to influence reproductive output which may ultimately lead to a low degree of reproductive skew. In this light, male bonobos are not only expected to try to influence female choice by inter-sexual affiliation, but also to vary their efforts in relation to female rank and expected female reproductive output. Bonobos are not really a sex reversal species but a complex intermingle of dominance relations may lead to a variety of reproductive strategies in both males and females. The first author currently further investigates whether males use alternative reproductive strategies, such as intersexual affiliation to influence female choice and/or use sperm competition.

Social and sexual preferences of female chimpanzees in the Taï Forest, Côte d'Ivoire

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Chimpanzee females are known to mate promiscuously, copulating with the majority of males and rejecting few solicitations. Although promiscuous mating is thought to provide many potential benefits to females, the question arises as to whether females are really so indiscriminate as to risk leaving paternity to chance. Relative to males, female chimpanzees have fewer gametes, a more constrained reproductive period, a shorter lifetime reproductive ability, and a considerably larger investment in the gestation and care of offspring. Consequently, females should carefully select high quality mating partners and enhance the survival of their offspring and maximize their reproductive success. The aim of this study is to determine if female chimpanzees exhibit sexual and social preferences for males, and if so, to examine how and when these preferences are expressed. Over 2200 hours of focal observation were collected on 14 estrous females from two communities. All stages of their reproductive cycle were sampled. For each female, detailed sexual and social behav-

ior were recorded, as well as responsibility for both association and proximity to the adult males. Female preferences were measured by quantifying female proceptive and receptive behavior, as well as by determining which individual was responsible for maintaining association and proximity. Preliminary results suggest that females show distinct preferences for particular males over others. Females showed a trend toward more selectivity during the peri-ovulatory period, and less selectivity outside of the peri-ovulatory period, suggesting a mixed reproductive strategy whereby females may potentially be able to influence paternity, while maintaining the benefits of promiscuous mating.

Mate choice in humans: theory and data

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In the past ten years, there has been an enormous improvement in our understanding of factors associated with mate choice in humans. In particular, a body of data has been generated on the role of fluctuating asymmetry, waist/hip ratio, directional biases in the human face and relative masculinization and feminization of the human face on mate choice in the opposite sex. Less impressive have been developments in theory but important theoretical constructs can help guide our understanding of the new empirical results. These include sex-antagonistic genes and the evolution of sex-biased mate choice. The purpose of this talk is to review the new theoretical work with special attention to the way in which theory may help us interpret the new empirical results.

Phylogenetic analyses of primate size evolution: the consequences of sexual selection

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We analyzed the relationship between primate mating system, size and size dimorphism by utilizing several phylogenetically-based methods. An independent contrast analysis of male and female size (log weight) showed that these are tightly correlated and that size dimorphism is not a simple allometric function of size. We found no relationship between mating system and sexual dimorphism in strepsirrhines but a strong relationship in haplorhines. By matched-pairs analysis, where sister groups were matched according to whether the mating system predicted higher or lower intra-sexual selection on male size, haplorhine species in more polygynous clades (with a predicted higher sexual selection) were significantly more dimorphic, had larger males, and also, but to a lesser degree, larger females. Both independent contrast and matched-pairs analyses are non-directional and correlational. By using a directional test, we investigated how a transition in mating system affects size and dimorphism. Here, each observation is the sum of change in dimorphism or size in a

clade that is defined by a common origin of a mating system. Generally, dimorphism, as well as male and female size, increased after an expected increase in sexual selection, and decreased after an expected decrease in sexual selection. The pattern was, however, not significant for all of the alternative character reconstructions. In clades with an expected increase in sexual selection male size increased more than female size. This pattern was significant for all character reconstructions. The directional investigation indicates that the magnitude of change in haplorhine dimorphism is larger after an increase in sexual selection than after a decrease, and, for some reconstructions, that the magnitude of size increase is larger than the magnitude of size decrease for both sexes. Possible reasons for these patterns are discussed, as well as their implications as being one possible mechanism behind Cope's rule, i.e. general size increase in many phylogenetic lineages.

Alternative reproductive strategies in primates: the case of orangutan bimaturism

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That interactions with social partners influence an individual's motivational state, and through this its physiological development and condition, has been known since long. The suppression of reproductive processes by, for instance, the presence of a dominant same sex conspecific has been documented for many species, and also for primates. Often these are reversible, sometimes they are not. In some cases an individual moves into a "waiting room strategy" to bide his time: better social opportunities. Especially for certain non-mammalian species switch points in the developmental trajectory have been described, where an individual has the "choice" for alternative fitness optimizing strategies. They can be an aspect of phenotypic flexibility, but may also be genetically predisposed. In either case a frequency dependent choice or selection mechanism is likely to play a role. In primates, such alternative strategies also seem to exist. One of the most striking examples of a candidate for this is the bimaturism that has been observed in orangutans and mandrills. The evidence for the existence of such alternative trajectories will be reviewed, and the evidence of our own long-term investigations on the reproductive success of the two morphs of adult male orangutans will be presented.

Intersexual conflict and primate social behavior

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It is increasingly recognized that a third component of sexual selection, mating conflict between the sexes, may account for behavioral, physiological and morphological features in a variety of mammals. In species in which infanticide by males poses a serious potential threat to infant survival, we expect that counter-strategies by fe-

males and likely sires have evolved. One of the counter-strategies involves sexual behavior: polyandrous mating by the female may improve infant fitness by diluting actual paternity distribution and confusing paternity assessment. These impacts of polyandry may reduce the risk of infanticidal attacks by males in the mating pool, and may also increase the number of defenders of infants in case of attacks. I show that the dominant male in a primate group and the female about to conceive an infant have a conflict of interest, where the optimum probability of paternity is higher for the male than the female. The extent to which this conflict of interest is expressed in behavioral terms depends on the male potential for coercion. Where the latter is high, I predict that dominant males will attempt to prevent matings with other males by directing aggression at both rival males and the female, and that females will evolve alternative means of paternity dilution. I then test these predictions by examining the relationships between male coercion potential and (1) harassment of females in the mating context, and (2) aspects of reproductive physiology in different primate radiations. The results suggest a strong effect of infanticide risk on harassment and female reproductive biology in primates.

Mate guarding in captive baboons

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In the wild, baboons often exhibit consortships in which the male follows the female closely, mates exclusively with her, while both travel with the troop. Mate guarding can be so rigid that it constrains male foraging activity. When living in large social groups, captive baboons exhibit similar mate guarding. This study examined the behavior of eleven young adult and full adult males living in four large groups. Each group contained 2 to 4 males, 10 to 20 adult females, 5 to 10 adolescent females, and several juveniles and infants. Each group lived in indoor/outdoor enclosures where the outdoor yards provided approximately 520 m² of horizontal space and numerous climbing structures. Data collection included focal animal sampling on each male, supplemented with *ad lib.* observations collected outside sample sessions. The preliminary results reveal several interesting aspects of mate guarding behavior in baboons. The alpha male in each group showed less rigorous mate guarding than the beta male. In one group, created by merging two one-male groups, mate guarding exhibited by these two males was strictly focused on "their" females; their consort activity was directed at only those females with whom they had a long history. The three captive born males showed no effort to participate in mate guarding; two of these were human reared and were never observed to copulate and the other had been mother-reared and mated in a normal manner and frequency. Females played a key role in maintaining consortships - looking back, pausing or slowing their movements, or exhibiting other behaviors to help assure proximity with the consort partner. Grooming rates between consort pairs were higher than grooming rates between these individuals and non-partners. This study provides evidence that certain aspects of baboon reproductive strategy are fundamental to this species and are exhibited even in captive conditions.

Determinants of male mating success in chacma baboons

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There is evidence that a general relationship between male dominance rank and mating success found in primates also stands for savannah baboons. However, the strength of this relationship differs among the savannah baboon subspecies and male rank in chacma baboons (*Papio cynocephalus ursinus*) was found to be of more importance than in the other subspecies. This can be explained with the absence of male coalitions and less pronounced effects of female choice. Chacma baboons are therefore ideally suited to study determinants of mating success other than the above. Although the priority-of-access model explains the proportion of time spent in consortship for males of different rank in chacmas, highest-ranking males usually consorted less often than expected. This study, conducted in the Drakensberg Mountains of Natal and at De Hoop in the Western Cape, demonstrates that mating success of high-ranking males is primarily correlated with the average number of cycling females during the tenure of high-ranking males. Neither the total number of males nor the number of females in a troop had a significant effect on mating success. In addition, males also consorted on fewer days than expected because they were found to identify cycles with higher probability of conception. There is also some evidence that older high-ranking males, probably with more knowledge about reproductive state of females, have a higher mating success than recently immigrated high-ranking males. The reason why males do not consort on as many days as possible could be explained with energetic costs involved in consorting. Drakensberg baboons live in a more challenging environment than Western Cape baboons. They were found to forage for longer hours and had less social and resting time than Western Cape baboons. Consorting Drakensberg males decreased foraging time by 10 %, whereas foraging time for Western Cape males remained similar during consorting and non-consorting periods. These findings indicate that costs involved in consorting are higher in the Drakensberg, and this explains why high-ranking males consorted on fewer days than males in the Western Cape.

Large primate aggregations: limits to female - female networks?

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Several primate species and populations form large aggregations with often more than 200 individuals. Among these species are geladas (*Theropithecus gelada*), hamadryas baboons (*Papio hamadryas hamadryas*), mandrills (*Mandrillus sphinx*), drills (*Mandrillus leucophaeus*), Guinea Baboons (*Papio hamadryas papio*), golden snub-nosed monkeys (*Pygathrix roxellana*) and a population of Angolan colobus

(*Colobus angolensis*) in the Nyungwe Forest in Rwanda. The largest groups in neotropical primates with up to 120 individuals are found in the uakaris (*Cacajao calvus*). The supposedly ecological causes for the formation of such large aggregations vary between taxa. For example, in hamadryas baboons it is thought to be the limited availability of sleeping cliffs. However, all of these taxa also show a tendency to form one-male units within larger groups. Phylogenetically, these one-male units within larger groups may derive from single one-male units, which united to form larger groups, as in the case of the Colobines and probably the uakaris, or from multi-male, multi-female groups which split into distinct one-male units, as in baboons. Either way, it seems that large aggregations are incompatible with a typical multi-male, multi-female group structure. To account for this relationship, we propose the following hypothesis. In large aggregations of more than 100-150 individuals it is impossible for a female to maintain social relationships with most other group members. She would be surrounded by a number of individuals with which no social relationship exists and which are potentially dangerous, including harassing and potentially infanticidal males. In such a situation, other females may not be effective coalition partner and a female-female social network would not represent the best solution to this problem. It is in the females' interest to form a stable relationship with a more powerful coalition partner - a male. Female-female relationships are loosened or given up in favor of female-male relationships in this situation.

Sexual swellings: the female primates' peacock tail?

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The conspicuousness of perineal sexual swellings in females of some Old World primates have stimulated zoologists ever since Darwin to link their evolution to sexual selection theory. In a recent field study, Domb & Pagel (*Nature* 410, 204-206; 2001) found support for the "reliable indicator hypothesis," which proposes that sexual swellings can be regarded as a costly handicap that honestly signals female quality. Under this hypothesis, swellings function in female-female competition over mates and therefore represent a reversal of sexual selection. However, Domb and Pagel's field research ignored intra-individual variability of swelling characters and the possibility that body mass could explain their few significant results. Moreover, they removed a class of females from the analysis that are expected to show the strongest patterns (synchronously mating females), and independent research has not supported the reliable indicator hypothesis. Thus, in contrast to Domb & Pagel, we found no relationship of swelling characteristics (size or duration) and female reproductive quality in a population of captive hamadryas baboons. Finally, in interspecific comparative tests that examined the evolution of exaggerated sexual swelling, we found no association between exaggerated sexual swellings and female mating competition, as measured using the adult sex ratio, female canine size, and ex-

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pected female mating synchrony. Within species, the least fertile females, or those least likely to raise surviving offspring, often have larger swellings. The data on sexual swellings and their correlates are more consistent with the many-males or paternity confusion hypotheses, in which females mate with more than one male per estrous cycle to reduce the risk of infanticide. Infanticide committed by males involves sexual selection through intrasexual competition, but anti-infanticide hypotheses do not postulate a reversal in sexual selection as proposed by the reliable indicator hypothesis. A swelling, which by its longer duration and/or larger size, increases the survival of infants, thus increasing the female's fitness, would be selected in the course of evolution.