Selected Publication Abstracts of
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Beehner, J.C., Nguyen, N., Wango, E., Alberts, S.C., Altmann, J. (2006) The endocrinology of pregnancy and fetal loss in wild baboons. *Hormones and Behavior.* (E publication in advance, February 17, 2006)

An impressive body of research has focused on the mechanisms by which the steroid estrogens (E), progestins (P), and glucocorticoids (GC) ensure successful pregnancy. With the advance of non-invasive techniques to measure steroids in urine and feces, steroid hormones are routinely monitored to detect pregnancy in wild mammalian species, but hormone data on fetal loss have been sparse. Here, we examine fecal steroid hormones from five groups of wild yellow baboons (*Papio cynocephalus*) in the Amboseli basin of Kenya to compare the hormones of successful pregnancies to those ending in fetal loss or stillbirth. Using a combination of longitudinal and cross-sectional data, we analyzed three steroid hormones (E, P, GC) and related metabolites from 5 years of fecal samples across 188 pregnancies. Our results document the course of steroid hormone concentrations across successful baboon pregnancy in the wild and demonstrate that fecal estrogens predicted impending fetal loss starting 2 months before the externally observed loss. By also considering an additional 450 pregnancies for which we did not have hormonal data, we determined that the probability for fetal loss for Amboseli baboons was 13.9%, and that fetal mortality occurred throughout gestation (91 losses occurred in 656 pregnancies; rates were the same for pregnancies with and without hormonal data). These results demonstrate that our longstanding method for early detection of pregnancies based on observation of external indicators closely matches hormonal identification of pregnancy in wild baboons.

Gesquiere, L.R., Altmann, J., Alberts, S.C., Khan, M.Z., Couret, J., Yu, J.C., Endres, C.S., Lynch, J.W., Ogola, P. & Wango, E. (2005) Coming of age: steroid hormones of wild immature baboons, Papio cynocephalus. *Amer. J. Primatol.* 67: 83-100.

Large gaps exist in our knowledge about common patterns and variability in the endocrinology of immature nonhuman primates, and even normal hormonal profiles during that life stage are lacking for wild populations. In the present study we present steroid profiles for a wild population of baboons (Papio cynocephalus) from infancy through reproductive maturation, obtained by noninvasive fecal analyses. Fecal concentrations of glucocorticoid (fGC) and testosterone (fT) metabolites for males, and of fGC, estrogen (fE), and progestin (fP) metabolites for females were measured by radioimmunoassay (RIA). In males, infancy was characterized by high and declining levels of fGC and fT, whereas steroid concentrations were low during the juvenile years. During the months immediately prior to testicular enlargement, fT (but not fGC) concentration tended to increase. Males that matured early consistently had higher fT and fGC concentrations than those that matured late, but not significantly so at any age. Individual differences in fT concentrations were stable across ages, and average individual fT and fGC concentrations were positively correlated. For females, high and declining levels of fE characterized infancy, and values increased again after 3.5 years of age, as some females reached menarche by that age. Both W and fGC were relatively low and constant throughout infancy and the juvenile period. During the months immediately prior to

menarche, fGC concentration significantly decreased, while no changes were observed for fE levels. fP exhibited a complicated pattern of decrease that was subsequently followed by a more modest and nonsignificant increase as menarche approached. Early- (EM) and late-maturing (LM) females differed only in fP concentration; the higher fP concentrations in EM females reached significance at 4-4.5 years of age. Maternal rank at offspring conception did not predict concentrations of any hormone for either sex. Our results demonstrate the presence of individual endocrine variability, which could have important consequences for the timing of sexual maturation and subsequently for individual reproductive success. Further evaluation of the factors that affect hormone concentrations during the juvenile and adolescent periods should lead to a better understanding of mechanisms of life-history variability.

Altmann, J. and Alberts, S.C. (2005) Growth rates in a wild population: Ecological influences and maternal effects. *Behav. Ecol. Sociobiol.* 57: 490-501.

Growth rate is a life-history trait often linked to various fitness components, including survival, age of first reproduction, and fecundity. Here we present an analysis of growth-rate variability in a wild population of savannah baboons (Papio cynocephalus). We found that relative juvenile size was a stable individual trait during the juvenile period: individuals generally remained consistently large-for-age or small-for-age throughout development. Resource availability, which varied greatly in the study population (between completely wild-foraging and partially food-enhanced social groups), had major effects on growth. Sexual maturity was accelerated for animals in the food-enhanced foraging condition, and the extent and ontogeny of sexual dimorphism differed with resource availability. Maternal characteristics also had significant effects on growth. Under both foraging conditions, females of high dominance rank and multiparous females had relatively large-for-age juveniles. Large relative juvenile size predicted earlier age of sexual maturation for both males and females in the wild-feeding condition. This confirmed that maternal effects were pervasive and contributed to differences among individuals in fitness components.

Altmann, J., Lynch, J.W., Nguyen, N., Alberts, S.C. & Gesquiere, L.R. (2004) Life-history correlates of steroid concentrations in wild peripartum baboon. *Amer. J. Primatol.* 64: 95-106.

Steroid concentrations during late pregnancy and early lactation may be affected by both a female's reproductive history and her current condition, and may in turn predict subsequent life-history events, such as offspring survival. This study investigated these relationships in a wild primate population through the use of fecal steroid analysis in repeated sampling of peripartum baboons (Papio cynocephalus). Fecal samples were collected from 32 females in five groups within the Amboseli basin during 8 weeks prior to parturition and 13 weeks postpartum. From December 1999 through February 2002, 176 fecal samples were collected from individuals representing 39 peripartum periods. Fecal concentrations of progestins (fP), estrogen metabolites (fE), glucocorticoids (fGC), and testosterone metabolites (fT) were measured by radioimmunoassay. Steroid concentrations declined from late pregnancy to lactation, and the decline was greatest and most precipitous for fE and M. Primiparous females had significantly higher mean fE concentrations in each of the last 2 months of pregnancy compared to multiparous females. Among multiparous females, fE and fT were significantly higher during late pregnancy in females carrying a male fetus compared to those carrying a female fetus. During early lactation, high fT in young mothers predicted subsequent infant death during the first year of life. These findings illustrate the potential power of repeated fecal-steroid

sampling to elucidate mechanisms of life-history variability in natural populations. They also document significant differences in hormone profiles among subgroups, and highlight that such normative subgroup information is essential for interpreting individual variability in hormone-behavior associations.

Silk, J.B., Alberts, S.C. and Altmann, J. (2004) Patterns of Coalition Formation by Adult Female Baboons in Amboseli, Kenya. *Anim. Behav.* 67: 573-582.

Coalitionary support in agonistic interactions is generally thought to be costly to the actor and beneficial to the recipient. Explanations for such cooperative interactions usually invoke kin selection, reciprocal altruism or mutualism. We evaluated the role of these factors and individual benefits in shaping the pattern of coalitionary activity among adult female savannah baboons, Papio cynocephalus, in Amboseli, Kenya. There is a broad consensus that, when ecological conditions favour collective defence of resources, selection favours investment in social relationships with those likely to provide coalitionary support. The primary features of social organization in female-bonded groups, including female philopatry, linear dominance hierarchies, acquisition of maternal rank and well-differentiated female relationships, are thought to be functionally linked to the existence of alliances between females. Female savannah baboons display these characteristics, but the frequency and function of their coalitionary aggression is disputed. In our five study groups, 4-6% of all disputes between females led to intervention by third parties. Adult females selectively supported close maternal kin. There was no evidence that females traded grooming for support or reciprocated support with nonkin. High-ranking females participated in coalitionary aggression most frequently, perhaps because they derived more benefits from group membership than other females did or could provide support at lower cost. Females typically supported the higher ranking of two contestants when they intervened in disputes between subordinates, so most coalitions reinforced the existing dominance hierarchy. Results indicate that female baboons participate in coalitionary aggression in a manner strongly influenced by nepotism and individual benefits.

Silk, J.B., Alberts, S.C. and Altmann, J. (2003) Social bonds of female baboons enhance infant survival. *Science* 302: 1231-1234.

Among nonhuman primates, females often form strong bonds with kin and other group members. These relationships are thought to have adaptive value for females, but direct effects of sociality on fitness have never been demonstrated. We present 16 years of behavioral data from a well-studied population of wild baboons, which demonstrate that sociality of adult females is positively associated with infant survival, an important component of variation in female lifetime fitness. The effects of sociality on infant survival are independent of the effects of dominance rank, group membership, and environmental conditions. Our results are consistent with the evidence that social support has beneficial effects on human health and well-being across the life span. For humans and other primates, sociality has adaptive value.

Buchan, J.C., Alberts, S.C., Silk, J.B. & Altmann, J. (2003) True paternal care in a multi-male primate society. *Nature* 425: 179-181.

Although male parental care is rare among mammals 1, adult males of many cercopithecine primate species provide care for infants and juveniles. This care is often in the form of grooming, carrying, support in agonistic interactions, and protection against infanticide(2,3). For these behaviours to be interpreted as true parental care, males must

selectively direct care towards their own offspring and this care must result in fitness benefits(4). With the exception of males defending probable offspring from infanticide(5), male primates living in multi-male, multi-female social groups have not been shown to selectively direct care towards their own offspring(6,7). We determined paternity for 75 juveniles in a population of wild savannah baboons (Papio cynocephalus) and collected data on interventions in agonistic disputes by adult males on behalf of juveniles as a form of male care. Here we show that adult males differentiate their offspring from unrelated juveniles and selectively support their offspring in agonistic disputes. As support in agonistic disputes is likely to contribute to rank acquisition and protect juveniles from injury and stress(2,3,5), this can be considered true parental care.

Lynch, J.W., Khan, M.Z., Altmann, J., Njahira, M.N. and Rubenstein, N. (2003) Concentrations of four fecal steroids in wild baboons: short-term storage conditions and consequences for data interpretation. *Gen. Comp. Endo.* 132: 264-271.

One source of both bias and "noise" in fecal steroid analysis is temporal change in steroid concentrations resulting from duration or conditions of fecal sample storage. However, no consensus currently exists regarding correct procedures or precautions necessary for fecal sample storage, and conditions vary widely within field endocrinology literature. This study considered the effects of short-term, weeks-long, storage conditions on quantifiable fecal testosterone (fT), glucocorticoids (fGC), estrogens (fE), and progestagen (fP) metabolite concentrations in wild baboons (Papio cynocephalus). Quadruplicate subsamples of fecal samples (n = 29) collected at Amboseli National Park and its environs were subjected to four different storage conditions prior to lyophilization, in order to determine the effects of storage on subsequent steroid concentrations, as assessed by I-125 radioimmunoassays. As expected, the best alternative to the "initial condition" of lyophilization at three days after collection was to freeze fecal samples at -20 degreesC for two weeks prior to lyophilization. This storage method resulted in no significant change from initial steroid concentrations for fE, fT, or fP, although fGC showed a slight but significant decline. Storage for two weeks in a charcoal refrigerator caused a mean increase in all four steroid concentrations. However, the results from this storage condition were robust in terms of practical questions asked of the data: fE and fP values still reflected pregnant versus non-pregnant states in baboon females; a fGC profile constructed by age class resembled that created from the samples from the initial condition, although slightly inflated across age classes; and there were only moderate changes in relative fT concentrations across adult males. Knowledge of the effects of storage upon each steroid analyzed within one's study is a necessary component in determining the optimal compromise for storage protocol in a particular research project.

Altmann, S.A. & Altmann, J. (2003) The transformation of behaviour field studies. *Anim. Behav.* 65: 413-423.

As areas of science mature, they pass through three, broadly overlapping stages of development, characterized respectively by description, explanation and synthesis. Field research on animal behaviour is making the transition from an area with a preponderance of purely descriptive studies to one that also includes the development and testing of verifiable hypotheses about the structure, causes and consequences of behaviour. We survey several reasons for this transformation of behaviour field studies and some of the major trends that characterize it, including: (1) patterns discerned in our cumulative knowledge of natural history; (2) increased support for behaviour field studies; (3) interfaces with related areas of science; (4) the development of observational sampling

methods and other aspects of data sampling and analysis; (5) the development of models of behaviour's adaptive functions and life-history consequences; (6) long-term field sites that make possible complete life histories, increased attention to individual differences and intergenerational studies of behaviour; and (7) the development of techniques for remote tracking of animals and for noninvasive, hands-off sampling of a range of behavioural, physiological, genetic and environmental phenomena.

Banks, W.A., Altmann, J., Sapolsky, R.M., Phillips-Conroy, J.E. and Morley, J.E. (2003) Serum Leptin Levels as a Marker for a Syndrome X-like Condition in Wild Baboons. *J. Clin. Endo. and Metab.* 88: 1234-1240.

We measured serum leptin levels in two groupings of wild male baboons, one with access to abundant quantities of food from gardens and garbage dumps near human habitations (Garbage; n = 11) and one without access (No Garbage; n =10). A Garbage subgroup had high leptin levels (Garbage HL), whereas the rest of the Garbage group had low leptin levels (Garbage LL) similar to those in the No Garbage group. The Garbage HL individuals were obese, with higher mass, body mass index, and leptin to mass ratios; were insulin to resistant, with elevations in serum insulin, glucose, and insulin to glucose ratios; and were hyperlipidemic. This syndrome X-like condition occurred only in the Garbage HL subset. The Garbage LL subset did not differ from the No Garbage individuals in mass, body mass index, leptin to mass ratio, insulin, glucose, or insulin to glucose ratios. The highest cholesterol levels, however, occurred in the Garbage LL individuals, suggesting that susceptibility to hyperlipidemia is distinguishable from susceptibility to obesity and insulin resistance. The differences were not explained by age or social status. These results show that a subgroup of wild baboons is susceptible to developing obesity and insulin resistance and that this susceptibility is not related to age or social rank.

Smith, K., Alberts, S.C. and Altmann, J. (2003) Wild female baboons bias their social behaviour towards paternal half-sisters. *Proc. Roy. Soc. Ldn.* 270: 503-510.

Adult female cercopithecines have long been known to bias their social behaviour towards close maternal kin. However, much less is understood about the behaviour of paternal kin, especially in wild populations. Here, we show that wild adult female baboons bias their affiliative behaviour towards their adult paternal half-sisters in the same manner and to the same extent that they bias their behaviour towards adult maternal half-sisters. Females appear to rely heavily on social familiarity as a means of biasing their behaviour towards paternal half-sisters, but may use phenotype matching as well.

Alberts, S.C., Watts, H.E. & Altmann, J. (2003) Queuing and queue-jumping: Long term patterns of reproductive skew among male savannah baboons. *Anim. Behav.* 65: 821-840.

In many animals, variance in male mating success is strongly correlated with male dominance rank or some other measure of fighting ability. Studies in primates, however, have varied greatly in whether they detect a relationship between male dominance rank and mating success. This variability has led to debate about the nature of the relation between rank and mating success in male primates. We contribute to the resolution of this debate by presenting an analysis of the relationship between dominance rank and male mating success over 32 group-years in a population of wild savannah baboons. When data were pooled over the entire period, higher-ranking males had greater access to fertile females. However, when we examined successive 6-month blocks, we found

variance in the extent to which rank predicted mating success. In some periods, the dominance hierarchy functioned as a queue in which males waited for mating opportunities, so that rank predicted mating success. In other periods, the queuing system broke down, and rank failed to predict mating success when many adult males were in the group, when males in the group differed greatly in age, 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 of baboons and between species of primates. Our long-term results provide strong support for the proposition that this variance is not an artefact 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.

Hahn, N.E., Proulx, D., Muruthi, P.M., Alberts, S. & Altmann, J. (2003) Gastrointestinal parasites in free-ranging Kenyan baboons. *Intl. J. Primatol.* 24: 271-279.

We screened fecal samples from 3 groups of wild-living baboons (*Papio cynocephalus* and *P. anubis*), involved in longitudinal behavioral studies, for evidence of gastrointestinal parasites. The two objectives of the study were: 1) to compare parasites from two of the groups with different foraging behavior from the same area and 2) to obtain fecal parasitic data on 3 groups of baboons to provide baseline reference data. We sampled individual baboons opportunistically from Lodge and Hook's groups, Amboseli National Park and from Mpala Group, Mpala Wildlife Research Centre, Kenya. Lodge Group baboons supplemented foraging on wild foods by daily foraging in human-source refuse, whereas Hook's and Mpala groups did not. We collected fecal samples from 55, 30 and 42 individuals in Hook's, Lodge and Mpala groups, respectively, and processed them via ether sedimentation. We identified strongylids, *Streptopharagus* sp., *Physaloptera* sp., *Trichuris* sp., *Enterobius* sp., and *Strongyloides* sp., in the feces, but no parasite directly attributable to exposure to people. Garbage- and wild-feeding Amboseli baboons differed in the prevalence of *Streptopharagus* sp., *Physaloptera* sp. and *Trichuris* sp.

Altmann, J. & Alberts, S.C. (2003) Variability in reproductive success viewed from a life-history perspective in baboons. *Am. J. Hum. Biol.*, 15: 401-409.

Nonhuman primates, like humans, mature slowly and have low fertility during a relatively long life. As data have accumulated on life-history patterns of nonhuman primates, comparative studies have yielded important insights into the evolution of this slow life-history style of primates. However, in order to understand selection pressures and evolutionary potential within species, it is important to complement comparative studies with detailed studies of life-history variability within species and to identify sources of this variability. Here we present a summary of how foraging environment, social status, and group size (a measure of population density) contribute to within-population variance in reproductive success for savannah baboons. We also discuss the extent to which savannah baboons, with their highly flexible and adaptable behavior, change their foraging environments by shifting home ranges and seeking rich food sources and how low-ranking females, which disproportionately bear the costs of social life, may mitigate those costs.

Zinner, D., Alberts, S., Nunn, C.L. & Altmann, J. (2002) Significance of primate sexual swelling. *Nature* 420: 142-143.

Exaggerated sexual signals are likely to be shaped by sexual selection, but few studies have examined signal evolution in females. Domb and Pagel[1] have presented support for the hypothesis that individual differences in exaggerated sexual swellings in female primates are reliable indicators of differences in female quality[2]. However, our re-analysis of their data casts doubt on their conclusions.

Khan, M.Z., Altmann, J., Isani, S.S. & Yu, J. (2002) A matter of time: evaluation the storage of fecal samples for steroid analysis. *Gen. Comp. Endo.* 128: 57-64.

The extraction and immunoassay of fecal steroids is an increasingly common technique, used in both captive and field studies to provide an approximation of an animal's circulating concentration of hormones through non-invasive methods. Storage of fecal samples is of critical concern because fecal bacteria metabolize fecal steroids within hours after deposit. Ethanol is often used as a preservative for fecal samples stored for several hours at room temperature. We examined the stability of fecal estrogen (fE) and glucocorticoid (fGC) metabolites from baboon (*Papio cynocephalus*) samples in a 95% ethanol solution at ambient temperature and at −20 °C over the course of six months, to determine the effect of storage on steroid concentrations. As measured by radioimmunoassay, fE metabolite concentrations increased by 122% at 90 days and fGC metabolite concentrations increased by 92% at 120 days. After peaking, both hormones declined to near initial concentrations by 180 days in ambient temperature samples. In samples stored at sub-zero temperatures, fGC metabolite concentrations showed a similar but dampened pattern, while fE metabolite concentrations exhibited small and variable changes with no consistent trend. We discuss explanations for the dynamic pattern of changing fecal metabolite concentrations and offer practical and analytical guidance to field workers for situations in which ideal conditions for stabilizing hormones are not available.

Bronikowski, A.M., Alberts, S.C., Altmann, J., Packer, C., Carey, K.D. & Tatar, M. (2002) Aging Baboon: comparative demography in a nonhuman primate. *Proc. Natl. Acad. Sci.* 99: 9591-9595.

Why do closely related primate genera vary in longevity, and what does this teach us about human aging? Life tables of female baboons (Papio hamadryas) in two wild populations of East Africa and in a large captive population in San Antonio, Texas, provide striking similarities and contrasts to human mortality patterns. For captive baboons at the Southwest Foundation for Biomedical Research, we estimate the doubling time of adult mortality rate as 4.8 years. Wild females in free-living populations in Tanzania and in Kenya showed doubling times of 3.5 and 3.8 years, respectively. Although these values are considerably faster than the estimates of 7-8 years for humans, these primates share a demographic feature of human aging: within each taxon populations primarily vary in the level of Gompertz mortality intercept (frailty) and vary little in the demographic rate of aging. Environmental and genetic factors within taxa appear to affect the level of frailty underlying senescence. In contrast, primate taxa are differentiated by rates of demographic aging, even if they cannot be characterized by species-specific lifespan.

Kemnitz, J.W., Sapolsky, R.M., Altmann, J., Muruthi, P.M., Mott, G.E. & Stefanick, M.L. (2002) Effects of food availability on serum insulin and lipid concentrations in free-ranging Baboons. *Amer. J. Primatol.* 57: 13-19.

The relationship between food availability and metabolic physiology was studied in groups of free-ranging baboons (*Papio* spp.) living in the Amboseli National Park and the Masai Mara National Reserve of Kenya. Three groups subsisted entirely on natural forage, while two other groups lived near tourist facilities and often consumed food wastes from these lodges. The refuse provided a very accessible food source with relatively high caloric density. Consumption of the refuse was associated with reduced locomotion. Sexually mature individuals from all five groups were sedated surreptitiously in the early morning and blood samples were collected. Compared to animals foraging exclusively in the wild, animals that supplemented their diet with the refuse items had two- to threefold elevations in serum insulin concentrations, as well as increased total cholesterol (C), HDL-C, and VLDL+LDL-C levels. No sex differences in physiological measures were observed except in body mass. Elevated serum insulin, and cholesterol and lipoprotein concentrations influence the development of cardiovascular disease and have been shown to be subject to dietary manipulation and exercise under controlled conditions. The present results suggest potentially deleterious effects of a highly accessible, calorically dense food source, and associated reduction of physical activity for baboons living in an otherwise natural environment.

Semple, S., McComb, K., Alberts, S., and Altmann, J. (2002) Information content of female copulation calls in yellow baboons. *Am. J. Primatol*. 56: 43-56.

In a wide variety of animal species, females produce vocalizations just before, during, or immediately after copulation. Observational and experimental evidence indicates that these copulation calls are sexually selected traits, functioning to promote competition between males for access to the calling female. In this paper, we present an acoustic analysis of variation in the form of copulation calls of female yellow baboons, Papio cynocephalus cynocephalus. In particular, we examine whether information about three factors-the calling female's reproductive state, the occurrence or absence of ejaculation, and the dominance rank of the mating male-is encoded in call structure and hence is potentially available to male receivers attending to the signal. Although several features of copulation calls were correlated with each of these factors, when all three were included in multiple regressions only reproductive state and rank of the mating male had independent effects on call form. These findings indicate that female copulation calls in this species signal information about the proximity to ovulation of the calling female and also the relative competitive strength of her mating partner

Altmann, J., Alberts, S.C., Altmann, S.A. and Roy, S.B. (2002) Dramatic change in local climate patterns in the Amboseli basin. *Afr. J. Ecol*. 40: 248-251.

Weather patterns, landscape characteristics, and animal distributions are intimately, albeit complexly, related on various spatial scales from highly local to global (e.g. Kullman, 1996; Le Houerou, 1989; Lean & Warrilow, 1989; Shukla, Nobre & Sellers, 1990). The Amboseli basin area of southern Kenya has experienced extensive habitat changes since the early 1960's. These include dramatic loss of tree and shrub cover, increase in areas of open all-year water, and concomitant changes in populations of large mammals and water birds (e.g. Western & van Praet, 1973; Struhsaker, 1976; Young & Lindsay, 1988; Altmann, 1998). Here we report for the first time patterns of temperature and rainfall in Amboseli for the 25-year period beginning in 1976. These data were gathered to evaluate direct and indirect effects of weather on the Amboseli baboons, *Papio cynocephalus* (e.g. Altmann, 1980; Stelzner & Hausfater, 1986;

Stelzner, 1988; Bronikowski & Altmann, 1996; Altmann, 1998) as part of a long-term investigation into the biology of that population.

Ryan, K.K. and Altmann, J. (2001) Selection for male choice based primarily on mate compatibility in the oldfield mouse, *Peromyscus polionotus rhoadsi*. *Behav. Ecol. Sociobiol*. 50: 436-440.

Despite the consensus that mate choice acts as a mechanism for selection of secondary sexual traits, the evolutionary forces affecting mate preferences themselves remain controversial. In this study, we first demonstrated selection acting directly on the mate preferences of monogamous male oldfield mice, *Peromyscus polionotus rhoadsi*. One group of male oldfield mice were allowed to express a social preference between two potential mates, and were subsequently paired with either their preferred or rejected female. Among these pairs, those containing preferred females produced more offspring than did those containing rejected females. We next demonstrated that this fitness advantage depended primarily on compatibility between the members of a mated pair. A second group of male oldfield mice were not allowed the opportunity to express a social reference between potential mates. Rather, these males were paired with females that had been either preferred or rejected by males in the first group. Among these pairs, those containing preferred females did not produce more offspring than those containing rejected females. In other words, individual mate preferences had fitness consequences only for those males that expressed them, demonstrating that these preferences were based primarily on compatibility between mates.

Combes, S.L. and Altmann, J. (2001) Status change during adulthood: life-history by-product or kin selection based on reproductive value? *Proc. R. Soc. Lond. Ser. B-Biol. Sci*. 268: 1367-1373.

When dominance status predicts fitness, most adaptive models of dominance relationships among cercopithecine primate females predict lifetime maintenance of status. These models and alternative ones positing rank decline as a non-adaptive by-product have remained largely untested, however, because lifetime status of older adults has been virtually unknown for natural populations. In a 25-year study of adult female savannah baboons (Papio cynocephalus), in each of three social groups, rank losses were common among the 66 females that lived past median adult age. These losses were not accounted for by loss in relative rank from group growth or by loss in absolute rank from reversals in rank between members of different maternal families or between sisters. Rather, females that had mature daughters experienced loss of dominance status to these offspring, a characteristic of all bur the top-ranking matriline of each group. Among proposed hypotheses for rank reversals between adults, that of kin selection based on relative reproductive value is most clearly supported by these data. In contrast, observed patterns of rank loss are not consistent with alternative models that postulate that changes during adult lifespan are a product elf accumulated risk, physical decline during ageing, or coalitionary support among females within or between matrilines.

Alberts, S.C. and Altmann, J. (2001) Immigration and hybridization patterns of yellow and anubis baboons in and around Amboseli, Kenya. *Am. J. Primatol*. 53: 139-154.

In 1986, Samuels and Altmann reported evidence for a hybrid zone between Papio anubis and Papio cynocephalus in Amboseli, Kenya, in a baboon population that has been the subject of long-term study since 1971 [Samuels & Altmann, International

Journal of Primatology 7:131-138, 1986]. In the current report we document ongoing patterns of hybridization in Amboseli between anubis and yellow baboons. In July 2000, we exhaustively scored living members of study groups for their degree of hybridity, using seven phenotypic characteristics (five in juveniles). We also scored all former members of study groups on the basis of photographic records, field notes, and observer recollections. A total of five anubis males and 11 males with hybrid phenotypes have immigrated into study groups over the course of the long-term study, and immigrations by hybrid males have increased in frequency over time. Further, the increasing frequency of hybrid phenotypes among animals born into study groups indicates that anubis and hybrid males have successfully reproduced in study groups. However, hybrid phenotypes and anubis immigrations were limited to groups in the southwestern portion of the Amboseli basin, with no hybrids occurring in the six eastern groups. Finally, we present evidence that anubis and hybrid males in Amboseli exhibit patterns of natal dispersal that are different from those of yellow males in Amboseli: males with anubis or hybrid phenotypes were significantly more likely to immigrate as juveniles or young subadults than were yellow males.

Smith, K.L., Alberts, S.C., Bayes, M.K., Bruford, M.W., Altmann, J. & Ober, C. (2000) Cross-species amplification, non-invasive genotyping, and non-Mendelian inheritance of human STRPs in Savannah baboons. *Am. J. Primatol*. 51: 219-227.

AB Twenty-mine human microsatellite primer pairs were screened for their utility in the cross-species amplification of baboon DNA derived from both blood and feces as part of a larger study to identify paternal half sisters in a population of wild baboons (Papio cynocephalus). Forty-one percent (12/29) of the human primers successfully amplified baboon DNA. Of these 12 primers, six amplified fragments that were both polymorphic and heterozygous (mean number of alleles = 6, mean heterozygosity = 87%) and yielded repeatable results. However, only five of these six simple tandem repeat polymorphisms (STRPs) showed patterns of Mendelian inheritance (i.e., mothers and offspring shared at least one allele at each locus), and were therefore useful for determining relatedness between individuals. Analysis of the sixth primer revealed non-Mendelian inheritance, i.e., three of the six known mother-daughter pairs had no shared alleles. This failure was probably due to non-specific fragment amplification, and may have resulted from a different STRP locus being amplified in mother and daughter. This finding highlights the importance of sampling DNA from known parent-offspring pairs when screening microsatellite primers for genetic studies. Multiple, independent replications of genotypes and Mendelian checks are both particularly important when using cross-species amplification or when using a low-quality source of DNA.

Sapolsky, R.M., Alberts, S.C. and Altmann, J. (1997) Hypercortisolism associated with social subordinance or social isolation among wild baboons. *Arch. Gen. Psychiatry* 54: 1137-1143.

The phenomena of basal hypercortisolism and of dexamethasone resistance have long intrigued biological psychiatrists, and much is still unknown as to the causes and consequences of such adrenocortical hyperactivity in various neuropsychiatric disorders. We have analyzed basal cortisol concentrations and adrenocortical responsiveness to dexamethasone in a population of wild baboons living in a national park in Kenya. We tested whether social subordinance in a primate is associated with dexamethasone resistance. Furthermore, we examined whether individual differences in adrenocortical measurements were predicted by the extent of social affiliation in these animals.

Methods: Seventy yellow baboons (Papio cynocephalus) were anesthetized and injected with 5 mg of dexamethasone; the cortisol response was monitored for 6 hours. The animals were of both sexes in a range of ages and had known ranks in the dominance hierarchies within their troops. Extensive behavioral data were available for a subset of ii adult males who were anesthetized under circumstances that also allowed for the determination of basal cortisol concentrations. Results: The socially subordinate baboons were less responsive to dexamethasone than were the dominant ones; as one manifestation of this, postdexamethasone cortisol values were more than 3 times higher in the dozen lowest-ranking animals compared with the dozen highest. In addition, socially isolated males had elevated basal cortisol concentrations and showed a trend toward relative dexamethasone resistance.

Conclusions: Our findings indicate that social status and degree of social affilitation can influence adrenocortical profiles; specifically, social subordinance or social isolation were associated in our study with hypercortisolism or feedback resistance.

Margulis, S.W. and Altmann, J. (1997) Behavioural risk factors in the reproduction of inbred and outbred oldfield mice. *Anim. Behav*. 54: 397-408.

The present study investigated two rarely measured aspects of inbreeding depression: the relationship between inbreeding and behaviour, and the possibility that inbred individuals that survive infancy may still suffer from inbreeding depression by failing to breed or failing to show appropriate mating or parental behaviours. Specifically, the relationship between (1) behaviour at pairing and reproductive success, (2) inbreeding and reproductive success and (3) inbreeding and pairing behaviour, was examined in two subspecies of the oldfield mouse, Peromyscus polionotus. Effects of parental and offspring inbreeding were separated through experimental design and analysis. Activity level during the first 25 days after pairing predicted future reproductive success: pairs that remained less active during the nocturnal (active) period were significantly less likely to breed than pairs that remained more active. Inbred females took significantly longer to produce their first litters and were less likely to produce litters than were outbred females, independently of whether females were related to their mates (i.e. whether their offspring would be inbred). Inactive pairs averaged fewer surviving pups than did active pairs. Inbreeding coefficient of female was a significant predictor of activity level in one of the two subspecies, suggesting that inbreeding may affect behaviour. Inbred adult females showed inbreeding depression in the form of lower conception rates and fewer surviving offspring, although the specific traits affected differed for the two subspecies. The implications for captive breeding programs, and likely causes of the subspecific differences, are discussed.

Bronikowski, A.M. and Altmann, J. (1996) Foraging in a variable environment: Weather patterns and the behavioral ecology of baboons. *Behav. Ecol. Sociobiol*. 39: 1-25.

We investigated the long-standing premise in behavioral ecology that the environment affects behavior and demography. We did this by evaluating the extent to which year-to-year variability in the behavioral ecology of a nonhuman primate population could be modeled from meteorological patterns. Data on activity profiles and home range use for baboons (Papio cynocephalus) in Amboseli, Kenya, were obtained over a 10-year period for three social groups: two completely wild-foraging ones, and a third that supplemented its diet with refuse from a nearby tourist lodge. The relationships across years among activity budgeting, travel distance, group size, and measures of temperature and rainfall

patterns differed among the social groups. Although meteorological variation generally correlated with behavioral variation in the completely wild-foraging groups, different weather variables and direction of relationships resulted for each group. In addition, different relationships among variables were found before and after home-range shifts. The food-enhanced group spent half as much time foraging as did the other groups and therefore could be used to evaluate the relative extent to which foraging time was a limiting factor for resting and social time. Under their relaxed ecological conditions, the food-enhanced animals increased resting time much more than social time. These findings, combined with supplementary information on the population, lead us to suggest that baboons use a suite of interrelated responses to ecological variability that includes not only changes in activity budgets, but also home-range shifts, changes in the length of the active period, and changes in group size through fissions. Moreover, our results imply that group differences as well as interpopulational and interspecific differences in behavioral ecology provide significant sources of variability. Therefore, social groups rather than populations may be the appropriate unit of analysis for understanding the behavioral ecology of baboons and other highly social primates. The different patterns we observed among groups may have fitness consequences for the individuals in those groups and thereby affect population structure over time.

Alberts, S.C., Altmann, J. and Wilson, M.L. (1996) Mate guarding constrains foraging activity of male baboons. *Anim. Behav*. 51: 269-1277.

For many species, mate guarding results in dramatic departures from normal behaviour that reflect compromised attention to feeding and other activities. Such departures have previously been difficult to document in primates, however. Data were gathered on two aspects of male behaviour that were predicted to be constrained during consortships, individual travel distance and duration of feeding bouts, for wild male baboons, Papio cynocephalus, in and out of mate-guarding episodes. In each case, consorting males were compared with themselves outside of consortships, and, in the case of distance traveled, they were compared also with non-consorting males matched for sample time and location. Males traveled significantly shorter distances while consorting than while not consorting, with the result that consorting males traveled distances similar to those traveled by females. Males also had significantly shorter feeding bouts while consorting. The shorter travel distances and feeding bouts experienced by consorting males may represent important constraints on male foraging activity, and probably result in decreased energy intake during mate guarding. Seasonal and non-seasonal breeding patterns will have different consequences for the magnitude of fluctuations in energy stores and depletions experienced during mate guarding, and costs of mate guarding in species that breed non-seasonally will be more difficult to document because they are necessarily smaller and temporally dispersed. When considered across the lifespan, however, mate guarding costs to non-seasonal breeders may equal or exceed costs to seasonal breeders.

Altmann, J., Alberts, S.C., Haines, S.A., Dubach, J., Muruthi, P., Coote, T., Geffen, E., Cheesman, D.J., Mututua, R.S., Saiyalel, S.N., Wayne, R.K., Lacy, R.C. and Bruford, M.W. (1996) Behavior predicts genetic structure in a wild primate group. *Proc. Natl. Acad. Sci*. U.S.A. 93: 5797-5801.

The predictability of genetic structure from social structure and differential mating success was tested in wild baboons. Baboon populations are subdivided into cohesive social groups that include multiple adults of both sexes. As in many mammals, males are

the dispersing sex. Social structure and behavior successfully predicted molecular genetic measures of relatedness and variance in reproductive success. In the first quantitative test of the priority-of-access model among wild primates, the reproductive priority of dominant males was confirmed by molecular genetic analysis. However, the resultant high short-term variance in reproductive success did not translate into equally high long-term variance because male dominance status was unstable. An important consequence of high but unstable short-term variance is that age cohorts will tend to be paternal sibships and social groups will be genetically substructured by age.

Alberts, S.C. and Altmann, J. (1995) Preparation and Activation – Determinants of age at reproductive maturity in male baboons. *Behav. Ecol. Sociobiol*. 36: 397-406.

Age at maturity is a particularly important life history trait, but maturational data are rare for males in natural populations of mammals. Here we provide information on three maturational milestones and their social and demographic correlates among 43 wild male baboons, Papio cynocephalus, in a natural population in Amboseli National Park, Kenya. We examined (1) age at testicular enlargement, which signals puberty and the onset of subadulthood, (2) age at attainment of adult dominance rank, which we consider to be the beginning of adulthood, and (3) age at first sexual consortship, which is the best measure available for age at first reproduction in male baboons. Testicular enlargement (median age = 5.69 rears) occurred earlier among sons of high ranking mothers, and was not influenced by rainfall or seasonality. Attainment of adult dominance rank (median age = 7.41 years) was also accelerated among sons of high-ranking mothers, and among males whose mothers had died while the males were juveniles. First sexual consortship (median age = 7.92 years) was not influenced directly by maternal characteristics, but attainment of adult dominance rank always preceded first consortship, The lag time between attainment of adult rank and first consortship (median = 2.5 months; range = 5-526 days), was predicted by the number of sexually cycling females in the group when the male attained rank, and by how high ranking the male became in his first months as an adult. We suggest that the age at which a male baboon is ready to begin reproducing is influenced by a relatively stable maternal characteristic that exerts its influence early in development, but the timing with which this potential is realized depends on activation by more proximate, often stochastic triggers such as female availability. This two-level organization of influences is likely to contribute to the variance both in age at first reproduction and in life-time fitness. Differences in the relative magnitude of the two levels will lead to both intra- and interspecific variability in the opportunity for maternal selection and sexual selection.

Alberts, S.C. and Altmann, J. (1995) Balancing costs and opportunities – dispersal in male baboons. *Am. Nat*. 145: 279-306.

Young male baboons typically disperse from their group of birth as they near adult size and may continue to migrate between social groups throughout their lives. Long-term data on dispersal and residence patterns of male baboons in Amboseli National Park, Kenya, were available for 110 males in the population, including 43 that were monitored during their natal dispersal. These data enabled us to provide not only a detailed evaluation of the effects of reproductive competition on dispersal but also the first direct estimates of the costs of dispersal in male primates and one of the few direct estimates of fitness costs associated with breeding in the natal group. Males underwent natal dispersal at a median age of 8.5 yr (range, 6.8-13.4 yr) and subsequently remained in nonnatal groups for a median tenure of 24 mo (range, 1-138 mo). Half of the males in the study engaged in

moderate to extensive reproductive activity before natal dispersal. Reproductive costs associated with breeding in the natal group were suggested by the high mortality of offspring for whom natal males were their likely fathers, even though maternal relatives avoided mating with each other. Dispersal involved considerable time spent alone, and therefore the costs of dispersal were substantial, because of mortality risks and missed reproductive opportunities during dispersal. Female availability and male mating success apparently affected both natal and secondary dispersal patterns. We present a model of dispersal tendency in order to explicate the ways in which differences in population density, predation risk, and the distribution of mating opportunities among groups might result in complex dispersal patterns that are consistent with both the results of the present study and the disparate empirical reports in the literature.

Altmann, J., Schoeller, D., Altmann, S.A., Muruthi, P., Sapolsky, R.M. (1993) Body size and fatness of free-living baboons reflect food availability and activity levels. *Am. J. Primatol*. 30: 149-161.

We used morphometric techniques and isotope-labeled water to investigate the influence of abundant, accessible food and resultant low activity levels on body size and fatness in free-living adolescent and adult baboons as compared to animals in the same population that experienced more typical, wild-feeding conditions. Females that had access to abundant food from a nearby garbage dump averaged 16.7 kg body mass, 50% more than their wild-feeding counterparts in adjacent home ranges. Little of the difference was due to lean mass: the animals with an accessible abundance of food averaged 23.2% body fat in contrast to 1.9% for the wild-feeding animals. Significant differences between feeding conditions were found for all measured skinfolds and for upper arm circumference but not for linear measurements. Differences between feeding conditions were less for males than for females, perhaps reflecting persistent effects of nutritional conditions during the first eight years of life before dispersal from the group of birth. The difference in fatness between feeding conditions was similar to the difference between humans with frank obesity and those that are considered lean, but in both cases the percentages of body fat in the baboons were considerably less than those observed in humans. In levels of fatness, the relatively sedentary animals resembled their counterparts in group-housed captive conditions.

Phillips-Conroy, J.E., Hildebolt, C.F., Altmann, J., Jolly, C.J., Muruthi, P. (1993) Periodontal health in free-ranging baboons of Ethiopia and Kenya. *Am. J. Phys. Anthropol*. 90: 359-371.

Frontal and lateral intraoral photographs of 19 baboons from the Awash National Park, Ethiopia and 37 baboons from Amboseli National Park, Kenya, were used to assess periodontal health. The Awash baboons, and two groups (Alto's and Hook's) at Amboseli, fed entirely from natural sources, but baboons from the third Amboseli group (Lodge) fed largely on food refuse from one of the park's lodges. Juveniles and adults were evaluated separately. Intraoral photographs were seriated based on visual appraisals of periodontal health. In both age groups, the best periodontal health was seen in Awash animals; Alto's and Hook's animals were intermediate, and the poorest health was seen in the Lodge sample. The periodontal health decreased with age in adult baboons, as reported in humans. Geochemistry, genetics, age, and diet (particularly variations in bacterial flora) were considered as factors contributing to the intergroup differences. Although it is not possible at present to exclude any of these as a

contributing cause, we consider that diet in the broad sense (including food, water, and contamination by oral bacteria of human origin) probably plays a major role.

Margulis, S.W., Altmann, J. and Ober, C. (1993) Sex-Biased lactational duration in a human population and its reproductive costs. *Behav. Ecol. Sociobiol*. 32: 41-45.

We tested the proposition that among humans (1) differences in lactational duration result in differences in costs of reproduction even under rich nutritional conditions; and (2) elimination of factors postulated to favor male-biased parental care will be reflected in elimination or reversal of sex-biased care. To do so, we examined the relationship between lactational duration and fertility among Hutterites, a communal-living human population in which the levels of nutritional resources and fertility are high, breast-feeding is the norm, contraceptive use is limited and the collective social and economic system results in low resource variance among individuals. We demonstrate that even under good nutritional conditions, duration of nursing was a significant predictor of the length of time to next pregnancy and that nursing continued to suppress fertility after the resumption of menses. Moreover, we find that daughters were nursed longer than sons, leading to a longer interval to next pregnancy. We examine this uncommon, but not unique, finding of female-biased human parental care in the light of Hutterite social structure, and we explore the consistency of this finding with the most applicable models of parental investment.

Moses, L.E., Gale, L.C. and Altmann, J. (1992) Methods for analysis of unbalanced, longitudinal, growth data. *Am. J. Primatol*. 28: 49-59.

We describe an approach to analysis of growth that does not depend on assumptions about the underlying functional growth pattern and that allows for multiple observations arising from individual-specific, irregularly spaced data. We produce estimated growth curves for predefined subject groups by using LOWESS, a nonparametric smoothing algorithm. We describe how statistical significance of curve features may be evaluated by using the "jackknife," a sample re-use method; this technique can be used to assess differences between subject groups. We then obtain residuals at each data point by reference to the estimated curve. Consistency of residuals is evaluated as a characteristic of individual subjects, and in the presence of individual consistency, relative size-for-age is then scored by the average residual for each individual. This allows study of relationships between relative size and other individual characteristics such as birth order, dominance rank, or age of maturation. Finally, we indicate flexibility of these methods and alternatives, propose uses related to other questions about growth, and suggest potential applications to variables other than body size. Appendices demonstrate application of the LOWESS and jackknife algorithms to the problem of testing sex differences in growth.

Altmann, J., Alberts, S. and Sapolsky, R.M. (1992) Endocrine and developmental correlates of unilateral cryptorchidism in a wild baboon. *Am. J. Primatol*. 26: 309-314.

A wild, group-living 8.5-year-old adult baboon was found to have only a single palpable testicle, the only case of cryptorchidism found among more than 200 males that we have examined. This young adult had an unusually small body size for his age, one that was comparable to that of immature males two years younger, and during maturation his body mass was increasingly small for his age. As a young adult, he also had very low testosterone concentrations, which, in combination with his small size, history of impaired growth, and the absence of any obvious scars around the scrotum, suggest that this is a

case of spontaneous unilateral cryptorchidism of unknown cause rather than one of monorchidism arising from injury. Despite striking differences in his growth, adult body size, and testosterone levels, the male's cryptorchidism seemed to have relatively little effect on his social and sexual maturation in his natal group. Nonetheless, it may be related to his inability to gain entry into another group after dispersal.

Altmann, J. and Samuels, A. (1992) Costs of parental care – infant-carrying in baboons. *Behav. Ecol. Sociobiol*. 29: 391-398.

Infant-carrying, the most costly form of primate parental care other than lactation, was investigated in savannah baboons of Amboseli, Kenya. Measurements of physical growth, counts and length of paces, and simultaneous records of carrying and locomotion were used to evaluate the time, distance, and energetic expenditure of infant-carrying. Finally, we modeled the energetics of independent infant locomotion and considered ontogenetic patterns in the alternative energetic costs of carrying versus independent infant locomotion under assumptions of complete nutritional dependency. The youngest infants were carried by their mothers during all travel and foraging, for a total of 8-10 km/day. By 8 months of age, both carrying time and distance were almost zero. However, daily carrying distance, unlike carrying time, did not decline in the first few months, because older infants were carried disproportionately during rapid travel and, consequently, for greater travel distances per unit carrying time. Females of low dominance rank carried their infants the most; the highest ranking mothers not only carried their infants least but biased their carrying against sons. Although carrying a growing infant is an increasingly costly behavior, during the period of nutritional dependence energetic costs to the mother are appreciably greater if an infant travels independently instead of being carried by its mother. Yet infants increased locomotor independence at a younger age than predicted by a simple model of material energetic efficiency. Trade-offs in energetic economy may enhance a mother's future reproduction at the expense of her present infant, may enhance survival of the present infant by promoting early acquisition of developmentally essential skills, or may suggest the importance of additional factors that influence the mother's and infant's behavior.

Sapolsky, R.M. and Altmann, J. (1991) Incidence of hypercortisolism and dexamethasone resistance increases with age among wild baboons. *Biol. Psychiatry* 30: 1008-1016.

While many features of the adrenocortical axis are unchanged with age in humans, there is a pattern of senescent hypercortisolism. This occurs basally, following threshold doses of dexamethasone, and in synergy with depression or Alzheimer's disease. An understanding of neuroendocrine aging is important, for both its gerontological implications, and determination of normative values for comparison with neuropsychiatric states. We have investigated whether aging is associated with hypercortisolism in a population of wild primates. The subjects were 108 yellow baboons (Papio cynocephalus) that have been under long-term study of Amboseli National Park in Kenya. Animals were anesthetized by blowgun under similar circumstances that allow for determination of basal cortisol concentrations. Sixty minutes later, 5.0 mg dexamethasone was administered to each animal, and cortisol determinations were made on serum collected immediately before administration and 6 hr later. Basal cortisol concentrations rose with age ($p < 0.028$; $r = 0.23$). This occurred in a nonprogressive manner, in that there were no differences in concentrations among the youngest three quartiles of animals, whereas animals in the oldest quartile (older than approximately 16

years) had significantly higher values. In addition, there was a significant increase in postdexamethasone cortisol concentrations with age ($p < 0.01$; $r = 0.31$). This feature emerged progressively with age in both sexes. A number of possible artifactual causes of this senescent pattern could be eliminated, including medication confound, coincident disease, and body weight. These findings suggest that hypercortisolism and glucocorticoid feedback resistance might be general features of primate aging.

Muruthi, P., Altmann, J. and Altmann, S. (1991) Resource base, parity, and reproductive condition affect females feeding time and nutrient intake within and between groups of a baboon population. *Oecologia* 87: 467-472.

We examined within-and between-group differences in aspects of feeding and nutrient intake among adult females of a single population of baboons (Papio cynocephalus) in Amboseli National Park, Kenya. Differences in time spent feeding, daily energy and protein intake and feeding efficiency (nutrient intake per minute spent feeding) reflected differences in resource base, reproductive condition and parity. Baboons that partially fed from a lodge garbage dump spent less than half the time feeding than those that were feeding totally in the wild. During this greatly reduced feeding time, the garbage-feeding group had a similar daily energy intake and only a slightly lower daily protein intake relative to wild-feeding baboons. Consequently, the feeding efficiency of the semi-provisioned baboons was appreciably higher than that of the non-provisioned baboons. For the totally wild-feeding baboons, samples were large enough to permit analyses of feeding time and nutrient intake during different reproductive states and parity. Females spent more time feeding and had higher daily energy and protein intake when they were pregnant or lactating than when they were sexually cycling. Nulliparous females spent more time feeding than their multiparous counterparts. The daily energy intake of nulliparous females was higher than that of their multiparous counterparts, but their daily protein intakes did not differ significantly. Pregnant or lactating and nulliparous females had higher feeding efficiency than their sexually cycling and multiparous counterparts. The two nulliparous females in the garbage-feeding group spent more time feeding but did not take in more energy or protein per day than their multiparous counterparts.

Altmann, M. and Altmann, J. (1991) Models of status-correlated bias in offspring sex-ratio. *Am. Nat.* 137: 542-555.

We study a simple model describing the genealogic structure of a population in which the sex ratio of offspring varies with a parent's position in a social hierarchy. This model is based on species in which one sex disperses and in which rank in a stable social hierarchy for the other sex is inherited" by the offspring of that sex. We find that biased production of offspring in such a social system has important implications for group-size regulation, for the genetic relationships among individuals at any given time and across generations, and for the disparity between the social environment experienced by a parent and its offspring. The general model predicts that group size is tightly regulated and that group size is unstable in groups with underproduction by high-ranking mothers. We then further examine the particular case of the model in which the nondispersing sex (females) is overproduced by higher-ranking parents. In this case, we find that females are unusually closely related; all females in a group have a common female ancestor 5-10 generations back. Moreover, daughters of mothers in the middle of the hierarchy experience the largest intergenerational disparity. In contrast to daughters of high- and low-ranking females, they occupy ranks much lower than their mothers'.

Samuels, A. and Altmann, J. (1991) Baboons of the Amboseli basin – demographic stability and change. *Int. J. Primatol*. 12: 1-19.

A cross-sectional demographic analysis of the entire baboon population of the Amboseli basin of southern Kenya was undertaken to complement the longitudinal, intensive studies of a subpopulation. The present survey documented the extent and persistence of the influx of anubis baboons into the predominantly cynocephalus community and provided another example of the nonrandom dispersal patterns of cercopithecine males. In addition, the survey confirmed continued demographic stability of the basin-wide baboon population and even growth in groups that had access to better feeding conditions, despite decline of the baboons' preferred habitat and expansion of human activities into wildlife areas. Conflicts with activities of humans, however, indicate that the present well-being of the Amboseli baboon population may be short-lived.