vealed by the equation Y = 0.24X - 4.98. These measurements provide important data for comparative analysis within the subfamily Colobinae. Furthermore, the data indicate that group size of *Simias concolor* in a primary rainforest habitat in North Siberut is considerably larger than that reported from other sites on the Mentawai Islands, thus emphasising the conservation importance of this region for this rare and endemic species.

Adaptive Strategies for the Use of Fallback Foods in Apes

Mark E. Harrison

Wildlife Research Group, The Anatomy School, University of Cambridge, Cambridge, UK E-Mail: harrison_me@hotmail.com

Key Words: Apes • Fallback food • Ecology

It has recently been suggested that the evolutionary importance of fallback foods (FBF) apply more to processing adaptations (e.g., gut morphology and dentition), whereas the evolutionary importance of preferred foods apply more to harvesting adaptations (i.e., increased search/travel efficiency), and that two classes of FBF exist: staple – available and eaten year-round, $\leq 100\%$ of the diet - and filler - may not be eaten for long periods, never 100% of the diet. In this paper, I test this idea on apes and find that, generally, it is well supported. First, I compare the FBFs used by the different species and their level of reliance on these (gorilla > chimpanzee > orangutan > gibbon). Next, I compare 14 characteristics (covering travel, tool use, cranio-dental, digestive and life history adaptations) indicative of FBF dependence. I find that, while these characteristics generally fit the above level of reliance on FBFs (with gorillas and gibbons unambiguously adapted primarily for the exploitation of FBF and preferred foods, respectively), some unexpected discrepancies do occur. Despite chimpanzee's proposed slightly greater reliance on FBFs than orangutans, orangutan cranio-dental and digestive morphology appears better adapted for FBF exploitation than that of chimpanzees. This is most probably due to the nature of the two species' main FBF: figs for chimpanzees, and bark and leaves for orangutans. While the former have many of the properties normally exhibited by preferred foods (patchy distribution and easy processing), the latter are difficult to masticate and digest (due to their high toughness and fibre content) and are low in energy, leading to adaptations in orangutans more suited for processing fibrous foods. It is clear that FBF exploitation has a dramatic influence on ape ecology and, consequently, is likely to have been very important in hominoid evolution. Bearing this in mind, and considering the possible bias of dental morphology for exploiting FBFs rather than preferred foods/overall dietary composition, care should be taken when attempting to assess extinct hominoid diet through teeth.

Development of a Liquid Chromatography-Tandem Mass Spectrometry Method for the Quantification of Endogenous Steroids in Primate Urine

Barbara Hauser, Tobias Deschner, Christophe Boesche

Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Leipzig, Germany

E-Mail: bhauser@eva.mpg.de

336

 $\textit{Key Words: Baboon} \cdot \textit{Oestrone} \cdot \textit{Pregnandiol} \cdot \textit{Cortisol} \cdot \textit{Testosterone} \cdot \textit{Mass}$ spectrometry

A quantitative method using liquid chromatography-tandem mass spectrometry (LC-MS/ MS) was developed for the simultaneous determination of 23 endogenous steroids in primate

urine. The introduced method includes oestrone, pregnandiol, cortisol, testosterone and several human urinary glucocorticoid and androgen metabolites. As the method is intended for the analysis of steroid hormones in behavioural studies on wild-living primates, it was adapted for a sample volume of 200 μ l urine. The sample preparation consisted of an enzymatic hydrolysis of steroid glucuronides using β -glucuronidase from *E. coli* followed by a solvolytic cleavage of steroid sulphates employing sulphuric acid/ethyl acetate. The extraction of steroids from urine was optimized with respect to pH during extraction, type of ether and the amount of enzyme necessary for complete hydrolysis of glucuronides. The method was validated with respect to detection limits, recovery of extraction, intra- and inter-day precision and reproducibility of hydrolysis and solvolysis. The proportion of steroid hormone excreted as sulphate was determined for 21 steroids in chimpanzee urine, in order to evaluate the necessity of this step. The solvolysis proved to be essential for all investigated steroids except for pregnandiol, tetrahydrocortisol and tetrahydrocortisone, which were found to be less than 10% in the solvolysis fraction. As a first application, the ovarian cycle profile of oestrone and pregnandiol was investigated in three captive bonobos.

The More Males, the More Dominant Are Female Primates

Charlotte K. Hemelrijk, Jan Wantia, Karin Isler

Theoretical Biology, Centre for Ecological and Evolutionary Studies, University of Groningen, Haren, The Netherlands E-Mail: c.k.hemelrijk@rug.nl

 $\textit{Key Words: Dominance relationships} \cdot \textit{Aggression} \cdot \textit{Female dominance} \cdot \textit{Group composition}$

Although models and empirical data have shown that dominance relationships (also those between the sexes) are, at least in part, a consequence of the self-reinforcing effect of winning and losing fights (the so-called winner-loser effect), this phenomenon has been debated. To contribute to this discussion, we try to explain how groups may differ in their degree of female dominance over males. Since groups differ in composition, we investigated how group composition may influence female dominance over males through self-reinforcing effects. For this, we combined a modelling study with an empirical investigation on 22 species throughout the Primate order. We used an earlier model, called DomWorld, because it has shown that self-reinforcing effects in combination with a high intensity and frequency of aggression increase female dominance over males. In the model, individuals are made only to group and compete, whereby winning and losing fights are self-reinforcing. The sexes differ only in their fighting power: males start with a higher initial dominance value and a higher intensity of aggression than females. Results show that in the model female dominance increases with the number of males in the group, which is due to the higher percentage of interactions with individuals that have a higher intensity of aggression (males). Similarly, in our comparative study (using contrast methods), female dominance increases with the percentage of males in the group. This correlation is also related to the percentage of competitive interactions of both sexes with males and is not due to sexual dimorphism. Though this supports the importance of winner-loser effects for dominance relationships, we also investiged alternative explanations for this phenomenon. Similar analyses in other species are needed to prove that this is a general phenomenon.