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BRIEF REPORTS

# Effects of Food Availability on Serum Insulin and Lipid Concentrations in Free-Ranging Baboons

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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. Am. J. Primatol. 57:13–19, 2002. 

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## INTRODUCTION

Eating habits and physical activity have large effects on the maintenance of health or progression of disease. Diets that elevate serum cholesterol increase the development of atherosclerosis and coronary heart disease (CHD) [McGill, 1979]. Exercise can improve insulin sensitivity and reduce insulin levels, which will reduce the risk of developing diabetes mellitus, hypertension, and heart disease [Ginsberg, 2000]. Hyperinsulinemia may exacerbate the deleterious effects of elevated cholesterol by further increasing cholesterol synthesis, altering the lipoprotein profile, and stimulating cell proliferation in the arterial wall [Stout, 1985; but see also Jarrett, 1988]. Physical inactivity, social stress, and other factors also contribute to the development of insulin resistance and cardiovascular disease [Walker et al., 1999; van Baak & Borghouts, 2000; Winston, 1988].

The effects of diet and reduced physical activity have been investigated in a variety of animal models of human disease in controlled conditions. Numerous experimental studies with captive nonhuman primates have found a significant correlation between obesity and reduced physical activity, and between plasma lipoproteins and atherosclerosis [McGill et al., 1981b]. In contrast, the effects of diet and activity on lipid measures or obesity in nonhuman primates in self-selecting situations, analogous to those in humans, are not comparably documented. In this report we describe the results of measurements from two groups of baboons (hereafter referred to as "lodge groups"), from two different locales, that consumed a mixed diet (some of which contained refuse items) and adopted a relatively sedentary lifestyle. In each locale, these animals were contrasted with other groups living in adjacent ranges whose diet and behavior were more typical of wild baboons (referred to as "wild-foraging groups").

## METHODS

### Sites and Subjects

Data were collected from June through September, the dry season, at two study sites: Amboseli National Park and Masai Mara National Reserve, both in Kenya. The baboons at both sites had been extensively studied previously and became well habituated to observers. Study groups included ones that were entirely wild-foraging and others that were eating a diet derived principally from refuse at tourist lodges. A variety of behavioral and endocrinological data on these group have been reported (e.g., Amboseli [Altmann et al., 1993, 1996; Altmann & Muruthi, 1988; Muruthi et al., 1991], and Masai Mara [Sapolsky, 1986; Sapolsky and Mott, 1987]).

In Amboseli, the 35 female and 29 male subjects (*Papio cynocephalus*) were members of three study groups: two completely wild-foraging and one lodge group. The females were at least 40 months of age, while the males were at least 96 months old. Late-gestational or nursing females were excluded. In the Masai Mara, a site where research and detailed demographic records have focused primarily on males, 30 male subjects (*Papio anubis*) were studied from two social groups: one completely wild-foraging and one lodge group. The wild-foraging groups subsist entirely on a natural diet that is almost entirely vegetarian, consisting primarily of grass blades and corms, various parts of Acacia trees, shrubs, and tubers. Considerable time and locomotion are required on a daily basis for obtaining and extracting these foods. The lodge groups relied predominantly on food waste that is

available in a concentrated supply throughout the year from a nearby lodge's refuse dump. As a result, they travel only a third of the distance, spend less than half the time feeding compared to the wild-feeding groups, and are larger and fatter [Altmann & Muruthi, 1988; Muruthi et al., 1991; Altmann et al., 1993]. Nonetheless, estimated daily energy intake in the wild groups did not differ significantly from those of the lodge group for Amboseli females, the one class of individuals for which such comparative data are available [Muruthi et al., 1991].

## Field Methods

Individuals were anesthetized with phencyclidine HCl (approximately 2 mg/kg/body weight) in the Mara, and Telazol® (tiletamine hydrochloride and zolazepam; Fort Dodge Laboratories, Inc., Fort Dodge, IA) in Amboseli, using injection by a syringe propelled from a blowpipe at less than 10 m. Both are dissociative anesthetics, with similar mechanisms of action at glutamatergic receptors. Telezol® was not yet available when the data were collected in the Mara, and was used for the more recent Amboseli studies because of tighter regulatory restrictions on access to phencyclidine. Unpublished data from the Mara population indicate no change in the endpoints measured as a result of anesthetic exposure. To preclude anticipatory stress or loss of habituation, animals were darted only when their backs were turned. To control for diurnal variability in physiological variables, darting was done as early as possible— only between 0700 and 1000 hr in Mara, and between 0730 and 1030 hr in Amboseli. Animals had typically eaten some amount during that time period, with the pattern of eating being similar at the two field sites. Thus, insulin data most conservatively represent "random" rather than "fasted" levels.

Within 15 min of darting, blood samples were collected and each animal was weighed to the nearest 0.1 kg. In Amboseli, other morphometric measures were taken, and fatness was also measured for females through the use of labeled water [methods in Altmann et al., 1993].

## Sample Handling and Laboratory Methods

All blood samples were put on ice immediately after collection. They were centrifuged and serum was frozen within 1 hr.

Insulin was measured by radioimmunoassay (Cambridge Medical Technology, Billerica, MA) and glucose was measured by the glucose oxidase method at the Wisconsin Regional Primate Research Center (J.W.K.).

Analysis of lipid levels for the Amboseli baboons was conducted at Stanford University (M.L.S.). Plasma total cholesterol was measured enzymatically. HDL-cholesterol was measured by dextran sulfate-magnesium precipitation [Warnick et al., 1982], followed by enzymatic determination of cholesterol. Levels of VLDL+LDL-cholesterol (VLDL+LDL-C) were calculated as the difference between total cholesterol and HDL-C. Lipids for the Masai Mara baboons were similarly measured at the University of Texas Health Science Center at San Antonio (G.E.M.). Total cholesterol and HDL-cholesterol (HDL-C) were measured enzymatically [Allain et al., 1974], the latter after precipitation of VLDL+LDL-C with heparin-manganese [Mott et al., 1982]. VLDL+LDC-C was calculated as above. Apolipoproteins A-I and B were quantitated by electroimmunoassay [Mott et al., 1982]. Lipid measurements at both laboratories were consistently within specified limits as monitored by the Centers for Disease Control National Heart, Lung and Blood Institute Lipid Standardization Program.

**TABLE I. Serum Insulin and Lipoprotein Concentrations by Diet Group for Female Baboons, Amboseli National Park**

| Measurement | Wild-foraging groups (n = 14) | Lodge group (n = 11) | $P$[a] |
|---|---|---|---|
| Insulin (μU/mL) | 21 ± 2[b] | 72 ± 11 | < 0.001 |
| Glucose (mg/dL) | 72 ± 4 | 79 ± 5 | NS |
| Total cholesterol (mg/dL) | 111 ± 10 | 128 ± 9 | NS |
| HDL-C (mg/dL) | 49 ± 4 | 77 ± 9 | 0.005 |
| VLDL-C plus LDL-C (mg/dL) | 52 ± 7 | 47 ± 7 | NS |
| Body mass (kg) | 10.6 ± 0.6 | 15.2 ± 1.4 | 0.004 |

[a]Indicated probabilities are based on t-tests with 23 degrees of freedom.
[b]Mean ± SEM.
NS, not significant ($P > 0.1$).

Data were evaluated by Student's *t*-tests and Pearson's product moment coefficient of correlation with subsequent *t*-tests.

## RESULTS

### Amboseli

Lodge group members of both sexes had approximately threefold higher insulin (IRI) levels than the baboons in the wild-foraging groups (Tables I and II). These animals also had higher HDL-C, and the lodge males had elevated total cholesterol levels. Lodge females were heavier than their fully wild-foraging counterparts (Table I), but male body mass did not differ significantly between foraging conditions (Table II).

Body mass was significantly correlated with age within each sex × diet group ($0.56 < r < 0.82$, $P < 0.01$), but diet groups did not differ significantly in age. There were no statistically significant sex differences in insulin or metabolite measures.

### Masai Mara

Insulin (IRI) concentration was twofold higher in the lodge group than in the wild-foraging group (Table III). Total cholesterol, VLDL+LDL-C, and HDL-C were higher in the lodge group than in the fully wild-foraging group. Across both groups, Apo B was correlated with VLDL+LDL-C ($r = 0.87$, $P < 0.01$), and Apo A-I correlated with HDL-C ($r = 0.61$, $P < 0.01$), as expected.

**TABLE II. Serum Insulin and Lipoprotein Concentrations by Diet Group for Male Baboons, Amboseli National Park**

| Measurement | Wild-foraging groups (n = 28) | Lodge group (n = 22) | $P$[a] |
|---|---|---|---|
| Insulin (μU/mL) | 22 ± 4[b] | 62 ± 18 | 0.02 |
| Glucose (mg/dL) | 72 ± 3 | 81 ± 4 | NS |
| Total cholesterol (mg/dL) | 89 ± 6 | 123 ± 5 | <0.001 |
| HDL-C (mg/dL) | 49 ± 4 | 73 ± 4 | <0.001 |
| VLDL-C plus LDL-C (mg/dL) | 40 ± 4 | 50 ± 4 | 0.007 |
| Body mass (kg) | 20.6 ± 1.3 | 24.2 ± 2.2 | NS |

[a]Indicated probabilities are based on t-tests with 49 degrees of freedom.
[b]Mean ± SEM.
NS, not significant ($P > 0.1$).

**TABLE III. Serum Insulin and Lipoprotein Concentrations by Diet Group for Male Baboons, Masai Mara National Reserve**

| Measurement | Wild-foraging groups (n = 19) | Lodge group (n = 9) | $P$[a] |
|---|---|---|---|
| Insulin (μU/mL) | 32 ± 6[b] | 69 ± 16 | 0.01 |
| Glucose (mg/dL) | 52 ± 0.4 | 50 ± 0.4 | NS |
| Total cholesterol (mg/dL) | 66 ± 3 | 87 ± 7 | < 0.03 |
| HDL-C (mg/dL) | 38 ± 3 | 48 ± 3 | < 0.06 |
| VLDL-C plus LDL-C (mg/dL) | 28 ± 1 | 39 ± 6 | < 0.02 |
| Apo A-1 (mg/dL) | 72 ± 5 | 80 ± 3 | 0.10 |
| Apo B (mg/dL) | 22 ± 1 | 27 ± 3 | < 0.06 |
| Body mass (kg) | 26.5 ± 0.8 | 28.1 ± 1.2 | NS |

[a]Indicated probabilities are based on t-tests with 26 degrees of freedom except for body mass, where df = 25 and IRI where df = 28.
[b]Mean ± SEM.
NS, not significant ($P > 0.1$).

## DISCUSSION

Although the effects of food availability and reduced activity have been investigated in captive animal models of human metabolic disorders, these studies usually involved conditions beyond the animals' control. In this study voluntary differences in eating patterns and lifestyle were associated with elevated serum insulin and cholesterol levels in the lodge groups compared to wild-foraging baboons. Lodge groups ate fresh refuse intensively and spent less time traveling than completely wild-foraging groups. The differences in metabolic measures between diet groups within each site were similar. The higher lipid values at Amboseli compared to Masai Mara may be due to different activity levels, amounts of refuse consumed, or differences in the subspecies at each site— possibilities that cannot be determined in the current investigation.

Elevated insulin concentration can result from increased adiposity or reduced physical activity [Bjorntorp, 1976; Horton, 1986; Walker et al., 1999; van Baak & Borghouts, 2000]. Among the Amboseli animals, in which measures of fatness were obtained, lodge females weighed more than the wild-foraging ones, had higher body-mass index and greater skinfold values, and higher percentage of body fat as measured by labeled water [Altmann et al., 1993]. Older lodge females were strikingly obese compared to age peers in wild groups. However, their fatness levels were similar to those in well-provisioned, group-housed captive animals, and these animals were considerably leaner than singly-housed captive animals with richer diets and lower activity levels [Altmann et al., 1993]. The relative physical inactivity in the lodge group might have shifted body composition from lean tissue to fat. Although lodge females were heavier and fatter than wild-foraging ones, adult males did not differ in body mass between diet groups. One possible explanation is that females had resided their whole lives in the same groups and, therefore, with the same diet conditions, whereas adult males probably immigrated into the study groups, and potentially the diet conditions, during or after adolescence. Lower levels of physical activity have been documented previously for the lodge group in Amboseli [Altmann & Muruthi, 1988; Muruthi et al., 1991]. Similar observations have been made for baboons at Gilgil, Kenya [Forthman-Quick & Demment, 1988].

The differences among groups probably were not attributable to genetic differences; at each site lodge and wild-foraging groups form a single genetic population, have adjacent ranges, and males transfer between the two types of groups.

Therefore, the changes in cholesterol profiles in the lodge groups compared to the males of the wild-foraging groups are likely due to diet and activity levels. This increase in VLDL+LDL-C concentrations in lodge males, as well as the increase in HDL-C in male and female lodge animals at both sites is typical of the significant increase in HDL-C for baboons in captivity fed diets high in cholesterol and saturated fats [McGill et al., 1981a]. The relative hyperinsulinemia of the lodge groups also may have contributed to the differing cholesterol levels. Of note, the insulin and cholesterol elevations in the lodge groups were not extreme, as compared to captive primates on atherogenic diets.

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