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RESEARCH ARTICLE

High-Fiber Diet Promotes Weight Loss and Affects Maternal Behavior in Vervet Monkeys

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The dramatic increase in obesity in western societies has shifted the emphasis in nutrition research from the problems of undernutrition to the adverse consequences of being overweight. As with humans, Old World monkeys are at increased risk for type II diabetes and other chronic diseases when they gain excessive weight. To prevent overweight and obesity, promote animal health, and provide a more natural level of fiber in the diet, the standard commercial monkey chow diet at a vervet monkey breeding colony was changed to a higher fiber formulation in 2004. The new diet was also higher in protein and lower in carbohydrate and energy density than the standard diet. Because maternal behavior is known to be sensitive to differences in resource availability, data on weight and mother–infant interactions for 147 mothers with 279 infants born from 2000 through 2006 were assessed for effects of the diet change. The results showed that, even though food was provided ad libitum, the mean body weight of breeding females was 10% lower after the transition to the high-fiber diet. Behaviorally, mothers on the high-fiber diet were significantly more rejecting to their infants, and their infants had to play a greater role in maintaining ventral contact in the first few months of their lives. The effects of the diet change on maternal rejection were significantly related to the mother's body weight, with lower-weight mothers scoring higher in maternal rejection. These results demonstrate that maternal behavior is responsive to changes in maternal condition, and that beneficial changes in the diet may have unintended consequences on behavior. Am. J. Primatol. 71:1–8, 2009.

Key words: diet; maternal behavior; weight loss; fiber

INTRODUCTION

Obesity has become a problem of epidemic proportion in Western society, with evidence that excess weight increases risk for type II diabetes, cardiovascular disease, and early mortality [Lewis et al., 2009]. This has led to considerable interest in the ideal weight loss diet and the effects of dietary components on health [Anderson et al., 2009; Brehm & D'Alessio, 2008; Gaesser, 2007]. Recent results have demonstrated the benefits of long-term caloric restriction in delaying age-related decline and disease onset in nonhuman primates [Colman et al., 2009; Ingram et al., 2007]. More moderate dietary adjustments by increasing dietary fiber have also been shown to promote weight loss and reduce risk of chronic disease in humans [Anderson et al., 2009; Howarth et al., 2001]. For example, Stubbs et al. [1998] covertly modified the energy density of the diet and found that people spontaneously lost weight on a high-fiber, low-fat diet compared with diets with higher energy density. In Western populations, individuals who eat a higher-fiber diet are at lower risk for hypertension, stroke, cardiovascular disease, diabetes, and obesity [reviewed in Anderson et al., 2009].

The standard primate laboratory chow diet is designed to provide all of the nutrients necessary for Old World monkey health and reproduction, but when fed an ad libitum chow diet, some Old World monkeys gain excessive weight and a small percentage develop type II diabetes [Hansen, 1989; Wagner et al., 2001]. The same trend has been observed at the Vervet Research Colony (VRC), a multigenerational breeding colony for socially housed vervet

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monkeys (*Chlorocebus aethiops sabaeus*). Vervets born and reared in the colony tend to be heavier than wild-caught vervets, and approximately 3% of adults develop hyperglycemia [Horrocks, 1986; Kavanagh et al., 2007]. In an attempt to reduce the risk of diabetes and promote animal health at the VRC, the standard laboratory chow diet was replaced with a new diet that contained a more natural level of dietary fiber and a lower energy density in 2004. The high-fiber diet was also higher in protein and lower in carbohydrates than the standard diet.

This article reports on the effects of the high-fiber diet on weight regulation and maternal behavior of breeding females at the VRC. Investment in reproduction and offspring care is known to be sensitive to the availability of resources and an adequate food supply for female mammals [Clutton Brock, 1991]. Nutrient requirements for pregnancy and lactation include an increase in calories, protein, and calcium above the levels required for non-reproducing females [Picciano, 2003; Speakman, 2008]. Parental investment theory postulates that females must balance their own metabolic needs with those of their current and future offspring in allocating energy for lactation and infant care [Trivers, 1974]. This balance will depend, to a certain extent, on the condition of the mother, local resource availability, and the mother's work load [Hauser & Fairbanks, 1988; Lee, 1987; Rosenblum & Andrews, 1994]. Under suboptimal conditions, mothers would be expected to delay reproduction and/or reduce investment in current offspring [Lee et al., 1991].

Earlier research at the VRC has demonstrated that interbirth interval and the quality of maternal care is influenced by the mother's condition, environmental risk factors, and by investment in earlier offspring [Fairbanks & McGuire, 1987, 1995; Fairbanks, 1988, 1996]. The data presented here show that maternal behavior is also influenced by relatively subtle changes in diet composition. Breeding females lost weight after the transition from the standard diet to a high-fiber diet, and that weight loss affected the quality of maternal care.

METHODS

Subjects

Subjects for this analysis were vervet monkeys, *Chlorocebus aethiops sabaeus*, residing at the VRC, a facility jointly managed by UCLA and the Department of Veterans Affairs Greater Los Angeles Healthcare System. The sample included 147 mothers with 279 infants (148 male, 131 female) born from 2000 through 2006 at the colony. The mothers and infants lived in 16 stable matrilineal social groups, housed in large outdoor enclosures. Mothers were colony-born, mother-reared, and between 3 and 14 years of age in the year of their infant's birth (mean age = 8.0). Maternal parity varied from 1 to 11 (mean = 3.8). Commercial chow was provided once per day in the morning in sufficient quantities to ensure that food was available throughout the day. The chow diet was supplemented with fresh fruits, vegetables, and forage 2–3 days per week.

All individuals were captured once a year between December and March for weighing, veterinary examination, TB testing, and sample collection. This is a time of year when most females are cycling or in the first few months of pregnancy. Gestation for vervets is approximately 165 days [Rowell, 1970]. The birth season at the VRC peaks in July–August, and 75% of infants in this study were born between June and September.

Diet Composition

The composition of the two diets is shown in Table I. The initial diet (Purina LabDiet Monkey Diet 5038) is a commonly used diet for laboratory Old World monkeys. It contains 69% of calories from carbohydrate (primarily from corn and wheat), 18% of calories from protein (primarily soy), and 13% of calories from fat, with 5% of weight as crude fiber. This diet is referred to here as the ''standard diet.'' The transition to the new diet was initiated on April 19, 2004, by mixing 10% of the new diet with 90% of the standard diet. The proportion of the new diet was increased weekly to 100% by the end of June, 2004. The new diet (Purina LabDiet Fiber-Balanced Monkey Diet 5052) had more than twice as much fiber (primarily from soybean hulls), was higher in protein, and somewhat lower in carbohydrates. The amount of fat was similar, but the source was changed from primarily animal fat to vegetable oil. This diet is referred to here as the ''high-fiber'' diet.

Mothers of infants born in 2000–2003 were fed the standard diet throughout gestation and lactation ($n = 88$ male, 91 female infants). The 2004 birth cohort was transitional: all infants were conceived on the standard diet and mothers were exposed to an increasing percentage of the high-fiber diet at some point during gestation or lactation ($n = 33$ male, 20 female infants). Mothers of infants born in 2005–2006 were fed the high-fiber diet from conception through lactation ($n = 27$ male, 20 female infants). Mothers in the three diet groups did not differ significantly in mean age (Anova: $F = 0.82$,

TABLE I. Composition of Standard and High-Fiber Diets

Composition	Standard	High-fiber
Fiber (crude)	5%	12%
Calories from protein	18%	27%
Fat	13%	15%
Carbohydrate	69%	58%
Metabolizable energy, kcal/g	3.22	2.87

2,276, $P = 0.44$), parity (Anova: $F = 2.50$, 2,276, $P = 0.08$), or infant sex (Chi square: $\chi^2 = 3.26$, df = 2, $P = 0.20$). Other than the diet composition, there were no significant changes in animal care staff, animal husbandry, or colony management practices during the time periods considered here.

Behavioral Data Collection

Mother infant observations were focused on the second and third month of life. This is a time when infants are in ventral contact with their mothers about 50% of the time, when infants are actively leaving and returning to the mother, and when individual differences in maternal protectiveness are most evident [Fairbanks, 1988]. Weaning usually does not begin until the infant is older, at 4–5 months of age [Fairbanks & McGuire, 1987].

Each mother–infant dyad was observed for six 5-min focal animal observations and 12 instantaneous point samples per week from week 5 through week 12 after birth, with half of the observations in the morning and half in the afternoon. Coded behaviors between mothers and infants during focal animal samples included: approach (mother or infant moves from beyond to within 1-m); leave (mother or infant moves from within to beyond 1-m); make ventral contact (mother or infant initiates ventral contact); break ventral contact (mother or infant terminates ventral contact); restrain (mother manually prevents infant from leaving); rejection (mother prevents infant from making contact or nursing by threatening, biting, or pushing the infant away); and groom (mother grooms infant's fur). Incidence of each of the above behaviors was transformed to frequency per hour of observation. Mother–infant contact was measured as the percentage of instantaneous point samples that the infant was in ventral contact with the mother. This data collection system has been used in our laboratory for 3 decades and has been shown to be effective in recording effects of social, environmental, and individual influences on maternal behavior and infant development [reviewed in Fairbanks, 1996].

The research protocol was reviewed and approved annually by the UCLA Animal Research Committee and by the Department of Veterans Affairs Greater Los Angeles Healthcare System Animal Care and Use Committee. All procedures adhered to USDA guidelines for the care and use of nonhuman primates.

Data Analysis

The general analysis strategy treated each mother–infant dyad as an independent case, even though some mothers were repeated across infants and across diet groups. One-way analysis of variance was conducted across the three diet groups (standard, transition, high-fiber) with significant main effects followed by Duncan's multiple range test to differentiate differences between groups. To insure that the main findings also held within subjects, a secondary analysis was performed for the 18 mothers with data for one or more infants under both the standard and high-fiber diet conditions using paired *t*-tests. Pearson product moment correlations (r) and partial correlations were used to assess linear relationships among variables.

Principal components analysis was used to reduce the seven coded maternal behaviors to independent dimensions before analysis, with factor scores used as the primary dependent variables. For factors that showed significant diet effects, the contribution of individual behaviors was then evaluated. The infant's role in maintaining contact was calculated as follows: Infant Contact Index = infant makes contact/(infant makes contact + mother makes contact).

Four mother–infant dyads with behavioral data were excluded from this study owing to adoption, infant illness, or clinical intervention during the behavioral data collection period. Three of these were in the Standard diet Group and one in the Transitional Group.

RESULTS

Effect of Diet on Body Weight

Figure 1 shows the mean (±SE) body weight for mothers in this sample, measured at the beginning of the year, by diet group. There was a significant reduction in mean female body weight in the years following the shift to the high-fiber diet (Anova: $F = 7.46$, df = 2,276, $P < 0.001$). On the standard diet, the weight of breeding females in this sample averaged 5.1 kg (range: 3.1–8.8 kg). Because weight was measured at the beginning of the year before the diet change was initiated, the mothers in the

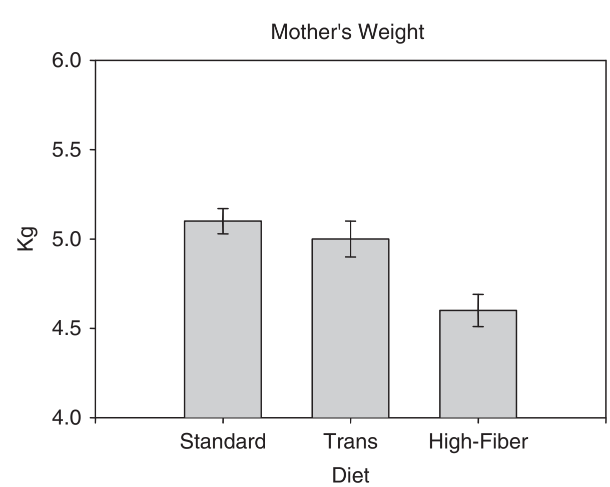

Fig. 1. Mean (±SE) weight at the beginning of the year for vervet mothers on the standard, transitional, and high-fiber diets.

transition diet group did not differ from mothers in the standard diet group. Following the diet change, mothers in the high fiber diet group had a mean weight of 4.6 kg (3.1–6.2 kg), which was significantly less than the weights for mothers in the standard diet and transition diet groups ($P<0.05$).

Other than weight loss, the diet change did not produce any measurable negative effects on morbidity or mortality for adult females and infants. The number of adult females in this age group (3–14 years) who died or were euthanized for clinical reasons continued to be low following the diet change (Standard: 1.8%; Transition: 1.2%; High-fiber: 1.3%), and there were no clinical cases of diarrhea or other illness associated with the diet change in the medical records. There were also no negative effects of the new diet on neonatal mortality, including abortion, stillbirth, and neonatal death (Standard: 22.8%; Transition: 15.8%; New: 20.5%).

Effects of Diet on Maternal Behavior

Principle components analysis of maternal behavior produced two factors with eigenvalues >1.2. The first factor (Table II), labeled Maternal Rejection, loads heavily on mother breaks contact, mother leaves, and mother rejects infant. The second factor, labeled Maternal Protectiveness, loads positively on mother makes contact, mother restrains, mother approaches, and mother grooms infant.

TABLE II. Principle Components Analysis of Maternal Behavior Toward Infants

Behavior: mother to infant	Factor 1: Rejection	Factor 2: Protectiveness
Reject	0.777	0.150
Break ventral contact	0.792	0.251
Leave	0.750	0.204
Restrain	−0.533	0.677
Make ventral contact	−0.301	0.858
Approach	0.386	0.497
Groom	−0.095	0.440

Figure 2 shows the mean (±SE) for the two maternal behavior factors by the three diet groups. As the figure indicates, the diet change had a major effect on maternal rejection (Anova: $F=6.41$, df = 2,276, $P<0.01$). Maternal Rejection Factor scores in the transition year did not differ from those on the standard diet, but mothers who went through all of gestation and lactation on the high-fiber diet scored significantly higher on the Maternal Rejection Factor compared with mothers on the standard and transitional diet ($P<0.01$). In contrast, the Maternal Protectiveness Factor scores did not differ significantly by diet group ($F=1.50$, df = 2,276, $P=0.23$).

Table III shows the means (±SE) for the individual maternal behaviors that went into the Maternal Rejection Factor by diet group. There were significant diet effects for mother rejects and mother leaves. The effects of diet on the Maternal Rejection Factor were not influenced by including infant sex, mother's age, or mother's parity in the Anova model (Diet: $F=5.98$, df = 2,271, $P<0.01$; Infant sex, Mother's age, Mother's parity: all P's >0.50).

Within-Mother Analysis of Diet Change

To determine whether the above effects on maternal rejection were true within-mother as well as between mothers, analysis of diet effects were rerun using only mothers with infants in both diet conditions and a within-subjects design. Eighteen mothers observed with 2–6 infants each were included in this analysis. Mean Maternal Rejection Factor score for infants on the standard diet is compared with mean Maternal Rejection score on the

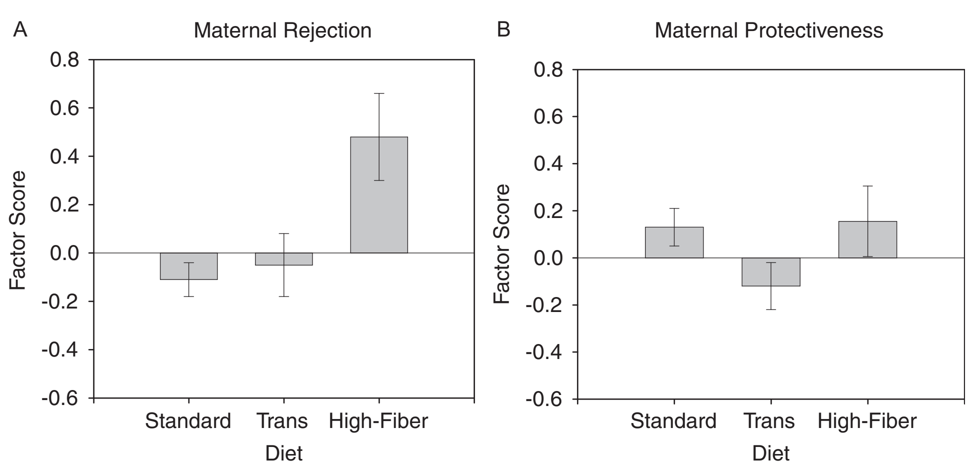

Fig. 2. (**A**) Mean (±SE) Maternal Rejection Factor score by diet group and (**B**) Mean (±SE) Maternal Protectiveness Factor score by diet group.

TABLE III. Mean Frequency Per Hour (+SE) and ANOVA Results for Individual Behaviors in Maternal Rejection Factor by Diet Group

Maternal behavior	Standard	Transitional	High-fiber	F	P
Reject	0.3 (+0.04)	0.3 (+0.1)	0.6 (+0.1)	5.94	<0.01
Break ventral contact	0.4 (+0.1)	0.3 (+0.1)	0.5 (+0.1)	1.50	0.22
Leave	3.4 (+0.2)	3.7 (+0.3)	4.9 (+0.4)	6.69	<0.01

high-fiber diet in Figure 3. Fifteen of the 18 mothers were more rejecting to infants conceived and born on the high-fiber diet than to their infants conceived and born on the standard diet. The average Maternal Rejection score increased +0.77 SD on the high-fiber diet for mothers with infants under both diet conditions (Paired: $t = 3.00$, df = 17, $P < 0.01$).

Relationship of Maternal Behavior to Mother's Weight

For females on the standard diet, the mother's weight at the beginning of the year was not related to her Maternal Rejection Factor scores ($r = 0.08$, $N = 177$, $P = 0.31$). In contrast, after the diet change, there were significant negative correlations between mother's body weight at the beginning of the year and Maternal Rejection scores (Transition: $r = -0.30$, $N = 53$, $P < 0.05$; High-fiber: $r = -0.37$, $N = 47$, $P < 0.01$). Mothers who weighed the least were more likely to be rejecting to their infants during the first few months of life (Fig. 4).

Because maternal weight increases with age and parity, it was important to determine if these demographic variables were influencing the above relationship. The results indicated that neither mother's age nor parity were significantly correlated with Maternal Rejection scores in this sample (Mother's age: Standard: $r = -0.09$, Transition: $r = -0.06$, High-fiber: $r = -0.02$, all P's > 0.20; Parity: Standard: $r = -0.07$, Transition: $r = 0.02$, High-fiber: $r = -0.13$, all P's > 0.30). The relationship between mother's weight and Maternal Rejection in the transition and high-fiber diet groups held independent of maternal age and parity (Transition: partial $r = -0.30$, $N = 53$, $P < 0.05$; High-fiber: partial $r = -0.50$, $N = 47$, $P = 0.001$).

Infant Role in Maintaining Ventral Contact

The role of the infant in maintaining ventral contact with the mother also changed with the maternal diet. There was a significant effect of diet condition on the Infant Contact Index scores ($F = 13.4$, df = 2,276, $P < 0.001$; Fig. 5A). On the standard diet, infants initiated less than half of the mother–infant ventral contacts. The infants' role in contact initiation increased during the diet transition year and continued to increase on the high-fiber diet to 60% of the ventral contacts.

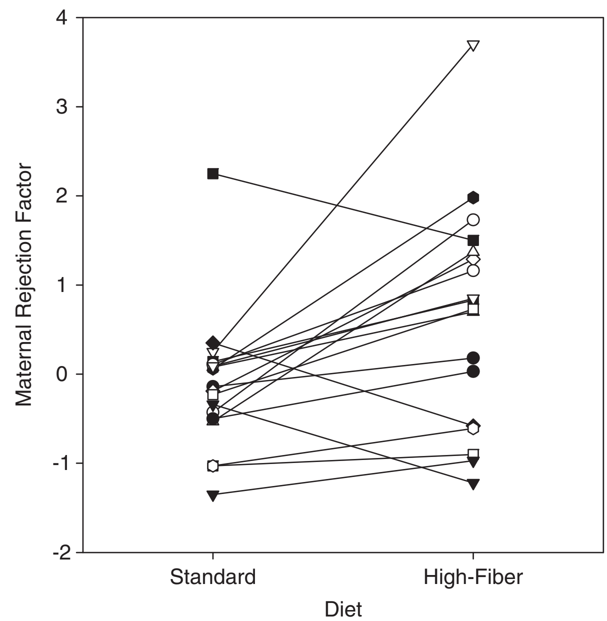

Fig. 3. Within-mother changes in Maternal Rejection Factor score on standard and high-fiber diet.

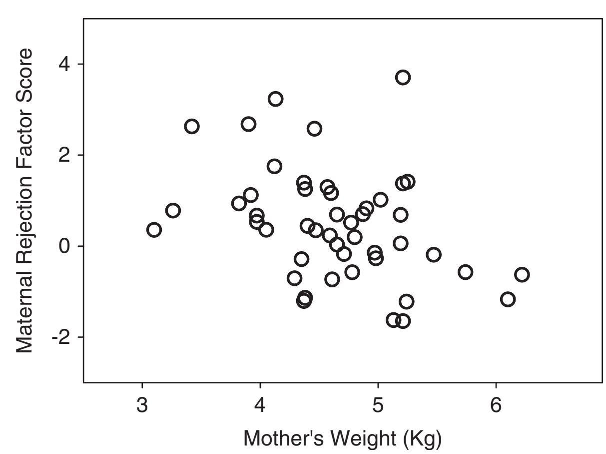

Fig. 4. Mother's weight by Maternal Rejection Factor score for mothers on the high-fiber diet.

The increasing role of the infants in maintaining contact counteracted the mothers' attempts to reduce contact. More rejecting mothers on the high-fiber diet spent significantly less time in ventral contact with their infants ($r = -0.51$, $N = 47$,

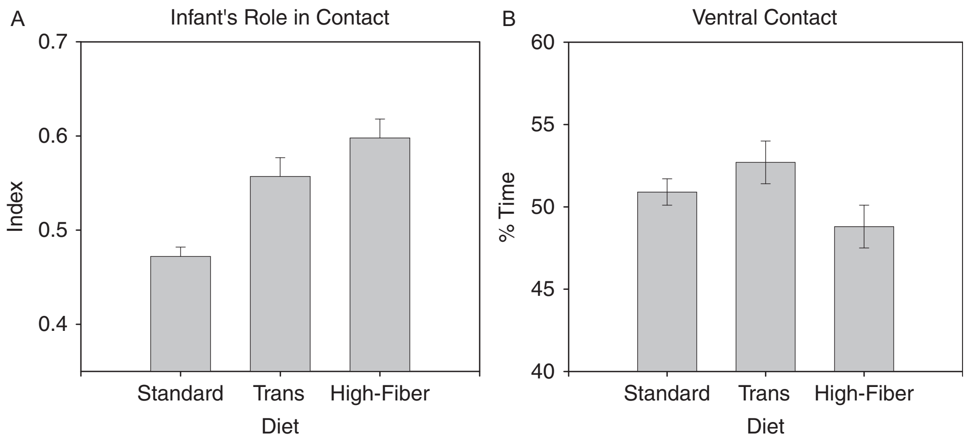

Fig. 5. (**A**) Mean (±SE) Infant Contact Index score by diet group and (**B**) Mean (±SE) percentage time in ventral contact for mother–infant dyads by diet group.

$P<0.001$), but Infant Contact Index scores increased as Maternal Rejection scores increased ($r=0.47$, $N=47$, $P<0.001$). This resulted in a slight but not significant reduction in mother–infant ventral contact time on the high-fiber diet ($F=1.96$, df = 2,276, $P=0.14$), shown in Figure 5B.

DISCUSSION

Increasing the amount of fiber and protein in the diet led to a spontaneous weight loss for vervet monkey breeding females, a result that is consistent with findings from human studies on the effects of fiber and protein on body weight. Research has shown that dietary fiber increases satiety, slows gastric emptying, and decreases post-meal hunger, thus reducing caloric intake, and fiber also has secondary effects of interfering with nutrient absorption and increasing caloric excretion [reviewed in Howarth et al., 2001]. Several randomized clinical trials have demonstrated the effectiveness of adding fiber to the diet in promoting weight loss in overweight people [Anderson et al., 2009; Yao & Roberts, 2001]. Protein content has also been associated with increases in satiety and weight loss in human studies [Berenshaw et al., 2008; Meckling & Sherfey, 2007]. Results from the VRC demonstrate that this type of diet-induced weight loss does not rely on intention or weight loss objectives.

The high-fiber diet reduced female weight to 4.6 kg, a level that is still heavier than an adult female of this species in the wild [Caribbean vervet: Mean = 3.3 kg; Horrocks, 1986]. There was also no indication that the diet change increased morbidity or mortality for adult females or infants at the VRC. Nevertheless, the weight loss diet led mothers to limit and control their young infants' access to the nipple. The fact that there was a direct relationship between the mother's weight and her behavior supports the idea that weight loss was an important intermediary between the diet components and maternal behavior, and reinforces the view that maternal behavior is highly sensitive to maternal condition and resource availability.

An earlier comparison of vervet mothers from the VRC with females in wild groups at Amboseli National Park in Kenya showed that changes in mother–infant contact over time followed a relatively invariant developmental trajectory, but mother–infant interactions differed [Hauser & Fairbanks, 1988]. Mothers in the field were more rejecting and less protective than mothers in the captive social groups, and infants in the field played a greater role in maintaining mother–infant contact. The diet change reported here led the captive mothers to more closely resemble vervet mothers in the field in both body weight, and in maternal and infant behavior. This suggests that the level of maternal rejection seen in the high-fiber diet is within the normal range, and that well-fed captive mothers on the standard diet may be unusually indulgent. Infants were able to compensate for their mothers' behavior and maintain comparable and appropriate levels of mother–infant contact, in the field and on both captive diets.

The results of this study demonstrate that a relatively subtle change in maternal diet can have significant effects on the mother–infant relationship for vervet monkeys. This type of variation in maternal behavior has been shown to have long-term consequences for offspring growth, behavioral development, stress-reactivity, and adult mothering behavior in nonhuman primates [Fairbanks, 1989, 1996; Maestripieri, 2009]. Similar effects of variation in maternal care in rodents have recently been shown to affect epigenetic programming of offspring via DNA methylation [Champagne & Curley, 2009; McGowan et al., 2008]. This suggests the possibility that diet-induced changes in maternal behavior could produce measurable changes in gene expression of nonhuman primates by similar mechanisms.

It should be noted that this is not the first study to suggest that a ''healthy'' nutritional context might unexpectedly or adversely affect behavior. Controlled studies have shown that male cynomolgus monkeys (*Macaca fascicularis*) consuming a diet relatively low in fat and cholesterol are more aggressive and less affiliative than counterparts consuming diets high in fat and cholesterol [Kaplan et al., 1991, 1994]. One of these studies focused on juveniles and showed further that consumption of a diet low in fat and cholesterol was accompanied by reduced central nervous system serotonergic activity as well as increased aggression [Fontenot et al., 1996]. By substituting vegetable for animal fat, the high-fiber diet used in this study significantly reduced cholesterol levels in VRC females (manuscript in preparation). This reduction in cholesterol may have contributed, along with the reduction in body weight, to the observed increases in maternal rejection.

In conclusion, maintenance of a healthy body weight has important implications for health and longevity in humans and nonhuman animals, and the search for effective weight loss diets is an important part of our nation's response to the current epidemic of obesity and obesity-related diseases. The results of this study suggest that the solution will not be simple, and there are likely to be unintended behavioral and mood effects of otherwise beneficial changes in diet and body weight.

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