Arboreal Adaptations of Body Fat in Wild Toque Macaques (*Macaca sinica*) and the Evolution of Adiposity in Primates

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ABSTRACT There is a paucity of information on body composition and fat patterning in wild nonhuman primates. Dissected adipose tissue from wild toque macaques (Macaca sinica) (WTM), feeding on a natural diet, accounted for 2.1% of body weight. This was far less than fatness reported for nonhuman primates raised in captivity or for contemporary humans. In WTM, fatness increased with age and diet richness, but did not differ by sex. In WTM (none of which were obese) intra-abdominal fat filled first, and "excess" fat was stored peripherally in a ratio of about 6:1. Intermuscular fat was minimal (0.1%). The superficial paunch held <15% of subcutaneous fat weight in contrast to its much larger proportions in obese humans and captive monkeys where most added fat accumulates subcutaneously. With increasing total adipos-

Various adaptations for arboreal life in mammals have been reviewed, particularly among nonhuman primates (Cartmill, 1972, 1992; Clutton-Brock and Harvey, 1977; Garber, 2011; Rosenberger, 2011; Zihlman et al., 2011a,b). These considerations, however, have overlooked the role of adipose tissue, despite the fact that all mammals, including humans, share a typical anatomical structure and distribution of adipose tissue, and homologous fat depots across species exhibit a range of adaptations to different ecologies and life-histories (Pond, 1978, 2012; Eaton et al., 1988).

Fatness in nonhuman primates, on the other hand, has been studied extensively, but almost exclusively among captive or food-provisioned subjects and often with a focus on obesity or health (Kaufman et al., 2007; Shigetoh et al., 2009; Shively et al. 2009). Individual differences in body fat have been linked to a number of variables: for example, gender and age (Coelho et al., 1984; Enzi et al., 1986; Schwartz and Kemnitz, 1992; Saad et al., 1997); genetics (Bouchard, 1997; Comuzzie et al., 2003; Kavanagh et al., 2007; Loos and Bouchard, 2008); reproduction (Campbell et al., 2004); levels of activity (Stern, 1984; Altmann et al., 1993; Jayo et al., 1993); environmental and seasonal variations (Muroyama et al., 2006; Garcia et al., 2010; Leonard and Katzmarzyk, 2010); behavioral stress and disease (Després and Lemieux, 2006; Kyrou and Tsigos, 2008); and culture and race in humans (Lindgärde et al., 2004; Moore et al., 2004). These studies made clear that adiposity touches many important aspects of primate biology.

ity, accumulating fat shifted in its distribution among eight different main internal and peripheral deposit areas—consistent with maintaining body balance and a low center of gravity. The available data suggest that, in arboreal primates, adaptations for agile locomotion and terminal branch feeding set constraints on the quantity and distribution of fat. The absence of a higher percentage of body fat in females and neonates (as are typical of humans) suggests that arboreal adaptations preclude the development of fat-dependent, large-brained infants and the adipose-rich mothers needed to sustain them. The lifestyle and body composition of wild primates represent a more appropriate model for early human foragers than well-fed captive monkeys do. Am J Phys Anthropol 152:333–344, 2013. © 2013 Wiley Periodicals, Inc.

From the point of view of primate evolution it is desirable to understand adiposity in ecological and social settings that most closely resemble ancestral conditions, such as might be found in contemporary nonhuman primates living in their natural environments (Foley, 1993; Bellisari, 2008). To this end, the study aims were to measure the amount and anatomical distribution of adipose tissue in a wild arboreal anthropoid primate, the toque macaque (Macaca sinica) of Sri Lanka, to compare this information with that from other studies and to relate it to the evolution of adiposity in primates. Hypotheses were considered that relate adipose patterning to the following: (1) food stress; (2) age, sex and differences in energy balance; (3) thermal insulation; (4) anatomical adaptation for arboreal life; and (5) its pivotal role in the evolution of hominids.

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METHODS AND MATERIALS

Study population

Toque macaques are typical above-the-branch primate quadrupeds (Grand, 1984) that use all levels of the forest canopy, and forage on a diversity of ripe fruit, young leaves and insects (Hladik and Hladik, 1972). The macaques living in the Nature Sanctuary and Archeological Reserve at Polonnaruwa, Sri Lanka, have been studied continuously over four decades (1968–2013). These macaques' natural dry evergreen forest habitat, and aspects of their demography, ecology, behavior, physical development, and epidemiology have been described earlier (Dittus, 1977; Cheverud et al., 1992; Ekanayake et al., 2007).

The standing population included over 1,000 known macaques distributed among 33 independent social groups. All macaques were individually identified by their natural markings and tattoos (Dittus and Thorington, 1981), and their life-histories were monitored from birth to death (Dittus, 2004). The ages of all individuals in this sample were based on known birth-dates. The 22 macaques sampled for necropsy originated from 11 (of the 33) different social groups and involved 12 females (age range 0.01–31.6 years) and 10 males (age range 1.1–21.4 years). The causes of death for these specimens were as follows: natural (2), conspecific aggression (4), dog bite (1), road kill (12), electrocution (2) and uncertain (1).

The methods of field observation and measurement comply with all institutional and governmental regulations regarding the ethical treatment of research subjects.

Morphometric measurement

An earlier study by Cheverud and Dittus (1992) had described the method for somatometric measurements of live-trapped (and released) macaques at Polonnaruwa. The crown-rump length refers to the distance between the vertex (top of head) and the caudal tip of the ischial tuberosities, and was measured using a caliper. This length, sometimes referred to as "sitting height," was used as a reference denominator because most dissected fat occurred in this body trunk region.

Fat dissection and weighing

Several methods have been used to measure body fat in primates, including skinfold thickness (Durnin and Womersley, 1974; Lohman, 1981), electrical conductivity (Sutcliffe and Smith, 1995; Wirsing et al., 2002), body water (Lewis et al., 1986; Garcia et al., 2004), and others. These approaches have limitations insofar as they are proxies for estimating total body fat, or make only partial distinctions among deposition sites, for example, using computed tomography (Enzi et al., 1986). They are also challenging to conduct under field conditions. The most appropriate method for present aims involved dissection (Pond and Mattacks, 1987). Specimens were weighed and measured soon after death before rigor mortis had set in, and most were dissected on the same day, a few were kept frozen (wrapped in polythene against dehydration) and thawed within 1-4 days for necropsy.

Total body weights were recorded from a spring scale (Salter, Thermoscale). Dissected body fat was weighed on a more sensitive scale (Ohaus, Scout Electronic Balance) accurate to one-hundredth of a gram. Dissected fat was sorted and weighed according to different fat depots in the three major body regions: subcutaneous, intermuscular and body cavity. Subcutaneous fat included all that present between the skin and immediate underlying muscle. Intermuscular fat was found among muscle bands. Fat of the body cavity included all that found among the omentum and mesentery surrounding the internal organs and along the dorsal inner wall. For one individual, fat from different regions had been accidently combined during weighing, and that sample was omitted where distinctions by body region were made.

Expressions of fat weight and statistical analyses

An animal's absolute quantity of fat can be expected to differ with body size. To adjust for this effect, the weight of dissected fat was expressed per unit body size. The latter was estimated as the cubic function of crown-rump body length (dm^3) . Fat weight was expressed as gm/dm³, and was referred to as the fat weight index (FWI). For statistical comparisons the FWI was preferred to the simpler estimate of "fatness," that is, fat weight as a percentage of total body weight, where the numerator is not independent of the denominator. Also, total body weight includes variable weights of stomach and intestinal contents that can be problematic to estimate.

The linear relation between age and fat weight (FWI) was tested for constant variance and for normality using the Shapiro–Wilk test, applying non-linear models of regression. The software packages of SAS (SAS Institute, Cary, NC, 2002) and SigmaPlot® v. 11.0 (Systat Software, Inc., Chicago, Illinois) were used for analysis. The Mann–Whitney Rank Sum Test was applied where distributions of FWI data failed tests for normality and equal variance.

RESULTS

The proportion of fat weight to total body weight

Toque macagues in their natural environment normally appeared lean or thin on visual inspection (Berman and Schwartz, 1988), but some of the adult males were hefty with muscles. Obese monkeys, with folds of fat draping from their bodies, as are common in captive or provisioned environments, were absent from wild toque macaques (n > 5,000 observed). The total body weights and skeletal proportions of the necropsied toque macaques (n = 22) fell well within the range of a much larger sample (n = 274) of live weights and somatometric measures taken earlier from this same population, for which Cheverud et al. (1992) had determined that most variation in body weight was due to differences in skeletal size and muscle mass. In the present study, dissections of the 22 carcasses indicated that total fat weight made up from 0.0 to 11.0% of total body weight, the mean proportion of body fat was $3.2\% \pm 2.5\%$ (Table 1), and the median was 2.5%.

The relation between total fat weight, age and sex

The mean fat weights of males $(1.71 \pm 0.64 \text{ gm/dm}^3)$ and females $(1.60 \pm 1.95 \text{ gm/dm}^3)$ of all ages did not differ significantly (Mann–Whitney U-test, NS), nor did they differ for males $(1.91 \pm 0.83 \text{ gm/dm}^3)$ and females $(2.32 \pm 2.63 \text{ gm/dm}^3)$ older than 5.5 years (*t* test =

FAT ADAPTATIONS IN A WILD ARBOREAL PRIMATE

	at Polonnar	uwa, Sri Lanka			
Measure	Body wt (kg); mean ± St Dev (range)	Fat wt (gm); mean ± St Dev (range)	Fat wt as % of total body weight		
Females $(n = 12)$	$2.37 \pm 1.25 \ (0.26 - 4.83)$				
Subcutaneous fat		$42.0 \pm 90.8 \; (0.0 - 326.0)$	$1.2 \pm 1.8 \; (0.0 - 6.7)$		
Intermuscular fat		$3.4 \pm 3.7 \ (0.0 - 10.2)$	$0.1 \pm 0.1 (0.0-0.3)$		
Intra-abdominal fat		$57.3 \pm 86.9 \ (0.0-315.6)$	$1.9 \pm 2.3 \ (0.0-9.0)$		
Total fat		$101.3 \pm 146.2 \; (0.0 - 433.1)$	$3.2 \pm 3.3 (0.0 - 11.0)$		
Males $(n = 10)$	$3.46 \pm 1.55 \ (1.22 - 5.19)$				
Subcutaneous fat		$29.3 \pm 22.6 \ (10.1 - 81.2)$	$0.8 \pm 0.4 \ (0.4 - 1.6)$		
Intermuscular fat		$4.8 \pm 3.1 \ (0.9 - 8.9)$	$0.1 \pm 0.1 (0.0-0.4)$		
Intra-abdominal fat		$81.2 \pm 59.1 \ (17.0 - 184.0)$	$2.2 \pm 0.9 \; (1.4 - 3.6)$		
Total fat		1149 + 797(270 - 2667)	$31 \pm 11(20 - 52)$		

TABLE 1. Comparisons of body weights, total fat weights, and percentage of fatness among wild toque macaques (Macaca sinica) at Polonnaruwa, Sri Lanka



Fig. 1. The total weight of dissectible adipose tissue in wild toque macaques in relation to age.

0.337, df = 9, P = 0.744). Therefore, fat weights were combined by sex in further analyses.

There was a positive relation between total fat weight (FWI) and age (Fig. 1). An ANOVA using FWI as the dependent variable and age and sex as the two independent variables indicated a significant difference by age (F = 15.33, P < 0.001) but not by sex (F = 0.91, P = 0.352), although the residuals in females were greater than those in males. Only one neonate (age 0.01 year) was necropsied, but the discovery of zero dissectible body fat was supported by numerous visual observations of other neonates as well as by estimates of their body fat using skinfold thickness (Dittus, unpublished).

The influence of diet on total fat weight

The 22 macaques sampled for necropsy originated from nine social groups that fed predominantly on natural forest foods (>90% of foraging time), and three groups that supplemented their natural diet through regular access (>20% of foraging time) to human garbage from houses or temples on the periphery of the study area (Dittus, 2012). Visual comparisons suggested that some of these garbage-eating macaques were fatter than those whose diet was more natural.

Individual macaques whose diet comprised mostly natural forest foods (n = 13) had a mean of 2.1% body fat whereas those with access to garbage (n = 9) had a mean of 4.8% body fat. The mean FWI of the former set $(0.97 \pm 0.54 \text{ gm/dm}^3)$ was significantly less (P < 0.01) than that of the latter (2.64 \pm 1.85 gm/dm³). This difference was accentuated among adults, where macaques feeding on garbage had three to four times significantly (P < 0.03) more fat weight than those restricted to a natural diet (Table 2).

The distribution of dissected fat depots by body region

Fat weight was compared according to its percentage distribution among the three main fatty regions of the body: subcutaneous (23.3%), intermuscular (3.8%), and body cavity (72.8%) (Fig. 2).

Inside the body cavity, 74.5% of the adipose tissue was distributed among the omentum and mesentery holding the intestines and other organs. Fat depots along the dorsal wall of the body cavity comprised 17.5% surrounding the kidneys, and 4.2% toward the pelvic area along the spine. Small amounts (4%) were found in the region of the heart and lungs (Fig. 3).

The largest proportions of subcutaneous fat lay in the deeply recessed pockets of the groin (32.2%) and axillas (20.6%) (Fig. 4). The abdomen (paunch) contributed 14.0%, with a greater proportion of fat (10.2%) lying anterior to the navel than posterior to it (3.8%). The hump (upper back and neck) held 12.3% of subcutaneous fat, and smaller depots occurred on the limbs (11.0%), lower back (5.3%), chest (3.6%), and throat (0.9%). There was virtually no dissectible subcutaneous fat on the head (<0.1\%), limbs distal to the elbows or knees, and tail 1–2 cm distal to its base. The bulk (79.1%) of subcutaneous fat was balanced between anterior (32.9%) and posterior depots (groin, 32.2%) of the trunk's long axis, with a smaller concentration midway on the ventral paunch (14.0%).

The relation between subcutaneous fat and intra-abdominal fat

The weights of intra-abdominal and subcutaneous fat depots were consistent in their differences and highly correlated across 21 individuals (Pearson's product-moment correlation coefficient, r = 0.826, df = 19, P < 0.0001). Using visceral fat weight as the independent regression variable (Fig. 5), there was a significant increase of 1 gm/dm³ of subcutaneous fat for every 6 gm/dm³ increase in intra-abdominal fat ($r_{adj}^2 = 0.455$, F = 17.727, P < 0.001). Relating this to diet, both subcutaneous and visceral fat depots were heavier in garbage feeders than in natural diet feeders, but this difference

	Fat weight as g	% of total body weight		Fat weight index (gm/dm ³)						
	Natural diet	Garbage supplemented diet	Natural diet	Garbage supplemented diet	Mann–Whitney test P					
Total fat, adults										
(age > 5.5 year)	n = 6	n = 5	n = 6	n = 5						
Mean ± SD	$2.0~\pm~1.2$	6.3 ± 3.5	0.90 ± 0.58	3.61 ± 2.02	< 0.03					
Range	(0.2 - 3.4)	(2.1 - 11.0)	(0.07 - 1.44)	(1.10-5.72)						
Total fat,										
all ages	n = 13	n = 9	n = 13	n = 9						
Mean \pm SD	2.1 ± 1.1	4.8 ± 3.2	0.97 ± 0.54	2.64 ± 1.85	< 0.01					
Range	(0.0 - 3.5)	(2.0-11.0)	(0.00 - 1.84)	(1.10-5.72)						
Subcutaneous										
fat, all ages	n = 13	n = 8	n = 13	n = 8						
Mean \pm SD	0.7 ± 0.4	0.9 ± 0.5	0.31 ± 0.20	0.48 ± 0.26	NS					
Range	(0.0 - 1.3)	(0.4 - 1.6)	(0.00-0.66)	(0.18 - 0.83)						
Intra-abdominal										
fat, all ages	n = 13	n = 8	n = 13	n = 8						
Mean \pm SD	1.3 ± 0.7	3.2 ± 2.5	0.61 ± 0.33	1.70 ± 1.31	< 0.01					
Range	(0.00–2.6) (1.4–9.0)		(0.0 - 1.07)	(0.69 - 4.65)						

TABLE 2.	Comparison	of fat	weights	by	body	region	between	toque	macaques	whose	diet	was ai	ll natural	and	those	whose	natural
diet was supplemented with garbage																	



Fig. 2. The proportional distribution of dissectible body fat among body regions in wild toque macaques.

was greater and statistically significant only for visceral fat (Table 2). These data point to a distributional bias toward greater accumulation of visceral fat than subcutaneous fat with increasing total body fat (up to 11.0% of body weight in this sample).

DISCUSSION

The primary function of white adipose tissue in vertebrates evolved as a readily deposited, slowly mobilized lipid store suitable for taking up circulatory fatty acids following rich meals and also for supporting prolonged fasts with low rates of energy expenditure (Pond, 1978, 2012; Friedman and Halaas, 1998). Adipose tissue acts as an energy buffer between environmental fluctuations in energy availability and an animal's needs to access it for daily living and reproduction. These considerations suggest the following hypotheses regarding the anatomical properties of adipose tissue of nonhuman primates in their arboreal niche and its role in primate evolution: (1) primates accumulate or lose adipose tissue in relation to

% Anatomical distribution of intra-abdominal fat



Fig. 3. The proportional distribution of adipose tissue among different anatomical areas inside the body cavity of toque macaques.

environmental food stress; (2) the development of adiposity follows differences in energy needs by age and sex; (3) adipose tissue acts as insulation against cold temperatures; (4) the amount and anatomical distribution of adipose tissue reflect constraints for arboreal locomotion and feeding; and (5) in the transition from the arboreal nonhuman primate niche to the terrestrial one in hominids, arboreal constraints on adiposity were shed and this had a profound effect on the evolution of adiposity and life-history of hominids.

Adiposity in relation to feeding ecology and life-history

Most information on primate body composition has come from primates in captivity where their activity is limited and food is provisioned liberally. Under such conditions, rhesus macaques (*Macaca mulatta*) had 9–32% body fat (Walker et al., 1984); pig-tailed macaques



Fig. 4. The proportional distribution of subcutaneous adipose tissue among different superficial anatomical areas in toque macaques.

(*M. nemestrina*) were considered normal at 9-13% body fat, and obese at 40% body fat (Walike et al., 1977); in cynomolgus macaques (*M. fascicularis*) body fat ranged from 0.6 to 27.9%; and species of lemur (Lemuridae) had 7-40% body fat (Pereira and Pond, 1995).

The obesifying life-styles of these captive animals contrasts with that of wild monkeys which forage actively for many hours (up to 80% of daytime), often on poor quality diets, and in habitats where their food supply set limits to overall population growth (Dittus, 1977, 1980, 2012). Rates of maturation for skeletal and total body size of primates in their natural habitats are considerably slower than in their well-fed counterparts under captive or semicaptive management (Altmann et al., 1977; Phillips-Conroy and Jolly, 1988; Cheverud et al., 1992). One would expect lesser fat reserves in these wild monkeys as well (Leigh, 1994). Indeed, Banks et al. (2001) found that leptin levels were three times greater in captive baboons than among wild ones in Africa. Whitten and Turner (2008) found no association between measures of adiposity and serum leptin in wild vervet monkeys (Chlorocebus aethiops) reflecting the extremely low fat storage in wild cercopithecine primates. Altmann et al. (1993) examined body fat in relation to diet among free-living baboons (P. cynocephalus) inhabiting the Amboseli National Park, Kenya. Total body fat was 23% in the baboons that fed primarily from a hotel garbage dump, considerably more than the 4.8% of body fat in toque macaques that had some access to human foods (Table 2). However, when these species fed only on natural foods, total fat levels were low and nearly identical: 1.9% for baboons and 2.1% for toque macaques. In both species, individuals on a natural diet had a significantly lower percentage of body fat than their garbage feeding counterparts (ibid.), and were at levels far below those seen among captive primates.

There were no spontaneously "obese" wild toque macaques by the loosely defined laboratory standard of obesity being 15–40% of body weight. Field estimates of fatness in baboons and toque macaques surviving on natural diets are closer to Pond and Mattacks' (1987) estimate of 2% (or less) body fat for wild-living mam-



Fig. 5. The relation between the weights of subcutaneous and visceral fat deposits among 21 toque macaques.

mals, than to the 5% that these authors had suggested as a normal optimum for primates—a prediction that they had based, in part, on captive-fed macaques. In general, low body fat appears to have been the norm in primate evolutionary history as also indicated by the central role of leptin in the physiological regulation of adiposity. Leptin was originally thought of as an antiobesity hormone; however, recent studies indicate that it is best viewed as a "starvation hormone" whose major role is to signal an energy deficit rather than a surfeit (Prentice et al., 2002; Whitten and Turner, 2008).

The close relation between adiposity and the availability of environmental energy is well illustrated by studies of the orangutan (*Pongo pygmaeus*). Although fatness has not been measured, Knott's (1998) analyses of urinary ketones (bi-products of adipose tissue metabolism) in wild orangutans suggest that these apes accumulate substantial fat stores during seasons of food abundance, particularly during the supra-annual mast fruiting events that characterize Southeast Asian rainforests. The ability to store much fat is critical to its survival during often prolonged and unpredictable seasons of food scarcity during which its lipid stores are depleted (MacKinnon, 1974; Galdikas, 1988; Knott, 1998). The orangutan lives for long periods on a negative energy budget (Harrison et al., 2010).

Adiposity in relation to age, gender, and reproduction

It follows that adiposity would be expected to vary with age and gender because of the energy requirements of development and reproduction.

In humans, adipose reserves and distribution affect reproductive maturation, fertility and lactation (McFarland, 1996; Pond, 1996; Vitzmanos and Marti-Henneberg, 2000; Lassek and Gaulin, 2007). The same phenomenon has been shown in well-fed nonhuman primates (reviewed by McFarland, 1996). Wild primates, with minimal adiposity, also show a correspondence between reproductive status and comparatively small changes in adiposity: *P. cynocephalus* (Altmann and Muruthis, 1988), vervet monkeys *Chlorocebus aethiops* (Whitten and Turner, 2008), or in the body condition of *M. sinica* (Dittus, 1998).

In toque macaques there was no significant difference by gender in total fatness (Table 1) measured across all ages, nor among adults only. This was true also of M. fascicularis (Pond and Mattacks, 1987), M. nemestrina (Walike et al., 1977), wild baboons Papio anubis, and P. hamadryas (Banks et al, 2001), squirrel monkeys Saimiri sciureus (Russo et al., 1980), and marmosets, Callithrix jacchus, (Power et al., 2001). According to Pond (1992), sex differences in the amount of fat are minimal in the great majority of mammals, including most primates. Exceptions to this have been noted in a number of primate studies, the common thread among them being (a) a provisioned food supply, (b) the development of obesity, and (c) fatter females than males among the adults: rhesus, M. mulatta, (Schwartz and Kemnitz, 1992; but see Hudson et al., 1996); baboons, P. cynocephalus (Coelho et al., 1984; Rutenberg et al., 1987); Japanese macaques, M. fuscata (Muroyama et al., 2006); and chimpanzees, Pan troglodytes (Bribiescas and Anestis, 2010). The contradictory data from these studies imply that sexual dimorphism in fatness, whereby females develop greater adiposity than males in adulthood, is an inherent potential capacity in nonhuman primates that normally is not developed in nature (where populations are often food-limited), and its manifestation is an artifact of unusual food-rich conditions, that are likely to be absent or only transient in nature.

Mean fatness did not differ by sex under natural conditions. Notwithstanding, plasticity in adult female adiposity would be expected to occur, especially in relation to the energetic demands of reproduction (Gittleman and Thompson, 1988). In this cross-sectional study of fatness in toque macaques, the residuals of mean fatness were indeed greater in females than in males. In an independent longitudinal study of variation in body condition of nongravid adult female toque macaques, deviations in body weight about an individual's own mean weight were used as a proxy for estimating condition. Each of 33 females had been weighed 10 to 20 times over a period of 18 years; their body conditions fluctuated by 5-18% about their own mean weights in relation to social and environmental differences, and weights were inversely related to the stage of lactation (Dittus, 1998). The data illustrate the degree of variation in female body condition (as mediated presumably mostly by adipose tissue) and its trend toward negative energy balance during lactation. The latter is more likely to occur in natural than food-enriched environments (Rosetta et al., 2011).

In well-nourished human populations, women normally develop heavier fat deposits than men (Saad, 1997; Wells, 2006). Lohman (1981) had offered that the typical (Western) "reference man" has 15% body fat and the typical "reference woman" 27%. Humans with traditional subsistence level life-styles show far lower adiposity, but women are generally at least marginally fatter than men (Abbie, 1967; Truswell and Hansen, 1976), suggesting that sexual dimorphism in fatness is an evolved trait peculiar to humans and is manifest under a range of environments (Norgan, 1997; Pond, 1998; Wells, 2006, 2012a).

The development of adiposity over a lifetime has been of interest for nonhuman primates (Russo et al., 1980; Coelho et al., 1984; Power et al., 2001) as well as humans (Skerlj, 1959; Enzi et al., 1986; Kuzawa, 1998). Adolph and Heggeness (1971) observed that nonhuman primates do not begin to deposit white fat until after birth. This was borne out in toque macaques (Fig. 1) and other species: rhesus, *M. mulatta* (Schwartz and Kemnitz, 1992), baboons, *P. cynocephalus* (Coelho et al., 1984) and squirrel monkeys, *Saimiri sciureus* (Russo et al., 1980).

An increase of mean adiposity with age implies a continuous accumulation of body fat as animals grow older, but this clearly was not the case for all adult individuals, as some very old toque macaques had low adiposity (Fig. 1). Old (>20 year) male and female toque macaques generally decrease in body weight and limb and body circumferences (Cheverud et al., 1992) and although some of this weight loss is due to muscle loss, observations suggest a loss of fat as well. In colony-managed rhesus (*M. mulatta*), the body-mass index (BMI) [an index of adiposity (Garrow, 1983)] also showed a general increase with age but a decline in old age (Schwartz and Kemnitz, 1992) when energetic demands for reproduction wane.

Among humans, adiposity changes with age for similar reasons as it does in nonhuman primates (Leonard and Katzmarzyk, 2010), but it is disproportionately greater in women than in men (Enzi et al., 1986; Shimokota, 1989). In humans, ethnicity (Kuzawa et al., 2007; Moore et al., 2004) and sexual selection are additional factors affecting the distribution of adipose tissue between the sexes among adults (Cant, 1981; Pond, 1992; Wells, 2006; Dixson et al., 2010). Nonhuman primates and humans share basic energetic functions of adiposity, but in humans this is modified in amounts and distributional emphasis not found among their arboreal ancestors.

Adipose tissue and the thermo insulation hypothesis

Many large, naturally obese mammals occur in areas with cold winters-giving rise to the widely held belief that superficial adipose tissue is an adaptation to thermal insulation. Anatomical investigations of many mammalian species have shown, however, that subcutaneous fat plays little or no role in thermo insulation of most terrestrial mammals, including humans (Pond, 1978, 2009). Fur plays a far greater role in thermo insulation than adipose tissue. For example, the subspecies of toque macaque (M. s. opisthomelas) that inhabits the frosty highlands of Sri Lanka appears no fatter than those of the warm lowlands (personal observation), and Hill (1942) quantified the conspicuously thicker and longer fur of the highland subspecies. Considering that 89% of adipose tissue in wild toque macaques is deposited either intra-abdominally or in anatomically recessed areas under the skin, its contribution towards thermal insulation of the body's surface area would appear to be minimal.

Notwithstanding, the thermo insulation idea has been evoked for primates. Paterson (1996), having noted greater fatness among Japanese macaques (M. fuscata) kept at Oregon than among those managed in the heat of Texas, attributed the difference in fatness to thermo insulation. He sidestepped the more conservative cause—namely, a far better food supply and lesser opportunity for exercise in the Oregon colony than in the Texas one. Similar explanations have been attempted to account for variations in the sexual dimorphism of fatness in human populations living at different latitudes, even though the relation between fatness and climate was inconsistent and cultural differences in exercise and diet were not well integrated in that study (Wells, 2012a). Both diet and exercise are major contributors to variation in human fatness (Stern, 1984), as well as to that among wild baboons (Altmann et al., 1993). The thermo insulation hypothesis is not well supported by current data from nonhuman or human primates.

Variation of adipose tissue patterning from comparative anatomical data

Do known anatomical variations in body fat reflect its adaptations? Pond (1978, 1984) and Pond and Mattacks (1985) examined the anatomical distribution of white adipose tissue in a variety of mammals by weighing dissected fat deposits from different regions of the body. They identified about a dozen distinct adipose depots that are homologous in cell structure, biochemistry, and gross anatomy among most terrestrial mammals, including humans. Pond and Mattacks' (1987) study of captive *M. fascicularis* and Pereira and Pond's (1995) study of captive lemurs come closest for comparisons to the present study of dissected adipose tissue in wild toque macaques.

A comparison of the anatomy of fat between *M. sinica* and *M. fascicularis* is particularly relevant, because of their similarities in body structure and size. Both are long-tailed arboreal macaques of similar weights (5–6 kg for males, 3–4 kg for females) and crown-rump lengths (410–490 mm for males, 364–435 mm for females) (Cheverud et al., 1992; Pond and Mattacks, 1987; Schillaci et al., 2007). The main differences between the macaque subjects in the two studies concern diet and total fatness: the mean percent dissectible fat from captive *M. fascicularis* (7.83% \pm 8.59% for males, and 7.44% \pm 8.34% for females) was more than twice that found among the free-living *M. sinica* (Table 1). One might expect this difference in total body fat to affect its proportional anatomical distribution.

Pond and Mattacks (1987, Fig. 3) examined the relationship between the ratio of superficial fat to intraabdominal fat and the total fatness in M. fascicularis. Lean M. fascicularis (having less than 17% body fat) correspond most closely in scale to the sample of necropsied toque macaques. In lean specimens of both species, visceral fat was about twice that of superficial fat, and both depots accumulated at constant rates with increasing mass of total body fat. There was an increase of about 1 gm/dm^3 of superficial fat for every 6 gm/dm^3 gain of abdominal fat (Fig. 5). There were no M. sinica with more than 11% total body fat to compare with the fatter M. fascicularis (17% or more fatness). Among the latter, however, with increasing total fatness, subcutaneous fat accumulated at a greater rate and far exceeded visceral fat (by >50%) among the most obese individuals (27% total body fat). Studies of dissected body fat in captive lemurs Eulemur fulvus and E. mongoz indicated a pattern similar to that found among the macaques (Pereira and Pond, 1995). In human subjects, the proportion of the total fat which was laid down subcutaneously rose with increasing obesity (Edwards, 1950; Allen et al., 1956), in a manner similar to that among the fattest M. fascicularis and E. mongoz.

The smallest amount of fat was dissected between the muscles, and constituted 3.8% of total body fat in *M. sinica* and about 3% in *M. fascicularis* and <5% in lemurs. The proportional distributions of dissected adipose tissue

among subcutaneous, visceral, and intermuscular depots (Fig. 2) were very similar in these species when these distributions were scaled for differences in total fatness (Pond and Mattacks, 1987).

It seems that in the evolution of adiposity in the primate lineage, internal depots developed ontogenetically as the priority site for storage, and as these depots filled up, "excess" fat was stored peripherally (Pond and Mattacks, 1987). It has been argued that subcutaneous depots were the first to wax and wane with change in the metabolic demands among several mammals, including human infants (Pond, 1978). In humans, where sexual selection is thought to play a role in the sexual dimorphism of fat distribution (Morris, 1967; Cant, 1981; Pond, 1992; Wells, 2006), the organization of fat depots may be modified still further. For example, Skerlj (1959) showed that almost all the increase in total fat in women after the age of 40 years is due to increased internal deposits; the subcutaneous deposits remain constant or decrease. This shift in fat distribution implies that sexual selection is relaxed among women of postreproductive age (Pond, 1992).

Variation in the anatomical distribution of intra-abdominal fat depots

In *M. sinica*, the intra-abdominal fat was highly skewed in its distribution (Fig. 3). Although M. fascicularis had more total body fat than M. sinica, the proportional distribution of intra-abdominal fat was similar, except that the mesenteries held somewhat less fat (66%, compared to 75% in M. sinica) and the dorsal wall of body cavity held proportionately more (34%, compared to 22% in *M. sinica*). In lean lemurs, *E. ful*vus, nearly 60% of intra-abdominal fat was on the dorsal wall, whereas in the obese E. mongoz it was among the mesenteries (Pereira and Pond, 1995). Fat on the dorsal wall of the body cavity can be enormous in humans (Pond, 1992). In M. sinica, the bulk (92%) of intra-abdominal fat (associated with the mesentery and kidney) occurred around the body's center of gravity. The distribution was similar for *M. fascicularis* and the lemurs.

Variation in the anatomical distribution of subcutaneous fat depots

The distribution of subcutaneous fat was not uniform over the surface of the body of M. sinica (Fig. 4). In captive-raised M. fascicularis, 49% of total body fat was subcutaneous (Pond and Mattacks, 1987, Table 2), this being twice that (23.3%) in the leaner *M. sinica* (Fig. 2); and its distribution among the different anatomical depots also differed. Thus, in the fatter M. fascicularis, the paunch held the major portion (56%) of subcutaneous fat compared to only 14% in M. sinica, whereas the axillas and groin depots combined held 26 and 52% in these species, respectively. Because of the heavy concentration of fat on the paunch of M. fascicularis, other smaller depots also were proportionally less (but greater in absolute weights) in *M. fascicularis* than in *M. sinica*. In both species the head, tail and distal segment of the limbs had little or no fat.

In lemurs, the pattern was the same insofar as lean lemurs had a minimal paunch, with fat concentrations in the axillas and groins, and obese lemurs had a "massive" paunch (Pereira and Pond, 1995). Similar observations have been made for *M. mulatta* (Kemnitz et al., 1989) and in a second study of M. fascicularis (Laber-Laird et al., 1991).

In the comparatively lean *M. sinica*, subcutaneous fat was distributed more evenly among depot sites than in their fatter counterparts, as no single depot exceeded 32.2% (groin), and this relatively heavy posterior depot was counterweighed by an equal amount (32.9%) at the two largest anterior depots combined (axillas and hump) (Fig. 4). Pereira and Pond (1995) have pointed out the impediment to locomotion of excess superficial fat accumulation in the axillas and groins of captive-raised obese lemurs. No such impediments were evident in wild toque macaques where these deposits were minimal and deeply recessed. Together these studies indicate that with increasing adiposity, peripheral fat accumulations shift away from the recessed depots by the shoulder (axilla) and hip (groin) joints, where they might impede locomotion, and towards the body's center of gravity at the central and ventral position of the paunch.

The distribution of adipose tissue in relation to body design for arboreal life

A review of mammalian life-histories indicated relatively small body sizes for arboreal forms (Eisenberg, 1981), and arboreal primates generally weigh less than their terrestrial counterparts (Clutton-Brock and Harvey, 1977). Small body size is a distinct advantage for arboreal folivores, frugivores and insectivores. Smaller species can move more freely through dense vegetation, and many nutritious food items such as young leaves, some fruit and insects are often located on thin terminal twigs, or in shrubs, that are unable to bear heavy bodies (Grand, 1972; Fleagle and Mittermeier, 1980; Wheatley, 1982; Harvey et al., 1987). A variety of skeletal, muscular, postural, and other adaptations for this ecological niche among primates have been reviewed (Schultz, 1970; Cartmill, 1972, 1992; Grand, 1972, 1977, 1984; Bolter and Zihlman, 2003; Garber, 2011; Rosenberger, 2011; Zihlman et al., 2011a,b).

The observations considered here suggest that arboreal primates also have evolved constraints in the amount and anatomical distribution of adipose tissue as adaptations to conserve energy and to promote agility in arboreal locomotion and feeding. The constraints on amount are shown by a low percentage of total body fat, normally about 2% of body weight, and also by an absence of fat in fetuses and neonates carried by the mother. Distributional adaptations consistent with a need for body balance and agility would be expected to differ according to the mode of arboreal mobility (quadrupedalism, brachiation, and use of prehensile tails). The macaques and lemurs considered here are typical above-the-branch quadrupedal primates (Grand, 1984) for which adaptations in fatness involve the following: (a) a distribution which concentrates fat reserves mostly intra-abdominally and towards the central ventral position of the torso, with (b) a lesser proportion stored peripherally, (c) in a manner that maintains a weight balance of peripheral depots between the anterior and posterior trunk-length axis, (d) a shift in peripheral fat accumulations towards the central ventral paunch with an increase of total fatness, and (e) an absence of adipose tissue on the tail and distal limbs. With increasing total body fat (among lean monkeys), an accumulation of most adipose tissue-both internally and peripherally, towards the body's ventral center-lowers the body's cen-

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ter of gravity closer to its supporting substrate and serves to stabilize arboreal mobility (Garber, 2011). Distributional trends accompanying obesity suggest a destabilizing influence (Pereira and Pond, 1995).

The patterns in adiposity found here are based on a limited sample of species. Notwithstanding, given that the Cercopithecoidea show a remarkable consistency and uniformity in skeleto-muscular anatomy in most bodily characters and in basic mode of locomotion (Schultz, 1970; Zihlman, personal communication), it is reasonable to expect similar homogeneity in adipose anatomy among these primates generally. The major morphological differences in this group are the widely distributed differences in tail length and an amazing variety of specific and subspecific differences in the coloration and pattern of their coats (Schultz, 1970).

Interestingly, the common design for above-the-branch quadrupedalists contrasts the unique arboreal adaptations of the orangutan. The ape's large body size limits its ability as an agile terminal branch feeder. Instead, it is anatomically suited to clamber in slow deliberate movements, distributing its weight with powerful long limbs among branches (Zihlman et al., 2011a). Its diet consists of hard-to-process fruit and other food items that generally are inaccessible to other sympatric primates, and these food items are most efficiently garnered by solitary or small mother-family units as opposed to large social groups (MacKinnon, 1974; Rodman, 1979; Wheatley, 1982, 1987; Galdikas, 1988; Mitani, 1989). Periodic substantial fatness of an otherwise large body and slow clambering go hand-in-hand in this niche adaptation for regular prolonged food stress, and orangutans bear the cost of social solitariness and slow reproduction; they have the longest interbirth interval (mean of 8 years) of any primate (Galdikas and Wood, 1990). Orangutans represent an anatomical outlier among the great apes and are unlikely candidates in the direct lineage to early hominids (Harrison et al., 2010). Their design is restricted to a single living genus and underscores the success of an alternate design, namely, above-the-branch quadrupedalism that is typical of many arboreal primates including the Old World Monkeys, which have a wider distribution and adaptations to different environments and climates than any other nonhuman primate (Schultz, 1970).

The data presented here are consistent with the hypothesis that the anatomical patterning of adipose tissue is an adaptation conforming to the constraints of arboreal locomotion and feeding. The configuration typical of arboreal above-the branch quadrupedalism is expected to differ compared to other modes of arboreal locomotion and feeding, for example, primates that clamber (Pongo), brachiate (Hylobatidae), use prehensile tails (many Platyrrhini), or leap and cling vertically (many Strepsirrhini).

Adipose tissue and the transition from anthropoid to humanoid evolution

The dearth of fat in nonhuman primate infants sharply contrasts with the abundance in human infants, which are among the fattest neonates among mammals (Prechtl, 1986; Kuzawa, 1998). The copious adipose tissue of human newborns has been considered critical to the normal development of the large human brain (Prechtl, 1986; Kuzawa, 1998). The paucity of fat among nonhuman primate infants suggests that the constraints on fatness concomitant with an arboreal life-style also set limits to the development of large brains. In other words, the evolutionary transition to the large-brained hominids from arboreal anthropoid ancestors hinged on abandoning the fat-limiting arboreal niche and adopting new "fat-friendly" terrestrial habits. No doubt, other changes also were involved in this adaptive shift (Foley and Lee, 1991).

Nevertheless, the importance of adipose tissue in this shift is further supported by the facts that women develop more adipose tissue than men, and maternal fatness and energy reserves promote fatness in their infants (Hull et al., 2008), which is critical to normal brain development (Kuzawa, 1998). These phenomena are consistent with the idea that sexual dimorphisms in fatness and its role in human female–female mate competition (in developing female traits sexually attractive to males) were linked to, and advertised, maternal ability to nurture and raise fat, healthy and large-brained offspring (Cant, 1981; Low et al., 1987). Such a sexually selected development was muted in their arboreal ancestors by natural selection (Byers and Dunn, 2012).

The evolution of adiposity among nonhuman primates and humans: Models from nature

Seasonal fluctuations in the availability of food and water, and unforeseeable droughts and cyclones affect tropical environments and their nonhuman primate inhabitants (Dittus, 1977, 1985), sometimes adversely by inflicting mortality and reduced reproduction (Struhsaker, 1973; Dittus, 1980; Strum and Western, 1982; Cheney et al., 1988; Lee and Hauser, 1998; Knott, 2005). Under similar ancestral ecologies, freedom from arboreal constraints on body fatness and the development of large brains may have served the first terrestrial hominids with alternative strategies for acquiring "energy capital" for offsetting environmental uncertainty of resource availability in new terrestrial habitats (Foley, 1987; Navarrete et al., 2011; Wells 2012b).

Yet, are there normal limits to fatness? Since the industrial revolution, most human populations have had to work less hard and have been able to eat more than previously (Stern, 1984). In this recent obesifying environment modern humans have developed increasing levels of adiposity, and the epidemic of obesity and associated disease are spreading worldwide (Mendez et al., 2005; Herbert et al., 2006; Bellisari, 2008). Seasonal reversible obesity is a natural phenomenon in some mammals, but these species do not suffer from the complications of obesity-related disorders observed in humans and captive-raised nonhuman primates. It has been argued that humans and other primates are not naturally and adaptively obese (Pond, 1998, 2012).

The normal lean macaques and baboons (at about 2% or less of total body fat), living in their natural habitats, offer a contrasting model for the study of primate body composition and the evolution of the human lineage. Indeed, similar to free-living nonhuman primates, the contemporary hunter-gathering Shuar and Yuwientsa people inhabiting the Amazonian rainforest of Ecuador regularly traveled long distances for up to 8–10 h in search of forest foods. Indices of fatness among their women were the lowest ever reported from any population of humans (Lindgärde et al., 2004). The same is

true of men of several hunter-gatherer societies (Eaton et al., 1988). Fat affects reproduction in captive-raised Macaca (Campbell et al., 2004; Rosetta et al., 2011) as well as humans (Norgan, 1997; Vizmanos et al., 2000), and women in well-studied hunter gatherer societies, such as the !Kung of southern Africa, experience far lower rates of reproduction than their fatter counterparts (McFarland, 1996). As purely hunter-gatherer lifestyles have largely vanished from the human landscape (Bodley, 1999), our understanding of the function of adipose tissue in human evolution can benefit from a closer examination of its role among our nonhuman primate relatives still foraging in the wild, keeping in mind that important differences—with respect to sexual selection in adiposity in particular-also set the human lineage apart from nonhuman primates.

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