

## RESEARCH ARTICLE

Validating Skinfold Thickness as a Proxy to Estimate Total Body Fat in Wild Toque Macaques (*Macaca sinica*) Using the Mass of Dissected Adipose TissueWOLFGANG P.J. DITTUS<sup>1,2,3\*</sup> AND K.A.SUNIL GUNATHILAKE<sup>3</sup><sup>1</sup>Conservation Ecology Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, District of Columbia<sup>2</sup>National Institute of Fundamental Studies, Kandy, Sri Lanka<sup>3</sup>Association for the Conservation of Primate Diversity, Polonnaruwa, Sri Lanka

Skinfold thickness (SFT) has been used often in non-human primates and humans as a proxy to estimate fatness (% body fat). We intended to validate the relation between SFT (in recently deceased specimens) and the mass of adipose tissue as determined from dissection of fresh carcasses of wild toque macaques (*Macaca sinica*). In adult male and female toque macaques body composition is normally 2% adipose tissue. Calipers for measuring SFT were suitable for measuring only some subcutaneous deposits of adipose tissue but were not suitable for measuring large fat deposits within the body cavity or minor intermuscular ones. The anatomical distribution of 13 different adipose deposits, in different body regions (subcutaneous, intra-abdominal and intermuscular) and their proportional size differences, were consistent in this species (as in other primates), though varying in total mass among individuals. These consistent allometric relationships were fundamental for estimating fatness of different body regions based on SFT. The best fit statistically significant correlations and regressions with the known masses of dissectible adipose tissue were evident between the SFT means of the seven sites measured, as well as with a single point on the abdomen anterior to the umbilicus. SFT related to total fat mass and intra-abdominal fat mass in curvilinear regressions and to subcutaneous fat mass in a linear relationship. To adjust for differences in body size among individuals, and to circumvent intangible variations in total body mass allocated, for example to the gastro-intestinal contents, dissected fat mass was estimated per unit body size (length of crown-rump)<sup>3</sup>. SFT had greater coefficients of correlation and regressions with this Fat Mass Index (g/dm<sup>3</sup>) than with Percent Body Fat. *Am. J. Primatol.* 77:618–632, 2015. © 2015 Wiley Periodicals, Inc.

**Key words:** wild primates; measuring adiposity; fat mass index; lean fatness; body composition

## INTRODUCTION

The anatomical distribution and structure of adipose tissue are homologous among mammals, including humans, and fatness is of interest because of its broad biological relevance [Dittus, 2013; Pond, 1998, 2012; Pond & Mattacks, 1985a,b]. In many wild animals, for example, fatness affects fecundity and survival [Pestrud & Pond, 2003]. Among primates, body fat has been linked to growth and development [Coelho et al., 1984; Saad et al., 1997; Schwartz & Kemnitz, 1992], reproduction [Campbell et al., 2004], levels of activity [Altmann et al., 1993; Jayo et al., 1993; Stern, 1984], behavioral stress and disease [Després & Lemieux, 2006; Kyrou & Tsigos, 2008], genetics [Bouchard, 1997; Comuzzie et al., 2003; Kavanagh et al., 2007; Loos & Bouchard, 2008], and an individual's environment [Garcia et al., 2010; Leonard & Katzmarzyk, 2010; Muroyama et al., 2006]. In humans, adiposity also varies with lifestyle

and race [Lindgärde et al., 2004; Moore et al., 2004]. Much attention, therefore, has been devoted to quantifying body composition.

**Aim: Estimating Adiposity in Wild Primates**

A variety of methods have been described for estimating body fat in primates. Non-invasive methods involve measures of skinfold thickness

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(SFT) [Durnin & Womersley, 1974; Lohman, 1981; Walker et al., 1984], limb circumferences [Coelho et al., 1984], and visual estimation [Berman & Schwartz, 1988]. Contrasts between adipose and other tissues in their physiological properties have served as a basis for estimating body composition using measures of electrical conductivity [Power et al., 2001; Sutcliffe & Smith, 1995; Wirsing et al., 2002], ultrasound [Walker et al., 1984], body water [Altmann et al., 1993; Garcia et al., 2004; Walike et al., 1977], densitometry [Womersley & Durnin, 1977], nuclear magnetic resonance [Lewis et al., 1986], X-ray absorptiometry [Colman et al., 1999], and computed tomography [e.g., Enzi et al., 1986; Shively et al., 2009]. Garrow [1983] reviewed the merits of many of these methods noting that SFT has been widely used because of its ease of measurement. All of these indices, however, represent proxies for body fat and few have been validated with direct measures of total body fat as determined either by necropsy or methods of chemical extraction [Lewis et al., 1986; Rutenberg et al., 1987]. The body mass index (BMI) is often cited in assessments of body composition and is easily derived from field data (body mass/length<sup>2</sup>). The BMI is a poor index for adiposity, however, because it does not distinguish between fat and other tissues (bone, muscle, alimentary tract contents) that contribute to total body mass [Garn et al., 1986; Garrow, 1983]. Consideration of BMI is therefore omitted in this report.

With the exception SFT, most methods for estimating body fat are impractical in field studies. We were interested, therefore, in developing a method for estimating fatness in wild primates under field conditions that would involve minimally invasive procedures. If wild monkeys can be temporarily captured and anesthetized, three measurements are easily obtained: total body mass, crown-rump length and the thickness of skinfolds. To resolve potential issues with indexing fatness in wild monkeys, we added an important fourth variable: the mass of dissected adipose tissue. "Total body fat" in this report excluded lipids in body fluids or tissue.

Our aim was to validate SFT and percent body fat with the mass of dissected white adipose tissue from fresh carcasses on the premise that such a validation would be applicable to live animals as well. This aim invites two preliminary considerations: low total body fat in wild primates and the allometry of fat deposits.

### Non-Invasive Methods Applied to Lean Primates

Most wild mammals normally are lean with less than 2% total body fat [Pond & Mattacks, 1987]; and this is true also of wild toque macaques [Dittus, 2013], baboons [Altmann et al., 1993; Banks et al.,

2001] and human hunter-gatherers [Lindgärde et al., 2004; Truswell & Hansen, 1976]. These low levels of fatness contrast with the usual 10% to 35% body fat found among food provisioned monkeys [Altmann et al., 1993; Dittus, 2013], and among many contemporary humans [Bellisari, 2008]. Even lean wild individuals differ noticeably, however, in degrees of fatness and robustness. Berman & Schwartz [1988] devised a method of quantifying observers' visual assessments in degrees of fatness among exotic rhesus macaques (*Macaca mulatta*) of the managed colony on Cayo Santiago, Puerto Rico. On their 7-point scale of obesity, all toque macaques feeding on a natural diet fall at or below the scale point of 2, which the authors considered as: "Neither thin nor fat, the monkey is sleek in appearance, skin is taut but does not protrude, and there is no loose flab." Visual assessment of obesity loses resolution when applied to the narrow range of total body fat found among wild primates. SFT would appear to offer a more objective and appropriate proxy for quantifying fatness in lean subjects.

### Allometric Anatomical Distribution of Adipose Tissue

Detailed anatomical studies involving the dissection of adipose tissue have been carried out in only a few primates, namely: captive cynomolgous macaques (*M. fascicularis*) and pig-tailed macaques (*M. nemestrina*) [Pond & Mattacks, 1987], wild toque macaques (*M. sinica*) [Dittus, 2013], and captive lemurs (*Eulemur fulvus* and *E. mongoz*) [Pereira & Pond, 1995]. These studies showed that, with increasing total fatness, the mass of adipose tissue showed a regular pattern of change in its proportional distribution: (a) intra-abdominal depots fill first, and "excess" fat is stored progressively beneath the skin, (b) the site for the accumulation of subcutaneous fat shifts away from the poles of the trunk (axilla and groin) towards the central ventral abdominal paunch, and (c) similar shifts towards the central ventral position occur within the body cavity.

### Hypotheses

In light of these considerations we hypothesized that SFT would (1) vary consistently in relation to the mass of dissectible adipose tissue beneath the skin, (2) predict fatness most reliably at sites on the body where the variation in fatness is high, and (3) at such sites, accurately predict not only total fat mass, but also its constituent subcutaneous and intra-abdominal fractions.

### METHODS

The methods of field observation and measurement comply with all regulations regarding the

ethical treatment of research subjects as prescribed by the National Institute of Fundamental Studies, Sri Lanka, and the Smithsonian Conservation Biology Institute, USA, and adhered to the American Society of Primatologists principles for the ethical treatment of primates. The animals investigated in this study were necropsied specimens, all of which were found dead prior to our investigations. Fresh carcasses of toque macaques are rarely found and our sample of 22 specimens was accumulated opportunistically over five years (1998–2002) from their natural forest environment at our study site in the Polonnaruwa Nature Sanctuary, Sri Lanka (see below).

### Study Population and Sampling

Toque macaques are endemic to Sri Lanka and are typical above-the-branch primate quadrupeds [Grand, 1984] that use all levels of the forest, and forage on a diversity of ripe fruit, young leaves, insects and the occasional small vertebrate [Dittus, 1977; Hladik & Hladik, 1972]. The macaques living in the Nature Sanctuary and Archeological Reserve at Polonnaruwa have been studied continuously over four decades (1968–2015). The natural dry-evergreen forest inhabited by the macaques and aspects of their demography, ecology, behavior, epidemiology, population genetics, physical growth, and functional anatomy have been described earlier [e.g., Cheverud et al., 1992; Dittus, 1977; Ekanayake et al., 2007; Grand, 1972, 1976]. Toque macaques live in closed and cohesive matrilineal societies with one or more immigrant breeding males. Competition for resources, and seasonally for mates, prevails in daily life and affects the macaques' rates of birth, death and physical growth [Dittus, 1977, 2004]. Population size is closely attuned to the availability of natural food and water in their habitat. In undisturbed natural forest environments net population growth is near zero, but the introduction of human food (mostly refuse) has stimulated exponential growth in affected groups [Dittus, 2012a].

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 & 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; females are physically mature or "adult" by 6 years old, and males by about 9 years old [Cheverud et al., 1992]. The 22 dead specimens in our sample were known when alive and originated from eleven (of the 33) different social groups. Their causes of death were: age and social rank related ( $N=2$ ), injury from conspecific aggression ( $N=4$ ), dog bite ( $N=11$ ), vehicular trauma ( $N=12$ ), electrocution ( $N=2$ ), and uncertain ( $N=1$ ). Total body

masses and measurements of SFT and morphometrics on intact bodies were recorded soon after death and before *rigor mortis*. Most specimens were dissected on the same day; a few were kept frozen (wrapped in polythene to protect against dehydration) and thawed within 1–4 days for necropsy. It is unlikely that the process of freezing and thawing during this short period adversely affected the adipose tissue or body composition from the point of view of these anatomical studies [Pond & Mattacks, 1985b].

The social groups from which the necropsied specimens originated differed in ecology: seven groups had fed predominantly on natural forest foods (> 90% of foraging time), and the other four had supplemented their natural diet through regular access (> 20% of foraging time) to human food refuse from houses or temples on the periphery of the study area [Dittus, 2012a]. Natural diet feeders ( $N=13$  individuals) had a mean of 2.1% body fat, whereas those with access to refuse ( $N=9$  individuals) had a mean of 4.8% body fat. Adult macaques feeding on refuse had 3 to 4 times significantly more ( $P < 0.03$ ) fat mass than those restricted to a natural diet [Dittus, 2013].

### Morphometric Measurement

A previous sample of 274 macaques from this population had been live-trapped and released unharmed in studies of physical growth and development [Cheverud & Dittus, 1992]. The methods for somatometric measurements described in that study were applied here. 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 with a resolution to the nearest millimeter. This measure is sometimes referred to as "sitting height" and it was used here as a reference denominator because most adipose tissue was anatomically distributed in this body trunk section (Fig. 1, Table I).

Skinfold thickness (SFT) was measured using a Lange Skinfold Caliper (Cambridge Scientific Industries, Cambridge, Maryland). The instrument was calibrated in millimeters and its accuracy was verified using a Vernier caliper. The thickness of a skinfold was estimated to the nearest 0.1 mm. The sites on the body selected for measuring skinfolds follow guidelines for humans [Durnin & Rahaman, 1967; Lohman, 1981] and macaques or baboons [Kemnitz et al., 1989; Muroyama et al., 2006; Small, 1981; Walike et al., 1977; Walker et al., 1984]. These sites were as follows. (1) Nape: neck at the dorsal midline. (2) Subscapular: upper back below tip of inferior angle of the scapula. (3) Suprailiac: lower back above the iliac crest. (4) Triceps: back of the upper arm midway between the acromion and olecranon. (5) Chest side: 3–5 cm lateral to the

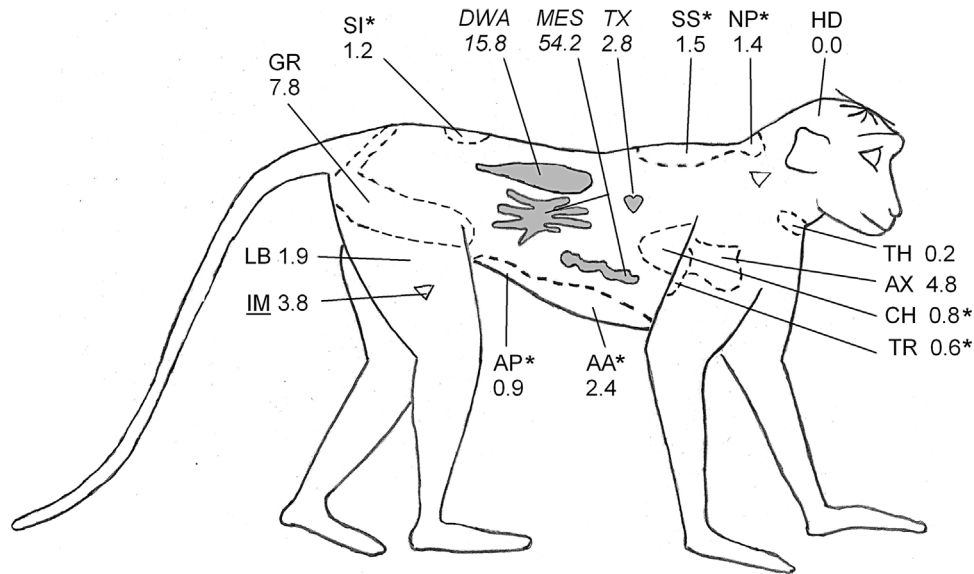


Fig. 1. The anatomical locations and percentage distributions of depots of adipose tissue and sites of measurement (\*) of Skinfold Thickness (SFT) for (i) subcutaneous fat (blank): AA (abdomen anterior to umbilicus), AP (abdomen posterior to umbilicus), AX (axilla), CH (chest side), GR (groin), HD (head), LB (limbs), NP (nape), SI (suprailiac), SS (subscapular), TH (throat and chin), TR (triceps); (ii) body cavity fat (shaded): DWA (dorsal wall of abdomen), MES (mesentery and omentum), TX (thorax); and (iii) IM (intermuscular fat).

nipples below the axilla. (6) Abdomen anterior to the umbilicus: midline between the umbilicus and sternum. (7) Abdomen posterior to the umbilicus: midline between the umbilicus and pelvic crest (Fig. 1). Hair had a negligible effect on measures of SFT because hair was sparse and fine on the ventral aspects of the body (abdomen, chest side) and at other sites the tips of the calipers were maneuvered to minimize the inclusion of hair. SFT measurement was subject to error between observers, and according to the exact location where the caliper was applied to the pinched skin [Ruiz et al., 1971]. In order to minimize caliper placement error, we took three measures of SFT at each of the seven sites. The means of these 21 measurements were reported as representative of an individual's mean skinfold thickness. Technical error in skinfold determination, by the same or two different examiners, translates into about 0.5% of total body fat in humans [Lohman, 1981], but this effect was not measured in macaques.

### Fat Dissection and Weighing

Total body masses were gauged using a spring scale (Thermoscale, Salter, UK) on intact bodies. Dissected body fat was weighed on a more sensitive scale (Scout Electronic Balance, Ohaus Corp., Florham Park, New Jersey, USA) accurate to 0.01 g. Adipose tissue was dissected, sorted and weighed according to body regions: subcutaneous, intermuscular and intra-abdominal. Subcutaneous fat included all that occurred between the skin and immediate

underlying muscle. Intermuscular fat lay within muscle bands. Fat of the body cavity included all that found among the mesentery, omentum and along the dorsal inner wall of the abdomen and thorax. Demarcation between different depots within these regions was clear (Fig. 1, Table I) and all dissectible adipose tissue was white in color. Distinct depots of brown adipose tissue were not found. Recent studies suggest that most depots are mixtures of white and brown adipocytes, the two cell types being closely similar, inter-convertible, and alternate versions within the same adipose organ [Cinti, 2011; Pond, 2012].

### Sites of SFT Measurement in Relation to the Anatomical Distribution of Adipose Tissue

Pond and Mattacks [1987] had described 13 anatomically distinct and homologous depots of adipose tissue in *Macaca* monkeys. Eight of these were subcutaneous, three were intra-abdominal and two were intermuscular. The depots dissected in the present study correspond to those described by Pond and Mattacks [1987]; but additionally, we distinguished among minor anatomical differences within these depots that allowed us to link SFT sites of measurement to the mass of the underlying subcutaneous adipose tissue (Fig. 1, Table I). For depots that were not measured for SFT, such as those of the inguinal area, we combined previously described superficial depots. Elsewhere, as in the paunch, we considered finer subdivisions within previously

**TABLE I. Sites for Measuring Skinfold Thickness (SFT) in Relation to the Mass and Percentage Distribution of all Dissected and Previously Defined Adipose Tissue Depots, and Their Anatomical Identification, From 15 Individual Toque Macaques**

Dissected adipose tissue depot	SFT site measured	Defined depot (Pond & Mattacks, 1987)	Adipose tissue mass (g)	% total adipose tissue	Anatomical identification of dissected and defined depots ( <i>ibid.</i> )
<b>Subcutaneous</b>					
Groin		GS + GV + BOT	122.4	7.8	GS (groin side): tissue anterior to femur, lateral to the abdominal wall and medial to the panniculus muscle, GV (groin ventral): tissue on the external surface of the abdominal wall, caudal to the umbilicus and between the hind limbs; BOT(base of tail): over the dorsal and posterior surface of the gluteal muscles and around the base of the tail.
Axilla		BA	78.1	4.8	BA (behind arm: tissue posterior to the humerus and in the axilla, extending posteriorly over the chest muscles
Triceps	X	BA	10.3	0.6	
Chest side	X	BA	13.8	0.8	
Neck	X	HUMP	22.5	1.4	HUMP: superficial adipose tissue over the spine between the dorsal crests of the scapulae
Subscapular	X	HUMP	24.2	1.5	
Abdomen anterior	X	PAU	38.6	2.4	PAU (paunch): superficial adipose tissue over the abdominal muscles from the sternum to the groin
Abdomen posterior	X	PAU	14.6	0.9	
Suprailiac	X	SKIN	20.2	1.2	SKIN: adipose tissue in all other subcutaneous depots.
Head		SKIN	0.3	0.0	
Limbs		SKIN	31.5	1.9	
Chin and throat		SKIN/IFS	3.3	0.2	
Subtotal			379.8	<b>23.3</b>	
<b>Body cavity</b>					
Abdominal, mesentery & omentum		OME + ATG	882.8	54.2	ATG (attached to the guts): mesentery, and OME (omentum)
Abdominal , dorsal wall kidney, pelvic		DWA	257.1	15.8	DWA (dorsal wall of abdomen): gonadal and retroperitoneal
Thorax		Pericardium + lungs	15.8	2.8	Pericardium, around heart and great vessels.
Subtotal			1,185.4	<b>72.8</b>	
<b>Intermuscular</b>		UMN + POP	62.1	<b>3.8</b>	UMN (under muscles of neck): tissue medial to the trapezius muscle , and POP; the popliteal depot between the biceps femoris, semitendinosus and semimembranosus muscles of the hind leg.
<b>Total</b>			1,627.3	<b>100.0</b>	

described depots (Table I). These depots comprise at least 95% of all dissectible adipose tissue [Pond & Mattacks, 1987].

All variables, including total fat mass, were known for 22 specimens; regional differences in fat mass were known for 21 of them. Within body regions we recorded masses for subcutaneous and intra-abdominal depots for 16 and 15 specimens, respectively. Differences in the available information on fat masses were due to sampling error and our inability to distinguish some depots in an injured specimen. Analyses used the maximum sample sizes where relevant.

**Measuring Adipose Tissue and Statistical Analyses**

The absolute quantity of adipose tissue can be expected to vary among animals according to body-size differences. We needed an accurate measure of individual differences in adiposity suitable for unbiased comparisons. The usual “fatness” expressed as a percentage of total body mass is problematic because, firstly, the numerator is not independent of the denominator. Secondly, total body mass can be influenced by variables such as organomegaly, pregnancy status and gastro-intestinal contents. Our sample did not include pregnant females or specimens with obvious organ abnormality. To control for body size differences, the mass of dissected adipose tissue was scaled according to the square-cube law. Body mass, which is equivalent to its volume, was estimated as the cubic function of crown-rump body length. Fatness was quantified as fat mass per unit body mass, or: total fat mass/(body height)<sup>3</sup>, expressed as g/dm<sup>3</sup>, and was referred to as the Fat Mass Index (FMI).

SigmaPlot<sup>®</sup> v. 11.0 software (Systat Software, Inc., Chicago, Illinois) was used for analysis of regression and correlation (Pearson Product Moment Correlation). In non-linear regression analyses, the distributions of data variables were tested for normality (using the Shapiro-Wilk test) and constant variance. Regression equations and lines were reported as either linear or curvilinear based on

the best fit value of the adjusted regression coefficient ( $r^2_{adj}$ ), its significance, and tests of the distributions of the original (not transformed) data. A *P*-value of less than or equal to 0.05 was considered as statistically significant.

**RESULTS**

**Independent, Incidental and Causative Variables of Fatness**

In order to estimate fatness in wild primates we selected independent variables that could be obtained most easily in the field from carcasses or from temporarily captured and sedated live macaques. These were: body mass, crown-rump length and SFT. We supplemented these variables with dissections of body fat from fresh carcasses in order to obtain an independent direct measure of body fat mass (Table II).

Our interest was to validate SFT as an independent variable from which fatness might be predicted. As an anatomical index, therefore, it is incidental to and differs from variables that may affect fatness, such as age, sex, and diet [Dittus, 2013] and behavioral and ecological factors that might influence body condition [Dittus, 1977; 1998].

There was no significant difference in the mean fat masses of males ( $1.71 \pm 0.64 \text{ g/dm}^3$ ) and females ( $1.60 \pm 1.95 \text{ g/dm}^3$ ) when compared across all ages (Mann–Whitney U-test, NS); nor did they differ for males ( $1.91 \pm 0.83 \text{ g/dm}^3$ ) and females ( $2.32 \pm 2.63 \text{ g/dm}^3$ ) older than 5.5 years (*t*-test = 0.337, *df* = 9, *P* = 0.744). An ANOVA using FMI 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). Fat masses were combined by sex in further analyses.

Mean fat mass (FMI) regressed positively on age ( $r^2_{adj} = 0.392$ , *df* = 21, *F* = 14.536, *P* < 0.01), but age was considered neither a practical variable for predicting fatness because exact age may be unknown in some sample populations, nor an empirically desirable one because it is implicated with

**TABLE II. Summary Statistics of Measures of Skinfold Thickness, Body Size, Fat Mass and Derived Indices of Total Fatness (Percent Body Fat and Fat Mass Index) Among Wild Toque Macaques (*Macaca sinica*)**

Measures	Female means or median* and range	Male means or median* and range
Sample size	12	10
Age	4.79 (0.01–31.61) y*	5.45 (1.06–21.42) y*
Body mass	2.37 (0.26–4.83) kg	3.46 (1.22–5.19) kg
Crown–rump length	36.1 (17.5–42.8) cm	39.1 (29.1–46.8) cm
Mean Skinfold thickness	1.9 (0.7–3.3) mm	2.2 (1.5–2.9) mm
Fat mass	101.3 (0.0–433.1) g	114.9 (27.0–266.7) g
Percent body fat	3.2 (0.0–11.0)	3.2 (2.0–5.2)
Fat Mass Index (FMI)	1.6 (0.0–5.7) g/dm <sup>3</sup>	1.7 (1.1–3.0) g/dm <sup>3</sup>

several other effects on fatness. SFT, on the other hand, is a biologically neutral index of fatness.

### Estimate of Skin Thickness

A fold of skin pinched with calipers measures the thickness of two layers of skin plus that of the adhering layer of adipose tissue. The thickness of the skin, *per se*, was not measured directly, but was estimated as SFT/2 from sites lacking dissectible fat beneath them, as observed often at the triceps and side of the chest. The thickness of the triceps skin of the infant (0.4 mm) was less than the mean skin thickness ( $0.7 \pm 0.2$  mm) of 9 individuals older than 0.5 years, but there was no statistically significant trend of skin thickness regressed on age ( $F = 2.171$ ,  $df = 9$ ,  $P = 0.1789$ ). Among macaques > 0.5 years old, males had slightly but significantly ( $P < 0.05$ ,  $df = 7$ ) thicker skin at the triceps ( $0.8 \pm 0.1$  mm,  $N = 5$ ) than females ( $0.6 \pm 0.1$  mm,  $N = 4$ ). Similar trends were found with skin thickness at the chest side and nape. Skin thickness varied as well by site of measurement on the body, being least at the chest side ( $0.5 \pm 0.1$  mm,  $N = 9$ ) but not significantly less than the slightly thicker skin at the triceps ( $0.6 \pm 0.2$  mm,  $N = 10$ ) (*t*-test,  $P = 0.06$ ,  $df = 17$ ), and both were significantly less than skin thickness at the nape ( $1.2 \pm 0.4$  mm,  $N = 7$ ) (Mann-Whitney tests,  $P = 0.008$  and  $P = 0.014$ , respectively). Only a few points or sites of measuring SFT lacked fat deposits suitable for

estimating skin thickness. No adjustments were made in the analyses of SFT data in relation to estimates of skin thickness alone.

### Variation in Skinfold Thickness (SFT) Among Anatomical Sites of Measurement

The SFT varied among individuals (Table II) and according to the site of measurement on the body (Table III). Overall (22 individuals, 154 measures) SFT ranged from 0.4 mm to 5.4 mm, with a mean and SD of  $2.0 \pm 0.7$  mm. The lowest mean measure of 0.7 mm was of an infant (age 0.01 years) and the greatest of 3.3 mm was of an adult female (age 21.3 years). The smallest measurements did not exceed 2.0 mm, with means above 1.0 mm, and were found at the triceps, and side of the chest. The thickest measurements, those in excess of 5.0 mm, were found at the nape (of the neck) and abdomen anterior to the umbilicus. With the exception of the nape, all mean measures were less than 3.0 mm. The minimal SFTs were all below 1.0 mm (Table III). The means of SFT per specimen were used for comparisons with individual fat masses (Table II).

In measuring the SFTs of the 22 specimens used in this report, it was evident that differences in SFT were consistent among the seven anatomical sites of measurement (Table III). It was of interest, therefore, to examine the correlations in SFT between pairs of measured sites. With the exception of pairs

**TABLE III. The Percent Distribution of Dissected Subcutaneous Fat Masses at Different Depots, the Mean and Range of Skinfold Thicknesses (SFT), and the Corresponding Correlation Coefficients Between SFT and the Mass of Dissected Subcutaneous Fat at the Seven Loci Where SFT Was Measured**

Anatomical location of subcutaneous adipose tissue depot	% of total subcutaneous fat mass at depot	SFT Mean $\pm$ SD <sup>†</sup> (mm)	SFT Range <sup>‡</sup> (mm)	Correlation: fat mass (FMI) and SFT at depot <sup>‡</sup>
Groin	32.23			
Axillas	20.56			
Chin & throat	0.87			
Head	0.08			
Limbs	8.29			
Nape	5.92	$3.0 \pm 1.0$	0.9–5.1	0.214 NS, $P = 0.43$
Subscapular	6.37	$2.8 \pm 0.8$	0.8–4.4	0.410 NS, $P = 0.12$
Suprailiac	5.32	$2.3 \pm 0.6$	0.9–3.7	0.507*
Chest sides	3.63	$1.1 \pm 0.2$	0.4–1.5	0.456 NS, $P = 0.08$
Triceps	2.71	$1.3 \pm 0.3$	0.7–1.9	0.165 NS, $P = 0.54$
Abdomen anterior to umbilicus	10.16	$2.1 \pm 1.0$	0.8–5.4	0.902****
Abdomen posterior to umbilicus	3.84	$1.5 \pm 0.7$	0.6–3.5	0.370 NS, $P = 0.16$
Sample Total	100.0	$2.0 \pm 0.7$	0.4–5.4	0.736**

NS, not significant.

<sup>†</sup> $N = 22$  macaques.

<sup>‡</sup> $N = 16$  macaques.

\* $P < 0.05$ .

\*\* $P < 0.01$ .

\*\*\* $P < 0.001$ .

\*\*\*\* $P < 0.0001$ .

**TABLE IV. Pearson’s Correlation Coefficients Between Pairs of SFT Measures at Different Anatomical Sites among N=22 Individuals**

	Abdomen posterior	Abdomen anterior	Triceps	Chest-side	Suprailiac	Subscapular
Nape	0.818 <sup>****</sup>	0.850 <sup>****</sup>	0.853 <sup>****</sup>	0.548 <sup>**</sup>	0.842 <sup>****</sup>	0.931 <sup>****</sup>
Subscapular	0.736 <sup>****</sup>	0.769 <sup>****</sup>	0.808 <sup>****</sup>	0.582 <sup>**</sup>	0.884 <sup>****</sup>	
Suprailiac	0.736 <sup>****</sup>	0.658 <sup>****</sup>	0.758 <sup>****</sup>	0.514 <sup>*</sup>		
Chest side	0.318 NS, $P = 0.15$	0.300 NS, $P = 0.18$	0.488 <sup>*</sup>			
Triceps	0.695 <sup>**</sup>	0.729 <sup>****</sup>				
Abdomen anterior	0.912 <sup>****</sup>					

NS, not significant.  
<sup>\*</sup> $P < 0.05$ .  
<sup>\*\*</sup> $P < 0.01$ .  
<sup>\*\*\*</sup> $P < 0.001$ .  
<sup>\*\*\*\*</sup> $P < 0.0001$ .

involving the side of the chest, all other pair-wise comparisons were highly significantly correlated (Table IV).

**SFT and the Mass of Adipose Tissue at Sites of SFT Measurement**

Fat was dissected, sorted into categories corresponding to anatomical location or depot, and weighed [Dittus, 2013]. The percentage distribution of fat mass among the three main fatty body regions was: subcutaneous (23.3%), intermuscular (3.8%) and body cavity (72.8%) (Table I). Only subcutaneous fat was accessible for measures of SFT, but some depots (axilla and groin) were inaccessible to calipers. Considering only subcutaneous adipose tissue, the percentage distribution of fat mass varied among the 12 subcutaneous depots and among the 7 points of measuring SFT (Table III).

We evaluated the correlations between SFT and the underlying mass of subcutaneous fat, as measured by the FMI. The means of SFTs, taken across all seven skinfold sites among 16 individuals, correlated significantly with the underlying masses of subcutaneous fat at these sites. Considering specific sites separately, the greatest significant correlation of this kind occurred in the depot of abdominal fat anterior to the umbilicus, and the weakest and non-significant correlations were found at the thinnest and least variable (in thickness) sites: the triceps and side of chest. The SFT at the all of the other sites were moderately thick and variable, but, with the exception of the suprailiac site, were not significantly correlated with their underlying fat masses (Table III).

**Predicting Total and Regional Body Fatness from Skinfold Thickness**

Previous investigators have obtained varying results of reliability in predicting fatness in both

human and nonhuman primates depending on which point on the skin was selected for measuring SFT. Using the correlations (Table III and IV) as guides we applied non-linear regressions of known masses of dissected adipose tissue (FMI) at the 7 points of measured SFT individually, and in combination. The best fit regression (linear or curvilinear) was determined by the magnitude of the regression coefficient ( $r^2_{adj}$ ), its statistical significance, the standard error of the estimated mean (SEE), passed tests for normality and equal variance in the distributions of the data, and how tightly the 95% confidence bands and 95% prediction bands fit the plotted data.

At necropsy we had separated fat deposits according to their anatomical distribution: subcutaneous, intermuscular and intra-abdominal. Although the absolute masses of these deposits differed among individuals, their relative proportions were consistent (Table I). We wished to determine how well measures of SFT predicted the fat masses (FMI) from these different body regions, in particular subcutaneous and visceral adipose deposits. SFT readings and masses of adipose tissue from these two regions were available for 21 individuals.

A regression of total fat mass (FMI) on mean SFT indicated a statistically significant curvilinear relationship (Fig. 2A), where SFT predicted total body fat mass (FMI). Separating total fatness into subcutaneous and intra-abdominal masses, SFT also statistically significantly predicted the mass (FMI) of intra-abdominal adipose tissue in a curvilinear plot (Fig. 2B), as well as the FMI of subcutaneous fat in a linear one (Fig. 2C). Similar statistically significant predictive relationships were found using only a single measure of SFT on the abdomen anterior to the umbilicus, where the greatest correlation ( $r = 0.902$ ,  $P < 0.0001$ ) between SFT and FMI had been found (Table III). The two estimates of SFT yielded similar levels of confidence in predicting total or regional fatness (Table V).



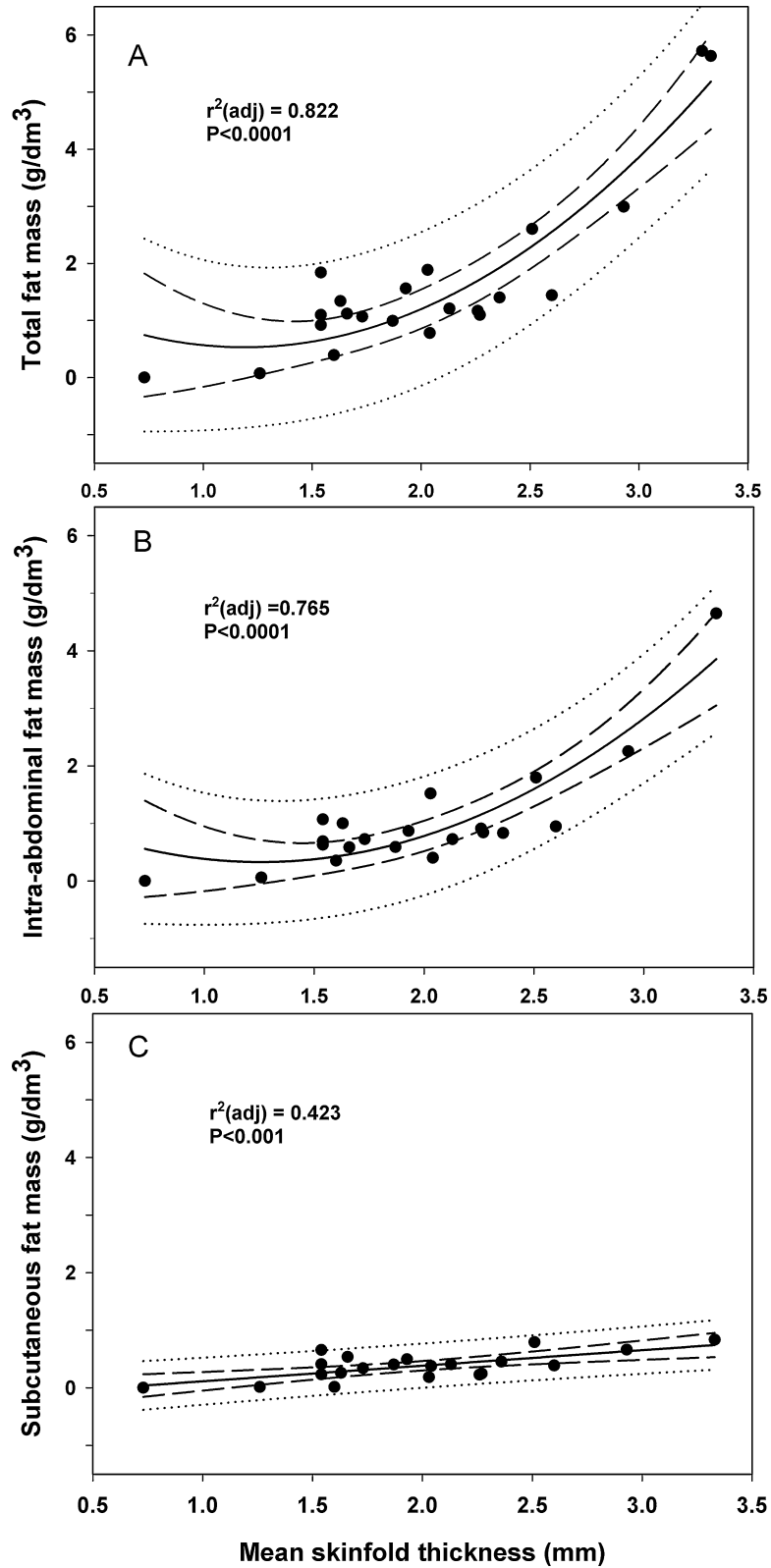


Fig. 2. **A.** Best-fit curvilinear regression of total mass of adipose tissue (FMI) on mean skinfold thickness. Individual data points (solid dots), regression (solid line), 95% confidence limits (dashed lines) and 95% prediction limits (dotted lines). **B.** Best-fit curvilinear regression of mass of intra-abdominal adipose tissue (FMI) on mean skinfold thickness; symbols as in (A). **C.** Best-fit linear regression of mass (FMI) of subcutaneous adipose tissue on mean skinfold thickness; symbols as in (A).

**TABLE V. The Best Fit Predictions (f) of the Total Mass of Adipose Tissue and That of Different Body Regions, Based on Regressions of Dissected Fat Mass (FMI) on Skinfold Thickness (SFT) From Different Anatomical Sites of Measuring SFT**

Regression of fat mass (FMI) on SFT	x = Skinfold thickness (mm)	
	Mean of all SFT measuring sites (N = 7)	Abdomen, anterior to umbilicus only (N = 1)
Total body fat (f <sub>T</sub> )		
Pearson r	0.916	0.929
r <sup>2</sup> adj	0.822	0.848
SEE	0.623	0.574
df	21	21
F	49.372****	59.680****
Prediction	$f_T = 1.959 - 2.411x + 1.016x^2$	$f_T = 0.349 + 0.173x + 0.162x^2$
Subcutaneous fat (f <sub>S</sub> )		
Pearson r	0.672	0.713
r <sup>2</sup> adj	0.423	0.482
SEE	0.179	0.169
df	20	20
F	15.667***	19.641***
Prediction	$f_S = 0.271x - 0.159$	$f_S = 0.021 + 0.182x$
Intra-abdominal fat (f <sub>A</sub> )		
Pearson r	0.888	0.903
r <sup>2</sup> adj	0.765	0.794
SEE	0.475	0.455
df	20	20
F	33.570****	39.613****
Prediction	$f_A = 1.624 - 2.061x + 0.821x^2$	$f_A = 0.697 - 0.417x + 0.246x^2$

\*\*\*P < 0.001.  
\*\*\*\*P < 0.0001.

**Using SFT to Predict Fatness in Terms of Percent Body Fat and FMI**

In toque macaques, FMI and Percent Body Fat (Table II) were highly correlated (Pearson’s  $r = 0.982$ ,  $df = 20$ ,  $P < 0.0001$ ). It was of interest to compare how well these two variables of known fatness related to SFT. With 20 degrees of freedom, the coefficients of correlation with mean SFT:  $r = 0.916$  ( $P < 0.001$ ) and  $r = 0.874$  ( $P < 0.001$ ), as well as the regression coefficients,  $r^2_{adj} = 0.822$  ( $P < 0.001$ ) and  $r^2_{adj} = 0.740$  ( $P < 0.001$ ), were somewhat greater with FMI than Percent Body Fat, respectively. The best fit estimates of fatness were curvilinear functions of mean SFT (e.g., Fig. 2A). Using mean SFT (mm) as the independent predictor variable (x), the equations for these regression relationships were:

$$\begin{aligned} \text{FMI (g/dm}^3\text{)} &= 1.959 - 2.411x + 1.016x^2 \\ \text{Percent Body Fat} &= 3.022 - 3.296x + 1.519x^2 \end{aligned}$$

**DISCUSSION**

**Fat Depots and SFT Sites of Measurement Differ in Reliability for Estimating Total Body Fat.**

The relation between skinfold thickness (SFT) and fatness has been reviewed before, particularly

for humans [Garrow, 1983; Lohman, 1981; Womersley & Durnin, 1977] and has been examined among non-human primates [Kemnitz et al., 1989; Murayama et al., 2006; Small, 1981; Walike et al., 1977; Walker et al., 1984]. Earlier studies (see Methods) served to guide the selection of points for measuring SFT of toque macaques.

Individuals differed in the mean thickness of their skinfolds, but the differences in SFTs among depots showed a regular pattern across individuals. This was indicated by statistically significant correlations in SFT between pairs of compared skinfold sites (Table IV) and reflected the consistent allometric variation in the distribution of underlying adipose tissue among different depots [Dittus, 2013]. The exception to this was those paired with the side of the chest, where correlations were low or not statistically significant because of consistently low fatness at this site; mean SFT at the chest side was similar to that of a double layer of skin thickness alone (Table III). Similarities in the SFT of some sites may be owed to little anatomical difference in fat mass; for example, the triceps and chest side measured different sections of the same depot (labeled “BA” in Table I and Fig. 1). Similarly, the nape and subscapular were different sections of the same HUMP (upper back) depot. On the other hand,

the PAU (paunch) depot differed in thickness anterior and posterior to the umbilicus (Table I and III).

#### *Hypotheses 1 and 2*

In our first hypothesis we predicted a consistent relationship between SFT and the mass of dissectible adipose tissue (FMI) at sites of SFT measurement. This prediction was generally supported by our results, but individual SFT sites differed in the strength of this relationship. Statistically highly significant relationships were found between FMI and the mean of SFT measurements at all 7 sites and at a single site on the abdomen anterior to the umbilicus (Table III). The absence of a statistically significant relation between FMI and SFT at sites of low fat mass or variability (triceps, chest side) supports our second hypothesis; namely, that SFT predicts fatness most reliably at sites on the body where the variation in fatness is high. Exceptions to the latter were SFT sites that were known to be subject to unusual measurement error (abdomen posterior to the umbilicus, nape and subscapular) (Table III, and see below).

Two prominent subcutaneous fat depots, the axilla and groin, together comprise more than 52% of total subcutaneous fat (Table III). These depots were not measured for SFT, however, because they were deeply recessed anatomically and not accessed easily with skinfold calipers. The triceps has been a much used point for measuring skinfolds in humans [e.g., Durnin & Rahaman, 1967; Hammond, 1955; Lohman, 1981] as well as monkeys [Kemnitz et al., 1989; Moruyama et al., 2006; Small, 1981; Walike et al., 1977; Walker et al., 1984], despite widespread use, it has been shown to be an unreliable indicator of fatness in humans [Ruiz et al., 1971]. Likewise, in rhesus monkeys, Walker et al. [1984] dismissed the triceps as well as the subscapular points, and Small [1981] discarded both the subscapular and suprailiac sites (in baboons) for measurement. In toque macaques, sections of the limbs (other than triceps) have slightly more than 8% of subcutaneous fat, but as in other non-human primates, it was sparsely distributed and not useful for comparisons of fatness [Pond & Mattacks, 1987].

Awareness of the sources of variation in SFT measurement is important in interpreting estimates of fatness based on SFT measures. Generally, when measuring SFT the caliper pinched only a small portion of an underlying fat deposit that extended over a larger surface area and varied in shape and size. This factor may introduce measurement error. For example, the thickness of abdominal adipose tissue posterior to the umbilicus tapers from thick near the umbilicus to thin or absent near the pelvic bone such that variation in SFT measures is easily introduced according to the exact point of caliper placement. A similar caution has been raised by Ruiz

et al. [1971] in using the triceps point in humans. We adjusted for this in toque macaques by measuring at three equally spaced points between the umbilicus and the pelvis. But initially this had not been done consistently for all individuals in our study, hence the correlation between SFT and underlying fat was less than what it might have been (and predictably should be) for subcutaneous fat posterior to the umbilicus (Table III). In other studies of cercopithecids, the abdomen posterior to the umbilicus has been used often to predict fatness (Kemnitz et al., 1989; Muroyama et al., 2006; Walike et al., 1977; Walker et al., 1984) but the influence of measurement error caused by much anatomical variation of this depot is not known.

The tautness of the skin with its adhering underlying fat layer affected ease of SFT measurement with calipers. SFT was most taut at the nape (among large sized bodies) and suprailiac points. This could be a source of measurement error, supporting similar observation in other cercopithecids [Small, 1981; Walker et al., 1984]. The thickness of skin in humans and non-human primates is independent of age among adults; skin is less thick among infants, slightly thicker in males than females, and varies primarily with anatomic location [Chiou & Blume-Pevtavi, 2004; Kramer & Bielitzki, 2012; Sandby-Møller et al., 2003]. Our estimates of skin thickness in toque macaque support these observations from other primates. Minor variations in skin thickness are likely to have a proportionately greater effect on SFT-based estimates of fatness in leaner than fatter individuals. Formulas for estimating fatness, therefore, should indicate the site of SFT measurement (Table V). Although SFT relates to the thickness of the subcutaneous adipose layer, it does not necessarily define it. Instead, SFT is an arbitrary sample (with respect to depot anatomy) and its value lies mainly in its consistent scaling relation to the dissected fat mass of the depot. It follows that variation in skin thickness between measurement sites or depots may affect SFT magnitude without biasing its predictive relationship to fatness, as long as skin thickness is constant at a particular site across individuals.

The strength of correlations between individuals' SFT sites of measurement and the underlying fat masses (FMI) varied. However, the sums of the subcutaneous fat masses at each of the seven sites correlated significantly with their SFT means (Table III). For purposes of prediction equations (Table V), these means are recommended as optimal because each site contributes independently to the prediction and those of low variability moderate those of high variability, essentially correcting for any potential bias introduced by individual sites. On the other hand, Lohman [1981] suggested that, in humans, as few as two SFT sites are sufficient to characterize the thickness of the subcutaneous layer.

Our data imply that a single site on the abdomen above the umbilicus may be sufficient in macaques. The abdominal SFT is easy to measure.

### SFT as a Proxy for Fatness of the Whole Body and Its Different Regions in Toque Macaques and Other Primates

With an increase of total body fat, there is a consistent allometric anatomical distribution of fat mass among adipose deposits in different parts of the body. This has been shown in lemurs [Pereira & Pond, 1995], macaques (*M. fascicularis* and *M. nemestrina*) [Laber-Laird et al., 1991; Pond & Mattacks, 1987], *M. sinica* [Dittus, 2013] and humans [Allen et al., 1956]. Therefore, a given measure of subcutaneous fat mass allows one to estimate total fatness as well as differences in regional fat deposits.

#### Hypothesis 3.

These allometric relationships lend empirical validity to our third hypothesis, namely, that SFT is a statistically reliable predictor (Table V) not only of total fatness (Fig. 2A), but also of its constituent regions: intra-abdominal (Fig. 2B) and subcutaneous fat (Fig. 2C) in this non-human primate. A similar relationship had been demonstrated long ago in humans [Allen et al., 1956].

Dittus [2013] argued that the amount and anatomical distribution of adipose tissue are adaptive traits for energy efficiency, agile locomotion and terminal branch feeding in arboreal primates. These adaptations include low total fatness (about 2% in wild primates), a near absence of dissectible fat in the fetus and neonate, the tail, and limb extremities distal to the elbow or knee. With increasing fatness (among lean monkeys), subcutaneous fat accumulations shift away from the poles of the trunk (axilla and groin) towards the central ventral abdominal paunch that, together with similar shifts of internal fat, lowers the body's center of gravity closer to the supporting substrate and serves to stabilize arboreal mobility. Adipose tissue should be viewed as subject to postural adaptations for arboreal life, in the same way as other anatomical systems have been considered to be [Cartmill, 1972, 1992; Clutton-Brock & Harvey 1977; Fleagle & Mittermeier, 1980; Garber, 2011; Grand, 1984; Rosenberger, 2011; Zihlman et al., 2011a,b]. The anatomical distribution of adipose tissue is consistent with a need for body balance and agility as well as with allometric development (Dittus, 2013; Reiss, 1989). Adipose anatomy, therefore, should differ according to the mode of locomotion and feeding, such as terrestrial and/or arboreal quadrupedalism (most Old World monkeys), brachiation (Hylobatidae), slow clambering (*Pongo*), vertical clinging and leaping (many Strepsirrhini), use of prehensile tails (many *Cebus*,

*Sapajus*, and atelines) and terrestrial bipedalism (humans).

The equations for predicting adiposity (Table V) would be expected to apply to any primate whose locomotor anatomy is comparable to that of the toque macaque. In principle, the method for predicting adiposity from SFT is expected to have wider taxonomic relevance, but the empirical constants (the relation between any SFT site and its underlying fat mass) would need to be established because they would differ according to the anatomical distribution of adipose tissue typical for a species' anatomy and mode of locomotion.

Considerations of SFT and adipose tissue patterning evoke the long-standing and widely held belief that superficial adipose tissue is an adaptation for thermal insulation in mammals inhabiting cold regions. This notion has been applied also to populations of humans [e.g., Wells, 2012] and monkeys [Paterson, 1996]. Anatomical investigations of many mammalian species have shown, however, that subcutaneous fat plays little or no role in thermal insulation of most terrestrial mammals, including humans [Pond, 1998 2012] and macaques [Dittus, 2013]. Fur plays a far greater role in thermal insulation than adipose tissue. Notwithstanding, adipose tissue does accumulate in many mammals [Pond 1998], including Japanese macaques [Hamada et al., 2003; Muroyama et al., 2006] as a source of energy to overcome periods of food shortage that are typical of most cold climates and a few tropical ones as well (e.g., the Asian rainforests inhabited by the orangutan [Knott, 1998]).

Body fat functions primarily as an energy reserve [Pond, 1998]. Its quantity is determined largely by a balance between the diet (energy input) and energy expenditure for survival and reproduction. Factors that affect this balance include, for example, seasonal and habitat variations in the food supply [Knott 1998; Muroyama et al., 2006; Pond, 1998], access to agricultural produce and level of activity [Altmann et al., 1993; Dittus 2013; Stern 1984], reproductive condition and social rank [Dittus, 1998; Garcia et al., 2010], physical growth [Cheverud et al., 1992] and health [Shively et al., 2009]. SFT, validated by a direct measure of fat mass, offers a convenient means for estimating an individual's total energy reserve (including its anatomical distribution), and for testing hypotheses concerning the role of body condition in the evolution of primate life-histories.

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