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Testosterone, Physical Activity, and Somatic Outcomes Among Filipino Males

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ABSTRACT Testosterone (T) facilitates male investment in reproduction in part through its anabolic effects on skeletal muscle. Traits like muscle and strength are energetically costly but are believed to enhance competitive ability in humans and other mammals. However, there are limited data on relationships between T and somatic outcomes in lean, non-western populations. We evaluate relationships between waking and pre-bed salivary T and adiposity, fat-free mass (FFM), arm muscle area (AMA), and grip strength (GS) in a large, population-based birth cohort of young adult Filipino males (20.8–22.6 years, $n = 872$). Data were collected as part of the Cebu Longitudinal Health and Nutrition Survey. Neither waking nor evening T predicted FFM, AMA, or GS. However, there were borderline or significant interactions between T and basketball playing (the most common team sport) and weight lifting as predictors of outcomes: higher waking T predicted higher FFM (activity $\times$ T interaction $P < 0.01$), AMA (interaction $P < 0.1$), and GS (interaction $P < 0.02$) among frequent basketball players, and GS (interaction $P < 0.09$) among the smaller sample of weight lifters. In contrast to clinical studies, but consistent with findings in several subsistence-level populations, T was positively related to adiposity in these lean young males, suggesting that energy status might regulate circulating T. Our findings support a role of the prewaking rise in T as a determinant of energetic allocation to lean mass and strength in the context of repeated muscular use and support the hypothesized role of T as a mediator of investment in costly somatic traits in human males. Am J Phys Anthropol 142:590–599, 2010.

As in other mammals, human adults face life history trade-offs between energetic allocation to reproductive effort and somatic maintenance (Stearns, 1989). The central importance of energetics to female reproductive status is illustrated by the exquisite sensitivity of female reproductive hormone production to energy intake, adiposity, and physical activity (Ellison, 2001). Given that successful female production requires extensive energetic investment in ovulation, gestation, and lactation, it is not surprising that female fecundity is modulated in response to multiple indices reflecting short and long-term access to energetic resources (Jasienska, 2001; Ellison, 2003).

In contrast to females, the trade-offs that determine variation in levels of male reproductive investment are less clear. Testosterone (T) is the primary male sex hormone, with wide ranging androgenic effects, and is a likely mediator of energetic allocation to male reproductive investment (Campbell and Leslie, 1995; Bribiescas, 2001; Ellison et al., 2002; Vitzthum et al., 2009). However, spermatogenesis itself is energetically inexpensive and only requires low levels of T to be sustained (Elia, 1992). T's primary reproductive function is instead thought to be indirect, operating through its effects on the soma and behavior, as described in a range of mammals (Field et al., 1985; Forger and Breedlove, 1987; Sapolsky, 1991; Muller and Wrangham, 2004; Beehner et al., 2006; Teichroeb and Sicotte, 2008). In clinical settings, T has been shown to have anabolic effects on skeletal muscle, leading to enhanced fat-free mass and strength (Bhasin et al., 2001; Sinha-Hikim et al., 2003; Storer et al., 2003). T also stimulates lipolysis in adipose tissue and inhibits the differentiation of adipogenic precursor cells, reducing the development and maintenance of adipose stores (Singh et al., 2003; Herbst and Bhasin, 2004; Woodhouse et al., 2004). These findings are complemented by large studies of US and European males showing that measures of adiposity, such as waist circumference and body mass index, are negatively associated with T (Gapstur et al., 2002; Jensen et al., 2004; Svartberg et al., 2004). These observations have contributed to a model in which T helps coordinate energetic allocation to costly somatic traits (e.g., muscle mass) and related behaviors that impact a male's mating opportunities via effects on competitive ability or attractiveness,

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at a cost to survival or maintenance functions, including adipose reserves (Bribiescas, 2001; Ellison, 2003).

Although a general model of T-driven somatic investment is well-supported in clinical work, the expected relationships between T and somatic traits have not been consistently found when investigated in subsistence-level societies. For instance, T has been found to relate positively to measures of lean mass in some (Lukas et al., 2004; Campbell et al., 2007) but not all (Campbell et al., 2003) studies in which this relationship has been evaluated, while others report inconsistent associations between T and BMI or body weight, which are a composite of lean mass and body fat (Bentley et al., 1993; Bribiescas, 1996; Ellison and Panter-Brick, 1996). In addition, at least three studies in subsistence-level societies have documented positive relationships between adiposity and T, contrary to expectations based upon the lipolytic effect of the hormone documented in clinical settings (Ellison and Panter-Brick, 1996; Campbell et al., 2003, 2007). Previous anthropological studies of T and body composition have tended to focus on relatively small samples and have used a variety of protocols when collecting samples and body composition data, which may have contributed to these discrepancies. These issues aside, support for the presumed role of T as a coordinator of somatic effort in human males, especially under conditions of subsistence-level activity and nutrition, remains equivocal.

Here we seek to shed light on the relationship between T, energetics, and somatic investment in a large sample of young adult Filipino males (age 20–22 years, n = 872). These men are representative of the population from which they are drawn in Cebu City, the Philippines and are characterized by a near absence of overweight and obesity. We carefully standardize timing of saliva collection at waking (AM) and in the evening (PM) and consider the role of diet, participation in physically demanding sports, and other potential influences that might confound or moderate the role of T as an influence on costly somatic traits.

MATERIALS AND METHODS

Study population

Data come from the Cebu Longitudinal Health and Nutrition Survey (CLHNS), a community-based birth cohort study of mothers and their infants born in 1983–84 (Adair et al., 1993, 2001; Kuzawa and Adair, 2003). Men were aged 20–22 at the time of this sampling. Body weight (kg), height (cm), waist circumference (cm), hip circumference (cm) and triceps, suprailiac, and subscapular skinfold thicknesses (mm) were measured using standard anthropometric techniques (Lohman et al., 1988). The body mass index (BMI) was calculated as the ratio of weight (kg)/height (m^2). Grip strength was measured to the closest kg in triplicate using a dynamometer with the average used in analyses. Percent body fat was calculated from triceps, suprailiac, and subscapular skinfold thicknesses using body density estimates and a body composition predictive formula validated for use in Asian populations (Durnin and Womersley, 1974; Deurenberg and Deurenberg-Yap, 2002). Fat mass and fat-free mass were calculated from their respective percentages of body weight. Upper arm muscle area (cm^2) was estimated from arm circumference and triceps skinfolds while adjusting for area of humerus (Frisancho, 1990). Dietary intake was measured using two 24-h recalls on consecutive days and the mean was used in analyses. Energy and fat intake were calculated using Philippines Food Composition Tables produced by the Food and Nutrition Research Institute of the Philippines (FNRI, 1997). This research was conducted under conditions of informed consent with human-subjects clearance from the Institutional Review Boards of the University of North Carolina, Chapel Hill and Northwestern University.

Testosterone measurement

Each participant was provided with instructions and two tubes for saliva collection. The first sample was collected immediately prior to bed. After collection, the tube was sealed and kept at room temperature. They were instructed to place the second tube next to their bed and to collect the second sample immediately upon waking the following morning. At each collection time, the participant was asked to record the time of collection. Both tubes were collected later that day by an interviewer, who placed the tubes on ice packs in a cooler. They were then transported to a freezer where they were stored at $-35^{\circ}C$ until shipment on dry ice to Northwestern University, where they were stored at $-80^{\circ}C$. They were thawed, centrifuged, supernatant separated, and aliquoted into smaller tubes for analysis of individual analytes.

Salivary T was analyzed at Northwestern University, using an immunoassay kit produced by Salimetrics (State College, PA; Kit No. 1-2402) and its associated protocols. The interassay coefficients of variation were 13.7% and 11.5% for high and low pools, respectively.

Sample selection

During the 2005 survey, 1,008 males of the original cohort of 1,633 liveborn males, ages 21.5 years (range 20.8–22.6 years), were located and interviewed. Of these, a final sample of 872 individuals agreed to participate in saliva collection, had sufficient sample for analysis and complete questionnaire data and biomarker assessments. The analysis subsample also excluded 17 individuals classified as obese (BMI $>$ 30), as the study's focus was on identifying allocations related to energetic trade-offs and excess adiposity was rare in the sample. Obesity is known to affect T levels through a variety of pathways, including aromatization of T into estrogen and reduced levels of sex-hormone binding globulin, leading to accelerated T clearance rates (Vermeulen et al., 1969; Schneider et al., 1979; Kley et al., 1980). Baseline characteristics of the final subsample of 872 males who were included in the present analyses were compared with those who were in the sample at baseline (singleton, liveborn infants). Those lost to follow-up were born to mothers who were more educated and with higher household assets scores at baseline, but there were no significant differences between our subsample here and the original baseline cohort in birth weight, birth length, parity, father's education, maternal height, or mother's or father's age at baseline.

Physical activity

We hypothesized that the relationship between T and somatic traits would be accentuated among regular participants in physically demanding sports. Measures of physical activity were reported as part of the standard

TABLE 1. Characteristics of Cebu males[a]

	Total sample (n = 872)	Range	Tertile of AM T			P-value[b]
			Tertile 1 (n = 291)	Tertile 2 (n = 291)	Tertile 3 (n = 290)	
Age (years)	21.5 ± 0.3	(20.8, 22.6)	21.5	21.5	21.5	0.94
AM T (pg ml^{-1})	191.1 ± 76.4	(26.1, 588.4)	116.2	181.7	275.5	0.00
PM T (pg ml^{-1})	117.7 ± 52.9	(2.6, 406.5)	102.6	116.3	134.2	0.00
Height (cm)	163.0 ± 5.9	(144.5, 181.2)	162.8	163.0	163.3	0.60
Weight (kg)	55.3 ± 8.0	(36.0, 89.0)	55.1	54.8	55.9	0.23
BMI	20.8 ± 2.5	(14.5, 29.9)	20.7	20.6	20.9	0.25
% underweight (BMI<18.5)[c]	15.9%		17.9%	16.9%	12.8%	0.21
% overweight (25≤BMI<30)[c]	7.1%		8.1%	7.1%	6.1%	0.64
% obese (BMI≥30)[c]	1.9%		2.0%	1.7%	2.0%	0.94
Waist circumference (cm)	71.6 ± 6.5	(56.5, 110.0)	71.5	71.0	72.2	0.08
Hip circumference (cm)	75.6 ± 6.4	(59.2, 104.0)	75.4	75.3	76.2	0.21
Waist-to-hip ratio	0.95 ± 0.04	(0.80, 1.19)	0.95	0.94	0.95	0.23
Triceps skin fold (mm)	10.4 ± 4.9	(3.0, 43.0)	10.2	10.2	10.9	0.06
Fat-free mass (kg)	46.5 ± 5.4	(32.6, 66.7)	46.6	46.2	46.7	0.06
Arm Muscle Area (cm^2)	34.6 ± 7.4	(14.2, 76.0)	34.7	34.0	35.2	0.15
Right grip strength (kg)[d]	73.7 ± 22.7	(17.0, 129.3)	73.8	72.0	75.3	0.29
Left grip strength (kg)[e]	69.9 ± 21.7	(5.0, 107.7)	69.7	66.2	75.4	0.15
Basketball player[f] (%)	22.9%		23.0%	21.7%	24.1%	0.78
Weight lifter (%)	4.1%		1.8%	5.8%	4.8%	0.03
Per capita household income (pesos)	90 ± 111	(0, 2110)	90	86	94	0.13
Daily energy intake (kcal)	2171 ± 882	(228, 5,809)	2,098	2,152	2,265	0.05

[a] mean ± SD.
[b] One-way ANOVA or chi-square across tertiles of AM T.
[c] Calculated before removal of 17 obese individuals from analysis sample (n = 889) using criteria of WHO (2000).
[d] Limited to right-handed individuals (n = 728).
[e] Limited to left-handed individuals (n = 135).
[f] Frequent basketball (three or more times per month).

CLHNS interview, and basketball was the most common sport reported. Among the 872 men in the sample, 266 reported playing some basketball. To limit our assessment to men who played regularly, we selected the 200 men (23% of the sample) who reported playing basketball three or more times each month as frequent basketball players. A total of 36 men (4%) reported lifting weights, and 10 of these were also frequent basketball players. Most of the men (n = 646) were categorized as less active, defined as not lifting weights and no or infrequent basketball playing. We evaluated whether the men who participated in sports differed from the less active men in ways that might influence our models. There were no differences in standing height between basketball players, weight lifters and less active men (ANOVA). Men who were less active were more likely to have graduated from high school when compared to frequent basketball players (Chi-square, $P < 0.003$).

Statistical analysis

All analyses were performed with version 10 of Stata (Stata Corporation, College Station, TX). Somatic variables, age, AM T (pg ml^{-1}), PM T (pg ml^{-1}) and daily food intake (kcal) were analyzed as continuous variables. Triceps, suprailiac, and subscapular skinfold thicknesses, fat mass, AM, and PM T were log-transformed to normalize the distributions. We first calculated mean levels of each variable stratified across tertiles of AM T (Table 1), and correlations were calculated to evaluate crude associations between T and somatic characteristics. Next, we used multiple regression to evaluate relationships between AM T and PM T and somatic outcomes as main effects and as interactions with activity patterns (Table 3 and 4), adjusting for covariates and potential confounders.

RESULTS

Characteristics of study subjects are reported in Table 1. Compared to similarly aged US males (NHANES; McDowell et al., 2005), Cebu males weighed less (mean: 55.3 kg vs. 83.4 kg), were shorter (mean: 163.0 cm vs. 176.7 cm), had lower BMI (mean: 20.8 vs. 26.6), and a smaller waist circumference (71.6 cm vs. 92.5 cm). Levels of overweight (7.1%) and obesity (1.9%) in our sample were low relative to 35.4 and 26.2% prevalence, respectively, reported in US men (NCHS, 2008). T followed the expected diurnal pattern. There were significant mean differences across tertiles of AM T for multiple measures of body composition, energy status, and energy intake.

Table 2 reports partial correlation coefficients between AM and PM T and somatic outcomes, adjusting for usual wake time (AM) and time of saliva collection (AM and PM). Consistent with findings from other lean populations with low average BMI, AM T was significantly positively correlated with percent body fat, fat mass, and suprailiac and subscapular skinfold thicknesses. Contrary to expectations, AM T was not related to any measure of lean mass or strength, and PM T was not significantly correlated with any somatic or energetic variable.

We hypothesized that the relationship between T and somatic traits would be more pronounced among men who regularly participated in physically demanding sports. Figure 1 shows geometric mean AM and PM T levels stratified on categories of sports participation. Frequent basketball players had significantly higher PM T than less active men, while weight lifters had signifi-

TABLE 2. Partial correlation coefficients (r) relating testosterone and somatic and energetic traits (n = 872)[a]

	Waking T	Evening T
Height	0.01	−0.01
Weight	0.04	0.01
Body mass index	0.04	0.02
Body fat %	0.08*	0.02
Fat mass[b]	0.09**	0.03
Waist circumference	0.03	0.004
Waist-to-hip ratio	−0.02	0.02
Triceps skin fold thickness	0.06	0.01
Subscapular skinfold thickness[b]	0.07*	0.04
Suprailiac skinfold thickness[b]	0.09**	0.01
Fat-free mass	0.01	0.01
Upper arm muscle area	0.04	0.05
Right hand grip strength[c]	0.04	−0.004
Left hand grip strength[d]	0.13	−0.003
Daily energy intake	0.05	−0.04

[a] log-transformed waking and evening salivary testosterone adjusted for usual wake time (AM) and time of saliva collection (AM & PM). *$P < 0.05$, **$P < 0.02$.
[b] log-transformed.
[c] Limited to right-handed individuals (n = 728).
[d] Limited to left-handed individuals (n = 135).

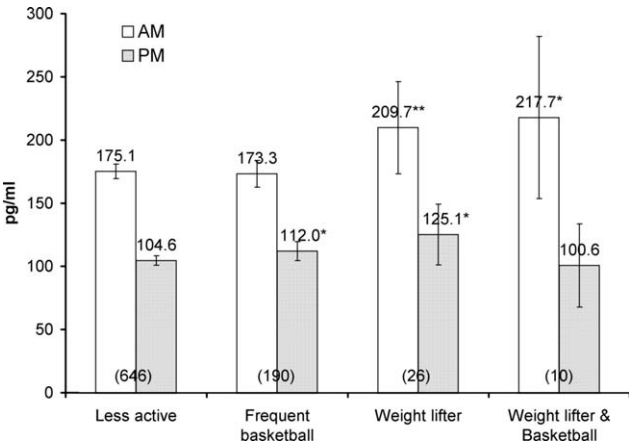

Fig. 1. Geometric mean waking (AM) and evening (PM) salivary testosterone by sports involvement. Values adjusted for usual wake time (AM) and time of saliva collection (AM and PM). Sample sizes in parentheses. Significant difference with less-active *$P < 0.1$, **$P < 0.05$.

cantly elevated AM T. Men who reported playing basketball and weight lifting had the highest AM T, but their PM T was about the same as that of less active men.

To evaluate the relationship between T and somatic outcomes, we next ran a series of multiple regression models beginning with a base model that evaluated the relationship between basketball playing or weight lifting as predictors of each somatic outcome, adjusting for height, age, and daily energy intake (coefficients not shown). We then added either AM or PM T to the base model. The final interaction model tested for a significant interaction between AM or PM T and sports participation as predictors of that outcome. Because only 10 men reported frequent basketball playing and lifting weights, they were counted as basketball players in models with basketball playing as a predictor and as weight lifters in models with weight lifting as a predictor.

In base models, frequent basketball players and weight lifters each had higher fat-free mass (FFM) (Table 3). There was a significant interaction between AM T and frequent basketball; with higher AM T predicting higher FFM among basketball players. In models including PM T, there was a borderline significant interaction between weight lifting and T, such that weight lifters with the lowest PM T had greatest FFM.

In models predicting arm muscle area (AMA), weight lifters had roughly 4 cm^2 additional AMA, which was a significant difference compared to nonweight lifters (Table 4). There was a borderline positive interaction between frequent basketball playing and AM T, with basketball players trending toward higher AMA when their AM T was relatively high. There was a borderline significant association between PM T and AMA in models adjusting for frequent basketball playing or weight lifting, respectively.

There was more consistent evidence for an interaction between sports participation and AM T in models predicting right grip strength in right-handed men (n = 728) (Table 5). There was a significant positive interaction between AM T and basketball playing in models predicting right grip strength, indicating that men with higher T had higher grip strength than men with lower T in this sports category. Similarly, AM T tended to be positively related to grip strength among weight lifters, although this interaction was not significant. When comparable models were run predicting left handed grip strength in left-handed men (n = 135), neither AM or PM T, or interactions with sports involvement, approached statistical significance (results not shown).

To help visualize the prominent interactions present in this sample, Figures 2 and 3 show best fitting regression lines and 95% confidence intervals between arm muscle area and right grip strength, respectively, and AM T, stratified on categories of sports participation. Here AM T values were logged residuals from a separate regression model that adjusted for time of saliva collection and usual wake time. Because these models are stratified on sports participation (unlike the above models, in which interactions between T and each sport were evaluated in separate models), we plotted the 10 men who were both basketball players and weight lifters as a separate category to avoid having to arbitrarily assign them to one sport. These figures show clearly that the positive relationship between AM T and both outcomes is limited to men who are involved with sports, with the steepest slopes found among the small sample of men who were involved with both sports.

DISCUSSION

In this lean sample of young adult males T is a positive predictor of traits related to muscularity and strength but primarily when combined with activities likely to impose demands on the musculature. Among physically active men in this sample, higher AM T predicts increased lean mass, arm muscle area, and grip strength. In contrast to expectations from US samples (Bhasin et al., 2001; Woodhouse et al., 2004), but consistent with findings in several subsistence-level populations (Ellison and Panter-Brick, 1996; Campbell et al., 2003, 2007), we found significant positive relationships between adiposity and salivary AM T. Together, our findings suggest that, under conditions of marginal energetic status, the anabolic effects of T on sexually dimorphic tissues may be greatest when combined with frequent muscular use (Ellison, 2001).

TABLE 3. Multiple regression models predicting fat-free mass (kg)[a]

			Waking T				Evening T			
	Base model	*P*	Main effects	*P*	Interaction	*P*	Main effects	*P*	Interaction	*P*
Basketball player	**0.82 (0.17, 1.47)**	**0.02**	**0.82** (0.17, 1.47)	**0.01**	**0.82** (0.17, 1.47)	**0.01**	**0.81** (0.15, 1.46)	**0.02**	**0.77** (0.12, 1.43)	**0.02**
T			−0.05 (−0.70, 0.61)	0.89	−0.56 (−1.32, 0.21)	0.15	0.20 (−0.40, 0.80)	0.52	0.01 (−0.66, 0.67)	0.98
BB X T					**1.96** (0.47, 3.46)	**0.01**			1.01 (−0.53, 2.55)	0.20
Model R^2	0.413		0.417		0.417		0.413		0.414	
Weight lifter	**1.31 (−0.07, 2.69)**	**0.07**	**1.33** (−0.06, 2.72)	**0.06**	**1.41** (−0.15, 2.97)	**0.08**	**1.29** (−0.10, 2.67)	**0.07**	**1.49** (0.09, 2.90)	**0.04**
T			−0.10 (−0.76, 0.56)	0.76	−0.09 (−0.76, 0.58)	0.79	0.21 (−0.39, 0.81)	0.50	0.33 (−0.28, 0.95)	0.29
WL X T					−0.44 (−4.42, 3.54)	0.83			**−2.51** (−5.31, 0.28)	**0.08**
Model R^2	0.411		0.411		0.411		0.411		0.413	

[a] β (95%CI). Models adjust for age, height and daily energy intake (coefficients not shown). Testosterone was separately adjusted for time of saliva collection (AM and PM) and usual wake time (AM). T = testosterone, BB = basketball player, WL = weight lifter. Coefficients consistent with a statistical trend or stronger ($P < 0.1$) in bold.

TABLE 4. Multiple regression models predicting arm muscle area (cm^2)[a]

			Waking T				Evening T			
	Base model	*P*	Main effects	*P*	Interaction	*P*	Main effects	*P*	Interaction	*P*
Basketball player	0.57 (−0.58, 1.71)	0.34	0.57 (−0.58, 1.71)	0.33	0.57 (−0.57, 1.71)	0.33	0.52 (−0.63, 1.66)	0.38	0.46 (−0.69, 1.61)	0.43
T			0.64 (−0.51, 1.80)	0.28	0.06 (−1.28, 1.40)	0.93	**0.94** (−0.12, 2.00)	**0.08**	0.60 (−0.57, 1.77)	0.31
BB X T					**2.24** (−0.40, 4.88)	**0.10**			1.81 (−0.89, 4.51)	0.19
Model R^2	0.036		0.037		0.040		0.039		0.041	
Weight lifter	**4.04 (1.63, 6.46)**	**0.001**	**3.96** (1.53, 6.38)	**0.001**	**3.00** (0.28, 5.72)	**0.03**	**3.95** (1.54, 6.37)	**0.00**	**4.24** (1.8, 6.69)	**0.01**
T			0.48 (−0.68, 1.63)	0.42	0.33 (−0.84, 1.49)	0.59	**0.89** (−0.16, 1.94)	**0.10**	**1.06** (−0.01, 2.14)	**0.05**
WL X T					5.34 (−1.60, 12.28)	0.13			−3.54 (−8.41, 1.33)	0.15
Model R^2	0.047		0.048		0.050		0.050		0.052	

[a] β (95%CI). Models adjust for age, height and daily energy intake (coefficients not shown). Testosterone was separately adjusted for time of saliva collection (AM and PM) and usual wake time (AM). T = testosterone, BB = basketball player, WL = weight lifter. Coefficients consistent with a statistical trend or stronger ($P < 0.1$) in bold.

TABLE 5. Multiple regression models predicting grip strength (kg)[a]

			Waking T				Evening T			
	Base models	*P*	Main effects	*P*	Interaction	*P*	Main effects	*P*	Interaction	*P*
Basketball player	1.13 (−2.80, 5.06)	0.58	0.51 (−1.27, 2.30)	0.57	0.50 (−1.28, 2.28)	0.58	0.50 (−1.28, 2.29)	0.58	0.36 (−1.43, 2.16)	0.69
T			0.79(−0.92, 2.50)	0.37	−0.35 (−2.32, 1.62)	0.73	0.15 (−1.46, 1.77)	0.85	−0.42 (−2.19, 1.35)	0.64
BB X T					**4.53** (0.59, 8.48)	**0.02**			3.36 (−0.92, 7.65)	0.12
Model R^2	0.044		0.045		0.052		0.044		0.047	
Weight lifter	**6.93 (−1.09, 14.95)**	**0.09**	3.00 (−0.66, 6.66)	0.11	1.03 (−3.26, 5.32)	0.64	**3.13** (−0.51, 6.78)	**0.09**	**3.15** (−0.58, 6.88)	**0.10**
T			0.64 (−1.08, 2.36)	0.46	0.39 (−1.35, 2.13)	0.66	0.11 (−1.50, 1.72)	0.90	0.11 (−1.53, 1.76)	0.89
WL X T					**9.11** (−1.30, 19.52)	**0.09**			−0.17 (−8.28, 7.93)	0.97
Model R^2	0.048		0.048		0.052		0.048		0.048	

[a] β (95%CI). Models predict right grip strength in right-handed men (n = 728) adjusting for age, height and daily energy intake (coefficients not shown). Testosterone was separately adjusted for time of saliva collection (AM and PM) and usual wake time (AM). T = testosterone, BB = basketball player, WL = weight lifter. Coefficients consistent with a statistical trend or stronger ($P < 0.1$) in bold.

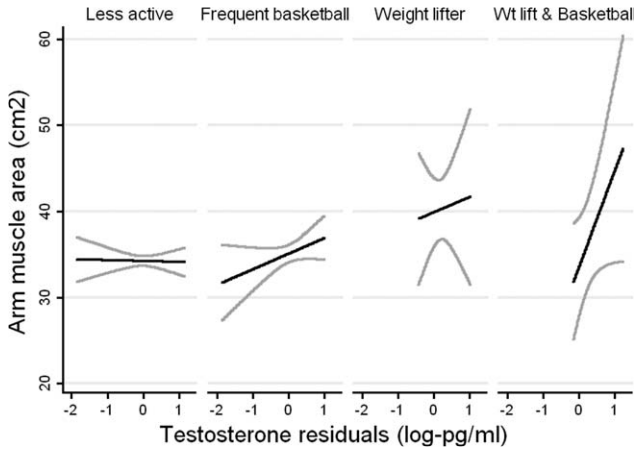

Fig. 2. Regression of arm muscle area on waking testosterone (log-pg ml^{-1}) stratified on involvement in sports. Dark line = best fit linear trend, light gray lines = 95% confidence interval. Testosterone = residuals from a separate regression adjusting for time of saliva collection and usual wake time. See Fig. 1 for sample sizes.

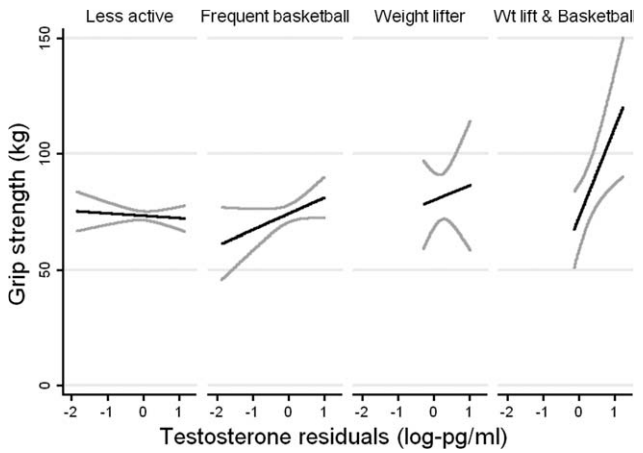

Fig. 3. Regression of right grip strength on waking testosterone (log-pg ml^{-1}) stratified on involvement in sports in right-handed individuals (n = 728). Dark line = best fit linear trend, light gray lines = 95% confidence interval. Testosterone = residuals from a separate regression adjusting for time of saliva collection and usual wake time. See Fig. 1 for sample sizes.

In the Philippines, the primary spectator and competitive sport is basketball, and amateur pick-up games are common in many Cebu neighborhoods. In our sample, 30% of men reported playing basketball at least once per month and 23% played frequently. Weight lifting was less common in our sample and was reported by only 4% of our respondents. T tended to be higher among men engaged in sports, with highest AM T found in weight lifters and elevated PM T found among basketball players. This finding could reflect trait-level variation in which men with higher T are motivated to participate in sports, although a large study of US men found no cross-sectional or longitudinal relationships between androgens and physical activity (Wolin et al., 2007). Conversely, sports participation might influence T. Endurance activities have been shown to reduce T production in short-term exercise bouts (Hoogeveen and Zonderland,

1996; Karkoulias et al., 2008) and over months of training (Urhausen et al., 1987; Wheeler et al., 1991; Tyndall et al., 1996). Although we lack data on basketball or weightlifting intensity, our finding that active men tend to have higher T does not support the notion that rigorous activity suppressed T in our sample. Alternatively, men who engage in sporting activities may also experience short-term increases in T, which may be related to competition (Elias, 1981; Kraemer et al., 1998; Salvador et al., 2003; Parmigiani et al., 2006). If men in our sample were engaged in competitive activity in the hours or days before sampling, this could contribute to T differences between active and inactive men. In future rounds of CLHNS data collection we hope to assess physical activity and competitive outcomes prior to sample collection to more fully address these possibilities.

The finding that T is a stronger predictor of metabolically-costly somatic investments among men reporting involvement in these physically demanding sports is consistent with prior work showing that the anabolic effects of T are accentuated when combined with strenuous physical activity (Bhasin et al., 2000; Casaburi et al., 2004; Kvorning et al., 2006). This use-driven pattern, matching allocation with function, could reflect an efficient means by which competitive ability is enhanced in proportion to use (Ellison, 2001) and is consistent with the hypothesized role of T as a mediator of male life history allocation and somatic investment (Bribiescas, 2001; Ellison, 2001). Given the metabolic costs of muscle mass, it would be maladaptive for males to indiscriminately maintain lean mass beyond the level of physical demand. In addition, the significantly lower T that we recently documented among the fathers in this sample of men would be expected to reduce these investments as reproductive priorities shift from mating activities to parenting (Kuzawa et al., 2009).

We found most consistent relationships between somatic outcomes and AM T, with less evidence for associations with PM T. To the extent that we are documenting a causal relationship between T and somatic traits, our findings suggest that T in the morning may be more important as a regulator of somatic investments. It is notable, however, that previous studies of subsistence-level populations have found mixed results in analyses of circadian T dynamics and body composition variables. Among the Kami (Nepal), males exhibited seasonal (winter) positive associations between mid-arm circumference and AM T but not PM T (Ellison and Panter-Brick, 1996). In contrast, PM T was found to be a positive predictor of lean mass for urban males in Zimbabwe whereas AM T was not (Lukas et al., 2004). PM T also predicted greater lean mass among a sample of Ariaal (Kenya) men, whereas relationships with AM T were unclear (Campbell et al., 2007). In Cebu, we collected morning samples immediately upon waking, which might have reduced the impact of uncontrolled circadian changes and improved our ability to detect relationships with waking samples (Axelsson et al., 2005). In addition, these studies did not consider a testosterone-by-activity interaction, which in our sample was necessary to identify significant relationships with somatic outcomes. Future work will be needed to clarify the importance of the overnight rise in T and the decline in T across the day, in combination with activity patterns, for the development and maintenance of T-dependent traits like body composition and strength.

T has been shown to have lipolytic effects in clinical studies (Woodhouse et al., 2004), which is believed to explain the common finding of a negative relationship between T and adiposity in large studies of US and European men (Gapstur et al., 2002; Jensen et al., 2004; Svartberg et al., 2004; Hall et al., 2008). A small but growing list of studies in subsistence-level populations have failed to find this expected inverse relationship between T and adiposity (Ellison and Panter-Brick, 1996; Campbell et al., 2003, 2007), although it was demonstrated in one such group (Campbell et al., 2006). Some of the inconsistencies in past findings may stem from differences in study design and measurement protocol, including the tendency for clinical studies to provide exogenous androgens coupled with more sophisticated lab-based body composition measurement techniques (Bhasin et al., 2001; Sinha-Hikim et al., 2003; Woodhouse et al., 2004). However, our findings, which are based upon a uniform sample collection protocol across a large, representative sample of men, are generally in agreement with findings from these smaller prior studies. The Filipino men in this sample had an average BMI of 20.8 kg m^{-2} and a greater percentage of our sample was underweight (15.9%) than the percentages of overweight and obese combined (WHO Consultation on Obesity, 2000). Thus our sample may have a similar metabolic and energetic status to subsistence-level societies, which could help explain the similarities in our findings. In addition to the positive association between adiposity and T in our sample, a link between T and energetics was also indicated by a significant positive gradient of energy intake across tertiles of AM T and a positive but nonsignificant correlation between energy intake and AM T ($P < 0.15$). That AM T is related to both caloric intake and energy status (adiposity) in our sample may suggest a responsiveness of T to acute and longer-term signals of energetic status (Bribiescas, 2001; Ellison, 2001, 2003; Campbell et al., 2003).

The physiological pathways that could account for these associations between energy intake, adiposity, and T are not clear. Sex hormone binding globulin (SHBG) may relate inversely to adiposity (Mohr et al., 2006; Gomez et al., 2007), mediated through the effects of adiposity on insulin and leptin. For instance, both leptin and insulin have been shown to relate inversely to SHBG in some samples of men, resulting in an increase in the fraction of circulating T that is unbound and thus reflected in salivary measures of free T (Pasquali et al., 1995; Söderberg et al., 2001; Gomez, 2007). In addition, in rodent models, leptin and insulin have been shown to modulate production of gonadotropin-releasing hormone, thereby influencing release of luteinizing hormone and testicular production of T (Bruning et al., 2000; Burcelin et al., 2003; Gamba and Pralong, 2006). Future analyses that include SHBG and metabolic hormones will be needed to clarify the pathways accounting for the positive association between T and adiposity documented in lean samples such as ours.

Several limitations of this study warrant mention. As is true for most prior studies of male reproductive ecology, the cross-sectional nature of our T samples prevents us from assessing how T and somatic outcomes change with time, which is critical to establishing causality. Planned, future follow-ups will help clarify whether baseline T predicts changes in somatic measures as the men in our sample age. In addition, we only have one AM and PM salivary sample for each participant, and past work has shown that collecting samples across several days and using the average in analyses enhances reliability (Dabbs, 1990). This study makes up for our

limited T measurements by collecting samples at highly standardized times of day in a sample of nearly 900 men, which exceeds the size of most prior studies in this area. It is important to note that our single measurements of AM and PM T do not introduce bias, but merely reduce the reliability of our T measures and thereby limits our ability to detect relationships between T and somatic phenotypes. Had we had an opportunity to collect additional saliva samples for each individual, some of the borderline-significant relationships that we documented would likely have passed the threshold for statistical significance. These limitations aside, it seems unlikely that our general conclusions would change. For instance, T was not close to being significantly related to most somatic outcomes until interacted on physical activity, suggesting that the absence of a relationship between these measures does not merely reflect the unreliability of our T estimates.

In summary, in this population of lean young adult Filipino men, we find evidence for dose-dependent anabolic effects of T on muscularity and strength when combined with physically demanding activity. This finding is generally consistent with previous studies demonstrating anabolic effects of T (Bhasin et al., 2001; Singh et al., 2003; Sinha-Hikim et al., 2003) and suggests that under conditions of energetic constraint T-driven investment in metabolically-costly lean mass is contingent upon functional loading (Ellison, 2001). Our finding of a positive relationship between T and adiposity is consistent with findings in several lean populations and may indicate that energetic status plays a more prominent role in the regulation of T and related somatic investments under conditions of marginal nutritional status. Our findings are generally in agreement with the proposed role of T as a mediator of somatic investment in male life history and complement the more common focus on the hormone's influence on the behavioral component of mating and competition.

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