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Costs and benefits of fat-free muscle mass in men: relationship to mating success, dietary requirements, and native immunity

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Abstract

On average, men have 61% more muscle mass than women (d=3), a sex difference which is developmentally related to their much higher levels of testosterone. Potential benefits of greater male muscle mass include increased mating opportunities, while potential costs include increased dietary requirements and decreased immune function. Using data on males aged 18–59 years from the third National Health and Nutrition Examination Survey and including other relevant variables, fat-free mass (FFM) and/or limb muscle volume (LMV) are significant predictors of the numbers of total and past-year self-reported sex partners, as well as age at first intercourse. On the cost side, FFM and LMV are strong positive predictors of daily energy intake and strong negative predictors of C-reactive protein and white blood cell count, measures of native immunity.
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1. Introduction

Despite claims of reduced levels of sexual dimorphism in the genus *Homo* (e.g., compared to *Australopithecus*) (McHenry, 1994; Plavcan, 2001), muscle mass and resulting muscular strength are very sexually dimorphic traits in contemporary humans. On average, men have approximately 61% more total muscle mass than women (Illner, Brinkmann, Heller, Bosy-Westphal, & Müller, 2000; Kim et al., 2004; Phillips, 1995; Shen, Punyanitya, Wang, Gallagher, & St. Onge, 2004; Wetter & Economos, 2004). Relatively more of this muscle mass is allocated to the upper body, with men having about 75% more arm muscle mass than women (Abe, Kearns, & Fukunaga, 2003; Fuller, Laskey, & Elia, 1992; Gallagher, Visser, Meersman, & Sepulveda, 1997; Nindl, Scoville, Sheehan, Leone, & Mello, 2002). Not surprisingly, this latter difference translates into approximately 90% greater upper body strength in men (Bohannon, 1997; Murray, Gore, Gardner, & Mollinger, 1985; Stoll et al., 2000).

The mean effect size for these sex differences in total and upper body muscle mass and strength is about 3, which indicates less than 10% overlap between the male and female distributions, with 99.9% of females falling below the male mean. An effect size of this magnitude also means that sex—a single dichotomous variable—explains roughly 70% of the variance in muscle mass and upper body strength in humans. The sex difference in upper-body muscle mass in humans is similar in magnitude to the sex difference in lean body mass in gorillas, the most sexually dimorphic primate (Zihlman & McFarland, 2000).

Sex differences in lower-body muscularity are nearly as large. In the legs, men's muscle mass is about 50% greater than that of women with a mean effect size of approximately 2 (Fuller et al., 1992; Lawler, Halliwill, Summer, Joyner, & Mulvagh, 1998; Shih, Wang, Heo, Wang, & Heymsfield, 2000), and lower body strength is about 65% greater with an effect size of about 3 (Bishop, Cureton, & Collins, 1987; Falkel, Sawka, Levine, & Pandolf, 1985; Wilmore, 1978).

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These substantial sex differences in muscle mass and strength suggest that there has been strong disruptive selection favoring greater male muscularity in the human lineage. In overall body weight comparisons, a female advantage in fat mass largely counterbalances a male advantage in muscle mass, making the sexes appear quite similar. But this gross similarity masks very different tissue investment strategies by males and females, which, in turn, suggests divergent selective histories, thus undermining conclusions about the human mating system based on overall body-weight dimorphism (e.g., Plavcan, 2001).

Why do humans exhibit such dramatic sexual dimorphism in muscle mass and strength? The ultimate answer rests in the history of selection that produced these sex differences. Because muscle would have been advantageous in aggressive competition for mating opportunities, sexual selection is a likely cause. Excess muscle may be a costly signal but in that case it would only be favored by selection if it conveyed information valuable to females in choosing mates, so such a suggestion raises the question: what is the function of excess muscle? Its obvious use and advantages in aggressive competition suggest that it evolved for that purpose.

The effects of such selection are potentially still observable—as preferences, outcomes, and tradeoffs—in contemporary populations. A number of studies have shown that women prefer muscular men (Dixson, Halliwell, East, Wignarajah, & Anderson, 2003, 2007; Frederick & Haselton, 2007), men with a larger chest size in relation to waist size (Swami & Tovee, 2005; Swami et al., 2007), and men with more upper-body muscle (Fan, Dai, Liu, & Wu, 2005). More muscular men report more sexual partners (Frederick & Haselton, 2007), as do men who score better in tests of muscular strength and physical fitness (Gallup, White, & Gallup, 2007; Honnekopp, Rudolpha, Beierb, Liebert, & Muller, 2007), and college athletes report almost twice as many sex partners in the past year as nonathletes (Faurie, Pontier, & Raymond, 2004). Men's greater muscle mass develops during puberty as testosterone levels increase; the amount of muscle is directly related to testosterone levels (Griggs et al., 1989), a conclusion supported behaviorally by the popularity of exogenous androgenic hormones among those seeking to increase muscle mass.

However, all adaptations entail costs and muscle mass is presumably no exception. Because muscle growth is supported by androgens the possible negative effects of testosterone on health—particularly its immunosuppressant effects (Folstad & Karter, 1992)—are relevant. Castrated males have longer life spans and lower infection rates than intact males in a variety of animals (Asdell, Doornenbal, Josh, & Sperling, 1967; Hamilton, 1948; Waters, Shen, & Glickman, 2000; Zuk & McKean, 1996), and testosterone supplementation increases both infection and mortality rates (Ahmed, Penhale, & Talal, 1985; Al-Afaleq & Homeida, 1998; Grossman, 1985; Hamilton & Mestler, 1969; Klein, 2000; Marker & Moore, 1988; May, 2007; Place, 2000; Salvador et al., 1996; Zuk & McKean, 1996).

In a meta-analysis of hormone manipulation studies with birds and mammals, Roberts et al. (2004) found only a weak effect of testosterone on immunity, but these authors neglected to group species by mating system and thus did not properly test the sexual-selection hypothesis. In both birds and mammals, sex differences in mortality are not universal but proportionate to the intensity of sexual selection (Promislow, 1992; Promislow, Montgomerie, & Martin 1992); in systematic cross species comparisons, sex differences in the rates of parasitism likewise parallel the force of sexual selection (Moore & Wilson, 2002).

Consistent with animal data, testosterone has also been shown to be negatively related to some measures of human immune function (Kanda, Tsuchida, & Tamaki, 1996; Muehlenbein & Bribiescas, 2005; Sthoeger, Chiorazzi, & Lahita, 1988) including C-reactive protein (CRP), a measure of native immunity (Davoodi et al., 2007; Kapoor, Clarke, Stanworth, Channer, & Jones, 2007; Yang, Lv, Huang, Xu, & Wu, 2005). Another measure of native immunity, the white blood cell count (WBCC) is negatively related to testosterone in birds (Al-Afaleq & Homeida, 1998). Sex differences in testosterone levels may explain why women have higher CRP levels (Khera et al., 2005) and higher WBCC than men (Bain, 1996). Native immunity is the immediate nonspecific immune response to infection, in contrast to the slower production of specific antibodies characteristic of acquired immunity (native immunity is often called "innate" or "natural" immunity in the medical literature; we avoid these terms because they are potentially confusing for readers of this Journal).

In support of the idea that testosterone has an adverse effect on immunity, mortality from infectious disease is substantially higher in males than in females (Owens, 2002). In the United States in 2004, age-adjusted deaths from infectious diseases were 42% higher in males compared with females, and still 31% higher excluding HIV-related deaths (based on data in Kung, Hoyert, Xu, & Murphs, 2008). The greater difference with HIV deaths included may also partially reflect testosterone's effects on risk-taking.

Another potential cost of higher muscle mass is an increase in energy needs. Skeletal muscle is the most significant determinant of differences in resting energy requirements and the major factor in total energy expenditure (Hayes et al., 2002; Zurlo, Larson, Bogardus, & Ravussin, 1990). Higher testosterone levels in males are associated with increased metabolic rates and concomitant energy demands (Ketterson et al., 1991; Marker & Moore, 1988; Welle, Jozefowicz, Forbes, & Riggs, 1992).

Thus, we test three predictions related to the costs and benefits of sexually dimorphic muscle mass in a large group of American men:

1) Muscularity will be positively related to the number of (self-reported) heterosexual sex partners and negatively related to the age at first intercourse,

2) Muscularity will be positively associated with substantially higher energy intake, and
3) Muscularity will be negatively related to native immunity, as measured by blood levels of CRP and WBCC.

2. Methods

To assess relationships among these and other variables, we used data from the third National Health and Nutrition Examination Survey (NHANES III), conducted from 1988 to 1994. The sample included 5536 males and 6492 females aged 18–59 with 38% non-Hispanic whites, 29% non-Hispanic blacks, 28% Hispanics, and 5% "other." Anthropometric data included height, weight, biacromial diameter, upper arm and thigh lengths, circumferences, and skinfolds.

The hypothesized predictor variable is "muscularity," and we operationalize it in two independent ways: fat-free mass (FFM) and limb muscle volume (LMV). To estimate overall muscularity, FFM was estimated from bioelectrical impedance (Chumlea, Guo, Kuczmarski, Flegal, & Johsson, 2002). Limb muscularity was based on the mean of separate estimates of muscle volumes for the upper arm and thigh. Upper-arm muscle volume was calculated from arm muscle area (Frisancho, 1981) times upper-arm length. Thigh-muscle volume was calculated by a similar method from comparable upper-leg data.

As body fat increases, skeletal muscle mass must also increase to support the additional weight. This muscle-to-support-fat is not the muscle we expect to increase copulatory success, and its effects must somehow be taken into account. In order to do so, we use body mass index (BMI), a well-established measure of overall fattiness, as a control variable in all of our statistical analyses.

Three self-report measures were used as indicators of copulatory success, a proxy for reproductive success in the absence of birth control (Perusse, 1993). NHANES III sample men were asked by a skilled interviewer about the number of lifetime and past-year female sexual partners, and age at first intercourse; responses are available from 5130 men aged 18–59 years.

To assess hypothesized costs of muscularity, caloric intake and immunity measures were extracted from NHANES III data. Detailed dietary histories based on 24-hour recall were obtained by a skilled NHANES interviewer and total energy intake calculated by matching the foods eaten to the USDA National Nutrient Database. Two measures of native immunity were available: white blood cell count (WBCC) and C-reactive protein (CRP). The WBCC is the number of circulating immune system cells per mm^3 of blood. CRP is an acute-phase protein, produced by liver and fat cells, which binds to pathogenic bacteria so that they can be destroyed by phagocytes, and thus provides an important element in native immunity, the early defense system against infections.

Two measures of physical activity were used as control variables in the analysis of daily energy intake. Leisure time physical activity data was available for 5504 men aged 18–59. The total amount of activity was calculated in metabolic equivalents (METs) based on the frequency of walking a mile or more, running, biking, swimming, aerobic dancing, other dancing, gardening, calisthenics, weight lifting, and up to four additional activities per person (one MET is 1 kcal/kg per hour, the approximate energy consumption of a person at rest). Leisure-time physical activity is of interest because it could elevate both muscle mass and dietary intake, obscuring the relationship between muscularity and caloric intake.

For the same reason, occupational exertion is also a potential confounding factor. Occupation, coded into 40 categories, was available for 4704 men aged 18–59 in NHANES III. We calculated the mean daily caloric expenditure for the sample males in each occupational category and divided by the mean for the whole sample. Clerical workers, for example, average 0.74 of the overall mean, while farm operators average 1.08. Each male in the sample was then assigned the mean value corresponding to his particular occupation for use as a control variable in evaluating other factors related to daily caloric expenditure.

Multiple linear regression was used to evaluate the relative predictive value of all independent variables (with BMI as a control variable for the measures of muscle mass). Predictor variables available to the regressions were FFM, LMV, BMI, height, age, marital status, family income, years of education, race/ethnicity, bone mineral density of the femur, serum testosterone (available for 1048 men), and occupational and leisure-time exertion. Outcome variables (each in a separate regression) were lifetime and last-year heterosexual sex partners, age at first coitus, daily energy intake, CRP and WBCC. Data

Table 1
Biomedical sex differences for participants aged 18–49 years, based on NHANES III sample

Variable	Male		Female		Sexual Dimorphism	
	Mean	S.D.	Mean	S.D.	Ratio	*d*
Age	33.0	8.6	33.0	3.7	1.00	0.00
Height, cm	176.4	7.3	163.0	6.7	1.08	1.75
Weight, kg	81.5	17.5	68.5	17.4	1.19	0.74
BMI	26.1	5.0	25.7	6.4	1.01	0.07
% Body fat	23.2	6.2	33.9	7.9	0.68	−1.52
Arm muscle, L	2.5	0.5	1.4	0.4	1.78	2.50
Thigh muscle, L	7.8	1.6	5.2	1.2	1.50	1.86
Fat free mass, kg	60.8	10.4	43.1	6.8	1.41	2.06
Energy intake, MJ	12.05	5.09	8.01	3.39	1.50	0.95
C-reactive protein	0.33	0.49	0.48	0.69	0.68	−0.27
WBCC	7.08	2.13	7.41	2.28	0.96	−0.15
Testosterone, ng/ml	5.69	1.91				

Sample size varies between 4244 and 4677 for males (except only 862 for testosterone), and between 4701 to 5482 for females.
All differences except age and BMI are significant at $p<.001$ using analysis of variance.

Table 2
Standardized regression coefficients from stepwise regression for the number of total sexual partners, partners during the past year, and age at first intercourse for men 18–59 years old in NHANES III

	Total Partners	Partners past year	Age at first intercourse
n	4774	4737	4167
Age	0.144***		0.137***
Married (1), unmarried (0)	−0.088***	−0.185***	0.090***
FFM	0.063**		
LMV		0.079***	−0.046**
BMI	−0.040***	−0.035*	
Education			0.062***
Occupational exertion			−0.036*
r^2	0.021***	0.049***	0.046***

* $p<.05$.
** $p<.01$.
*** $p<.001$.

analysis was performed using SPSS 15.0. Most analyses are for men aged 18–59 years because these years should bracket more than 95% of human male reproduction. In comparing males with females, a more restricted age group of 18–49 is used, because female measures tend to change after menopause.

3. Results

3.1. Descriptive statistics

For both sexes aged 18–49 in the NHANES III sample, Table 1 shows weighted means, standard deviations, sexual dimorphism (expressed as male mean/female mean), and effect sizes (d) for sex differences. Although there is only 19% dimorphism in weight and 1% dimorphism in BMI, dimorphism is 41% for fat-free mass, 78% for upper-arm muscle volume, and 50% for thigh muscle volume. Energy intake (+50%) is slightly more dimorphic than fat free mass. As expected, percent body fat and two measures of native immunity, CRP and WBCC, are dimorphic in the opposite direction, being significantly higher in women.

Table 3
Standardized regression coefficients for significant predictors for daily energy intake in men 18–59 years old in the NHANES III (n=4318)

	Beta
Age	−0.176***
BMI	−0.183***
FFM	0.246***
Leisure time activity (METs)	0.050**
Occupational exertion	0.084***
r^2	0.072***

** $p<.01$.
*** $p<.00001$.

Table 4
Standardized regression coefficients for significant predictors of CRP and WBC in men 18–59 years old (n=4935)

	CRP	WBCC
Age	0.086***	0.032*
FFM	−0.061**	−0.160***
BMI	0.133***	0.201***
r^2	0.019***	0.019***

* $p<.05$.
** $p<.01$.
*** $p<.00001$.

3.2. Association among predictors: testosterone and muscularity

Controlling for age and BMI, serum testosterone is positively related to FFM (r=0.174 $p<.000001$) and LMV (r=0.289, $p<.000001$).

3.3. Predicting number of female sex partners and age at first coitus from measures of muscularity

Stepwise regression was used to evaluate the effect of FFM, LMV, and the other variables listed in the methods on lifetime and past-year sexual partners and age at first intercourse. The results are shown in Table 2.

FFM is the more significant measure of muscularity for total partners and LMV is also significant if substituted for FFM in this regression (beta=.046, $p<.01$, r^2=.020). For partners in the past year, LMV is the significant predictor and, age is no longer significant. For age at first intercourse, LMV is again the significant muscularity factor in the regression along with age, marital status, education, and occupational exertion. Although height is correlated with total partners controlling for age (r=.047, $p<.01$), it is not significant in these multiple regressions.

If the sample is restricted to men with serum testosterone values, testosterone is not significant in the regressions for total partners and age at first intercourse. In the regression for partners in the past year, LMV (beta=.064, $p<.05$) and testosterone (beta=.088, $p<.01$) are both significant and 6.8% of the variance is explained.

Current marital status interacts with both FFM and reported mating success. Controlling for age, currently married men report 10.7 fewer lifetime sexual partners ($p<.001$), 1.1 fewer past-year partners ($p<.001$), and having first intercourse 1.2 years later ($p<.001$); controlling for age and BMI, they have 0.57 kg less FFM ($p<.01$). Conversely, controlling for age and BMI, each kilogram of FFM decreases the likelihood of being married by 1.3% ($p<.01$).

3.4. Predicting energy costs from measures of muscularity

Table 3 shows the results of the regression for energy intake. FFM is the strongest predictor of energy intake, followed by BMI, age, occupational exertion and leisure

activity. If LMV is substituted in the regression, the result is similar (beta=.098, $p<.05$).

3.5. Predicting native immunity from muscularity

Another possible cost associated with muscularity is lower native immunity as reflected in lower levels of C-reactive protein and WBCC, both of which are significantly higher in women (Table 1). In the regression, FFM is the strongest muscularity predictor, but substituting LMV gives a similar result (beta=−.056, $p<.001$, $r^2=.015$). Likewise, FFM is the stronger negative predictor for WBCC (Table 4). but if LMV is used in place of FFM, it has a similar effect, [beta =−.127, $p<.001$, and $r^2=.020$ ($p<.0000001$)]. Testosterone is not significant in either regression, but, controlling for age, is negatively related to CRP (−0.083, $p<.05$).

3.6. Visualizing the relationships

As detailed above, our statistical analyses use a multivariate approach to control for BMI, age, and other factors of interest. However, it is also desirable to visualize the magnitude of the observed relationships among muscularity and its costs. Since additional FFM is required to support additional fat (on average, 0.54 kg per kg fat in this sample), and because this relationship may change with age, we computed the residuals from a regression of FFM on age and BMI for NHANES III men. These residuals provide a measure of relative muscularity in the same way that residuals from the cross-species brain size/body size relationship give a measure of relative encephalization. Thus, in Fig. 1, the data are arranged by quintiles of relative muscularity, least muscular men on the left. As can be seen, after adjusting for age (by using residuals from a regression of each dependent variable separately on age), lifetime sex partners and caloric intake monotonically increase, and native immunity (as measured by WBCC) decreases, with increasing relative muscularity.

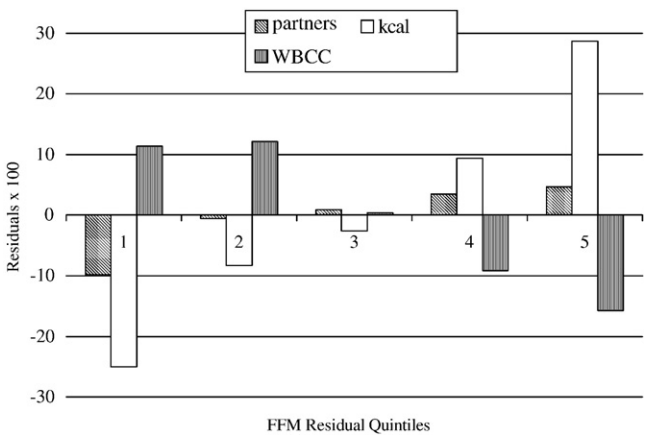

Fig. 1. Standardized residuals from regression with age for total sexual partners, energy intake, and white blood cell count in relation to quintiles of FFM residuals from regression with age and BMI.

4. Discussion

Because the population used in this study comprises well-nourished men with low exposure to infectious disease, this may influence the degree to which muscular phenotypes are expressed. Also, the number of self-reported sexual partners has limitations as a measure of potential reproductive success. Men with higher testosterone and increased muscle mass may be more prone than other men to exaggerate their number of sexual partners, while men with lower testosterone may be more accurate. However, women do report finding muscular men more attractive (Dixson et al., 2003, 2007; Fan et al., 2005) and also report that their most recent short-term sex partners are more muscular than other sex partners (Frederick & Haselton, 2007), giving some credence to the reported differences. With these qualifications in mind, it is worthwhile to evaluate the present findings.

When age, marital status, and BMI are controlled in men in the NHANES III sample, measures of current muscularity are significantly positively associated with the number of total sexual partners and partners in the past year and negatively with age at first intercourse. Although the variance explained is modest, the relationship with total partners and age at first intercourse is related to current muscularity for a sample varying in age from 18 to 59 years. As would be expected, current muscularity is more strongly related to the most current measure of copulatory success, partners in the past year. The significant relationship between muscularity and the number of sexual partners is consistent with the idea that the substantial human sexual dimorphism in muscle mass is at least partially a product of sexual selection in past environments where there was a high degree of male mating competition.

Male muscle mass is not free to escalate indefinitely, because it is also a significant handicap requiring substantially more dietary energy and testosterone to maintain. The increased dietary cost of increased muscle is confirmed by our finding that total energy intake is 50% higher in males and is strongly related to measures of muscle mass even when controlling for the amount of leisure-time physical activity and occupational exertion.

The higher testosterone levels in males, which support larger muscle masses, have been linked to decreases in immune system activity. This interpretation is supported by our findings of lower C-reactive protein and WBCC in males and a negative relationship between both of these and the two measures of muscle mass. Thus, males with higher muscle mass will be less able to respond quickly to the most common infectious agents which native immunity has evolved to combat. The stronger relationship of measures of costs and benefits with muscularity than with serum testosterone itself suggests that muscle mass may be a better reflection of bioactive androgens over time than a single measurement of serum testosterone.

In other animals where body mass is highly sexually dimorphic, it is functionally related to male-male competi-

tion for mates, suggesting that sex differences in mass and muscularity are often a product of sexual selection (Andersson, 1994). But in the case of humans, body size differences are relatively small, while differences in muscle mass and body fat are quite substantial. This discrepancy can be explained by two divergent selection pressures—for more muscle in men and for more fat in women (Lassek & Gaulin, 2006, 2007, 2008)—selection pressures which nearly cancel at the level of overall body mass. Selection favoring accumulation of brain-building resources in females and increased strength in males has produced two morphs that are similar in total mass but dramatically different in body composition. If the differing forces—favoring female fat accumulation and male muscle accumulation—are properly understood, an inference that the human lineage has experienced a long history of monogamy becomes dubious.

Data reported here suggest that male muscle mass is evolutionarily constrained. While it may provide advantages in terms of increased access to mates, it entails costs which make each increment of muscle harder to sustain. This pattern of results suggests conflicting pressures operating through sexual and natural selection. Sexual selection favors increased muscularity in males through its favorable effects on mate access, but natural selection favors lower levels of muscle mass than would result from sexual selection alone because muscularity has energetic and immune costs that presumably would elevate mortality from starvation and infection. If this interpretation is correct, then it is possible that there is a range of muscularity levels that produce equal net fitness effects with different contributions from fertility and survival, thus potentially explaining genetic variance in male muscularity.

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