

# The Paternal Provisioning Hypothesis: Effects of Workload and Testosterone Production on Men's Musculature

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**KEY WORDS** men's life history; parental investment; steroid physiology; workload; muscle mass

## ABSTRACT

**OBJECTIVES:** Testosterone supports male reproduction through a broad range of behavioral and physiological effects, including the maintenance of sexually dimorphic muscle used in male-male competition. Although it is often assumed that a persistent relationship exists between men's testosterone production and musculature, most studies either fail to find evidence for such a relationship, or document very weak associations. In nonhuman primates, by contrast, correlations between testosterone and muscle mass are higher. Here, we propose the "Paternal Provisioning Hypothesis," which predicts that men's skeletal muscle is less dependent on the effects of androgens than that of other primates, and more sensitive to the physical demands of men's work. This permits human fathers to downregulate testosterone, which has negative impacts on pair-bonding and parenting effort, but without sacrificing the strength and musculature necessary to provision mates and offspring.

**METHODS:** We tested predictions of the Paternal Provisioning Hypothesis by assessing parental status, salivary testosterone levels, anthropometry, and strength among 122 men (ages 18–78) at the Mogielica Human Ecology Study Site in rural Poland. We chose this population because men practice subsistence agriculture, regularly engaging in physically demanding labor. Grip and chest strength were assessed using a dynamometer, and upper-body musculature was estimated from arm muscle circumference.

**RESULTS:** In this population, testosterone showed no association with measures of strength or musculature, and was lower in older men and pair-bonded fathers. Marital and parental status and workload, by contrast, were positive predictors of muscle mass and strength measures.

**DISCUSSION:** These findings offer support for the Paternal Provisioning Hypothesis. *Am J Phys Anthropol* 000:000–000, 2015. © 2015 Wiley Periodicals, Inc.

The steroid hormone testosterone supports male reproduction through a broad range of morphological, physiological, and behavioral effects (Wingfield et al., 1990; Ketterson and Nolan, 1992, 1999; Krause, 2006). Accumulating evidence suggests that testosterone's primary function is to promote male mating effort (Ketterson and Nolan, 1992), with implications for two fundamental life history trade-offs: that between current and future reproduction, and that between quantity and quality of offspring (Trivers, 1972, Hill, 1993). Across vertebrates, elevated testosterone is associated with investment in male-male competition and mate-seeking behaviors (Fox, 1983; Wingfield et al., 1990; Ketterson and Nolan, 1992; Creel et al., 1997; Bribiescas, 2001). Consequently, in a range of species, testosterone reduces both paternal care and provisioning (i.e., investment in offspring quality; Wingfield et al. 1990, Smale et al., 2005; Lynn, 2008). Testosterone can also increase mortality from extrinsic and intrinsic causes, adversely affecting future reproduction (Wilson and Daly, 1985; Marler and Moore, 1988; Ketterson and Nolan, 1992; Kruger and Nesse, 2006; Redpath et al., 2006).

Sexually dimorphic traits—both ornaments and armaments—are supported by testosterone in many vertebrates (e.g., Lincoln, 1971, 1992; Whiting et al., 2003; Bókony et al., 2008). Such traits can increase mating success, but also incur energetic costs, and sometimes

decrease survival (Promislow, 1992, Promislow et al., 1992). In humans, muscle mass and strength are highly sexually dimorphic, and skeletal muscle hypertrophy is thought to have reproductive benefits via male-male competition and female choice (Dixson, 2009). However,

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muscle tissue is also metabolically active and energetically expensive, accounting for ~20% of men's basal metabolic rate (Bribiescas, 2001). Accordingly, testosterone has been hypothesized to directly mediate competing energy allocations between reproduction and survival in men, through the management of sexually dimorphic muscle mass (Bribiescas, 1996, 2001; Bribiescas et al., 2012).

This 'Somatic Allocation' model has been used to explain both inter- and intra-population variation in men's testosterone levels (Bentley et al., 1993; Bribiescas, 1996, 2001; Ellison and Panter-Brick, 1996; Campbell et al., 2003, 2007; Gettler et al., 2010). The model hypothesizes that increased energy availability promotes elevated testosterone, which supports muscular hypertrophy. Nutritional constraint, however, downregulates testosterone, producing a diminished, thriftier phenotype (Bribiescas, 1996, 2001).

Consistent with this hypothesis, men's testosterone levels fall on an urbanization gradient across populations (Bribiescas, 2001; Gray et al., 2006a, 2006b). Well-nourished, Westernized men exhibit the highest levels of testosterone, and the largest body sizes, while men involved in subsistence food production generally have suboptimal nutrition, reduced testosterone levels, and shorter stature (e.g., Stini, 1979; Ellison et al., 1989; Bentley et al., 1993; Bribiescas 1996, 2001; Gray et al., 2006a, 2006b). Nutritional constraints appear to have a similar effect on chimpanzees, as males living in the wild maintain smaller body sizes and lower levels of urinary testosterone than their well-fed, captive counterparts (Muller and Wrangham, 2005). The model has been less successful in predicting intra-population variation in testosterone, particularly among subsistence groups, in which men show little testosterone response to changes in food availability (e.g., Bentley et al., 1993; Ellison and Panter-Brick, 1996; for chimpanzees see Muller and Wrangham, 2005).

Implicit in the Somatic Allocation Hypothesis is an assumption that a direct, persistent link is maintained between testosterone and men's musculature, and that any effects of energy availability on muscle mass are mediated by testosterone. Evidence for this assumption, however, is weak. Whether variation in men's testosterone levels predicts variation in musculature, across populations, has rarely been examined. One exception is a study of Ariaal pastoralists, comparing salivary testosterone and anthropometry among sub-populations of settled and nomadic men (Campbell et al., 2006b). Interestingly, settled men had higher morning and evening testosterone than nomads. Fat free mass was not appreciably different between the two groups, however, suggesting that inter-population variation in men's testosterone did not produce differential expression of skeletal muscle phenotype. Within populations, some studies report relationships between measures of testosterone and muscle mass, but also find that testosterone predicts little of the variance in men's musculature (e.g., Lukas et al., 2004; Campbell et al., 2007; Lassek and Gaulin, 2009). Men's testosterone levels predicted only three percent of the variance in fat free mass within a large cohort of American men (Lassek and Gaulin, 2009;  $N = 1,048$ ), and in a study of Zimbabwean men, testosterone levels accounted for <1% of the variance in fat free mass (Lukas et al., 2004;  $N = 109$ ).

Other large- and small-scale studies have generally failed, within populations, to find any direct relationship between men's testosterone levels and their strength or

musculature (Kenyan Ariaal and Turkana men, Nepalese Taman and Kami men, and Filipino men: Ellison and Panter-Brick 1996; Campbell et al., 2003, 2006a, 2006b; Gettler et al., 2010). By contrast, although data are somewhat sparse in nonhuman primates, measures of testosterone and muscle mass appear to be correlated in chimpanzee males (Emery Thompson et al., 2012), baboons males (Muehlenbein et al., 2001), and in male pig-tailed and rhesus macaques (Muehlenbein et al., 2002). In relatively small cross-sectional samples of captive baboons ( $N = 21$ ), pig-tailed macaques ( $N = 41$ ), and rhesus macaques ( $N = 53$ ), moderate correlations were found between serum testosterone and upper-arm circumference (muscle mass estimate) after accounting for age (Muehlenbein et al., 2001, 2002). Despite small samples, testosterone levels explained 18% of the variance in baboon arm circumference, and 15 and 9% of the variance, respectively, in pig-tailed and rhesus macaque arm circumference. In wild chimpanzees, Emery Thompson et al. (2012) examined longitudinal data consisting of 60 accumulated observation-years for males in the community. Mean annual urinary testosterone in males showed a strong correlation with a measure of muscle mass from urinary creatinine, with testosterone explaining 35% of the variance. Why is a relationship between testosterone and musculature apparently so much easier to detect in nonhuman primate males than in men?

Although it makes intuitive sense that investment in sexually dimorphic muscle should be mediated by testosterone, specific features of human life history call the logic of this hypothesis into question. Distinct from most mammals, humans exhibit a sexual division of labor, with male provisioning of mates and offspring (Lancaster and Lancaster, 1983; Kaplan et al., 2000; Wood and Marlowe, 2013). In foraging societies, men specialize in hunting large game, a difficult, dangerous activity that requires strength and endurance (Murdock and Provost, 1973; Gurven and Hill, 2009; Lancaster and Kaplan, 2009; Apicella, 2014). In traditional, preindustrial, and industrial societies, a clear trend emerges in which men's physical work, on average, involves greater reliance on strength tasks, particularly episodic bursts of upper-body strength and force (Murdock and Provost, 1973; Wood and Eagly, 2002). This trend is manifested more prominently among societies, such as foragers and agriculturalists, in which a pronounced sexual division of labor is associated with greater reliance on strength tasks in male work roles (Ibid.). Although substantial variability in men's parenting effort appears within the cross cultural record (Gray and Anderson, 2010), evidence from a number of studies shows that men increase their workload according to the number and age of their dependents (Quinlan, 2000; Marlowe, 2003; Knoester and Eggebeen, 2006; Lee et al., 2007; Hooper, 2011; Wood and Marlowe, 2013), which, in an evolutionary context, suggests that fathers in particular need to maintain physical strength and musculature to support their provisioning efforts.

At the same time, considerable evidence suggests that testosterone has a negative impact on male parenting effort and pair bonding in humans, just as it does in many other species (reviewed in Gettler, 2014). For example, in various studies men with elevated testosterone were found to be less responsive and less sympathetic to infant cries (Fleming et al., 2002), less interested in infants or infant stimuli (Storey et al.,

2000; Roney et al., 2006; Weisman et al., 2014), less involved with families and parenting (Alvergne et al., 2009; Mascaro et al., 2013), less committed to their current partner (Caldwell Hooper et al., 2011), and more interested in extra-pair mating (McIntyre et al., 2006). And numerous cross-cultural studies have reported that investing fathers maintain lower testosterone levels than single childless men, including among American, Canadian, Chinese, Filipino, Hadza, Jamaican, Senegalese, and Swiss men (Storey et al., 2000; Fleming et al., 2002; Gray et al., 2002, 2006a, 2006b, 2007; Alvergne et al., 2009; Kuzawa et al., 2009; Muller et al., 2009; Gettler et al., 2011; Perini et al., 2012). Furthermore, more pronounced diurnal declines in testosterone have been observed in relation to indices of paternal involvement, providing further evidence for a suppressive effect of male parenting on testosterone production (Muller et al., 2009; Gettler et al., 2012). Lower testosterone levels during fatherhood have been interpreted as a physiological shift toward investment in a current partner and shared offspring, and away from male status competition and mate-seeking behavior (Gray et al., 2002; Kuzawa et al., 2009; Muller et al., 2009; Gettler et al., 2011). Accordingly, in societies where men have little direct involvement with offspring, or maintain nonexclusive pair bonds, marriage and fatherhood may not be associated with reduced testosterone (Gray, 2003; Muller et al., 2009).

The Somatic Allocation model posits that testosterone determines physiological investment in mating effort by increasing muscle mass, and thus, effectiveness in reproductive competition (Bribiescas, 1996, 2001; Bribiescas et al., 2012). The model assumes, however, that men's activity patterns remain constant (Bribiescas, 1996), whereas recent evidence indicates that men's work demands change substantially across the lifespan, and particularly with fatherhood (Hooper, 2011; Marlowe, 2003; Wood and Marlowe, 2013). This suggests an important puzzle: if men's muscle mass is predominantly supported by testosterone, which declines sharply during fatherhood, then would not men's physical capabilities be compromised at the precise time when their provisioning responsibilities intensify?

We propose the Paternal Provisioning Hypothesis, which predicts that the lack of evidence for a clear relationship between men's testosterone levels and their musculature reflects a real phenomenon in which men's skeletal muscle is less dependent on the effects of androgens than that of other primates. This permits men's musculature and strength to be augmented during fatherhood, despite suppressed testosterone levels, through the physical demands of increased provisioning. We tested predictions of this 'Paternal Provisioning' hypothesis in the Mogielica Human Ecology Study Site in southern Poland. We chose this population because men often practice subsistence agriculture, and regularly engage in physically demanding labor.

Mutually exclusive predictions can be derived from the Paternal Provisioning and Somatic Allocation Hypotheses. For the Paternal Provisioning Hypothesis to be tenable, the following predictions must be supported. Pair-bonded, involved fathers should show lower testosterone levels than childless men (P1). Fathers should have increased workloads compared to childless men (P2). Despite lower testosterone levels, however, fatherhood and intensified workload will positively affect both musculature (P3) and strength (P4).

In contrast, the Somatic Allocation Hypothesis proposes that testosterone is the primary driver of somatic allocation toward musculature. According to this competing perspective, higher testosterone levels should have a positive impact on muscle mass (CP1) and strength (CP2). Furthermore, if men experience a reduction in testosterone levels during fatherhood, then pair-bonded fathers should show decreased musculature (CP3) and strength (CP4).

## METHODS

### Study site and participants

In summer 2011, research was conducted at the Mogielica Human Ecology Study Site, in the rural village of Słopnice, southern Poland. Słopnice sprawls across 56.74 km<sup>2</sup> of high mountain terrain and has a total population of 6,198 (Statistical Office of Krakow, 2013). Seasonal and labor-intensive work has been documented in villages from this mountain region (Jasienska, 2013; Jasienska and Ellison, 2004). Mean body mass index of the sample was 26.56 (S.D. = 3.76), not unlike that of other Western populations (e.g., Finucane et al., 2011), which indicates that food availability was not limited, and is consistent with previous research conducted in this region (Jasienska and Ellison, 2004; Jasienska, 2013). And although the populace is rapidly transitioning to a Westernized lifestyle, it retains several characteristics that distinguish it from more developed regions of Europe, such as greater reliance on subsistence agriculture, physically demanding labor that is concentrated during the summer harvest, and higher completed fertility (Colleran, 2013; Jasienska and Ellison, 2004; Jasienska, 2013).

One hundred and twenty-two men participated in this study. Participants were healthy adult males residing in Słopnice, whose ages ranged from 18 to 78 years (mean: 38.93 years, S.D. = 16.97 years). In this sample, men's primary occupations included: 36% employed in building trades (e.g., bricklayer, carpenter, construction worker, framing), 17% worked as physical laborers in a variety of occupations (e.g., butcher, plumber, metal worker, mechanic, etc.), 15% were retired, 15% were white-collar workers (e.g., accountant, shop keep, soldier, supervisor, etc.), eight percent were farmers, and eight percent were students. Many participants practiced subsistence agriculture as a secondary occupation, particularly among retirees and students, such that 54% of the sample farmed as either a primary or secondary occupation. Table 1 provides further descriptive statistics for the study sample.

### Data collection

Men were recruited by advertisements posted on community bulletin boards and by referral sampling. We visited households using structured interviews to collect demographic, physical activity, and work data from men. Participants provided information regarding their age, marital and parental status, children's ages, and occupational status. Participants provided further information regarding work patterns: their profession, hours worked in a week, and physicality of their work. Participants were asked about additional sources of physical exertion, such as sports participation, weightlifting, or other

TABLE 1. Descriptive statistics of study sample

	Entire study sample $N = 122$	Single and childless men $N = 55$	Pair-bonded fathers $N = 67$
Mean age (yrs.)	38.93, S.D. = 16.97	31.38, S.D. = 17.83	45.13, S.D. = 13.45
Age distribution:			
18–29	38%	71%	10%
30–39	20%	9%	28%
40–49	16%	2%	28%
50–59	12%	5%	18%
60–69	5%	4%	6%
70–79	9%	7%	9%
Mean height (cm)	175.05, S.D. = 7.31	176.60, S.D. = 7.44	173.79, S.D. = 7.00
Mean weight (kg)	81.30, S.D. = 11.99	77.39, S.D. = 12.23	84.51, S.D. = 10.87
Mean body mass index	26.56, S.D. = 3.76	24.86, S.D. = 3.94	27.96, S.D. = 2.97
Mean body fat (%)	22.69, S.D. = 6.62	19.18, S.D. = 6.55	25.58, S.D. = 5.17
Sports and/or weightlifting	17%	25%	10%
Injuries interfering with work	20%	11%	27%

exercise, as well as injuries or illness that interfered with their work.

After the interview, height, weight, body fat percentage, and flexed arm circumference were collected. Body fat percentage was estimated from triceps skinfold using standard procedures (Donoghue, 2009). Following Sell et al. (2009), upper-body muscle mass was estimated using flexed arm circumference, which was measured at the widest point of the upper-arm with biceps maximally contracted. We adapted this method, because Sell et al. did not account for participants' body fat percentage, which also contributes to arm circumference. Accordingly, we use arm muscle circumference [upper-arm circumference – (triceps skinfold  $\times$  3.14)] of participants' flexed biceps for a more precise measure of muscularity (McWhirther and Pennington, 1994). Upper-body strength was estimated using a portable dynamometer to measure grip and chest strength. For grip strength, the participant's elbow was flexed at 90° with the forearm in neutral position, and participants used their dominant hand to squeeze the dynamometer with maximum effort (Mathiowetz et al., 1985). For chest strength, participants used both hands to grasp the dynamometer at the sternum and pressed hands together with maximum effort (Sell et al., 2009). Each strength test was repeated in triplicate, with the mean used for statistical analyses.

Circulating testosterone exhibits a diurnal rhythm in which secretion peaks in the morning and declines steadily throughout the day, until reaching an evening nadir (van Cauter, 1990). To account for diurnal fluctuation, participants provided morning and evening saliva samples. We also calculated proportional diurnal decline for morning to evening testosterone levels (AM T/PM T), such that higher positive values indicate more precipitous proportional decline. Morning samples were collected immediately after waking, and evening samples shortly before bedtime. Participants provided 4 ml of saliva via passive drool into a collection tube. Salivary testosterone levels correlate well with serum free testosterone, the fraction of circulating hormone available to target tissues (Wang et al., 1981; Goncharov et al., 2006). Participants were asked to refrain from eating, drinking alcoholic or caffeinated beverages, brushing teeth, engaging in sexual activity, and smoking for at least thirty minutes prior to providing samples, because these activities can influence salivary hormone measurements (Salimetrics, 2013).

Some participants were unable to complete chest strength or grip strength tests due to existing injuries ( $N = 4$  and  $N = 2$ , respectively), such as shoulder problems or missing fingers. One participant did not provide morning and evening saliva samples. This study was approved by the University of New Mexico Human Research Review Committee, and participants provided written informed consent.

### Statistical analysis

Before evaluating predictions, we constructed a correlation matrix of independent and dependent variables to assess bivariate relationships. Multiple regression analysis was used to evaluate predictions. Regression models employed a backward elimination procedure in which all independent variables were entered into the regression equation and were sequentially removed based on their partial correlation with the dependent variable. Age was correlated with several behavioral, demographic, and physiological traits examined in this study (Table 2), and was included as a predictor variable in all regression models. Because energetic factors can potentially affect testosterone levels (Ellison et al., 1989; Pritchard et al., 1998), as well as development of skeletal muscle tissue (Stini, 1979), body fat percentage was used as an indication of energy status in regression models predicting testosterone levels, muscle mass and strength.

Some of the questionnaire data employed categorical responses (e.g., marital and paternal status, physicality of workload, and medical conditions that interfere with work). These responses were dichotomized and converted into binary variables. For purposes of this analysis, marital and parental status were combined into a single binary variable (single men and childless men = 0, pair-bonded father = 1). This partitioning is justified, because although reductions in men's testosterone levels have been reported in the contexts of both pair bonds and parenting (Burnham et al., 2003; Gray et al., 2002, 2006a, 2006b, 2007; Alvergne et al., 2009; Muller et al., 2009; Gettler et al., 2011), the combination of pair bonding and fatherhood appears to produce the most suppressive effects on testosterone production (Kuzawa et al., 2009). Accordingly, inclusion in the pair-bonded father group was limited to men who were jointly fathers and married. A small portion of our sample consisted of newlyweds who were nulliparous ( $N = 4$ ), and widowers who

TABLE 2. Pearson correlation matrix of variables used in regression analysis

	Age	Arm muscle circum.	Body fat	Chest strength	Grip strength	Injuries	Marital/parental status	Morning T	Evening T	Diurnal decline T	Sports/weights	Work hrs. (heavy)	Work hrs. (total)	Work on others' farm
Age	1													
Arm muscle circumference	-0.42 <sup>a</sup>	1												
Body fat (%)	0.70 <sup>a</sup>	-0.16	1											
Chest strength	-0.44 <sup>a</sup>	0.69 <sup>a</sup>	-0.13	1										
Grip strength	-0.50 <sup>a</sup>	0.63 <sup>a</sup>	-0.18	0.76 <sup>a</sup>	1									
Injuries	0.46 <sup>a</sup>	-0.35 <sup>a</sup>	0.34 <sup>a</sup>	-0.29 <sup>a</sup>	-0.39 <sup>a</sup>	1								
Marital/parental status	0.47 <sup>a</sup>	0.04	0.48 <sup>a</sup>	0.09	0.01	0.20 <sup>b</sup>	1							
Morning salivary T	-0.46 <sup>a</sup>	0.18	-0.31 <sup>a</sup>	0.17	0.27 <sup>a</sup>	-0.32 <sup>a</sup>	-0.16	1						
Evening salivary T	-0.45 <sup>a</sup>	0.16	-0.36 <sup>a</sup>	0.10	0.11	-0.24 <sup>a</sup>	-0.38 <sup>a</sup>	0.64 <sup>a</sup>	1					
Diurnal decline in T	0.03	0.04	0.09	0.11	0.17	-0.07	0.29 <sup>a</sup>	0.28 <sup>a</sup>	-0.55 <sup>a</sup>	1				
Sports/weightlifting	-0.40 <sup>a</sup>	0.20 <sup>b</sup>	-0.39 <sup>a</sup>	0.17	0.06	-0.23 <sup>b</sup>	-0.20 <sup>b</sup>	0.15	0.29 <sup>a</sup>	-0.14	1			
Work hrs., heavy	0.05	0.26 <sup>a</sup>	0.09	0.35 <sup>a</sup>	0.19 <sup>b</sup>	0.14	0.22 <sup>b</sup>	-0.16	-0.12	-0.05	-0.09	1		
Work hrs., total	-0.04	0.22 <sup>b</sup>	0.10	0.35 <sup>a</sup>	0.22 <sup>b</sup>	0.04	0.26 <sup>a</sup>	-0.00	-0.15	0.16	-0.16	0.68 <sup>a</sup>	1	
Work on others' Farm	-0.24 <sup>a</sup>	0.08	-0.28 <sup>a</sup>	-0.05	0.01	-0.22 <sup>b</sup>	-0.13	0.17	0.10	0.06	0.14	-0.06	-0.00	1

<sup>a</sup>  $P < 0.01$

<sup>b</sup>  $P < 0.05$

See Statistical Analysis for description of variables; see Table 2 for summary of variables. Data were cube root transformed. Tests were two tailed.

were fathers but not currently partnered ( $N = 6$ ; two of the widowers' had a youngest child who was an adolescent, whereas the other widowers had adult children all older than 30 years of age). Married men without children as well as widowers were assigned to the "single men and childless men" group, while all other participants in this grouping were neither married nor had children. Two men in the sample were unwed fathers. One had had no interaction with his child or the mother of his child for nearly a decade, and he was assigned to the single and childless group. The other resided with his partner and newborn infant, provided childcare, and was saving money for a wedding. This participant was assigned to the "pair-bonded father" group. Taken together, marital and parental status, age, and body fat percentage were used to predict variation in men's morning and evening testosterone levels, as well as variation in diurnal testosterone decline (P1).

Participants reported number of days and hours normally worked in a week during the summer season when the survey was administered. Men's workload was examined as a function of marital and parental status (P2). Because injuries interfering with work were fairly common in this community (Table 1), participants' injuries were included in regression models predicting workload (no injuries interfering with work = 0, injuries interfering with work = 1). Total number of work hours was regressed on marital and parental status, age, and injuries. As a subsequent test of men's commitment to family provisioning, a similar regression analysis was conducted in which total work hours were regressed on age, injuries, and total number of children (instead of the binary variable representing marital and parental status).

Although most of the study population participated in physically demanding work, we were particularly interested in the effects of manual labor on phenotype. Accordingly, another measure of workload was created, which consisted of men's time spent in heavy manual labor. Participants provided ratings of the physicality of their work: sedentary, light, fairly heavy, or very heavy. Fairly and very heavy work hours were summed for a more direct assessment of physical work, and used as a predictor variable of muscle mass and strength measures. Many participants helped friends and family with their farm work during the summer harvest, but work contributed toward others' farms was sporadic and much less predictable than participants' own work schedule. To accommodate for weekly variability in participants' work toward others' farms, which was considerable, whether or not participants helped friends or family with farm work was converted to a binary variable (do not contribute work to others' farms = 0, contribute work to others' farms = 1). Finally, information about weightlifting and sporting activities was collected, which was also converted into a binary variable (no sports/weightlifting involvement = 0, sports/weightlifting involvement = 1). Because our analysis concentrated on upper-body strength, we limited inclusion of sporting activities to those involving more rigorous upper-body exercise. By this criterion, the most common forms of recreational physical activity in this sample were weightlifting 6%, volleyball 6%, and swimming 5%. However, a broader definition of sporting activities, which also included activities with

less direct upper-body involvement, such as soccer 25%, running 4%, and bicycling 4%, had a negligible impact on subsequent analyses.

Taken together, age, body fat percentage, injuries interfering with work, marital and parental status, morning or evening testosterone levels, heavy work hours, weightlifting/sports participation, and work contributed to others' farms were used to predict arm muscle circumference (P3), chest strength, and grip strength (P4), in separate regression models. Morning and evening testosterone were entered individually into models.

Predictions derived from the competing hypotheses described earlier can be evaluated in regression analyses of muscle mass and strength measures. If the Somatic Allocation Hypothesis is accurate, men's testosterone levels are expected to positively predict arm muscle circumference (CP1), and both chest and grip strength (CP2), while fatherhood is expected to be negatively associated with these variables (CP3,4). All non-binary variables were cube root transformed before analysis to better adhere to the assumptions of parametric statistics.

### Hormone analysis

Saliva was collected via passive drool in polypropylene tubes and frozen within eight hours of collection. Samples were analyzed for testosterone levels using an established enzyme immunoassay protocol (Salimetrics, State College, PA; Kit No. 1-2402) at the Hominoid Reproductive Ecology Laboratory, University of New Mexico. The assay manufacturers report a correlation of saliva and serum total testosterone of 0.96 and a limit of detection of  $\sim 1$  pg/ml. Frozen samples were thawed, vortexed, and centrifuged for 15 min prior to dispensing into the assay to break up and precipitate mucins. Inter-assay coefficients of variation (CVs) were 5.1% for high and 9.9% for low salivary control. Intra-assay CV for duplicate determinations averaged 5.7%.

### RESULTS

Table 2 presents a correlation matrix to illustrate bivariate relationships between the analyzed variables. Regression analysis was used to examine the effect of relationship and fertility status on men's testosterone levels (P1). As predicted, pair-bonded fathers exhibited lower evening testosterone as well as more pronounced diurnal decline in testosterone, although marital and parental status did not predict lower morning testosterone. Regressing morning testosterone levels on age, body fat percentage, and marital and parental status produced a significant model,  $\text{adj. } R^2 = 0.21$ ,  $F(1, 120) = 31.96$ ,  $P < 0.001$ . However, body fat percentage and marital and parental status were nonsignificant, while age negatively predicted morning testosterone levels ( $P < 0.001$ ). For evening testosterone levels, body fat percentage was not a significant predictor, and was eliminated from the model. Age and marital and parental status were negative predictors of evening testosterone ( $P < 0.001$  and  $P = 0.022$ , respectively), resulting in a significant model,  $\text{adj. } R^2 = 0.23$ ,  $F(2, 120) = 18.53$ ,  $P < 0.001$ . Greater diurnal decline in testosterone levels was predicted by marital and parental status ( $P = 0.001$ ), resulting in a significant model,  $\text{adj. } R^2 = 0.08$ ,  $F(1, 120) = 10.76$ ,  $P = 0.001$ . Neither age nor body fat percentage were significant predictors in this model (See Table 3).

To examine the effects of men's workload (P2), participants' total work hours were regressed on age, injuries interfering with work, and marital and parental status. As predicted, pair-bonded fathers worked more than single and childless men. This generated a significant model,  $\text{adj. } R^2 = 0.08$ ,  $F(2, 121) = 6.44$ ,  $P = 0.002$ , in which total work hours were negatively predicted by age ( $P = 0.039$ ) and positively predicted by marital and parental status ( $P < 0.001$ ). Injuries interfering with work were eliminated as a variable. Participants' total work hours was then regressed on age, injuries interfering with work, and number of children. This model was also significant, but less robust,  $\text{adj. } R^2 = 0.06$ ,  $F(2, 121) = 4.60$ ,  $P = 0.012$ . Total work hours was negatively predicted by age ( $P = 0.016$ ) and positively predicted by number of children ( $P = 0.003$ ). Injuries interfering with work were again eliminated. See Table 4 for analyses of men's workload.

Finally, we examined muscle mass and strength measures (P3, 4, and CP1-4). As predicted, marriage and fatherhood and workload had substantive effects on muscularity and strength. We regressed arm muscle circumference on: age, body fat percentage, heavy work hours, injuries interfering with work, marital and parental status, morning or evening testosterone levels, sports and weight lifting involvement, and work on others' farms. The overall model was significant,  $\text{adj. } R^2 = 0.32$ ,  $F(4, 120) = 15.32$ ,  $P < 0.001$ . Arm muscle circumference was negatively predicted by age ( $P < 0.001$ ) and injuries interfering with work ( $P = 0.008$ ), and positively predicted by heavy work hours ( $P < 0.001$ ), and marital and parental status ( $P = 0.009$ ). All other predictors were non-significant. Chest and grip strength were regressed on the same predictor variables, which produced significant models; chest strength:  $\text{adj. } R^2 = 0.42$ ,  $F(5, 116) = 18.03$ ,  $P < 0.001$ ; and grip strength:  $\text{adj. } R^2 = 0.40$ ,  $F(5, 118) = 16.59$ ,  $P < 0.001$ . Chest strength was negatively predicted by age ( $P < 0.001$ ) and injuries interfering with work ( $P = 0.013$ ), but positively predicted by body fat percentage ( $P = 0.028$ ), heavy work hours ( $P < 0.001$ ), and marital and parental status ( $P = 0.001$ ). The remaining predictors were non-significant and eliminated from the model. Grip strength was negatively predicted by age ( $P < 0.001$ ) and injuries interfering with work ( $P = 0.006$ ), and positively predicted by body fat percentage ( $P = 0.013$ ), heavy work hours ( $P = 0.011$ ), and marital and parental status ( $P = 0.019$ ; See Table 5). All other predictors were nonsignificant and eliminated.

Although we found strong support for the Paternal Provisioning Hypothesis, no support was found for the Somatic Allocation Hypothesis. Neither morning nor evening testosterone predicted muscle mass (CP1) or strength measures (CP2). No interaction effects of testosterone and workload were evident either on arm muscle circumference or chest and grip strength. Although pair-bonded fathers demonstrated lower evening testosterone levels, and greater diurnal decline in testosterone, than single and childless men, marriage and fatherhood did not produce a decrease in either musculature (CP3) or strength (CP4; Table 5). Instead, and consistent with the provisioning model of men's life history, pair-bonding, and parenting had a positive impact on musculature and strength, despite being associated with lower testosterone. See the Data Supplement for further details of regression analyses in which significant predictors were entered separately into models, so that the individual contributions of these variables could be observed.

TABLE 3. Summary of regression analyses predicting salivary testosterone measures

	<i>B</i>	SE ( <i>B</i> )	$\beta$	<i>T</i>	Sig. ( <i>P</i> )
<i>Regression model for evening T</i>					
Age	-0.47	0.12	-0.35	-3.89	<0.001
Marital and parental status	-0.27	0.12	-0.21	-2.32	0.022
<i>Regression model for diurnal T decline</i>					
Marital and parental status	0.08	0.03	0.29	3.28	0.001

TABLE 4. Summary of regression analyses predicting workload<sup>a</sup>

	<i>B</i>	SE ( <i>B</i> )	$\beta$	<i>T</i>	Sig. ( <i>P</i> )
<i>Regression models for total work hrs</i>					
Age	-0.54	0.26	-0.21	-2.09	0.039
Marital and parental status	0.88	0.25	0.35	3.56	<0.001
Age	-0.79	0.32	-0.30	-2.44	0.016
Number of children	0.65	0.22	0.37	3.00	0.003

<sup>a</sup> Marital/parental status and number of children were entered separately into models.

TABLE 5. Summary of regression analyses predicting chest strength, grip strength, and arm muscle circumference<sup>a</sup>

	<i>B</i>	SE ( <i>B</i> )	$\beta$	<i>T</i>	Sig. ( <i>P</i> )
<i>Regression model for arm muscle circum</i>					
Age	-0.09	0.02	-0.44	-4.66	<0.001
Heavy work hours	0.02	0.01	0.27	3.43	<0.001
Injuries interfering with work	-0.06	0.02	-0.23	-2.72	0.008
Marital and parental status	0.05	0.02	0.23	2.65	0.009
<i>Regression model for chest strength</i>					
Age	-0.56	0.09	-0.66	-6.39	<0.001
Body fat percentage	0.30	0.13	0.22	2.32	0.028
Heavy work hours	0.08	0.02	0.32	4.41	<0.001
Injuries interfering with work	-0.20	0.08	-0.20	-2.53	0.013
Marital and parental status	0.22	0.07	0.28	3.30	0.001
<i>Regression model for grip strength</i>					
Age	-0.45	0.07	-0.68	-6.19	<0.001
Body fat percentage	0.28	0.11	0.26	2.51	0.013
Heavy work hours	0.04	0.01	0.19	2.59	0.011
Injuries interfering with work	-0.19	0.07	-0.23	-2.80	0.006
Marital and parental status	0.13	0.06	0.20	2.39	0.019

<sup>a</sup> Morning and evening testosterone were entered separately into models.

## DISCUSSION

We contrasted competing models of men's life history by testing associations between parental status, workload, testosterone, and muscle mass in a rural Polish population. The Somatic Allocation Hypothesis has emphasized the role of testosterone in mediating trade-offs between survival and reproduction primarily through the maintenance of skeletal muscle (Bribiescas, 1996, 2001; Bribiescas et al., 2012). However, several studies have failed to show that natural variation in men's testosterone levels produces somatic effects on muscle mass, both between- and within-populations (Ellison and Panter-Brick 1996; Campbell et al., 2003, 2006a, 2006b; Gettler et al. 2010). Other studies report weak, inconsistent, or indirect relationships (Ellison and Panter-Brick 1996; Lukas et al., 2004; Campbell et al., 2007; Lassek and Gaulin, 2009; Gettler et al., 2010). We proposed an alternative model, the Paternal Provisioning Hypothesis, which recognizes the importance of men's provisioning responsibilities, and associated

changes in the testosterone production and physical activity patterns of involved fathers. We suggest that muscle mass and strength are augmented during fatherhood, despite suppressed testosterone levels, in response to the physical demands of intensified provisioning. We found support for this hypothesis. Pair-bonded fathers in our sample exhibited lower evening testosterone levels, along with a more precipitous decline in morning to evening testosterone, than single and childless men. And even within this community in which men's work normally involves demanding manual labor, lower testosterone among pair-bonded fathers did not negatively impact productivity. On the contrary, fathers calibrated their work patterns to family need, increasing labor with additional children.

No associations were found between marital and paternal status and morning testosterone levels. Many studies have reported stronger associations between evening testosterone levels and pair-bonding and parenting (e.g., Berg and Wynne-Edwards, 2001; Gray et al., 2002, 2004a, 2004b; Muller et al., 2009; Gettler et al., 2012).

One potential explanation is that evening testosterone reflects cumulative social interactions experienced throughout the day, whereas morning testosterone may be more reflective of baseline, dispositional differences between individuals (Gray et al., 2002, 2004a; Muller and Wrangham, 2004; Muller et al., 2009). If this is the case, then it is sensible to expect stronger relationships with evening testosterone, though this does not fully explain why some studies detect an influence of pair-bonding and parenting on morning testosterone while others do not.

In many small scale societies, men's provisioning is dependent on physical labor (Lancaster and Kaplan, 2009; Gurven and Hill, 2009; Wood and Marlowe, 2013; Apicella, 2014). In Slopnice, work often requires manual labor, and a strong, positive correlation exists between men's total work hours and heavy work hours (Table 2). The level of physical labor practiced among Slopnice men allows us to parse relative contributions of men's provisioning activities and testosterone levels in the maintenance of muscle mass. Indicative of male parenting effort, fathers exhibited both lower evening testosterone as well as higher productivity to accommodate family need. Fathers also maintained more upper-body muscle mass and strength than their childless counterparts. (See Figs. 1 and 2)

These findings are of interest because male secondary sexual characteristics, such as dimorphic musculature, are thought to represent investment in mating effort—supported by testosterone (Bribiescas, 1996, 2001). It seems likely that elevated testosterone during sexual maturation is associated with increased musculature in later adolescence, when males are investing heavily in mating effort. This close relationship is not evident, however, after fatherhood and during men's prime reproductive years. We observed a divergent relationship, in which enhanced musculature and strength was associated with men's parenting effort and decreased testosterone production. Among primates, this pattern may be unique to humans. The distinct reproductive ecology of humans, which places a premium on biparental care of altricial young and the sexual division of labor (Kaplan et al., 2000; Marlowe, 2003; Wood and Marlowe, 2013), likely renders a constant relationship between men's testosterone and muscle mass maladaptive. If men's muscle mass were primarily supported by testosterone, then physical capabilities would be compromised when testosterone levels decline during fatherhood—precisely when men need to increase productivity because of provisioning demands. Instead, paternal investment disrupts putative associations between mating effort and testosterone in relation to sexually dimorphic muscle, such that the labor demands of parenting effort determine musculature.

It is not our contention that men's circulating testosterone has no effect on muscle anabolism. Indeed, there is evidence for stronger associations between testosterone levels and measures of upper-body musculature among adolescent males, in both Western and non-Western populations (Danish boys: Hansen et al., 1999; Dogon boys: Beverly Strassmann, personal communication). These findings are consistent with some portion of the Somatic Allocation Hypothesis, but this relationship is weaker in adulthood, when men begin their reproductive careers. It is plausible that testosterone levels during puberty may have a lasting—potentially lifelong—impact on the development and maintenance of musculature,

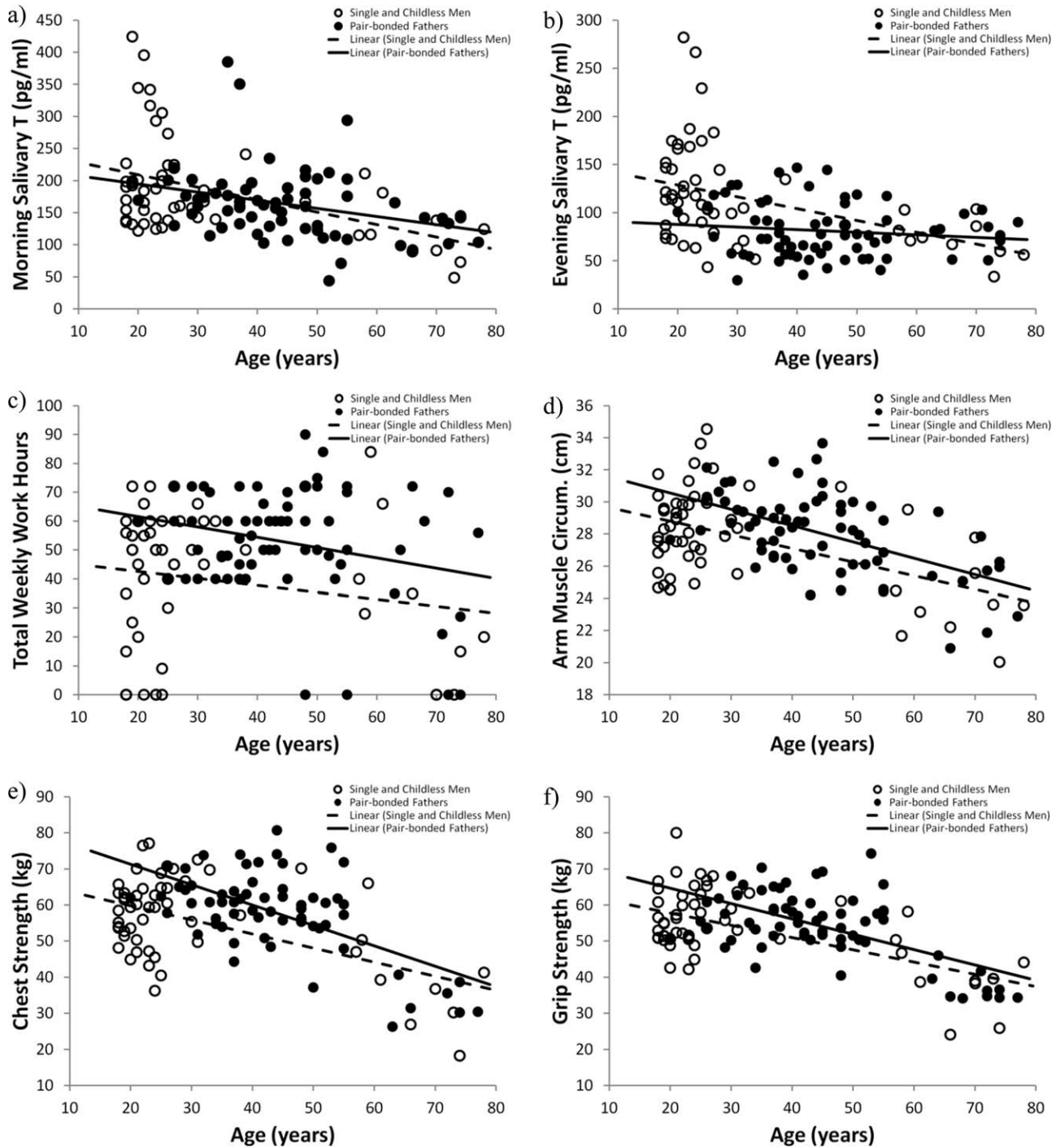
though longitudinal data are not available to speak to this point. However, it is clear that substantial plasticity exists in determination of adult musculature (Bhasin et al., 1996, 2000), and in this sample of rural Polish men, pair-bonded fathers allocated more time and effort toward work than single and childless men, along with greater somatic investment in strength (Figs 1 and 2). We propose that the influence of endogenous testosterone on men's skeletal muscle is secondary to, and superseded by, subsistence and provisioning activities.

The lack of associations between men's testosterone levels and their muscle mass and strength reported here is not altogether unexpected. Several studies examining such relationships report null findings, or find indirect, inconsistent, or weak relationships, particularly among non-Western groups (e.g., Ellison and Panter-Brick, 1996; Campbell et al., 2003, 2006a, 2006b; Lukas et al., 2004; Gettler et al., 2010). A cohort study, using a large sample of young Filipino men, found that salivary testosterone levels were not predictive of lean mass, arm muscle area, or grip strength (Gettler et al., 2010). However, an interaction effect emerged in which morning salivary testosterone among physically active sports participants predicted lean body mass, arm muscle area, and grip strength. And in a population sample of Zimbabwean men, a significant but weak relationship (explaining less than one percent of the variance) was reported between afternoon salivary testosterone and fat-free mass (Lukas et al., 2004). Among Ariaal pastoralists of Northern Kenya, no relationship was found between salivary testosterone and lean body mass (Campbell et al., 2003, 2006b). However, a subsequent study of the same population reported that arm muscle area and lean body mass were predicted by evening salivary testosterone after accounting for androgen receptor sensitivity, which was evaluated by genotyping for CAG repeats in the androgen receptor gene (Campbell et al., 2007). It is worth noting that the extent to which CAG repeats modulate transcriptional activity of the androgen receptor gene remains inconclusive, because experimental research has shown dose dependent effects of exogenous testosterone on men's anabolic response without interaction from CAG repeat length (Woodhouse et al., 2003). Thus, it would appear that a key component of the Somatic Allocation Hypothesis has not been supported empirically.

Experimental research investigating testosterone's effects on musculature within laboratory settings, although far removed from naturalistic conditions, has yielded mixed results. Although men receiving supra-physiologic doses of testosterone consistently demonstrate anabolic effects on skeletal muscle tissue (Bhasin et al., 1996, 2000, 2001), doses within a more normative physiological range generally do not produce lean mass accretion in eugonadal men (e.g., Fowler et al., 1965; Casner et al., 1971; Bower and Reardon, 1972; Johnson et al., 1972; Fahey and Brown, 1973; Golding et al., 1974; Loughton and Ruhling, 1977; Crist et al., 1983; Friedl et al., 1991; see Hartgens and Kuipers, 2004, for a comprehensive review).

A separate line of research investigating hormonal and somatic changes during prolonged bed rest has implications for discriminating between the effects of testosterone and physical activity on muscle tissue conservation. One study examined how exercise regimens influence men's body composition, strength, and hormone levels during 30 days of bed rest (Wade et al.,

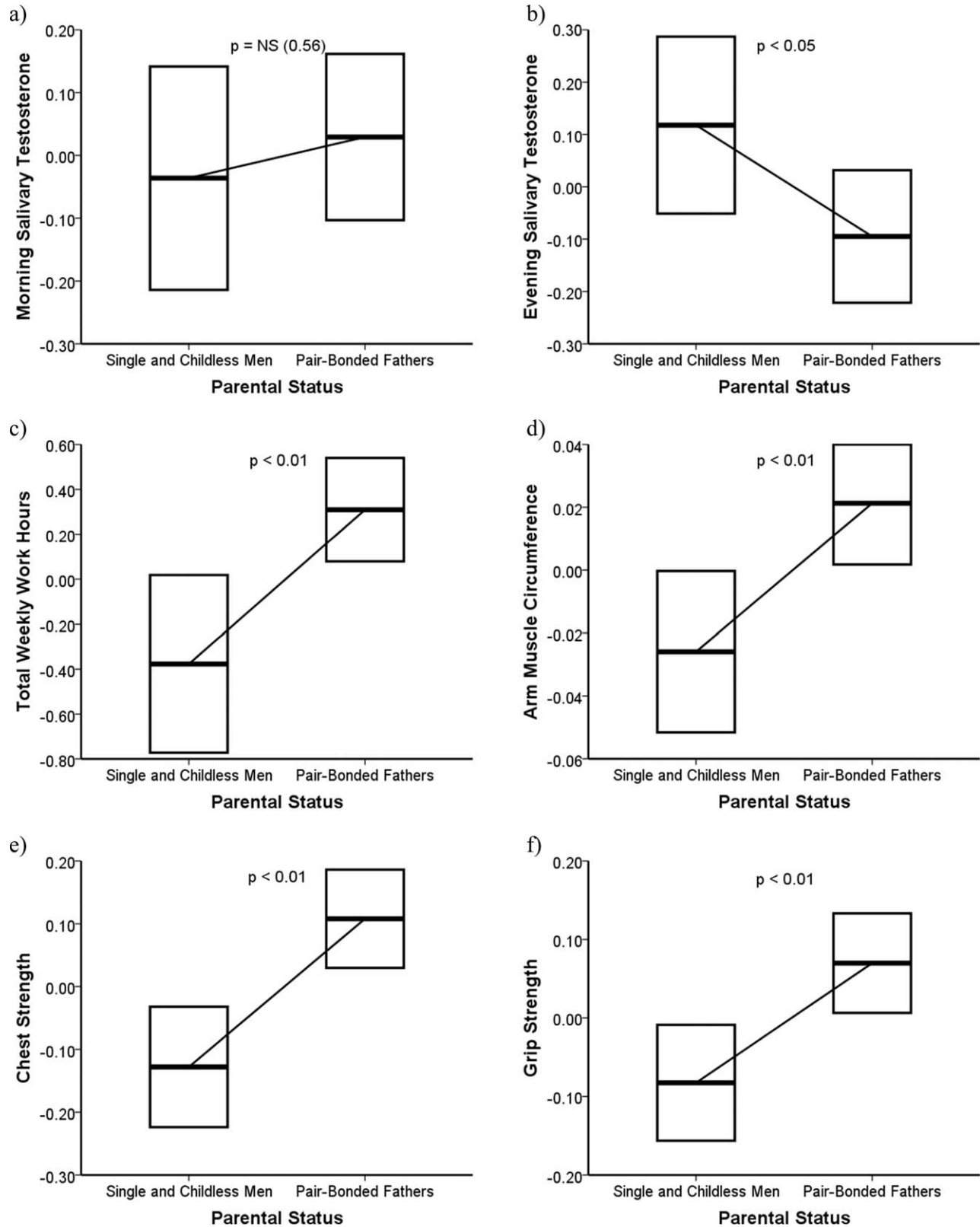




**Fig. 1.** Age decline in salivary morning and evening testosterone levels, workload, arm muscle circumference, chest and grip strength among single and childless men and pair-bonded fathers

2005). Healthy men were restricted to bed rest and assigned to one of three conditions. The control group avoided all exercise. A second group followed an exercise regimen intended to preserve lower body strength. The final group followed a regimen intended to preserve aerobic capacity. Exercise groups completed rigorous, 30-min programs twice a day for five days a week. Relative to pre-bed-rest baselines, plasma testosterone was decreased in exercise groups but not the control group.

Although exercise groups exhibited decreased testosterone levels, they maintained aerobic and muscular work capacities; the control group did not, despite unaltered steroid concentrations. In a second study (Zachwieja et al., 1999), men were restricted to 28 days of bed rest without exercise, but some received testosterone injections at supraphysiologic doses while others were given placebo. Men receiving testosterone gained lean body mass, but, nevertheless, showed reduction in lower- and



**Fig. 2.** Mean and 95% confidence intervals for morning and evening salivary testosterone, workload, arm muscle circumference, chest and grip strength among single and childless men and pair-bonded fathers. Values were adjusted for age as well as injuries interfering with work, and cube root transformed. All *t*-tests were two-tailed. A Satterthwaite approximation *t*-test was used for comparisons of morning testosterone means and workload means because of marginally unequal and significantly unequal sample variances, respectively.

upper-body strength comparable to controls, such that testosterone administration produced no appreciable benefit toward strength preservation in the absence of physical activity.

Experimental data have demonstrated relationships between testosterone administration and muscular development. However, these data also highlight inconsistencies in the relationship between testosterone and muscularity, in which physical workload appears to be a mediating factor. Physical activity has a protective effect on skeletal muscle tissue, even under adverse health conditions and suppressed testosterone production (e.g., AIDS: Bhasin et al., 2000; sarcopenia: Roth et al., 2000). Accordingly, observational and experimental data call into question assumptions that are present within existing models of male life history, particularly any model that hold men's activity level constant while emphasizing the effect of testosterone.

Recently, Trumble et al. (2013) documented acute increases in salivary testosterone after tree chopping in the Tsimane, a group of forager horticulturalists. They proposed that such increases might function to augment skeletal muscle capabilities during work, thus supporting male parenting effort. They further suggested that decreased testosterone would compromise men's parenting effort by impeding their provisioning abilities: "While many have argued that decreases in testosterone with fatherhood would increase investment in current offspring (Gray et al., 2002; Gettler et al., 2011), in subsistence populations dependents necessitate increased food production, and thus a diminished testosterone response during physical activity could have negative effects on physically intensive food production strategies." (355). Our data indicate that this second conjecture is incorrect. Pair-bonded fathers exhibited, concomitantly, lower evening testosterone levels, greater diurnal decline in testosterone, and increased strength and productivity.

There are also several reasons to doubt the functional interpretation for exercise-induced testosterone increases favored by Trumble et al. First, although transient elevations in testosterone with exercise are well documented, these generally result not from increased hormone production, but from 1) decreased clearance (because steroid hormones are cleared by the liver, their concentration increases with physical activity, as blood is shunted toward exercising muscles: Cadoux-Hudson et al., 1985; Terjung, 1979) and 2) decreased blood volume (during exercise water is absorbed into interstitial spaces, increasing blood concentration: Raastad et al., 2000). These effects can be observed in both men and women, and in a wide range of hormones, including estradiol, progesterone, prolactin, leptin, cortisol, DHEA, and DHEAS (e.g., Jurkowski et al., 1978; Bonen et al., 1979; Keizer et al., 1980, 1987; Bonen and Keizer, 1987; Fisher et al., 2001; Kraemer et al., 2001). A specific functional role for testosterone in this context is thus unlikely. Second, although steroid hormones exhibit an acute increase during exercise (reviewed in McMurray and Hackney, 2000), this is followed by prolonged suppression (Häkkinen and Pakarinen, 1993), particularly after sustained activity.

Trumble et al. (2013: 354) acknowledge that seasonal wood chopping among the Tsimane occurs over a truncated timeframe, and is likely not substantial enough to promote muscular development. However, they suggest that acute testosterone increases might amplify muscular performance in short-term contexts, and would con-

tribute to muscle hypertrophy with sustained work effort over more extended periods. A substantial body of research in exercise science, however, has failed to support these ideas. Fraysse et al. (2014), for example, found that in vivo androgen treatments had no immediate effect on the maximal force, power or fatigue resistance of muscles in mice, nor on their evoked calcium transient. They concluded that "androgens have no major rapid action on either intact fast skeletal muscle or isolated muscle fibres" (Fraysse et al. 2014: 11). In humans, a recent series of careful studies (which were precise enough to detect upregulated gene expression of striated muscle hypertrophy in response to consumption of 25 g of protein after exercise) demonstrated that exercise-induced increases in men's testosterone levels had no apparent influence on muscular performance, growth, or strength, either during or postexercise (West et al., 2009, 2010, 2012; West and Phillips, 2012). Wilkinson et al. (2006) demonstrated that muscular hypertrophy occurs in response to resistance exercise without acute increases in androgen concentration. Finally, a number of studies that are frequently cited (including by Trumble et al., 2013) to support an effect of postexercise testosterone increases on musculature (e.g., Ronnestad et al., 2011) have been shown to be seriously flawed, in both their methods and interpretation (Phillips, 2012; Schroeder et al., 2013).

To be clear, we are not disputing the fact that transient elevations in circulating testosterone are biologically meaningful. An extensive literature has found strong associations between acute testosterone increases and both mating and competitive motivation (reviewed in Archer, 2006). Such increases are generally due to increased steroid production rather than reduced clearance, being observed in response to competition and courtship displays that do not involve physical exertion (Mazur et al., 1992; Cohen et al., 1996; Roney et al., 2003; Steiner et al., 2010). Testosterone surges in response to sexual stimuli are associated with elevated LH levels, further suggesting that endocrinological fluctuation encouraging mating effort is specifically due to increased testosterone production (LaFerla et al., 1978; Stoleru et al., 1993). Given the experimental evidence that exercise-induced rises in testosterone have no effect on muscle performance, and the lack of evidence that such spikes represent investment in parenting effort, as opposed to a nonspecific physiological response to physical activity, we question the relevance of such increases to men's work.

In sum, we developed a model of men's life history, the Paternal Provisioning Hypothesis, which is consistent with observed changes in men's testosterone levels and workload across the life course. We find support for our hypothesis in a sample of rural Polish men, whose subsistence often relies on demanding physical labor. Although fatherhood predicted lower evening testosterone and more pronounced diurnal testosterone decline, indicative of parenting effort, fathers did not show muscle atrophy or diminished strength. Instead, fathers augmented strength and musculature in response to increased provisioning demands. We situate our findings within the larger evolutionary context of how human males apportion mating and parenting effort, and the adaptive effect on men's phenotypes. Although enhanced muscularity, presumably supported by elevated testosterone, is believed to represent investment in mating effort in younger men, this relationship appears to

change for married fathers. Human males may represent an outlier among primates, in which paternal provisioning disrupts the relationship between testosterone and muscle mass, becoming the primary driver of investment in dimorphic musculature.

Because of distinctive features of the human life course, it is difficult to position our results within a broader pattern of primate life history. Pair-bonding and biparental care among primates is rare, but convergent evolution of male parenting has been observed most extensively in the family Callitrichidae (Rutberg, 1983; Cleveland and Snowdon, 1984; Fernandez-Duque et al., 2009). Similar to humans, tamarin and marmoset males have shown reductions in circulating and urinary androgens in response to expectant mates, paternal experience, and olfactory cues of their infants (Nunes et al., 2001; Ziegler et al., 2004; Prudom et al., 2008). The sexual division of labor found in humans, however, is unprecedented among extant primates (Kaplan et al., 2000). Moreover, relative to other primate species in which males participate in offspring care, the slow life history of humans may result in an even more prolonged period of suppressed testosterone across the life course (Gettler et al., 2011). Human reproduction is exceptional in many respects, and characterized by remarkably altricial young, short interbirth intervals, lengthened juvenile periods, and multiple dependents of overlapping ages (Lancaster and Lancaster, 1983; Kaplan et al., 2000). We hypothesized that because men's life history places a premium on parenting effort and division of labor, men must augment their productivity and physical capabilities under conditions of prolonged, downregulated investment in mating effort and testosterone production.

Future research includes supplementing our cross-sectional analysis with longitudinal data to test additional predictions of our model. We do not suggest that the manner in which testosterone exposure affects pair-bonded fathers is fundamentally different from that of young single men. Rather, we propose that muscularity only becomes less dependent on androgenic stimulation because of a unique confluence of life history traits specific to human males. And although the convergence of these traits—reduced testosterone production, increased productivity, and augmented muscularity—is most pronounced during fatherhood, we expect a similar pattern in other contexts in which these coalesce at some level, not only between fathers and non-fathers but also, potentially, within individuals based on fluctuation in workload.

Toward this end, we have begun collecting and analyzing longitudinal seasonal data on Słopnice men (e.g., Alvarado et al., 2014; Klimek et al., 2014). Our analyses are preliminary, but agree with our overarching hypothesis (Alvarado et al., 2014). Men's workload intensified during the summer harvest, leading to reductions in body fat and testosterone production, but increases in strength and musculature, compared to a period of lower physical activity during the winter. Although humans are not seasonal breeders, it is instructive to draw comparative reference from seasonally breeding mammals in which seasonal rise in testosterone levels promotes heightened expression of secondary sexual characteristics, including dimorphic musculature, while returning to non-breeding testosterone baseline results in degeneration of these traits (Lincoln, 1971; Ben Saad and Bayle, 1985; Field et al., 1985; Forger and Breedlove, 1987;

Asher and Peterson, 1991). This contrasts with the pattern predicted by the Paternal Provisioning Hypothesis for humans, and the one identified in our longitudinal study of rural Polish men.

Potential physiological differences between humans and other primates underlying the link between testosterone and musculature remain a black box, and warrant further investigation. The peptide hormones human growth hormone (hGH) and insulin-like growth factor (IGF-1) exert intrinsically coupled mechanistic actions (Florini et al., 1996), which have been proposed to regulate muscle function and performance (reviewed in Rennie, 2003), and some researchers have employed an evolutionary perspective to posit regulatory adaptive effects of hGH on skeletal muscle phenotype (e.g., Bribiescas, 1996). However, a comprehensive meta-analysis that aggregated five decades of hGH research into a single dataset, and carefully calculated effect sizes across 44 studies, found that hGH administration did not enhance muscular performance, and actually had a degenerative influence on exercise capacity (Liu et al., 2008). Nor does IGF-1 administration have any appreciable effect on physical capabilities (Doessing et al., 2010). Furthermore, women maintain significantly higher levels of circulating hGH than men, making it improbable as a primary regulator of men's dimorphic musculature (e.g., Engstrom et al., 1998).

Repetitive bouts of exercise produce acute increases in the rate of muscle protein synthesis (Biolo et al., 1997; Phillips et al., 1997) and small net accretions that produce a chronic hypertrophic response from local intramuscular mechanisms (Rennie et al., 2004). Local mechanisms within skeletal muscle tissue that affect the rate of muscle protein synthesis include the p70S6K, JAK, STAT, and mTOR intracellular signaling pathways, which generate a synthetic response to muscle force production (Biolo et al., 1997; Phillips et al., 1997; West et al., 2009, 2010, 2012). These pathways represent promising areas for future research on differences between humans and non-human primates in muscle maintenance.

Future research will also involve more detailed comparisons of our dataset with other Polish samples, to enrich the existing ethnographic work on parenting and fatherhood among Polish men. An earlier study of urban Polish men found no significant difference in morning or evening salivary testosterone between fathers and non-fathers (Jasienska et al., 2012), though a relatively small number of nonfathers were included in the sample ( $N = 18$ ). Interestingly, fathers' testosterone levels interacted with educational achievement and number of children. Although our current analysis was not situated at examining these issues, these relationships warrant further investigation, and data collected from our sample of rural Polish men may help to further elucidate relationships between fathers' testosterone levels, educational and socioeconomic status, and parity.

Finally, our data provide valuable insight into the expression of men's testosterone levels across the life course, which may have important health implications. Development and maintenance of the prostate gland is regulated by androgenic hormones (O'Malley, 1971; Platz and Giovannucci, 2004), and rapidly rising rates of prostate cancer, though concentrated among Western nations, have become a global concern (Kamangar et al., 2006). Although large-scale epidemiological studies examining men's hormonal profiles near the time

prostate cancer develops often report null associations between prostate cancer cases and controls (Roddam et al., 2008), testosterone levels are most variable and highest during early adulthood, so that variation in men's testosterone levels is diminished and difficult to detect at older ages (Ellison et al., 2002; Kehinde et al., 2006). However, there is evidence that testosterone exposure across the lifespan is associated with prostate cancer risk (Alvarado, 2010, 2011). Accordingly, it is reasonable that allostatic diminution of men's testosterone production would have a protective effect on prostate cancer risk (reviewed in Alvarado, 2013). Investigating how socioecological factors interact with men's parenting effort and reproductive physiology can only work to elucidate observed trends in androgen-sensitive disease.

### LIMITATIONS

Our findings are subject to several limitations, most notably the cross-sectional nature of the study design. Hormone measures were based on two (one morning and one evening) saliva samples from each participant. Because of the variability inherent in hormonal data, potential relationships between testosterone, muscle mass, and strength may have been obscured beyond detection. However, we were able to detect clear relationships between testosterone and other variables, such as age and marital and parental status. Thus, it seems unlikely that measurement error was responsible for null relationships between testosterone and muscle mass and strength, which are absent in many studies.

Phenotypic correlation represents another potential confound (Stearns, 1992). Specifically, an alternative explanation for the positive associations between testosterone and muscularity among non-human primates is that robust phenotypes can incur the costs of both elevated testosterone and augmented muscle mass, without these traits being causally linked. However, in the context of our analysis, phenotypic correlation would imply that more robust phenotypes can 1) afford higher testosterone levels and greater muscularity, 2) are more attractive to potential mates, and 3) have higher probability of fertility. Instead, we found that although fathers work more and have greater muscularity and strength than childless men, they also had lower testosterone. More importantly, it is unlikely that phenotypic correlation can explain, concomitantly, why the relationship between testosterone and skeletal muscle appears much easier to detect in nonhuman primates than in humans. Phenotypic correlation is also inconsistent with our preliminary seasonal analyses, which indicate that, within individuals, relaxed work effort during the winter was associated with seasonal testosterone elevation, but muscular atrophy and strength loss, whereas heavy work during the summer harvest was associated with enhanced musculature and decreased salivary testosterone.

Our estimates of duration and physicality of work relied on participant appraisal, which may be susceptible to reporting error. Such error was likely minimal, however, given that self-reported work data were associated with anthropometric and physical performance measures (i.e., men reporting longer hours and heavier work exhibited greater upper-body musculature and strength).

Lastly, our analysis lacked a measure of paternal involvement. Consequently, we cannot examine the

importance of direct care as a predictor of testosterone suppression in fathers.

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