AMERICAN JOURNAL OF HUMAN BIOLOGY 15:196–208 (2003)

# Modeling Growth and Senescence in Physical Performance Among the Ache of Eastern Paraguay

ROBERT WALKER* AND KIM HILL
*Department of Anthropology, University of New Mexico, Albuquerque, New Mexico 87131*

*ABSTRACT* This article seeks to partially fill a paucity of available data on physical performance in hunter–gatherer societies. Quantitative data are presented on various physical performance measures conducted on the Ache of eastern Paraguay, hunter–gatherers up to the 1970s and now part-time foragers and horticulturists. The performance battery was conducted on most individuals over 10 years of age, allowing for cross-sectional examination of growth and senescence patterns across the lifespan for both sexes. These measures tend to display steep ascents and peak in the early 20s with slight declines thereafter with age for males, whereas females demonstrate peaks in performance earlier in life, with lower or no senescence rates thereafter. The result is a convergence in physical performance between men and women at later ages. We suggest that the female physiology faces reproductive constraints to performance early in life but shifts allocation to increased work output later in life during the long human postmenopausal stage. In contrast, the male physiology maximizes work output in early adult life. These schedules of physical performance are contrasted with schedules of food production ability, which tend to occur later in life, and therefore imply that skill rather than strength alone is an important component of the human foraging niche. Am. J. Hum. Biol. 15:196–208, 2003. 

Although anthropometric data such as body weight, height, and skinfolds are commonly collected in studies of traditional societies, we know of only a few anthropological studies that have conducted age-specific physical performance studies of foraging (or part-time foraging) societies. These include Canadian Inuit (Rode and Shephard, 1971, 1994), children in Botswana (Bock, 1995, 2002), Gidra hunters in Papua New Guinea (Ohtsuka, 1989), Hadza foragers in Tanzania (Marlowe, 2000; Blurton Jones and Marlowe, 2002), and several studies of traditional societies reviewed by Shephard (1978). More attention should be given to parametric modeling of these measures across the lifespan to allow for closer analysis of growth and senescence rates and better intergroup comparisons. Given that the genetic potential of human physiology evolved in a hunting and gathering context with high activity levels and food limitations, we feel information derived from these studies is critical to understanding human patterns of growth and senescence in both ancestral and modern peoples.

## MATERIALS AND METHODS

### *Study group*

All ethnographic evidence suggests that the Northern Ache were nomadic hunter–gatherers without horticulture before first peaceful contact in the 1970s (Hill and Hurtado, 1996; Clastres, 1998). Since then the Ache frequently trek into the forest with family groups and then return to a permanent reservation settlement after several days to a month. The Ache in this study have exclusive use rights to the Mbaracayu Reserve, where they are allowed to hunt with hands, machetes, and bows and arrows but not using firearms or dogs. In 1998 the Ache at the Arroyo Bandera settlement, where much of the data in this study were collected, spent 14% of all person days (range 0–50% for individuals) on trek (McMillan, 2001). Game animals comprise up to 80% of the Ache diet in the forest (Kaplan et al., 2000) but the settlement diet is based on a staple of sweet manioc planted in slash-and-burn fields.

Contract grant sponsors: University of New Mexico Research and Allocations Grant (to KH), Lewis R. Binford Graduate Fellowship, National Science Foundation Graduate Fellowship, Student Research and Allocations Committee Grant, Research, Projects, and Travel Grant, Latin American and Iberian Institute Research Grant (to RW).

*Correspondence to: R. Walker, Department of Anthropology, University of New Mexico, Albuquerque, NM 87131. E-mail: robwal@unm.edu webpage: http://www.unm.edu/~robwal

Received 25 November 2001; Revision received 18 October 2002; Accepted 19 November 2002

Published online in Wiley InterScience (www.interscience.wiley.com). DOI: 10.1002/ajhb.10135

Activity levels are high in the forest, where family groups often move camp each day. Men spend about 7 hours per day hunting in the forest (Hill and Hawkes, 1983) and women spend over 6 hours per day moving camp, harvesting and processing food, and conducting other miscellaneous work activities (Hurtado et al., 1985). On the reservation, leisure time increases but is often spent playing games of soccer and volleyball in the intense Paraguayan heat.

Food is limited for the Ache and, like other food-limited organisms, more food leads to increased fertility and survivorship (Hill and Hurtado, 1996). Growth rates also increase with increased food intake, as evidenced by several Ache children that were adopted into North American families and grew to be much taller and bigger than their age mates. For example, at age 22 one boy who was adopted at age 4 was 10 cm taller than the average of other boys his age that had grown up in reservation settlements (Hill and Hurtado, 1996). Ache boys and girls register around or below the lowest fifth percentile of American body mass and height. These observations suggest that growth patterns are indeed limited by food availability.

### *Field methods*

A physical performance battery was conducted between May 15 and August 5, 2000, on nearly all individuals over 10 years of age living at the Arroyo Bandera colony and between December 15 and 31, 2000, at Kuetuvy, a recently established Ache community. The battery included weight, arm diameter, grip strength (measured with a Smedley III), 50-m dash, pushups, pullups, and chinups. A summed measure of pushups, pullups, and chinups is a low-cost way to measure upper body strength, but suffers from variability introduced by differential motivation across individuals, as discussed below. Subscapular and tricep skinfolds were measured at Arroyo Bandera only. To increase sample size, weights and grip strengths were measured among men and women in a third Ache colony, Chupa Pou.

The original battery also included a step test to obtain an estimate of $VO_2$ max (rate of oxygen intake during maximal aerobic exercise and considered a valid measure of the functional capacity to perform work). $VO_2$ max is expressed in units of liters of oxygen consumed per minute and aerobic capacity is expressed in milliliters of oxygen consumed per minute per kilogram of body weight. The step test was conducted at heights of 20 and 30 cm for 5 minutes at 30 ascents per minute. Steady-state work output was estimated using the equation in Heyward (1998, p. 54). Heart rate was averaged over the last minute with a Polar Pacer 98 NV. Using the submaximal Astrand nomogram and appropriate sex and age corrections (calculation routine in Shephard, 1970) a rough estimate of $VO_2$ max was calculated for each step test height and averaged between the two. It would be preferable to perform a maximal $VO_2$ test and measure oxygen output directly, but this methodology was chosen for its cost-effective simplicity. The results, therefore, should be compared to other studies with caution, although the age-dependent and sex comparisons within the Ache population are sound.

Sick, injured, or elderly individuals did not perform certain activities at their own discretion. Also, due to time constraints, not all of the individuals in Kuetuvy conducted the $VO_2$ max tests. For skinfold measurements the final value is an average between both sides. Following previous studies, the grip strength measure is taken from the stronger hand.

Participants were asked to squeeze the Smedley III as hard as possible; perform their maximum number of pushups, pullups, and chinups; and run their fastest in the 50-m dash on a flat, grass-surface soccer field. Most participants of both sexes were openly competitive while performing these measures with the exception of pushups, where less than full effort was often noticed. In contrast, a few individuals clearly gave near exhaustive efforts to these tests. It is very difficult to control for variation caused by motivation. Participants were paid the equivalent of three American dollars upon completion of the physical performance tests.

### *Analytical methods*

The following model, which is the product of a logistic growth function and a linearly declining senescence function, is fit to physical performance data across the lifespan:

$$Y = \frac{(1 - S \cdot t_m) \cdot A}{1 + e^{-G(t-I)}}$$

where $Y$ represents the physical performance variable of interest; $S$ is the senescence parameter; A, B, and G are parameters of the logistic growth function. $t$ refers to age since birth and $t_m$ is age beyond sexual maturity (estimated at 18 years). Parameter $A$ is the asymptotic value of the logistic growth function, parameter $G$ represents the exponential rate of growth, and parameter $I$ estimates age at the inflection point (Zullinger et al., 1984).

The function ($1–S^* t_m$) models senescence as starting at age 18 and leading to a linear decline in performance. This appears to approximate the data rather well over the age range sampled. However, the true age pattern of senescence at later ages (60+) may not be captured by our methods because older individuals chose whether or not to participate. This decision suggests that some who declined would have performed poorly and introduces a sample bias toward those who perform best. If everyone had participated, we believe the results would have shown an accelerated decrease in ability at later ages.

The product of the growth and senescence functions gives the model an S-curved shape through development with a linear decline after maturity. The S-shape need not be marked, but will have an inflection point (I) at which time the rate of increase is maximal and begins to slow. The procedure used here allows for continuous modeling across the lifespan and is therefore preferable to modeling the data in two steps. Growth and senescence parameters can then be compared across physical performance measures and between the sexes.

The above model is fit to Ache data separately for males and females of all ages. The model is fit using the nonlinear modeling procedure in SAS (PROC NLIN; SAS, Cary, NC). Age is the only fixed effect in the model since it is the independent variable of interest. Maximum likelihood estimates and associated standard errors are given for each parameter in the model. For both male and female Ache, when the fitted model converges it is very similar in shape to nonparametric curve fitting (e.g., least ordinary weighted sum of squares or LOWESS) plots of performance by age. LOWESS smooth curves are useful to display subtle changes with age that may not be captured in the parametric model. The assumption of linearly declining grip strength with age appears to be appropriate for men and women.

## RESULTS

Table 1 gives means of anthropometrical measurements broken down into age groups and Table 2 gives means of physical performance activities. However, the modeling approach as described above is preferable to giving means for 5- or 10-year age intervals because we are interested in the true shape of the function and testing hypotheses concerning differences in the shapes of curves. Means and standard errors for age intervals are given for anthropometrics (Table 1) and physical performance measures (Table 2) to facilitate comparisons with previous studies where structural modeling is lacking. Both absolute and relative (measures divided out by body weight) are given because we are interested in both raw performance, driven largely by body size, as well as performance per unit of body weight. For example, aerobic capacity is the relative measure of $VO_2$ max.

Table 3 gives parameter estimates and 95% confidence intervals for the fitted model for grip strength (both sexes), 50-m dash speed, pushups plus pullups plus chinups, and absolute $VO_2$ max (males only). Aerobic capacity and relative grip strength do not model well because the shape of the age function does not fit the scheme of logistic growth coupled with linear senescence because body size is what drives the logistic growth model and these are relative measures.

### *Grip strength*

We can test the hypothesis of difference between the sexes in grip strength and find that men have higher asymptotic values, as evidenced by the 95% confidence interval for female A values that does not overlap with the lower A range for males. The inflection point (highest rate of increase in grip strength) occurs at age 10.5 for girls (95% CI = 9.9, 11.1) and occurs significantly later in boys, 12.8 years (12.2, 13.4).

The growth (G) and senescence (S) parameters for grip strength are very similar for both sexes, with girls increasing only slightly faster and reaching age at fastest increase (I) over 2 years earlier. The model suggests that men are stronger mostly because grip strength continues to increase until age 25, about 4 years later than the peak grip strength in women. Figure 1a,b compares model fits to LOWESS curves for both women's and men's grip strength, respectively. Relative grip strength (grip strength divided by body weight) is interesting because the male graph is rather unchanged, with peak values in the early 20s and subsequent senescence. However, women show almost no detectable senescence across the lifespan, and we see a convergence between men and women at later ages (Fig. 2).

### *Running velocity*

Figure 3 graphs LOWESS curves fit to 50-m dash speed (m/s) by age data for both sexes. In concert with the model parameters in Table 3, men's dash speed peaks at age 23, whereas increases in women's dash speed abruptly stops at about age 15 and begins to decline. Age 15 is near the mean age of menarche for Ache women (Hill and Hurtado, 1996) when further growth is probably shunted into reproductive function rather than muscular growth. Interestingly, the quick spike in women's dash speed is not unlike the beginning of increase in the boy's curve, with the big difference between the sexes occurring at about age 15, where girl's running speed peaks and boy's running speed continues to increase for around 8 more years. Senescence in performance is again significant for both sexes and nearly significantly steeper for men than women (Table 3) and approximately linear (Fig. 3).

### *Upper body strength*

Figure 4 graphs LOWESS curves fit to the summed number of pushups, pullups, and chinups by age data for both sexes. The women's data are clearly not easily modeled by our performance function since the performance by age pattern is nearly flat, with only a slight (insignificant) decrease with age (Fig. 4). The men's data, however, show increases to age 21, greatest increase at age 15.2, and a significant linear decline with senescence (Table 3).

### *Work capacity*

Figure 5 graphs LOWESS curves fit to estimated $VO_2$ max (l/min) by age data for

*TABLE 1. Means of anthropometric measurements with standard error of the means and sample sizes in parentheses—mean (SE., n)—separated by age groups*

| Females age | Weight (kg) | Height (cm) | Arm diam. (cm) | Subscap (mm) | Tricep (mm) |
|---|---|---|---|---|---|
| 9 to 14 | 40.33<br>(1.35, 53) | 135.91<br>(1.76, 34) | 7.07<br>(0.18, 28) | 12.33<br>(1.24, 15) | 11.03<br>(0.97, 15) |
| 15 to 19 | 56.40<br>(1.35, 18) | 150.33<br>(0.58, 9) | 8.31<br>(0.22, 11) | 18.10<br>(1.96, 5) | 15.40<br>(1.76, 5) |
| 20 to 29 | 57.28<br>(1.08, 18) | 146.75<br>(1.67, 8) | 8.56<br>(0.24, 6) | 20.33<br>(3.83, 3) | 14.50<br>(2.84, 3) |
| 30 to 39 | 58.77<br>(1.45, 26) | 147.94<br>(0.83, 16) | 8.56<br>(0.11, 14) | 15.31<br>(1.11, 8) | 13.19<br>(0.90, 8) |
| 40 to 49 | 56.72<br>(1.77, 18) | 150.63<br>(1.36, 8) | 8.19<br>(0.31, 8) | 16.25<br>(5.75, 2) | 12.75<br>(1.75. 2) |
| 50 to 59 | 50.23<br>(0.83, 19) | 147.71<br>(1.38, 7) | 8.08<br>(0.10, 11) | 12.71<br>(1.50, 7) | 10.93<br>(0.62, 7) |
| 60 + | 49.50<br>(2.65, 4) | 144.33<br>(1.01, 85) | 7.11<br>(0.12, 2) | | |
| **Males age** | **Weight (kg)** | **Height (cm)** | **Arm diam. (cm)** | **Subscap (mm)** | **Tricep (mm)** |
| 9 to 14 | 33.43<br>(1.27, 39) | 133.13<br>(1.70, 15) | 6.18<br>(0.17, 15) | 6.05<br>(0.17, 10) | 5.75<br>(0.32, 10) |
| 15 to 19 | 59.90<br>(1.44, 26) | 158.25<br>(1.66, 8) | 8.83<br>(0.25, 8) | 10.90<br>(0.80, 5) | 7.90<br>(0.19, 5) |
| 20 to 29 | 60.99<br>(1.15, 40) | 159.06<br>(0.69, 17) | 8.44<br>(0.13, 18) | 8.41<br>(0.32, 11) | 5.14<br>(0.41, 11) |
| 30 to 39 | 58.85<br>(1.08, 38) | 158.06<br>(1.30, 18) | 8.26<br>(0.13, 17) | 8.00<br>(0.53, 10) | 4.65<br>(0.37, 10) |
| 40 to 49 | 63.76<br>(1.54, 22) | 157.92<br>(1.10, 13) | 8.62<br>(0.19, 8) | 8.67<br>(0.93, 3) | 4.83<br>(0.60, 3) |
| 50 to 59 | 59.86<br>(1.12, 21) | 157.00<br>(1.78, 10) | 8.54<br>(0.14, 12) | 8.42<br>(0.47, 6) | 5.25<br>(0.36, 6) |
| 60 + | 57.51<br>(1.15, 7) | 146.00<br>(4.00, 2) | 8.13<br>(0.28, 4) | 6.50<br>(0.29, 3) | 4.33<br>(0.17, 3) |

*TABLE 2. Means of physical performance activities with standard error of the means and sample sizes in parentheses—mean (SE., n)—separated by age groups*

| Females age | Grip strength | Relative grip strength | Dash speed (m/s) | Push + pull + chin | Relative push + pull + chin | $VO_2$ max (L/min) | $VO_2$ max (ml/min/kg) |
|---|---|---|---|---|---|---|---|
| 9 to 14 | 20.57 (0.74, 54) | 0.51 (0.01, 53) | 5.07 (0.08, 28) | 15.15 (1.85, 27) | 0.44 (0.07, 26) | 1.97 (0.09, 27) | 52.05 (1.91, 27) |
| 15 to 19 | 28.94 (0.74, 18) | 0.52 (0.02, 18) | 5.05 (0.19, 11) | 15.27 (2.74, 11) | 0.28 (0.06, 11) | 2.78 (0.19, 11) | 49.76 (2.98, 11) |
| 20 to 29 | 26.64 (0.85, 18) | 0.52 (0.02, 18) | 5.13 (0.20, 6) | 19.33 (4.88, 6) | 0.35 (0.09, 6) | 2.40 (0.22, 6) | 42.39 (4.48, 6) |
| 30 to 39 | 28.20 (0.57, 27) | 0.49 (0.01, 26) | 4.48 (0.10, 13) | 10.08 (1.99, 13) | 0.18 (0.04, 13) | 2.48 (0.17, 10) | 42.79 (2.32, 10) |
| 40 to 49 | 27.75 (0.99, 18) | 0.49 (0.02, 18) | 4.78 (0.11, 7) | 19.14 (3.62, 7) | 0.35 (0.06, 7) | 3.11 (0.35, 6) | 55.48 (6.62, 6) |
| 50 to 59 | 23.58 (0.84, 19) | 0.47 (0.02, 18) | 4.39 (0.14, 11) | 10.91 (1.96, 11) | 0.21 (0.04, 11) | 2.31 (0.39, 2) | 45.34 (6.54, 2) |
| 60 + | 25.50 (2.03, 4) | 0.51 (0.02, 4) | | | | | |
| **Males age** | **Grip strength** | **Relative grip strength** | **Dash speed (m/s)** | **Push + pull + chin** | **Relative push + pull + chin** | **$VO_2$ max (L/min)** | **$VO_2$ max (ml/min/kg)** |
| 9 to 14 | 20.46 (1.01, 39) | 0.61 (0.01, 39) | 5.39 (0.13, 14) | 23.43 (2.10, 14) | 0.74 (0.06, 14) | 2.14 (0.20, 14) | 65.55 (2.27, 14) |
| 15 to 19 | 38.62 (1.08, 26) | 0.65 (0.01, 26) | 6.81 (0.17, 9) | 44.78 (4.23, 9) | 0.74 (0.09, 9) | 4.12 (0.18, 9) | 67.02 (4.51, 9) |
| 20 to 29 | 41.34 (1.02, 40) | 0.68 (0.01, 40) | 6.66 (0.10, 18) | 43.00 (3.54, 17) | 0.72 (0.06, 17) | 3.74 (0.26, 18) | 61.85 (3.93, 18) |
| 30 to 39 | 37.93 (0.88, 38) | 0.65 (0.01, 38) | 6.36 (0.15, 16) | 48.00 (4.97, 16) | 0.85 (0.10, 16) | 3.29 (0.28, 15) | 56.20 (3.79, 15) |
| 40 to 49 | 37.37 (1.09, 21) | 0.59 (0.02, 21) | 6.14 (0.30, 5) | 36.86 (1.93, 7) | 0.57 (0.02, 7) | 3.23 (0.33, 4) | 46.04 (2.98, 4) |
| 50 to 59 | 33.12 (0.97, 21) | 0.56 (0.02, 21) | 5.42 (0.16, 10) | 28.89 (3.65, 9) | 0.48 (0.07, 9) | 2.74 (0.33, 4) | 43.43 (5.22, 4) |
| 60 + | 31.00 (1.75, 6) | 0.54 (0.02, 6) | 4.91 (0.15, 3) | 25.67 (3.84, 3) | 0.45 (0.08, 3) | 2.64 (n/a, 1) | 45.46 (n/a, 1) |

*TABLE 3. Parameter estimates with 95% confidence intervals of the logistic growth and linear senescence model of various physical performance measures for both sexes*

| Model | | Parameter | | | |
|---|---|---|---|---|---|
| | | (A)symptote | (I)nflection | (G)rowth | (S)enescence |
| Female grip | | 33.5889 | 10.4888 | 0.3514 | 0.00552 |
| | 95% C.I. | (31.70, 35.48) | (9.88, 11.09) | (0.24, 0.46) | (0.004, 0.007) |
| Male grip | | 47.0572 | 12.7926 | 0.332 | 0.00733 |
| | 95% C.I. | (44.46, 49.66) | (12.17, 13.42) | (0.25, 0.42) | (0.006, 0.009) |
| Female dash speed | | 5.1158 | 5.8695 | 0.6753 | 0.00404 |
| | 95% C.I. | (4.92, 5.32) | (−2.20, 13.94) | (−0.72, 2.07) | (0.002, 0.006) |
| Male dash speed | | 7.3012 | 6.7106 | 0.2036 | 0.00723 |
| | 95% C.I. | (6.90, 7.70) | (4.76, 8.66) | (0.11, 0.29) | (0.006, 0.009) |
| Male push + pull + chin | | 63.5291 | 15.2033 | 0.1598 | 0.01440 |
| | 95% C.I. | (43.59, 83.46) | (10.33, 20.08) | (0.04, 0.27) | (0.009, 0.020) |
| Female $VO_2$ max | | 2.6024 | 9.2038 | 0.4402 | −0.00141 |
| | 95% C.I. | (2.22, 2.98) | (7.08, 11.33) | (−0.034, 0.915) | (−0.010, 0.0067) |
| Male $VO_2$ max | | 4.1476 | 11.9137 | 0.4220 | 0.0102 |
| | 95% C.I. | (3.66, 4.64) | (10.60, 13.23) | (0.12, 0.72) | (0.005, 0.015) |

both sexes. Nonetheless, the age-dependent pattern for men is similar to the previous physical performance measures with increases to age 21, maximum increase at age 11, and significant linear senescence (Table 3). However, the women's $VO_2$ max data demonstrate increases to about age 18, with no clear pattern of senescence. In fact, the few older women in the sample seem to be in excellent physical condition, despite their

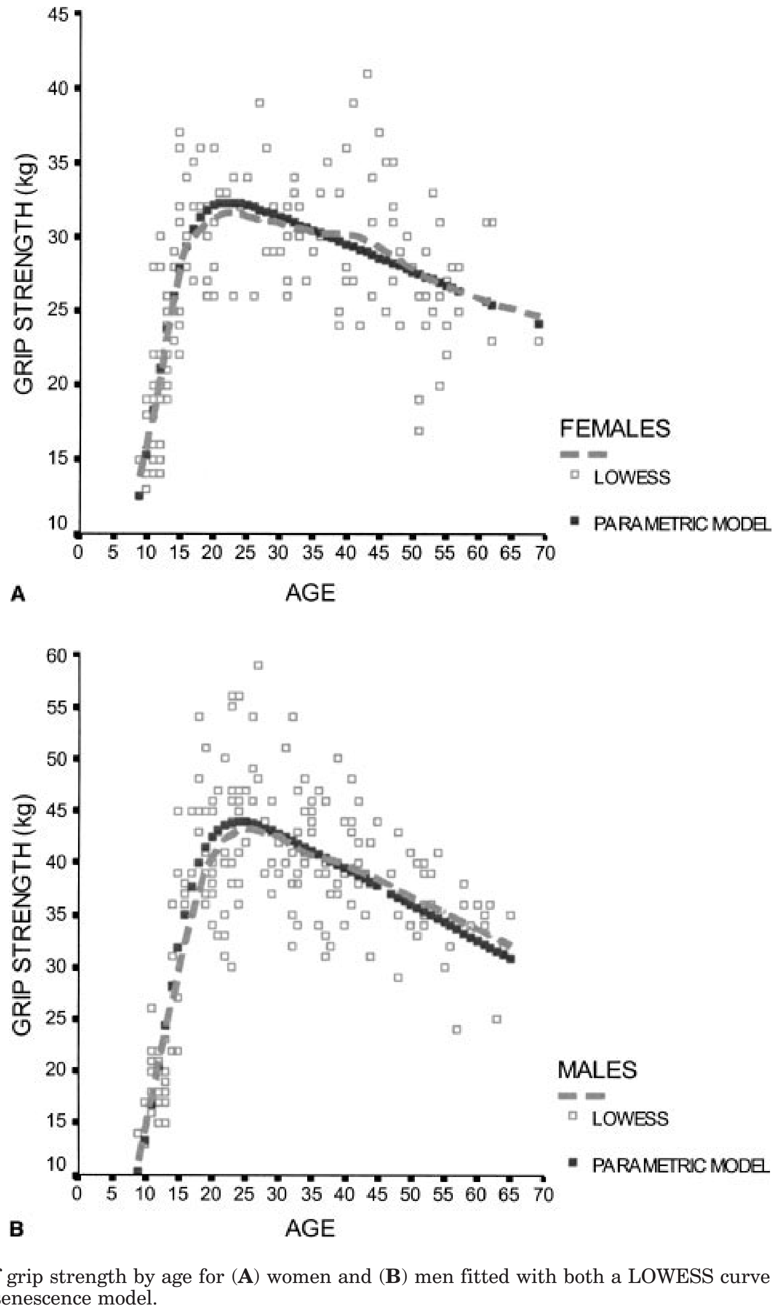


Fig. 1. Plot of grip strength by age for (**A**) women and (**B**) men fitted with both a LOWESS curve and the logistic growth/linear senescence model.

declining performance in grip strength and the 50-m dash. However, no women over 55 performed this exercise and so the true decline in later ages may not be captured.

Aerobic capacity (ml/min/kg) shows strikingly different patterns for women vs. men (Fig. 6). Women show the interesting pattern of highest values early and later in life, whereas men's aerobic capacity and $VO_2$ max measures show a similar age-specific pattern of highest values in the early 20s, with subsequent declines. Unfortunately, the sample size of

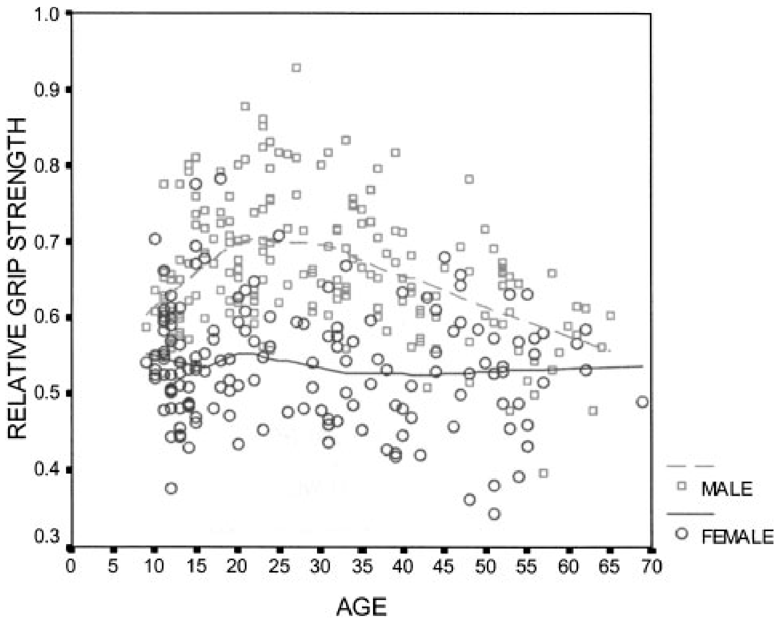


Fig. 2. Plot of grip strength divided by weight (no units) for men and women fitted with LOWESS curves.

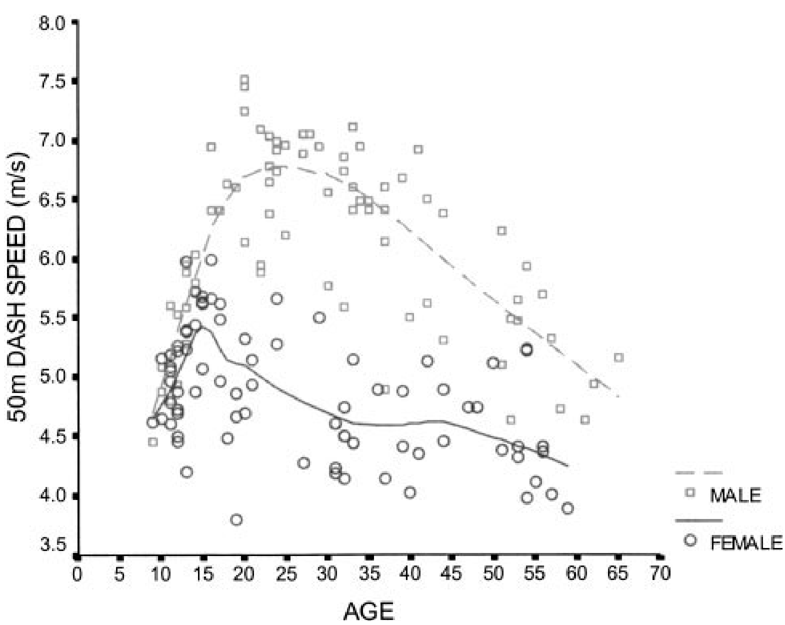


Fig. 3. 50-m dash speed (m/s) by age for men and women fitted with LOWESS curves. This measure is calculated by dividing 50 m by the time it takes to run that distance.

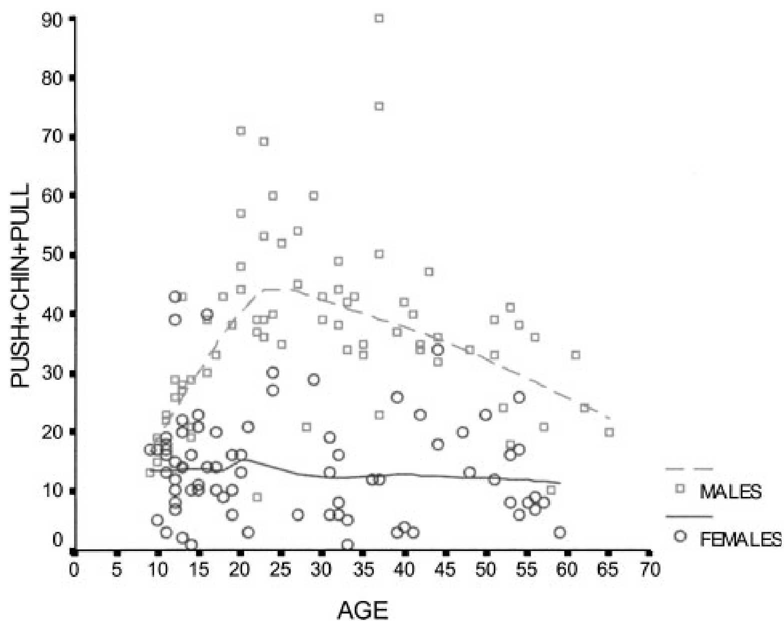


Fig. 4. Summed measure of pushups plus pullups plus chinups by age for men and women fitted with LOWESS curves.

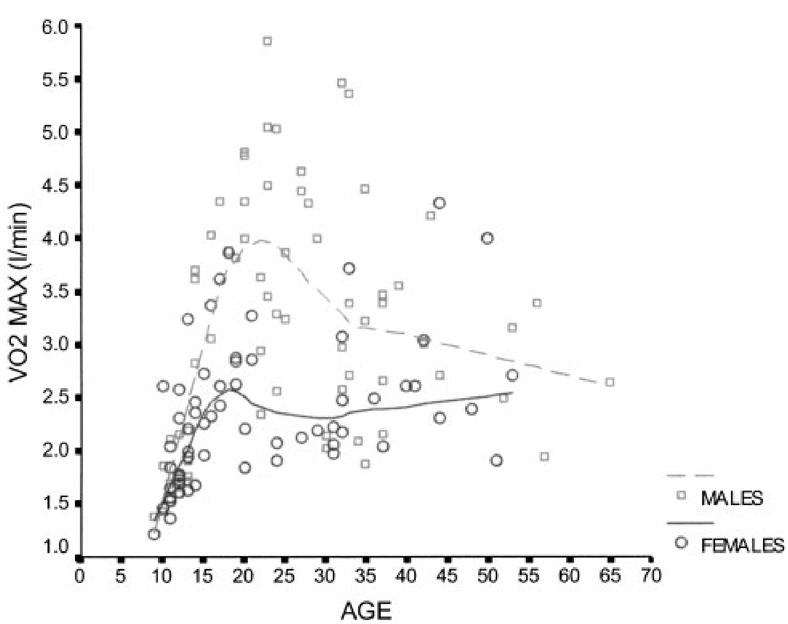


Fig. 5. $VO_2$ max (L/min) estimates by age for men and women fitted with LOWESS curves.

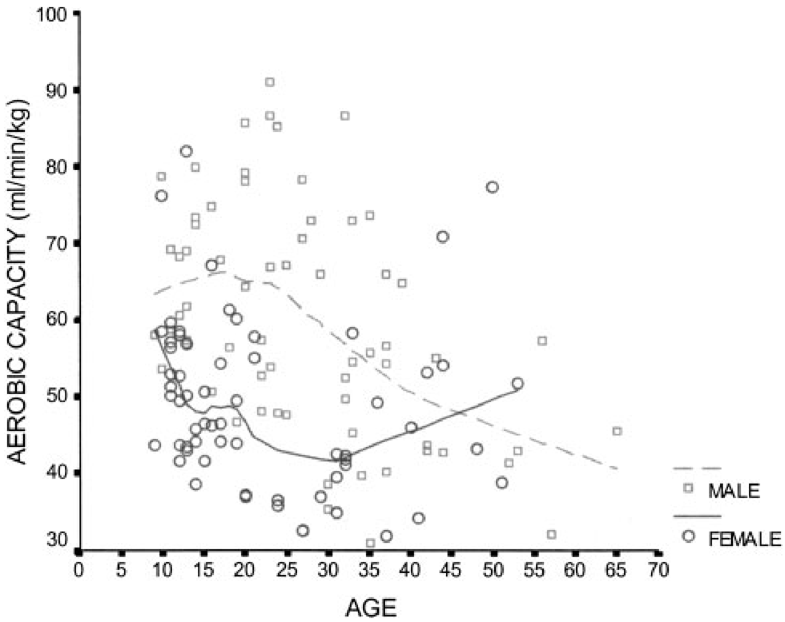


Fig. 6. Aerobic capacity (mL/min/kg) estimates by age for men and women fitted with LOWESS curves.

older individuals is small that this finding should serve as an initiative for other studies to further investigate aerobic capacity and $VO_2$ max of older women in traditional societies.

Figure 7 gives a sum of subscapular and tricep skinfolds across the lifespan. Subcutaneous fat layers in men show very little change across the lifespan, while women have the highest fat deposits in the late teens and early 20s, but declines in later ages. This observation shows why women's physical performance is hindered during the adult years and increases (e.g., aerobic capacity and $VO_2$ max), remains relatively constant (e.g., upper body strength), or at least senesces at a slower rate than male physical performance (every measure).

## DISCUSSION

This study suffers from the limitations of cross-sectional data. Although words such as "increase," "decline," and "change" are used, these should be interpreted with caution. However, body weight is one measure that has been repeated for 22 years for the Ache. Using these data, one can show that while there is some year-to-year variation in body size over this time span, there is no secular decline or increase in body size for age (unpubl. data). Therefore, given the high correlation between body size and physical performance, we assume that our cross-sectional data closely matches what would be found in a longitudinal study. Despite tight correlations between body size and performance, it is still very important to measure actual performance ability and body composition because we have found some interesting age- and sex-specific differences that are not apparent in analysis of only body weight.

Another more difficult problem is selection bias that occurs with age. Because age-specific mortality probably acts against weaker individuals, an effect that must become stronger with age, true age-dependent increases and decreases may be obscured by this age-based selection bias. We can only hope that low, rather steady rates of mortality from age 10 onwards for the Ache (Hill and Hurtado, 1996; Hill et al., 2002) do not overly hinder the results presented here.

Our cross-sectional analyses of physical performance measures across the lifespan demonstrate that men are strongest in their early 20s and experience linear declines in performance with senescence after the age of peak ability. The male pattern is seen in graphs of grip strength (Fig. 1b), relative grip strength (Fig. 2), 50-m dash speed

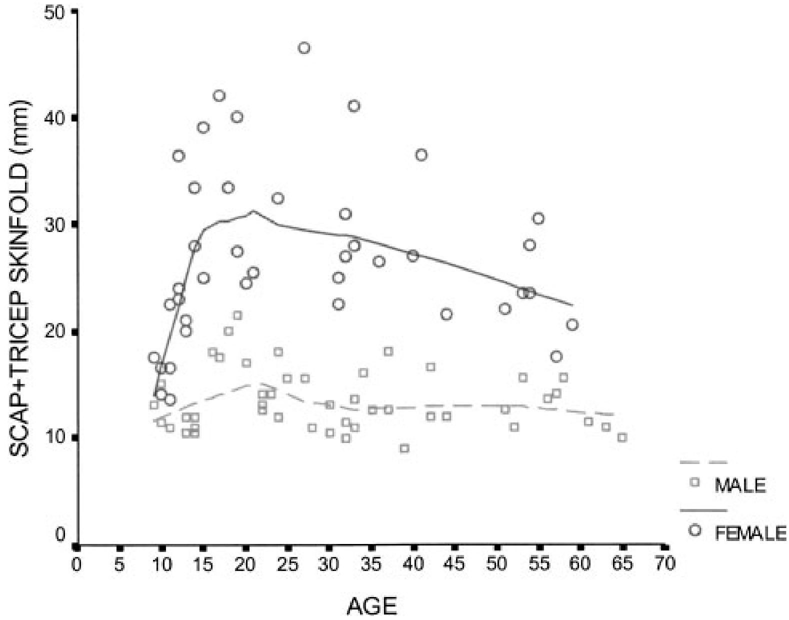


Fig. 7. Sum of tricep and subscapular skinfolds measures (mm) by age for men and women fitted with LOWESS curves.

(Fig. 3), upper body strength (Fig. 4), $VO_2$ max estimates (Fig. 5), and aerobic capacity (Fig. 6), suggesting that individuals in their late teens or early 20s are the strongest, fastest, and have the highest functional capacity of the cardiorespiratory system. However, women tend to reach performance peaks slightly earlier and senesce slower or not at all, depending on the measure. The most intriguing result is the age pattern of $VO_2$ max and aerobic capacity in females that suggests high work capacity before and after the adult reproductive years and a lower work capacity between ages 20 and 45.

There are two studies (Ohtsuka et al., 1987; Little and Johnson, 1986) that compare grip strength and grip strength per unit body weight (i.e., relative grip strength) among the Gidra of Papua New Guinea, Turkana of northwest Kenya, Zapotec speakers in southern Mexico, and modern Japanese, French, and Americans. Relative grip strength among Ache women appears to be unique in showing little to no senescence across the lifespan. Relative grip strength values for Ache women are intermediate between Zapotec and Turkana, and values for Ache men are comparable to Zapotec and Turkana. Gidra Papuans and modern men and women demonstrate larger relative grip strengths than the Ache at all ages (ibid.). Examining absolute grip strength, Little and Johnson (1986) state that all groups in their study (U.S., Turkana, Zapotec, and French) demonstrate age decrements between 2.0 and 2.5 kg per decade for men and between 1.0 and 2.2 kg per decade for women. Ache men decline at 1.7 kg per decade and women at 0.9. Rate of senescence in the Ache sample therefore appears to be slower than for the other groups, but the same pattern of more rapid senescence in men holds for all groups studied. However, senescence measured as a percentage decline may be approximately equal between the sexes.

Delayed development in food-limited populations has been well documented (Shephard, 1978; Little and Johnson, 1986; Curran-Everett, 1994). Whereas studies in food-abundant populations demonstrate greatest isometric muscle strength in the late teens (i.e., Swedes in Bäckman et al., 1995), undernourished traditional populations like the Ache tend to demonstrate performance peaks in the early- to mid-20s.

### *Age-specific food production*

These schedules of physical performance can be contrasted with schedules of food production ability, which tend to occur later in life, and therefore imply that skill is an important component of the human foraging niche. For example, Ache age-specific hunting performance measures—finding rates and probabilities of kill upon encounter for important prey and archery ability—look very different than strength schedules. Proficiency peaks in hunting ability tend to occur much later in life. Hunters at the peak return rate age of 40 years harvest on average 0.7 kg per hour, while hunters at the age of peak strength harvest at less than one-half that rate (Walker et al., 2002). And, at the peak return rate age of 40 years, men achieve only 75% of the absolute aerobic capacity to do work ($VO_2$ max) that characterizes them when they are 20 years younger.

Hunting return rate curves peak later in life for other societies as well—age 35 for the Hiwi (Kaplan et al., 2000), 40 for the Machiguenga and Piro (Gurven and Kaplan, n.d.), early or mid-40s to mid-50s for the Etolo (Dwyer, 1983), 45–50 for the Hadza (Marlowe, 2000). Gidra hunters around the ages of 35–45 have return rates four times higher than hunters in their late teens, despite the fact that both age groups had nearly equal grip strength measures (Ohtsuka, 1989). While some of these results may be partially due to effects of acculturation, these studies suggest that skill acquisition for several decades is an important component of traditional human hunting. Additionally, some extractive gathering activities, such as mongongo nut processing (Bock, 1995, 2002), Gidjingali shellfish collecting (Meehan, 1982), and Hadza (Blurton Jones and Marlowe, 2002) and Hiwi root digging (Kaplan et al., 2000) have return rate schedules with similar shapes as hunting curves. Although age-specific performance may be partially confounded by childcare, this probably indicates that success in these activities is based on learned skills rather than strength, especially since women's strength peaks even earlier in life than for men. However, as shown in Figures 5 and 6, work capacity may be high for women in their 40s and beyond as a combined result of decreasing fat (Fig. 7) and/or increased training levels, which leads to increased performance. Increased work time and output for older women has been shown for the Ache and Hiwi (Hurtado et al., 1992), Hadza (Hawkes et al., 1989, 1997), and the Agta (Headland, 1986).

The schedules of physical performance presented here can also be contrasted with data from Olympic athletes, as peak ages in ability appear to map onto skill-intensities of the activity. Even with drastic improvements over the last century in Olympic training, Schulz and Curnow (1988) have found that the age of peak performers in many events has remained nearly constant from 1896–1980. In women's short-distance running, peak performance is around age 22, medium-distance running age 24, long-distance running age 27, tennis age 24, and swimming age 18. In men's short-distance running, peak performance is around age 23, medium-distance running age 24, long-distance running age 27, jumping age 24, tennis age 24, and swimming age 20. Sports that require more precise motor control take longer to reach proficiency. For example, female golfers reach their prime at age 30, males at age 31, and male baseball players age 27 (Schulz and Curnow, 1988; Horn, 1988). These data demonstrate how age-dependent ability maps onto the level of skill investment needed to reach peak ability and suggests that none of these Olympic events requires as much skill as hunting and some other extractive foraging activities.

### *Sex differences*

Sex differences in physical performance schedules are almost certainly due to differences in body composition and higher investment in female reproductive organs. Girls have on average 50% more adipose tissue mass than boys from late adolescence into adulthood (Cameron, 1998; Norgan, 1998). While both sexes experience adolescent growth spurts in muscle mass accompanied by an increase in cardiorespiratory function, girls demonstrate levels relatively and absolutely lower than for boys (Bogin, 1999; Shephard, 1978). Human females differ from other primates and most mammals in having substantial subcutaneous adipose energy reserves to meet costs of reproduction (Prentice and Whitehead, 1987). The common ethnographic pattern of sequestering females at age of menarche, seen traditionally in the Ache (Hill and Hurtado, 1996), probably accentuates increases in percent body fat through both lower energy expenditure and increased food intake.

It makes sense that increased adipose tissue relative to muscle mass in women should have little effect on age-dependent grip strength schedules or other isometric muscle measures, but it clearly inhibits physical performance beginning in adolescence for 50-m dash, pushups, pullups, chinups, relative grip strength, $VO_2$ max, and aerobic capacity (Figs. 2–6). Increases in performance in these measures are attenuated because of tradeoffs associated with allocation to fat and reproductive tissue necessary for reproduction in women. This suggests that the female physiology faces reproductive constraints on performance early in life, whereas the male physiology maximizes work output in early adult life.

Shephard (1999) states that functional loss of physical performance can be countered with regular physical activity, but that continuously training athletes still show substantial effects of aging that is a reflection of decreases in cardiac pump function and muscle strength coupled with increasing impairment of heat tolerance. As we have shown for the Ache, also an active population, senescence still occurs in a predictable manner, similar to physically active modern populations. Bortz and Bortz (1996) find senescence rates in running, rowing, swimming, and $VO_2$ max of around 0.5% per year in active individuals. The rates of senescence for the physical performance tests measured here range from 0.4–1% per year decline starting at age 18 until the 50s–60s, where sample sizes become small. Senescence rates probably begin to accelerate at later ages, but since we allowed individuals to self-select into participation, the age of accelerated decline is not visible.

Interestingly, the exceptions appear to be women's $VO_2$ max, aerobic capacity, and upper body strength (pushups, pullups, and chinups). No decline is detectable in either $VO_2$ max or aerobic capacity, a result also found for indigenous Siberian women (Katzmarzyk et al., 1994), although decreases with age were found for Inuit women (Rode and Shephard, 1971, 1994). Women in modern societies who continue to gain considerable body fat after maturity show marked decline in aerobic performance with age (Schvartz and Reibold, 1990).

This pattern of high aerobic performance at young and old ages for indigenous women suggests that the female physiology faces reproductive constraints to performance early in life but shifts allocation to increased work output later in life during the long human postmenopausal stage. In contrast, the male physiology appears to be designed to maximize work output in early adult life, but more research on high-activity, non-contraceptive-using traditional societies is needed to verify these results.

## ACKNOWLEDGMENTS

We thank the Ache of Arroyo Bandera, Chupa Pou, and Kuetuvy for their patience and cooperation with this project. Discussions with Hilly Kaplan were the main motivation for the modeling procedure.

## LITERATURE CITED

Aoyagi Y, Shephard RJ. 1992. Aging and muscle function. Sports Med 14:376–396.

Bäckman E, Johansson V, Hager B, Sjoblom P, Henriksson G. 1995. Isometric muscle strength and muscular endurance in normal person aged between 17 and 70 years. Scand J Rehabil Med 27:109–117.

Blurton Jones N, Marlowe F. 2002. Selection for delayed maturity: does it take 20 years to learn to hunt and gather? Hum Nat 13:199–238.

Bock J. 1995. The determinants of variation in children's activities in a southern African community. Ph.D. Dissertation, University of New Mexico, Albuquerque, NM.

Bock J. 2002. Learning, life history, and productivity: children's lives in the Okavango Delta, Botswana. Hum Nat 13:199–238.

Bogin B. 1999. Patterns of human growth. Cambridge, UK: Cambridge University Press.

Bortz WM, Bortz WM. 1996. How fast do we age? Exercise performance over time as a biomarker. J Gerontol Series A Biol Sci Med Sci 51:M223–M225.

Cameron N. 1998. Fat and fat patterning. In: Ulijaszek SJ, Johnston FE, Preece MA, editors. The Cambridge encyclopedia of human growth and development. Cambridge, UK: Cambridge University Press. p 230–232.

Clastres P. 1998. Chronicle of the Guayaki Indians. Cambridge, MA: MIT Press.

Curran-Everett L. 1994. Accordance between VO2 max and behavior in Ngisonyoka Turkana. Am J Hum Biol 6:761–771.

Dwyer PD. 1983. Etolo hunting performance and energetics. Hum Ecol 11:145–174.

Greksa L. 1990. Developmental responses to high-altitude hypoxia in Bolivian children of European ancestry: a test of the developmental adaptation hypotheses. Am J Hum Biol 2:603–612.

Gurven M, Kaplan H. n.d. Determinants of time allocation to production across the lifespan among the Machiguenga and Piro Indians of Peru. Unpublished manuscript, University of New Mexico.

Hawkes K, O'Connell JF, Blurton Jones N. 1989. Hardworking Hadza grandmothers. In: Standen V, Foley R, editors. Comparative socioecology. London: Basil Blackwell. p 341–366.

Hawkes K, O'Connell JF, Blurton Jones NG. 1997. Hadza women's time allocation, and the evolution of long postmenopausal life spans. Curr Anthropol 38:551–575.

Headland T. 1986. Why foragers do not become farmers: a historical study of a changing ecosystem and its effect on a Negrito hunter-gatherer group in the Philippines. Honolulu: University of Hawaii.

Heyward VH. 1998. Advanced fitness assessment and exercise prescription. Champaign, IL: Human Kinetics.

Hill K, Hawkes K. 1983. Neotropical hunting among the Ache of eastern Paraguay. In: Hames RB, Vickers WT, editors. Adaptive responses of Native Amazonians. New York: Academic Press. p 139–188.

Hill K, Hurtado M. 1996. Ache life history: the ecology and demography of a foraging people. New York: Aldine de Gruyter.

Hill K, Boesch C, Goodall J, Pusey A, Williams J, Wrangham R. 2001. Mortality rates among wild chimpanzees. J Hum Evol 39.

Hurtado AM, Hawkes K, Hill K, Kaplan H. 1985. Female subsistence strategies among Ache hunter-gatherers of Eastern Paraguay. Hum Ecol 13:1–28.

Hurtado AM, Hill K, Kaplan H, Hurtado I. 1992. Trade-offs between female food acquisition and child care among Hiwi and Ache foragers. Hum Nat 3:185–216.

Kaplan H, Hill K, Lancaster J, Hurtado AM. 2000. A theory of human life history evolution: diet, intelligence, and longevity. Evol Anthropol 9:156–184.

Katzmarzyk PT, Leonard WR, Crawford MH, Sukernik RI. 1994. Predicted maximal oxygen consumption of indigenous Siberians. Am J Hum Biol 6:783–790.

Little MA, Johnson BR Jr. 1986. Grip strength, muscle fatigue, and body composition in nomadic Turkana pastoralists. Am J Phys Anthropol 69:335–344.

Malina RM, Buschang PH, Aronson WD, Selby HA. 1982. Aging in selected anthropometric dimensions in a rural Zapotec-speaking community in the valley of Oaxaca, Mexico. Soc Sci Med 16:217–222.

Marlowe F. 2000. The patriarch hypothesis: an alternative explanation of menopause. Hum Nat 11:27–42.

McMillan G. 2001. Ache residential grouping and social foraging. Ph.D. Disseration, University of New Mexico, Albuquerque, NM.

Meehan B. 1982. Shell bed to shell midden. Melbourne: Globe Press.

Norgan NG. 1998. Body composition. In: Ulijaszek SJ, Johnston FE, Preece MA, editors. The Cambridge encyclopedia of human growth and development. Cambridge, UK: Cambridge University Press. p 212–215.

Ohtsuka R. 1989. Hunting activity and aging among the Gidra Papuans: a biobehavioral analysis. Am J Phys Anthropol 80:31–39.

Ohtsuka R, Inaoka T, Kawabe T, Suzuki T. 1987. Grip strength and body composition of the Gidra Papuans in relation to ecological conditions. J Anthropol Soc Nippon 95:457–467.

Prentice AM, Whitehead RG. 1987. The energetics of human reproduction. Symp Zool Soc Lond 57:275–304.

Rode A, Shephard RJ. 1971. Cardiorespiratory fitness in an Arctic community. J Appl Physiol 31:519–526.

Rode A, Shephard RJ. 1994. Physiological consequences of acculturation: a 20-year study of fitness in an Inuit community. Eur J Appl Physiol 69:516–524.

Schulz R, Curnow C. 1988. Peak performance and age among superathletes: track and field, swimming, baseball, tennis, and golf. J Gerontol Psychol Sci 43:113–120.

Schvartz E, Reibold RC. 1990. Aerobic fitness norms for males and females aged 6 to 75 years: a review. Aerospace Med Assoc 61:3–11.

Shephard RJ. 1970. Computer program for solution of the Astrand nomogram and the calculation of body surface area. J Sports Med Phys Fitness 10:206–210.

Shephard RJ. 1978. Human physiological work capacity. Cambridge, UK: Cambridge University Press.

Shephard RJ. 1999. Age and physical work capacity. Exp Aging Res 25:331–343.

Walker RS, Hill K, Kaplan H, McMillan G. 2002. Age-dependency in hunting ability among the Ache of eastern Paraguay. J Hum Evol 42:639–657.

Zullinger EM, Ricklefs RE, Redford KH, Mace GM. 1984. Fitting sigmoidal equations to mammalian growth curves. J Mammal 65:607–636.