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TESTOSTERONE LEVELS CHANGE WITH SUBSISTENCE HUNTING EFFORT IN !KUNG SAN MEN

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SUMMARY

Although little is known empirically of the physiology of human hunting, arguments for innate biological bases of gender-dimorphic behaviors such as aggression frequently point to the role of hunting in human evolution. Study of !Kung San hunter-gatherer men demonstrated that the diurnal pattern in serum testosterone was altered during a six-day hunt, compared to pre- and post-hunt levels, due mainly to elevation of evening values. Hunting success did not correlate with any testosterone measures. The pattern of changes observed is most consistent with the known concomitants of moderate prolonged exercise.

INTRODUCTION

HUNTING AND GATHERING comprise the subsistence strategy pursued by humans for 95% of their history, and which has apparently shaped the characteristically human anatomy, physiology, behavior, and even intelligence (Washburn & Lancaster, 1968; Mayr, 1970, p. 385; Eaton & Konner, 1985). For this reason, the hunting-gathering niche is widely regarded as central to understanding both the evolution and the current substrates of human behavior. The study of certain contemporary hunter-gatherer populations can therefore provide a window on the adaptive context of human behavioral biology .

The recognized importance of hunting and gathering in human evolution, coupled with the observation that hunting of large game is engaged in almost exclusively by men in most known traditional cultures (D'Andrade, 1966; however, see Dahlberg, 1981), has often led to the inference that hunting forms the adaptive basis of male aggression. That men do engage more in certain aggressive, competitive and stressful activities has tended to reinforce this supposition. A predisposition to engage in these behaviors has been thought to be based on androgens, the dominant gonadal steroids in males. The relationship between testosterone (T), the most predominant potent androgen in plasma, and behavioral or environmental variables has therefore been extensively explored. However, no study has characterized the response of androgens to subsistence hunting, which is the presumed adaptive basis for these hormone-

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behavior relationships. Research on the physiology of human hunting has been limited to studies of endurance in one population of hunter-gatherer men (Nurse & Jenkins, 1977).

In the study reported herein, a naturalistic experiment was performed to explore the impact of hunting activity on circulating levels of T in !Kung San subsistence hunters. Previous studies of this population have provided key insights into basic human adaptive modes in, among others areas, nutrition, demography, lactation and behavioral ecology. In this instance, the fact that hunting by men is a routine basis of subsistence provided an opportunity to probe the relationship between hunting and T.

While there is no information on androgens in hunting, there is a large literature on the relation of T to context and behavior, both in men and in male non-human primates. Sensitivity of T levels to activity and experience has been most clearly demonstrated in the areas of stress, aggression and exercise. Each has characteristic effects. First, both physical and psychological stress have been consistently found to depress T (Mason, 1968; Kreuz *et al.*,1972; Opstad & Aakvaag, 1982). Second, aggressive or competitive/dominance encounters generally raise T levels, which also reflect the outcome of the encounter: T levels are elevated in winners and relatively depressed in losers (Rose *et al.*, 1975; Elias, 1981). In non-human primates, interactions of aggressive behavior and T, through both developmental and concurrent effects, are well-documented (Rose *et al.*, 1974). Similar effects may obtain in humans (Rubin *et al.*, 1981). While androgens and spontaneous aggressive behaviors have not been studied synchronously in men, some evidence links indirect behavior measures or overall personality ratings (aggressiveness, hostility) to T levels (Rose, 1975; Olweus *et al.*, 1980), although these findings have been difficult to replicate (Doering *et al.*, 1974; Monti *et al.*, 1977). Finally, exercise and physical effort are also paralleled by changes in serum T, which is an anabolic hormone that promotes energy release to support large muscle effort. Generally, sustained moderate-to-intense exercise appears to elevate T, although data from some studies have been equivocal (Kuoppasalmi *et al.*, 1980).

Study of T response to hunting in men who hunt for a living would provide a hormonal profile of this apparently prototypic, characteristically male activity. Further, it may answer the question of whether men experience hunting in a manner like, or unlike, the previously-reported patterns of response to stress, aggression, and exercise.

METHODS

The study participants were !Kung San, a Khoisan-speaking hunter-gatherer population of the Kalahari in northwestern Botswana and adjacent regions of Namibia and Angola. Numerous aspects of their biology, ecology and culture have been extensively studied (cited in Konner & Worthman, 1980), and their hunting practices have been described (Lee, 1968; 1979). Hunting supplies only a minority of the diet measured by weight, in this case 30%. Like many known hunter-gatherers, a marked division of labor restricts this activity almost completely to men. Adult men pursue game an average of three days a week, and vary widely in hunting inclination, talent and experience. Traditional prey species range from reptiles and game birds to eland and giraffe, and the strategies, equipment and effort involved vary accordingly. Methods employed include capture of small prey with bare hands, trapping, clubbing, stalking and shooting with small poisoned arrows, and organized group attacks with spears and dogs.

Six !Kung hunters, ages 25 to 45 years (35.8 ± 3.3), were the subjects of the main experiment. A 29-year-old Western male was also included as a control. Steroid hormone levels were monitored before, during and after a six-day hunt that took place in mid-August, a time of relatively cool, dry weather with conditions favorable for tracking. Baseline (pre-hunt) blood samples were drawn on the two days prior to departure of subjects for six days' hunting in a familiar environment in the Dobe area where game was said to be plentiful. Subjects returned to the village and were followed for two post-hunt days, for a total of 10 study days. Choice of prey and of hunting partners, methods and intensities were all left to the subjects' discretion. At the end of each day, brief individual interviews produced a written description of that day's activity. These were later coded by

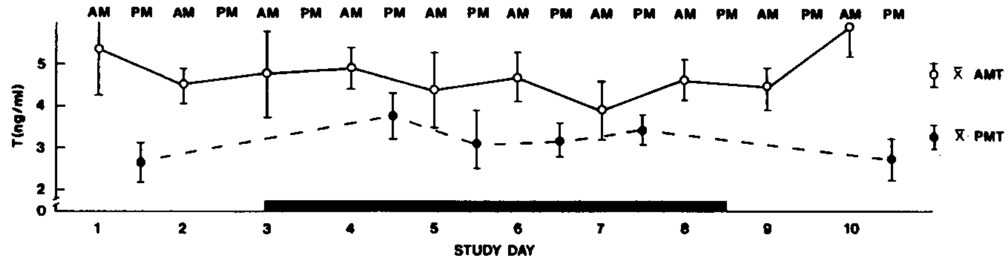

FIG. 1. Serum testosterone levels in six !Kung men in relation to hunting activity over a 10-day period. Men were followed for 10 consecutive days, with significant hunting effort expended on days 3-8. Mean values of T (ng/ml ± s.e.) are shown for the men at each sample point. Distance between the lines for AM and PM means roughly reflects AM-PM T. Values are these: Pre-hunt AM = 5.34 ± 1.10, Hunt AM (grand mean) = 4.42 ± 0.63, Post-hunt AM = 5.44 ± 0.81; Pre-hunt PM = 2.81 ± 0.39, Hunt PM (grand mean) = 3.43 ± 0.63, Post-hunt PM = 2.56 ± 0.40; Pre-hunt ΔT = 2.53 ± 0.99, Hunt ΔT (grand mean) = 1.00 ± 0.25, Post-hunt ΔT = 2.88 ± 0.71 ng/ml. Symbols: O——O AM T; ●-----● PM T; solid horizontal bar represents hunting period.

another investigator for daily intensity of hunting effort and degree of success or failure on an arbitrary scale (0 to 5 for effort; -3 to +3 for degree of failure/success). Subjects were also questioned about occurrence of intercourse. For a variety of reasons, including pregnancy or lactation of spouse, there was only one report of coitus during the entire study.

Blood was drawn daily either at 0700 h (AM) and 1900 h (PM) (days 1, 4-7 and 10), or at 0700 h only (days 2, 3, 8 and 9). Samples were withdrawn from the antecubital vein into 10 ml non-heparinized siliconized vacutainers, allowed to clot for 30 min, then spun on a hand-crank centrifuge. Serum was decanted and stored in liquid nitrogen until processing. Concentrations of T, estradiol (E_2) and progesterone (P) were determined simultaneously by celite partition chromatography and radioimmunoassay (RIA) according to a widely-used method (Coyotupa *et al.*, 1972). Blanks, pools, and unknowns were extracted in ether, frozen, decanted, dried, taken up in 1 ml isooctane (TMP), and applied to prepared celite microcolumns. With a 0.5 ml TMP rinse, the next 3.5 ml (TMP) eluate was collected for P RIA, the next 5.0 ml (TMP) discarded, the next 6.0 ml (benzene:TMP 30:70) saved for T RIA, the next 3.5 ml (ethyl acetate:TMP 15:85) discarded, and the last 3.5 ml (ethyl acetate:TMP 40:60) saved for E_2 RIA. Radiolabeled (high specific activity, ^3H quadruple-labeled) steroids were obtained from New England Nuclear. Specificities of antisera kindly supplied by Guy E. Abraham [S-741#2 (T), S-49#6 (P) and S-52#6 (E_2)] have been reported elsewhere (Abraham *et al.*, 1971; Coyotupa *et al.*, 1972). Assay sensitivity (mean for standard curve, in pg: P = 15; T = 8; E_2 = 12) and precision (mid-range pool, duplicates: intra-assay %CV for P = 3.9, T = 2.8, E_2 = 6.1; inter-assay %CV for P = 9.8, T = 5.2, E_2 = 12.5) were well within accepted limits.

Because it is conventional to use parametric statistics on measures such as these, all central tendencies are reported here as means ± s.e. However, the inferential statistics used throughout are nonparametric tests with more conservative assumptions.

RESULTS

Testosterone

Serum T levels for all !Kung subjects are plotted by sample point in Fig. 1. Values and ranges are comparable to those established for Western populations (Faiman & Winter, 1971). Evening as well as morning samples were drawn because it was reasoned that, if activity undertaken during the day affects T levels, that effect would best be discerned at the end of the day. In Western clinical populations, a marked diurnal variation in serum T levels has been reported, with evening values averaging around 30% lower than morning values (Nieschlag,

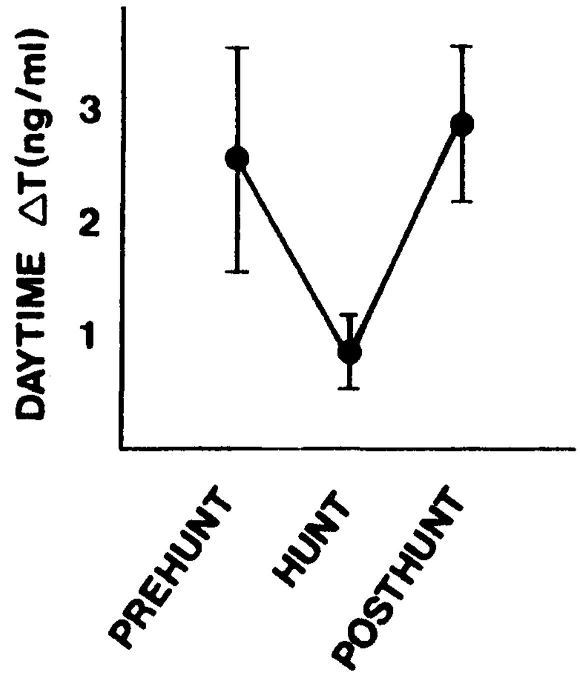

FIG. 2: Morning-to-evening difference in serum testosterone levels (ΔT) in six !Kung San men before, during and after a six-day hunt.

1974). Baseline values of !Kung hunters show similar diurnal variation. Pre-hunt (5.34 ± 1.10 ng/ml) and post-hunt (5.44 ± 0.81 ng/ml) AM levels differed significantly from the corresponding pre- and post-hunt PM levels (2.81 ± 0.39 and 2.56 ± 0.40 ng/ml, respectively). The magnitude of the daytime decline in T averaged 2.53 ± 0.99 ng/ml in pre-hunt and 2.88 ± 0.71 ng/ml in post-hunt samples, a morning-to evening drop of 44% ($p < .03$, Wilcoxon signed ranks test, two-tailed) and of 53% ($p = .031$), respectively. This was confirmed by samples taken from these and other men outside the main experimental period, and indeed, to a lesser extent by the values obtained during the six-day hunt itself (AM, 4.31 ± 0.17 ng/ml; PM, 3.43 ± 0.63 ng/ml; $p = .063$).

On hunt days, however, the morning-to-evening difference in T concentration (ΔT) was diminished to only 19.4% (Fig. 2). ΔT decreased by two-thirds of the pre-hunt mean to 0.85 ± 0.61 ng/ml during the hunt and returned to baseline values by the last post-hunt day. Comparison of mean ΔT during the hunt with that before the hunt approached significance ($p = .063$, Wilcoxon signed ranks test, two-tailed), while the hunt to post-hunt comparison was significant ($p = .031$). The primary cause of the reduction in diurnal T variation on hunt days was an increase in PM levels. Evening T was 2.81 ± 0.39 ng/ml pre-hunt, 3.47 ± 0.44 on four hunt days, and 2.56 ± 0.30 post-hunt. The difference between hunt and pre-hunt PM values approached significance (Wilcoxon signed ranks, $p = .063$, two-tailed), and the post-hunt decrease in PM values was significant ($p = .031$). There was no difference between pre- and post-hunt PM values. Although AM values were lower during than before or after the hunt, this effect did not approach significance; thus, if we had measured AM values only, no effect would have been discerned.

TABLE I. DAYTIME CHANGE (ΔT) AND EVENING VALUES (PM) OF TESTOSTERONE (T) BY INTENSITY OF HUNTING ACTIVITY. ΔT = AM-PM; AM = T VALUES AT 0700 H; PM = T VALUES AT 1900 H. SCALES OF HUNTING INTENSITY WITH REPRESENTATIVE BEHAVIORS: 0 = NO HUNTING; 1 = DESULTORY TRAPPING ONLY, NO SYSTEMATIC PURSUIT OF GAME; 2 = PERSISTENT SHOOTING OF FOWL, SETTING OF SNARES, BRIEF ASSISTANCE IN LARGE PREY HUNT; 3 = STEADY SEEKING OF GAME FOR PART OF DAY, SOME STALKING AND PURSUIT, ACTIVE HONEY COLLECTION; 4 = ALL-DAY HUNTING (SEEKING, TRACKING, STALKING) OF LARGER GAME, SOME PURSUIT; 5 = ALL-DAY INTENSE INVOLVEMENT, CONSTANT ACTIVITY (GENERALLY OCCURRED IN PURSUIT OF LARGE GAME).

	Hunting Activity Level											
	0		1		2		3		4		5	
T values (ng/ml)	ΔT	PM T	ΔT	PM T	ΔT	PM T	ΔT	PM T	ΔT	PM T	ΔT	PM T
mean	2.80	2.69	2.17	2.93	0.93	3.35	0.83	3.60	0.908	3.35	1.06	3.19
SD	1.93	0.94	---	---	0.40	1.39	1.58	1.19	1.90	0.99	2.02	1.16
s.e.	0.56	0.27	---	---	0.20	0.70	0.53	0.39	0.78	0.40	0.90	0.52
n of obs.	12		1		4		9		6		5	

Hunting effort and success

Mean effort score for all subjects on hunt days was 3.2 ± 1.27. Inspection of the relationship between intensity of activity and T over the entire study period (Table I) suggests that the daytime decline in T was significantly diminished at all but the most minimal hunting intensities. There were no significant differences in ΔT across hunting effort levels 1 (corresponding, for example, to desultory trapping of fowl) through 5 (represented by activity such as day-long pursuit, with dogs, of large game) (Spearman r = .139, .9>p>.5). Further, no relationship was observed between degree of hunting effort and evening values of T (Spearman r = -.095, .9>p>.5), nor was the level of morning T related to degree of effort expended thereafter over the day (Spearman r = .170, 4>p>.3).

Hunting success and failure averaged 0.1 ± 1.9 across all subjects. Hunt outcome was not correlated with T (Table II). On hunt days, neither evening T levels (Spearman r = -.150, .5>p>.4), nor ΔT (r = .040, .9>p>.5), nor AM T (r = -.061, .9>p>.5) nor even subsequent AM T (r = -.324, .2>p>.1) were statistically related to outcome of hunt. Furthermore, hunt effort bore no significant relationship to outcome (Spearman r = -.204, .9>p>.5). Hunters' T values on days of successful game procurement (i.e., in men who actually caught game or "owned" a group kill) were compared to values on days when they failed to catch game. This comparison showed no difference between successful and failed game procurement days in evening T (Student's t, p = .61), ΔT (p = .66), morning T (p = .98), or subsequent morning's T (p = .69).

Control

The Western control subject participated fully in activities on hunt days. His mean non-hunt values (pre-hunt AM 5.87, PM 2.14, ΔT 3.39; post-hunt AM 5.58, PM 2.28, ΔT 3.72 ng/ml) lie well within the range of both the !Kung men and Western men. During the hunt period, his T

TABLE II. MEAN TESTOSTERONE EVENING (PM) VALUES, AM-PM DIFFERENCE, AND MORNING LEVELS ON THE SUBSEQUENT DAY (POST-AM) BY DEGREE OF HUNTING SUCCESS. SUCCESS WAS CODED BY MAGNITUDE OF RETURN (NUMBER AND SIZE), WEIGHED AGAINST DEGREE OF EFFORT INVESTED FOR NO RETURN. NEGATIVE SCORES REFLECT DEGREE OF EFFORT EXPENDED IN FAILED HUNTS.

	Hunt Outcome						
	-3	-2	-1	0	1	2	3
T values (ng/ml)							
PM	3091 ± 1238	4151 ± 1108	3679 ± 1195	2928	3846 ± 920	3027 ± 1560	2619 ± 788
ΔT	1190 ± 344	-658 ± 2221	-129 ± 1160	-754	2251 ± 1743	773 ± 1837	725 ± 645
n of obs.	4	3	4	1	6	3	3
post-AM	4263 ± 2081	4451 ± 1427	4500 ± 2324	4810 ± 2565	4913 ± 1073	3961 ± 1381	2995 ± 711
n of obs†	4	4	6	6	8	4	3

† Numbers of observations for PM T and ΔT differ from those for post-AM because PM samples were not collected on all study days. There are considerably more zero-success scores for post-AM, because these include the initial day when men merely went out to the bush for the hunt and did set-up and reconnaissance (i.e., little effort and zero immediate return).

profile (mean AM 6.26, PM 5.21, ΔT 1.05 ng/ml) showed substantially the same pattern of change as did the !Kung hunters'. These data, though limited to a single subject, indicate that the hormone responses observed may not be population-specific.

Progesterone and estradiol

In view of reports attributing to !Kung San men a marked elevation of E_2 relative to women (Tobias, 1966), serum E_2 and P were also measured in a small sample of San men. Their averages for E_2 (38 pg/ml, range 10-118) and P (232 pg/ml, range 73-723) did not differ notably from the means (E_2, 21.2 ± 7.2 ; P, 212 pg/ml) reported for Western men (Abraham *et al.*, 1971), and they are about an order of magnitude lower than !Kung San women's values. !Kung women in a related study had overall mean T values of 209 pg/ml (range 81-476), at the lower end of the range of reported values for women in sedentary Western populations (Margoulis, 1981). While these findings for women differ sharply from a previous report on the San, those for men concur with it (Van de Walt *et al.*, 1978).

Hemoconcentration

In an effort to gauge whether the changes in evening T on hunt days might have been due to hemoconcentration effects, similar statistical analyses were performed for another of the hormones measured, progesterone. Application of the Wilcoxon signed ranks test showed no diurnal variability of P on non-hunt days; however, on hunt days there was a significant morning-to-evening difference in P (Wilcoxon signed ranks test, two-tailed, $p = .031$). This was due to both an increase in AM ($p = .031$) and a decrease in PM ($p = .031$) values of P, a change opposed to direct hemoconcentration.

DISCUSSION

Hunting was accompanied by marked alterations in the hunter's androgen profiles: it was associated mainly with maintenance of circulating T levels during the day, with a rapid return to baseline levels after the hunt period. Perhaps hunting involves the ability to maintain T levels over the day's activity, but further increments in activity level are not met with increases in androgen production that would abolish or reverse the diurnal pattern. Physically "most fit," or high performance, individuals do show maintenance of T with elevation of luteinizing hormone (LH) during high-intensity runs, or physical training (Remes *et al.*, 1976; Dessypris *et al.*, 1979). Otherwise, alterations of T levels during exercise are apparently achieved without changes in LH levels.

Hemoconcentration might have acted as a confounding variable in this study, for it has been shown to increase linearly with exercise intensity, and thus may produce apparent rises in plasma T without actual changes in production rates (Wilkerson *et al.*, 1980). Hunting in open savannah can entail water loss and considerable thermal stress, although the study took place during the Kalahari equivalent of a winter dry season, with moderate daytime temperatures. Humidity was minimal, but the men had an adequate water supply. Lack of a direct relationship between degree of effort and evening T levels argues against attribution of the observed changes to hemoconcentration alone. Absence of parallel effects on another hormone measured (P) also tends to discount hemoconcentration effects. Furthermore, to account for the observed increase in evening serum T on hunting days solely on this basis would require a 25% drop in blood volume against baseline, limited to evening values; this is unlikely.

Total serum T was determined in this study. However, only a fraction of this, the free T (unbound to the specific carrier protein, sex hormone binding globulin (SHBG)) appears to be physiologically active. Small changes in SHBG can therefore result in significant shifts in circulating free T. Studies of SHBG binding capacity responses to exercise and stress have shown either no change (Kuoppasalmi, 1980), or changes that would magnify, not reduce, the observed shift in total serum T (Aakvaag *et al.*, 1979; Remes *et al.*, 1979; Elias, 1981). Measures of total T may therefore be regarded as valid in the context of this study.

Several reports on human and animal fighting have not only related aggressive activity to subsequent increases in T levels, but also linked favorable outcomes to greater increases in T and unfavorable outcomes to decreases (Gordon *et al.*, 1979; Elias, 1981). If hunting were primarily a form of aggressive-competitive encounter of the sort involved in those investigations, we might expect to see a relationship between hunt outcome and T. We found none: hunting success or failure bore no relationship to any measure of T or ΔT before, during, or after the hunt. Because, as is discussed below, our coding of success-failure incorporated the fitness loss of failed effort, we also probed for a direct relationship between T and actual capture of prey. The data did not indicate an association between this measure of success and values of T (PM T, ΔT, or post-AM T).

Data from this study appear to suggest that outcome and effort expended are dissociated. This seems counter-intuitive but may be attributable largely to small sample sizes (both subjects and days), and partly to intrinsic differences among hunting strategies. High-effort pursuit of big game has high unit return but high risk of failure per attempt, while low-effort trapping of small prey has low risk of failure but low unit return. The manner in which success was coded incorporates this complexity and compounds further the effort-success dissociation, for the greater the degree of effort expended in unsuccessful hunting strategies, the greater the degree of failure. Daily activity records showed that all of the men used mixed hunting strategies; modulation of strategies and effort may partly account for the dissociation between hunt intensity and T levels. These data also indicate the potential import in humans of intelligent manipulation of complex behavior strategies for achieving desired goals within physiologic constraints.

Evolutionary arguments for the importance of hunting in shaping foundations of men's behavior have tended to focus on its aggressive, competitive and stressful components. Its basic nature as a form of effort, or work, has been less frequently considered. The data suggest that !Kung men do not experience subsistence hunting as mere stress, which depresses T levels, for the main effect was an increase in evening values. On the other hand, no interaction of hunt outcome and T levels was observed, in contrast to reports that T reflects success and failure in certain aggressive and dominance interactions. Rather, these data are most congruent with reported effects of moderate prolonged exercise. Studies of interactions of androgens and exercise have produced varied results, due largely to differences in subject population and the type, duration and intensity of activity studied. But there is fairly consistent evidence that sustained moderate-to-intense exercise elevates T (Galbo *et al.*, 1977; Remes *et al.*, 1979); intense exercise produces an increase when in progress, followed by a decrease (Kuoppasalmi *et al.*, 1976; Kuoppasalmi, 1980); and very prolonged intense exercise acts as a stressor, which depresses T (Morville *et al.*, 1979). The broader functional significance of and mechanism for such transient shifts in circulating T concentrations are not well understood.

Alternative explanations for hunt-related changes in androgen levels could arise from hunt-related changes in diet, or patterns of sexual or social activity. While the virtual absence of sexual intercourse during the study obviates a direct effect of intercourse, it is conceivable that removal from women during the hunt or even increased time in all-male groups might exert an effect. Moreover, the study did not control for diet, which might have been different during the hunt period.

The clear dissociation of hunting effort and daily outcome may be partly explained by the observation that men employed mixed, complex hunting strategies involving varying degrees of effort and probability of success. Manipulation of hunting strategy by the men may have buffered the physiologic impact of hunting activity by balancing degree of hunting effort against realized and expected hunting success. The limited time frame of this study, the small number of subjects, and the complexity of hunting behaviors all preclude formulation of more generalized interpretations. More complete characterization of the behavioral biology of human subsistence hunting will require coupling of hormonal and other physiologic measures with data on pattern and type of hunting strategies, time and energy allocation, and type and quantity of returns.

We conclude that subsistence hunting was associated with significant changes in testosterone patterns in !Kung hunters, due primarily to the maintenance of T concentrations during hunting days that is reflected in elevation of evening values. Diurnal variation in circulating T was hence markedly attenuated. It is also notable that shifts in T level were a consequence, not a primary cause, of the behaviors observed here; hormone changes followed and supported, not preceded, hunting activity. Studies of human behavioral biology might consider the ways in which the dominant context of human evolution, the hunting-gathering niche, may have selected for efficient, appropriate responses to subsistence-related effort.

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