

Differential Reproductive Success and Body Size in !Kung San People from Northern Namibia

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ABSTRACT

The associations patterns between reproductive success, measured by the total number of offspring, number of living offspring and number of dead offspring, and parental body size, estimated by stature, body weight and Body mass index, were tested in 65 female and 103 male members of a !Kung San population ageing between 25 and 40 years ($x = 30.2$ yr.) from northern Namibia. In both sexes a significant interaction between fertility patterns and body dimensions was found. Nevertheless, the association patterns differed markedly between the two sexes. While in males tallness and an improved weight status was associated significantly with a higher number of surviving offspring, smaller and lighter females had significantly more surviving children. In males a directional selection towards increased stature and better weight status is in accordance with the well known secular trend of acceleration. In females first of all the postpartum changes in body composition and body weight, resulting from exhausting infant feeding practices seem to support the maternal depletion hypothesis.

Introduction

Man today is the product of millions of years of evolution, fashioned by the process of natural and sexual selection. According to Mather¹ three types of natural selection can be distinguished: 1) a directional type, favouring one extreme, 2) a balanced type, favouring an average phenotype and 3) a destabilizing type, in which the extreme phenotypes seem to

have the highest fitness. Several studies were carried out to test which type of selection is the best to explain the evolution and recent variation of body size. Especially the impact of maternal height and weight on fertility and infant mortality was tested. While some studies, evaluating the fertility body size interactions mentioned above, tended to support the hypothesis of balanced selection^{2–6}, the results of other investigations plead for

the more directional type of selection^{7–10}. However, the results of those studies indicating a directional kind of selection are not homogeneous: Frisancho et al.⁷ and Devi et al.⁹ reported a significantly negative association between maternal body size and number of surviving offspring, with other words the offspring of smaller mothers had a better chance to survive than the offspring of taller mothers for two samples from poor undernourished populations in South America and India. These results are in contradiction to the well documented trend of acceleration. This so-called secular trend towards an increase in average stature, a decreased average age of menarche and a delayed termination of reproductive phase was described since more than 150 years¹¹. As theoretical explanations technological development and/or a generally improved socio-economic situation, comprising improved nutrition, hygiene availability and quality of health care, were discussed. There is some evidence that not only industrial populations are affected by this trend, but also in non-westernized societies culture change and modernisation promote secular changes of body size^{12–14}. Hausmann and Wilmsen¹⁵ observed an increase of average stature in !Kung children after an improvement of their diet especially after an increase of their daily protein intake. On the other hand a selectional process towards a higher reproductive success of taller mothers was even proved for traditional societies. Martorell et al.¹⁰ found a positive and significant association between maternal stature and number of surviving offspring. The children of taller mothers had a far better chance to survive than the children of smaller mothers. Unfortunately only few studies considered the impact of paternal body build on fertility outcome^{16–18}. One of the traditional populations for which the phenomenon of secular acceleration was found

are the Khoisan living Namibia, Botswana and South Africa. Especially for San people from southern Africa a trend towards increasing stature was reported during the first half of our century¹⁹. However, a strong sexual dimorphism was observed: the absolute increase in stature was almost twice as great in males as in females¹². As a result, there was an increase in sexual dimorphism in stature within this population. Between 1915 and 1950 the difference in mean stature between males and females had increased by 16.3mm¹². These results may be interpreted as a sexual dimorphism in natural selection. In the present study the hypothesis that there is a sex difference in the type of selection in San populations is tested. The interaction between differential fertility patterns, first of all the number of surviving offspring and body size, described by stature, body weight and body mass index was analysed in a sample of !Kung San people from Namibia.

Material and Methods

Subjects

Data for the present study were collected at various locations of the Nyae-Nyae-area in the Bushmenland of northern Namibia. The study comprised 65 female and 103 male northern Bushman language speaking !Kung San ageing between 25 and 40 years ($x = 0.2$) living in an area up to 70 km around Tsumkwe the administrative centre of northern Bushmanland. Most probands followed to a certain extend a traditional lifestyle as hunter gatherers, living in small more or less permanent camps consisting 7 to 15 grass huts near waterholes. The great majority of probands had contact to westernised lifestyle as a result of temporary occupation of single band members at cattle farms.

Fertility data

All probands belonged or had belonged to the sexually active group of their society. The probands were interviewed with regard to the number of their living and dead offspring. Abortions were excluded from the analyses. In the !Kung San population extramarital intercourse is frequent and therefore in case of the male probands all children they accepted as their own offspring were included into the analyses.

Fertility on the individual level was described by following variables:

- C, D+A = total number of children, dead and alive
- C, D = total number of children, dead
- C, A = total number of children, alive

Anthropometrics

Stature and body weight of each proband were measured according to the methods described in Knussmann²⁰. Body mass index (BMI) (Body weight/stature square) was calculated. Individual weight status was classified using BMI categories according to the recommendations of the WHO²¹.

- Thinness: grade 1: 17.0–18.49
(mild thinness)
grade 2: 16.0–16.99
(moderate thinness)
grade 3: < 16.0
(severe thinness)
- Normal range: 18.50–24.99
- Overweight: grade 1: 25.00–29.99
grade 2: 30.00–39.99
grade 3: > 40.00

Statistical analyses

Statistical analyses were carried out using SPSS for Windows (Version 6.1) according to Buehl and Zoefel²². After computing descriptive statistics (mean, standard deviation, Median, Variance, Range, Skewness, Kurtosis) Duncan analyses were calculated in order to test group dif-

ferences with respect of their statistical significance. Additionally multiple regression analyses were performed.

Results

Body size

Descriptive statistics of all body size variables are demonstrated in Table 1. As to be expected in human populations males surpassed females in stature as well as in body weight. Furthermore the average weight status estimated by using the body mass index was better in male probands. Nevertheless the BMI of !Kung San women showed a far higher variance than the BMI of !Kung San males. While no male could be classified as overweight according to the WHO definitions of weight status, 3% of the females corresponded to the definition of mild overweight (BMI 25.0–29.99). Furthermore the percentage of severe thinness (BMI < 16.0) was extremely higher in female probands 14.9% versus 5.4% (see Table 2).

Fertility parameters

Sample parameters of the fertility variables are listed in Table 1. Women reported a higher number of total offspring as well as dead and living offspring than men. With the exception of the total number of children females exhibited a higher variance of the fertility variables than men.

Body size and fertility

Comparing the interaction between body size and fertility parameters, the two sexes differed markedly. This was true of all body size variables. Within the female proband group, childless women exhibited the significantly highest stature values ($p < 0.01$) and women who had given births to more than 4 children showed the significantly lowest statures, while fathers of more than four children were taller, however only insignificantly,

TABLE 1
DESCRIPTIVE STATISTICS OF BODY SIZE VARIABLES AND FERTILITY VARIABLES

Variable	Mean	SD	Median	Min-max	Variance	Skewness	Kurtosis
Males Stature	160.4	58.1	160.4	145.5–174.8	3369.9	0.02	–0.25
Body weight	49.4	6.9	48.6	33.2–68.2	47.8	0.38	0.02
BMI	19.2	2.0	19.0	12.6–23.7	4.1	0.02	–0.05
C, A+D	3.1	2.8	3.0	0–11	7.6	0.73	0.01
C, D	0.9	1.4	0.0	0–6	1.8	1.82	2.88
C, A	2.3	1.9	2.0	0–8	3.9	0.62	–0.39
Females Stature	148.9	53.4	149.0	137.0–161.7	2853.9	–0.11	0.01
Body weight	42.2	6.6	43.0	28.6–64.5	43.2	0.53	1.43
BMI	19.0	2.6	18.9	14.5–26.9	6.9	0.56	0.43
C, A+D	4.4	2.6	4.0	0–12	6.9	0.36	–0.12
C, D	1.2	1.5	1.0	0–5	2.1	1.28	0.84
C, A	3.2	2.1	3.0	0–9	4.4	0.29	–0.50

Legend: C, A+D = Number of children, alive and dead
 C, D = Number of dead children
 C, A = Number of living children

TABLE 2
WEIGHT STATUS

	Females	Males
Severe Thinness	14.9%	5.4%
Moderate Thinness	10.4%	8.0%
Mild Thinness	14.9%	29.5%
Normal weight	56.7%	57.1%
Overweight grade 1	3%	0.0%

than childless men and fathers of 1 to 3 children. Considering the number of dead offspring only, males with more than four dead children were significantly smaller ($p < 0.05$) and lighter ($p < 0.01$) than males without dead offspring or males with 1–3 dead children. Within the female proband group no significant relationship between the number of dead offspring and body size was observed. Regarding the living offspring women, without any living offspring were significantly

taller ($p < 0.05$) and heavier ($p < 0.05$) than the mothers of 1–3 children or mothers of more than 4 children. In contrast, the fathers of more than 4 living children were taller and significantly heavier ($p < 0.05$) than men without living offspring and the fathers of 1–3 living children (see Tables 3 and 4, Figures 1–4).

The results of the Duncan analyses were corroborated by the multiple regression analyses: While male stature and body weight showed no significant impact on the number dead as well as living offspring, in females body weight and the number of living offspring were significantly related (see Tables 5–7).

The associations between higher stature as well as higher body weight and lower number of dead offspring in the male proband group can be seen in the scatter plots, too. The scatterplots demonstrated also the increase of the number of living offspring with increasing paternal stature (see Figure 5). Within the fe-

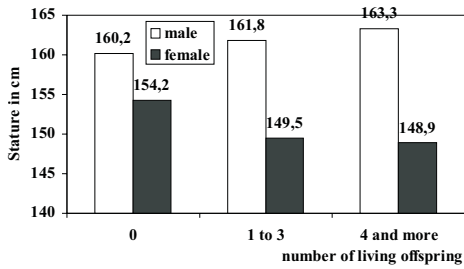


Fig. 1. Stature and living offspring.

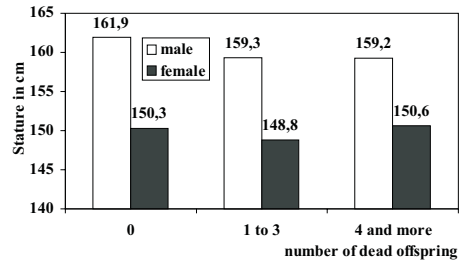


Fig. 2. Stature and number of dead offspring.

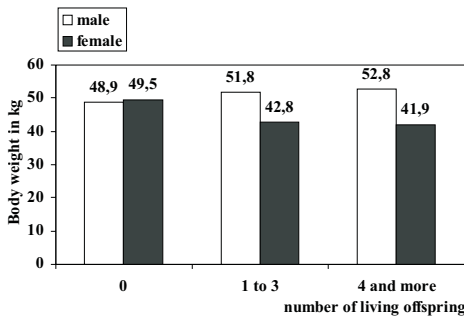


Fig. 3. Body weight and living offspring.

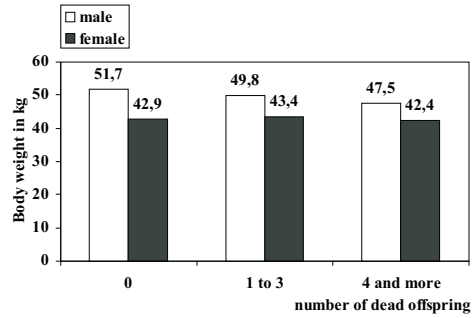


Fig. 4. Body weight and dead offspring.

TABLE 3
MALE BODY SIZE AND FERTILITY

Total number of offspring	0		1–3		4 and more		F-value
	x	SD	x	SD	x	SD	
Stature	160.1	4.9	161.8	5.4	162.0	6.1	1.3 n.s.
Body weight	49.5	5.9	51.7	6.9	50.2	7.3	1.0 n.s.
BMI	19.7	1.7	19.3	2.0	19.1	2.1	0.9 n.s.
Number of living offspring							
Stature	160.1	4.8	161.8	5.6	163.2	5.9	2.1 n.s.
Body weight	48.9	5.9	51.8	7.2	52.8	5.8	3.2 p < 0.005
BMI	19.2	1.7	19.7	2.1	19.7	1.6	1.9 n.s.
Number of dead offspring							
Stature	161.9	5.1	159.3	6.1	159.2	2.5	2.8 p < 0.05
Body weight	51.7	6.1	49.8	7.8	47.5	5.9	4.3 p < 0.01
BMI	19.6	1.8	19.6	2.1	18.6	2.6	3.1 p < 0.05

TABLE 4
FEMALE BODY SIZE AND FERTILITY

Total number of offspring	0		1–3		4 and more		F-value
	x	SD	x	SD	x	SD	
Stature	157.5	5.8	149.7	4.7	148.9	4.2	4.7 p < 0.01
Body weight	45.9	2.4	43.7	6.4	42.1	6.2	3.1 p < 0.05
BMI	18.6	1.9	19.4	2.4	18.9	2.2	1.3 n.s.
Number of living offspring							
Stature	154.2	7.1	149.5	4.8	148.9	3.9	3.1 p < 0.05
Body weight	49.5	8.6	42.8	4.9	41.9	7.0	3.3 p < 0.05
BMI	20.9	3.9	19.2	2.1	18.8	2.7	1.4 n.s.
Number of dead offspring							
Stature	150.3	4.9	148.8	4.8	150.6	4.7	0.9 n.s.
Body weight	42.9	5.6	43.4	7.1	42.4	5.7	0.9 n.s.
BMI	18.9	2.0	19.5	0.3	18.7	2.8	0.7 n.s.

TABLE 5
MULTIPLE REGRESSION ANALYSES: MALE BODY SIZE AND FERTILITY PATTERNS

Dependent variable: number of living offspring				
Variable	B	SE of B	Beta	T
Stature	0.01	0.01	0.08	0.64 n.s.
Body weight	-0.02	0.04	-0.06	-0.51 n.s.
(Constant)	-1.25	5.91		-0.21 n.s.
Multiple r = 0.06; r square = 0.01; F = 0.21 n.s.				
Dependent variable: number of dead offspring				
Variable	B	SE of B	Beta	T
Stature	-0.01	0.01	-0.06	-0.46 n.s.
Body weight	-0.02	0.02	-0.09	-0.73 n.s.
(Constant)	3.93	3.99		0.98 n.s.
Multiple r = 0.15; r square = 0.02; F = 1.05 n.s.				

male proband group the scatterplots showed the drastic decrease of living as well as dead offspring with increasing stature as well as body weight (see Figure 6).

Discussion

The interaction between body size and fertility is of special interest in recent

population studies such as for explanation of secular trends as well as in an evolutionary context^{10,17}. Several studies yielded a significant association between body size and reproductive success^{3,5,16–18,23,24}. However, the majority of these studies considered exclusively the impact of maternal body dimensions on fertility patterns. In the present studies a

TABLE 6
MULTIPLE REGRESSION ANALYSES: FEMALE BODY SIZE AND FERTILITY PATTERNS

Dependent variable: number of living offspring				
Variable	B	SE of B	Beta	T
Stature	-0.01	0.01	-0.03	-0.23 n.s.
Body weight	-0.08	0.04	-0.26	-2.37 p < 0.05
(Constant)	8.599	7.21		1.19 n.s.
Multiple r = 0.28; r square = 0.08; F = 3.25 P < 0.05				
Dependent variable: number of dead offspring				
Variable	B	SE of B	Beta	T
Stature	-0.01	0.01	-0.19	-1.36 n.s.
Body weight	0.01	0.03	0.06	0.41 n.s.
(Constant)	8.28	5.16		1.61 n.s.
Multiple r = 0.17; r square = 0.03; F = 0.94 n.s.				

TABLE 7
MULTIPLE REGRESSION ANALYSES: FEMALE BODY WEIGHT AND FERTILITY PATTERNS

Dependent variable: body weight				
Variable	B	SE of B	Beta	T
Dead offspring	-0.04	0.54	-0.01	-0.08 n.s.
Living offspring	-0.88	0.38	-0.28	-2.31 p < 0.02
(Constant)	45.85	1.55		29.1 p < 0.000
Multiple r = 0.28; r square = 0.08, F = 5.46 p < 0.02				

possible sex bias of the impact of stature and body weight as well as weight status on reproductive success was tested. This hypothesis could be proved because the interaction between body size and fertility patterns differed markedly between the two sexes. In males the number of living offspring was associated with higher stature and increased body weight. This result may be interpreted as a process of directional selection favouring taller and heavier men, which may be responsible for the well known secular trend of increasing stature within the San populations which was documented for the first half of the 20th century, additionally to the well known parameters such as cul-

ture change, acculturation or modernisation¹². This directional selection may be due to the complex interaction between body build, first of all stature and body weight, and socio-economic rank. A taller stature and an improved weight status indicate a better access to important resources and improved nutrition since childhood. The better socio-economic situation of the family of taller males allowed them to exhaust their genetical potential to a high degree during growth and development during childhood and pubertal growth spurt. Furthermore this improved social situation increased the chances to become a high ranking male during adulthood. This higher social sta-

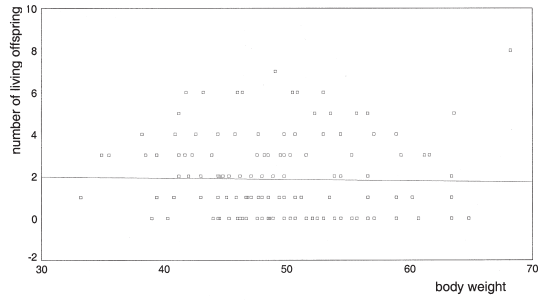


Fig. 5a. Male body weight and number of living offspring.

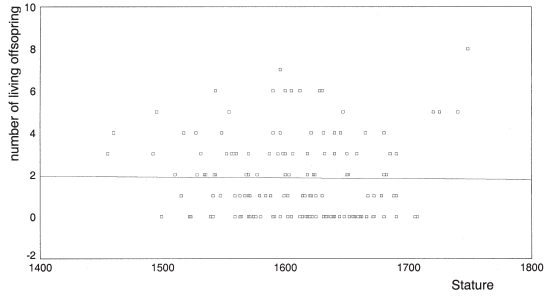


Fig. 5b. Male stature and living offspring.

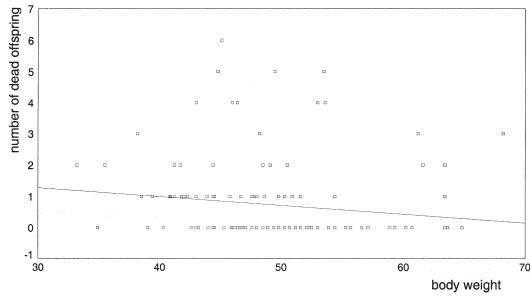


Fig. 5c. Male body weight and dead offspring.

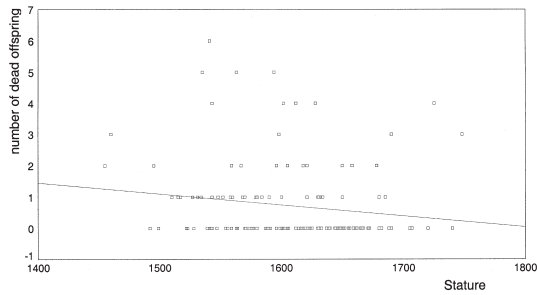


Fig. 5d. Male stature and number of dead offspring.

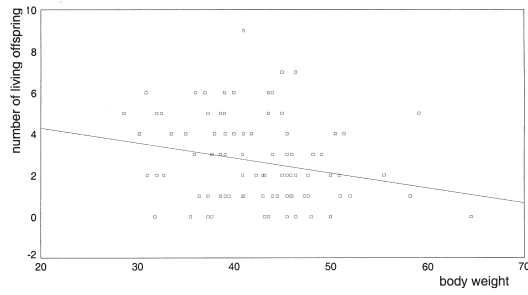


Fig. 6a. Female body weight and number of living offspring.

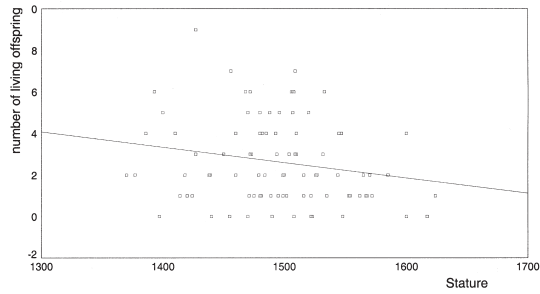


Fig. 6b. Female stature and number of living offspring.

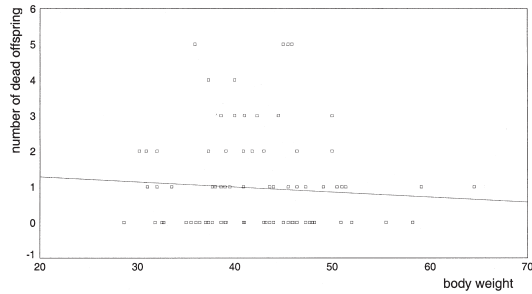


Fig. 6c. Female body weight and number of dead offspring.

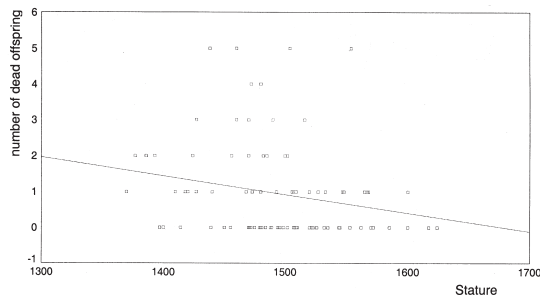


Fig. 6d. Female stature and number of dead offspring.

tus enables the male to get a better access to resources during adult life and this improved the weight status too. A better weight status also increase male fertility. On the one hand it is well known, that undernutrition may result in a loss of libido, a decrease of prostate fluid, a decrease of sperm number and sperm mobility²⁵, on the other hand male status, in traditional societies seen in male stature and weight status influences the female choice. It is a well known female strategy to choose males of higher status because this kind of mate selection improves the chances of their offspring to survive and become high ranking, too. Therefore younger and healthier and therefore more fertile females mates males of higher status and increase male fertility in this way too.

In females body size and fertility are also associated. During the early seventies the so-called »frisch-hypothesis« or the »hypothesis of critical weight« was postulated by Rose Frisch and co-workers^{25–27}. According to this hypothesis a distinct body weight or a sufficient amount of subcutaneous fat tissue is essential for the regular onset and maintenance of ovulatory menstrual cycles. The higher the amount of adipose tissue, the earlier menarche occurred and the higher is the chance to experience ovulatory cycles. In this way the nutritional status influences female fertility outcome. Several studies documented this positive association between female body fat and reproductive success^{28,29}. Otherwise it must be stated, that a high amount of adipose tissue may also be an indicator for reduced fertility or sterility because several pathological disturbances of female sex hormone secretion such as the polycystic ovarian syndrome may be associated with increased overall and especially abdominal fatness³⁰. But in contrast to males, in females body size not only influences fertility, body size is also influenced by fer-

tility patterns. While obviously in males the number of offspring itself does not effect the body size especially the body weight female body size is affected by number of pregnancies in many ways: First of all body composition, fat distribution and the breadth dimensions of the pelvis are affected by pregnancy and childbearing^{31–37}. Furthermore the enormous somatic stress during the late stages of pregnancy and child carrying practices after birth may result in changes of the profile of the vertebral column and in a decrease of stature³⁸. In the present study women with a high number of living offspring were smaller and especially lighter than childless females or mothers of less than 3 living children. At first this result is in contradiction to the Frisch-hypothesis, postulating a positive association between maternal body dimensions, especially body weight and body fat, and reproductive success, however the results of the present study support the maternal depletion hypothesis. Jeliffe and Maddock³⁹ reported for the first time a high prevalence of protein-calorie malnutrition among multiparous women in NewGuinea and called this phenomenon »maternal depletion syndrome«. In contrast, several other investigations yielded no evidence for the real existence of this »maternal depletion syndrome«^{40–43}. Even for Kavango women, living – as the San women under discussion in the northern part of Namibia – no depletion of maternal weight status dependent on number of living offspring was found²⁴. According to Tracer³⁶ fertility associated maternal depletion occurred in a population of Au in Papua NewGuinea. Tracer³⁶ pointed out, that it is essential for studies of maternal nutritional depletion to take account of heterogeneity within the population in access to resources, breast-feeding practices and long-term patterns of reproduction. Especially the type of breast-feeding practices seems to be important

for the development of maternal nutritional depletion: San women exhibit various specific nursing patterns i.e. a prolonged duration of lactation (up to 4 years and more) and short but frequent feeds (up to five times per hour)⁴⁴ resulted in a dramatic reduction of female body fat and lead to a more rapid decrease in body fat and body weight than longer, less frequent feeds⁴⁵. Furthermore the utilisation of the body fat stores is the major source of energy during the lactation period for San women. For a hunter-gatherer population living a harsh, extremely dry climate such as the Kalahari semi-desert it is impossible for lactating women to compensate the extra energy costs of lactation by increased food consumption or decreased physical activity.

As mentioned in the introduction section a secular trend towards an increased average stature was documented for the !Kung San during this century. On the one hand this increased stature may be due to drastic changes in life style towards a more sedentary way of life with access to wage earning⁴⁶ and improvement of diet¹⁵ on the other hand there is no explanation for the sex bias in increase average stature reported by Tobias¹². Although there is a well known

sex bias in access to modernisation, females are more traditional than males, according to the results of the present paper there is a sex bias in natural selection: while in males a directional type of selection towards an increased stature and advanced weight status was observed for the !Kung San people of this study, in females none of the three types of selection mentioned in the introduction could be proved. In a previous paper¹⁷ it was shown, that taller males had not only more surviving offspring but also more surviving sons and smaller males had more surviving daughters. This may be interpreted as a directional selection in males but not in females. Although in females, an increased number of living offspring was associated significantly with decreased stature and weight, no directional selection may be assumed. The significant correlation between number of living offspring and low weight and poor weight status seems to be a result of postpartum changes in maternal body size and body composition according to the maternal depletion hypothesis postulated by Jelliffe and Maddocks³⁹ and not of an a priori selectional process.

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REPRODUKTIVNI USPJEH U ODNOSU NA GRAĐU TIJELA U !KUNG SAN POPULACIJI IZ SJEVERNE NAMIBIJE

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