## Socioecological Aspects of Human Reproduction in Sub-Saharan Africa

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### ABSTRACT

The purpose of this study was to compare fertility outcome of two populations of northern Namibia, following different ways of subsistence. The total number of offspring, but also the number of dead and surviving offspring was compared between 236 !Kung San (91 females, 145 males) hunter gatherers and 248 Kavango (87 females, 161 males) horticultural pastoralists and a small number of Kavango people living in the urban center of Rundu. While no typical differences in fertility outcome between the study populations could be observed in males, marked differences were found for the female sample. As to be expected traditional Kavango women had given birth to a higher number of children and these children had a higher chance to survive in comparison to those of !Kung San women. On the other hand Kavango females living in urban centers reported a significantly lower number of offspring. It can be concluded that even in recent populations fertility differences according to subsistence patterns are observable.

Key words: reproductive ecology, subsistence, !Kung San, Kavango

### Introduction

Human reproductive ecology is the study of human reproduction as an aspect of human biology that is responsive to ecological context<sup>1</sup>. Furthermore, human reproductive ecology as a field is located in the larger domain of evolutionary ecology, distinct in its motivation and goals from clinical, epidemiological and demographic approaches to the study of human reproduction and fertility. During the last 3 decades first of all the interaction between female fertility and environmental stress factors was analyzed, while human male reproductive ecology is as yet underdeveloped, both empirically and theoretically, although new studies in this area are promising<sup>1</sup>. The preference of the analysis of female reproductive performance may be due to the fact that the female reproductive system is particularly vulnerable to effects of the environment<sup>1–3</sup>. Several ecological variables such as energy balance, lactational habits, dietary consumption, nutritional sta-

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tus, individual workload, but also climate and altitude seems to influence human ovarian function<sup>4</sup>. In general increasing somatic but also psychic stress effects ovarian function and leads to a gradual decrease of ovarian function, in the worst case to secondary amenorrhoea<sup>4</sup>. Variations in ovarian function associated with variations in energy balance or workload as a consequence of subsistence ecology has been documented first of all in three populations - the Lese of Zaires Ituri forest<sup>5,6</sup>, the Tamang of highland Nepal<sup>7</sup> and rural Polish farm women outside Crakow<sup>8</sup>. In all samples it was documented that during periods of nutritional stress or increased workload progesterone levels, ovulatory frequency and duration of menstrual bleeding declined parallel to average body weight while cycle length increased. Therefore subsistence ecology seems to influence female reproductive function.

The impact of subsistence patterns on reproductive performance has been discussed for nearly three decades. More than 25 years ago Campbell and Wood<sup>9</sup> published that there were no significant differences observable in total fertility among hunter-gatherers, horticulturalists and agriculturalists. Stimulated by these results, Bentley et al.<sup>10</sup> analyzed the fertility data of 57 populations (12 foraging, 14 horticultural and 31 agricultural) and found lower fertility rates among foragers and horticulturalists in comparison to populations using intensive agriculture. In detail the mean fertility rate of foragers was 5.7, that of horticulturalists 5.9 and the fertility rate of agriculturalists was 6.3. In contrast to the results presented by Campbell and Wood<sup>9</sup>, these findings are in accordance with the well known assumption, that social and economic changes such as the Neolithic transition, and a general improvement of subsistence techniques leading to a reduction of workload on the one hand and a more balanced energy situation on the other hand may result in an increase of fertility and so in an enlargement of populations<sup>11,12</sup>.

In the present study we tested this hypothesis using fertility data of females as well as males of three populations with natural fertility living in the northern part of Namibia near the international border to Angola.

## **Material and Methods**

## Study population

The field research was conducted in various locations of the Kavango district and the Nyae-Nyae area of the Bushmanland in northern Namibia. Altogether 484 probands were enrolled in the present study. The study population could be divided into two major subgroups: 236 !Kung San and 248 Kavango people. The !Kung San sample comprised 91 !Kung San females ageing between 18 and 65 years (x=30.7, SD =11.6) and 145 !Kung San males ageing between 18 and 65 years (x=31.5, SD=11.5) living in an area up to 70 km around Tsumkwe, the administrative center of northern Bushmanland. The Kavango sample comprised 87 females ageing between 18 and 60 years (x=28.2, SD=9.7) and 161 males ageing between 18 and 60 years (x=25.4). SD=4.5). All Kavango probands belonged to the southern Bantu speaking Kavango people which can be divided into five matrilinear tribes: Kwangali, Mbunza, Sambyu, Gciriku and Mbukshu. Members of all tribes are included in the present sample. For a more detail description see previous publications<sup>13–20</sup>.

## Subsistence patterns

Among the !Kung San sample most probands followed a traditional lifestyle as hunter and gatherers to a certain extent, living in small more or less permanent camps consisting of 7 to 15 grass huts near waterholes. However, the great majority of probands had contact to westernized lifestyle as a result of temporary occupation of band members at cattle farms and hunting ranches.

The Kavango live north and south of the Okavango river, which forms the border between Angola and Namibia. As a result of the continuous civil war in Angola, today, most Kavango live south of the river, in Namibia. The inhabitants of the Namibian Kavango district traditionally practice a mixed subsistence of cattle pastoralism and horticulture, and when they live close enough to it, they fish in the Okavango river. Only a minority of the Kavango is engaged in some kind of occupation with regular cash income. The present Kavango sample was divided into two subsamples. On the one hand 63 males and 24 females who lived in Rundu. the administrative center of the Kavango district, as wage earning employees. They belonged to the minority of Kavango engaged in productive labor. Their social status, westernized nutritional habits and physical appearance differed markedly from those Kavango living in rural areas. The second subsample comprised people from rural areas around Rundu. They lived in traditional kraals as horticultural pastoralists, earning no regular cash income. Their nutrition consisted in vegetables and animal products, such as milk and occasionally meat. from their own plot. Additionally, fish from the Okavango river played an important role in their nutritional habits.

## Reproductive history

Data regarding reproductive history were collected retrospectively by an interview of each proband using a standardized questionnaire. The following parameters of reproductive history were obtained:

- Total number of offspring, dead and alive  $(C_{d+a})$ ;
- Total number daughters, dead and alive  $(D_{d+a})$ ;

- Total number of sons, dead and alive  $(S_{d+a});$
- Total number of offspring, dead (C<sub>d</sub>);
- Total number of daughters, dead  $(D_d)$ ;
- Total number of sons, dead  $(S_d)$ ;
- Total number of offspring, alive (C<sub>a</sub>);
- Total number of daughters, alive  $(D_a)$ ;
- Total number of sons, alive  $(S_a)$ .

#### Statistical analyses

The statistical analyses were carried out using SPSS program version 10.0. After computing descriptive statistics (means, standard deviations, range), group differences were tested with respect of their statistical significance. Since no normal distribution could be assumed distribution free procedures were applied predominantly.

### Results

#### Definition of age groups

In a first step of analysis 6 age groups were defined. Age group 1 comprised all subjects younger than 20 years at the time of investigation. Age group 2 comprised all subjects between the ages of 20 and 25 years. Subjects ageing between 26 and 30 years were classified as members of age group 3. Subjects ageing between 31 and 35 years were defined as members of age group 4. Age group 5 comprised all subjects ageing between 36 and 40 years, while all subjects older than 40 were classified as members of age group 6. Unfortunately no Kavango male from urban areas included in the present sample was older than 30 years.

## Comparison between male and female subjects

In nearly all age groups female probands reported a higher total number of offspring than their male counterparts. Especially the number of dead sons and daughters was markedly higher among female probands.

# Comparison of fertility parameters according to subsistence patterns

In the first and second age group urban Kavango females exhibited the significantly lowest number of dead as well as living offspring, while Kavango females from rural areas had given birth to the significantly highest number of offspring. This was also true of age group 4 and 6. In age group 3 we found the highest total number of offspring among Kavango females from urban areas, while Kavango females from rural areas exhibited the lowest number of total offspring. Regarding the sex of living and dead offspring no singular trend was observable. Among Kavango females of age groups 1, 2, 3, 5 and 6 the number of living sons surpassed the number of living daughters. This was only true of the !Kung San women of the age groups 2 and 4 (see Table 1).

Concerning the fertility outcome of the male subjects, it turned out, that Kavango males always reported a higher number of total offspring and – with the exception of age group 5 – also a higher number of living offspring than their !Kung San counterparts. According to the sex distribution of the living offspring, no clear trend was observable among the male probands (see Table 2).

## Discussion

According to Bentley et al.<sup>10</sup> subsistence patterns have a marked influence on fertility rate per se. Differences in daily or seasonal workload, temporary food shortages, duration of lactation and patterns of birth spacing, but also life style habits such as nomadism versus sedentary life style influence first of all female reproductive performance via effects on the ovarian function<sup>1,7,21</sup>. Changes in subsistence patterns often lead to alterations in fertility outcome<sup>11,12,22</sup>. The transition from nomadism and forager subsistence, which was typical for nearly 99% of our history<sup>23</sup>, to a more sedentary lifestyle and horticultural or agricultural subsistence during the Neolithic transition resulted in a marked increase of affected populations<sup>11,12</sup>. Several causes for this population increase are discussed. such as the reduction of the mortality rate or an improvement of the nutritional situation. A stable food base is one of the byproducts of sedentism and leads to an earlier sexual maturation in girls and a longer reproductive span within the female population, because a positive energy balance is of special importance for female sexual maturation and the maintenance of ovulatory cycles<sup>1,4</sup>. On the other hand, a more sedentary lifestyle enables women to give birth in shorter intervals. Nomadism requires mobility of the whole group, this is also true of mothers with dependent toddlers. However, it is nearly impossible to carry more than one child and therefore long interbirth intervals are absolutely necessary among populations following a nomadic lifesty $le^{21,24}$ . In the present paper we compared fertility outcome of more or less nomadic Kung San people and sedentary Kavango people. The !Kung San belonged to the few recent populations following a predominantly nomadic lifestyle without domesticated milk producing animals such as cattle or goats. Nancy Howell<sup>25</sup> described the !Kung San fertility as extraordinary low, averaging a little more than 4 births per women<sup>25</sup>. San women produce their offspring at relatively widely spaced intervals, averaging four to five years between children. These are extraordinary long birth intervals for a population of natural fertility, however these long birth intervals are an ideal adaptation to the harsh ecological situation of Kalahari semidesert<sup>24,26</sup>. Proximate causes for the of birth intervals seem to be the very typical nursing patterns of !Kung San women,

Variable	Kavango urban X (SD)	Kavango rural X (SD)	!Kung X (SD)	p
Č <sub>d+a</sub>	0.33 (0.5)	1.67 (0.8)	0.82 (0.8)	< 0.00'
$D_{d+a}$	0.17 (0.4)	0.67 (0.9)	0.45(0.7)	ns
$S_{d+a}$	0.17 (0.4)	1.00 (0.7)	0.36(0.5)	< 0.01
$\tilde{C}_d$	_	0.33 (0.7)	0.11 (0.3)	ns
$D_d^u$	-	0.11 (0.3)	_	ns
$\mathbf{S}_{\mathbf{d}}^{\mathbf{u}}$	_	0.22 (0.4)	0.11 (0.3)	ns
Č,a	0.33(0.5)	1.33 (0.9)	0.73 (0.6)	< 0.04
Da	0.17(0.4)	0.56 (0.9)	0.45 (0.7)	ns
S,a	0.17(0.1) 0.17(0.4)	0.78 (0.7)	0.10(0.1) 0.27(0.5)	< 0.049
Age group 2				
Č <sub>d+a</sub>	1.01 (0.6)	2.55(1.4)	2.35(1.5)	< 0.048
$D_{d+a}$	0.83 (0.8)	1.50 (0.9)	1.23(1.2)	ns
$S_{d+a}$	0.17(0.4)	1.05(1.1)	1.13 (1.1)	n.s
$C_d$	_	0.30 (0.5)	0.68 (1.1)	n.s
$D_d$	_	0.20 (0.4)	0.45 (0.8)	n.s
$S_d$		0.10 (0.3)	0.23 (0.5)	ns
$C_{,a}$	1.00 (0.6)	2.25(1.3)	1.68(1.1)	< 0.05
$\begin{array}{c} \mathrm{D_a} \\ \mathrm{S_{,a}} \end{array}$	$0.83 (0.8) \\ 0.17 (0.4)$	$\begin{array}{c} 1.30 \ (0.9) \\ 0.95 \ (0.9) \end{array}$	$0.77 (0.7) \\ 0.90 (1.0)$	<0.05 ns
Age group 3	0.17 (0.4)	0.33 (0.3)	0.30 (1.0)	115
C <sub>d+a</sub>	5.00(3.5)	4.38 (1.8)	4.55 (2.3)	ns
$D_{d+a}$	1.33 (0.6)	1.81 (1.1)	2.35(1.9)	ns
$S_{d+a}$	3.67 (3.2)	2.56 (1.2)	2.20 (1.5)	ns
$C_d$	0.33 (0.6)	0.69(0.9)	1.55 (1.6)	ns
$D_d$	0.00 (0.0)	0.19 (0.4)	0.70 (1.1)	ns
$S_d$	0.33 (0.6)	0.50 (0.7)	0.85 (0.9)	ns
$C_{,a}$	4.67 (3.2)	3.69(1.7)	3.00 (1.6)	
				ns
$\mathbf{D}_{\mathbf{a}}$ $\mathbf{S}_{\mathbf{a}}$	$1.33 (0.6) \\ 3.33 (3.1)$	1.63(0.8) 2.06(1.0)	$\frac{1.65\ (1.4)}{1.35\ (1.0)}$	ns <0.026
Age group 4	0.00 (0.1)	2.00 (1.0)	1.55 (1.0)	<0.020
C <sub>d+a</sub>	4.25(1.3)	5.00 (1.7)	5.14(1.1)	ns
$D_{d+a}$	2.75(0.9)	2.33 (0.6)	1.86 (1.2)	ns
$S_{d+a}$	1.50 (0.6)	2.67(1.5)	3.29 (1.3)	ns
$C_d$	0.50 (0.6)	0.67(1.2)	0.29 (0.5)	ns
$\mathbf{D}_{\mathbf{d}}$	0.00 (0.0)	0.01 (1.2)	0.14 (0.4)	ns
$\mathbf{S}_{d}$	0.50 (0.6)	0.67 (1.2)	0.14(0.4) 0.14(0.4)	ns
		4.33 (1.5)		
C,a	3.75(0.9)		4.86(0.7)	ns
Da	2.75(0.9)	2.33(0.6)	1.71(1.1)	ns
<u>S,a</u> Age group 5	1.00 (0.1)	2.00 (1.7)	3.14 (1.1)	< 0.018
C <sub>d+a</sub>	6.67 (3.5)	7.44 (2.2)	5.17 (3.4)	ns
	3.33 (1.2)	3.67(1.8)	3.17 (2.1)	ns
D <sub>d+a</sub>		3.78 (1.7)	2.00 (2.1)	
$S_{d+a}$	3.33(2.5)			ns
$C_d$	1.67(2.1)	1.33(1.6)	0.67(0.8)	ns
Dd	0.67(1.2)	0.22(0.4)	0.17(0.4)	ns
$\mathbf{S}_{d}$	1.00(0.9)	1.11 (1.6)	0.50(0.6)	ns
C,a	5.00 (1.7)	6.11 (2.2)	4.50 (2.8)	ns
$D_a$	2.67(1.2)	3.44(1.9)	3.00(2.1)	ns
S,a	2.33 (1.5)	2.67 (1.1)	1.50 (1.6)	ns
Age group 6	5 50 (9 5)	000 (00)	5 60 (2 9)	
C <sub>d+a</sub>	5.50(3.5)	8.83 (2.8)	5.69(3.2)	ns
D <sub>d+a</sub>	1.50(0.7)	4.33 (1.9)	3.25(2.4)	ns
$S_{d+a}$	4.00(2.8)	4.50(2.4)	2.44(1.6)	ns
$C_d$	1.00 (1.1)	2.67(1.6)	1.81(1.6)	ns
$D_d$	_	1.33 (1.2)	1.19 (1.5)	ns
$S_d$	1.00(0.1)	1.33 (1.9)	0.63 (0.7)	ns
$C_{,a}$	4.50 (3.5)	6.17(1.6)	3.88(2.6)	ns
$D_a$	1.50(0.7)	3.00 (0.9)	2.06(1.8)	ns
S,a				

## S. Kirchengast and C. Neubert: Fertility Patterns, Coll. Antropol. 28 Suppl. 2 (2004) 175–182

Variable	Kavango urban X (SD)	Kavango rural	!Kung X (SD)	_ p
		X (SD)		
Age group 1				
$C_{d+a}$	0.42(0.7)	0.06 (0.3)	0.40 (0.8)	ns
$D_{d+a}$	0.33(0.5)	0.06 (0.3)	0.13(0.4)	ns
$S_{d+a}$	0.08 (0.3)	_	0.27(0.6)	ns
$\tilde{C}_d$	_	-	_	
$D_d$	_	_	_	
$S_d$				
	0.42 (0.7)	0.06 (0.3)	0.40(0.8)	
C,a			0.40(0.8)	ns
$D_a$	0.33 (0.5)	0.06 (0.3)	0.13(0.4)	ns
S,a	0.08 (0.3)	_	0.27 (0.6)	ns
Age group 2				
$C_{d+a}$	1.00 (1.2)	1.30 (1.5)	0.88(1.2)	ns
$D_{d+a}$	0.44 (0.9)	0.58 (0.8)	0.35(0.7)	ns
$S_{d+a}$	0.56 (0.7)	0.73 (0.8)	0.56(1.0)	ns
$C_d$	0.04 (0.2)	0.15 (0.6)	0.14(0.4)	ns
$\mathbf{D}_{\mathbf{d}}$	0.04 (0.2)	0.03 (0.2)	0.02(0.2)	ns
	0.04 (0.2)			
$S_d$	-	0.12(0.4)	0.12(0.4)	ns
C,a	09 (1.2)	1.15(1.3)	0.74(1.0)	ns
$D_a$	0.39(0.9)	0.55(0.8)	0.33(0.6)	ns
S,a	0.56 (0.7)	0.61 (0.7)	0.42 (0.8)	ns
Age group 3				
$C_{d+a}$	2.33(1.3)	2.75(2.2)	2.32(1.9)	ns
$D_{d+a}$	1.56 (0.9)	1.50(1.4)	1.11(1.2)	ns
$S_{d+a}$	0.78 (0.7)	1.25(1.3)	1.21 (1.2)	ns
$C_d$	0.44 (0.5)	0.29 (0.6)	0.71(0.9)	ns
$D_d$	0.44(0.5)	0.18 (0.5)	0.34(0.6)	ns
$\mathbf{S}_{d}$	_	0.11 (0.3)	0.37 (0.6)	< 0.04
Č,a	1.89 (1.2)	2.46 (1.8)	1.63(1.3)	ns
	1.11 (0.8)	1.32(1.1)	0.79(0.9)	
Da				ns
S,a	0.78 (0.7)	1.14 (1.2)	0.82 (0.9)	ns
Age group 4	9.17 (1.5)	0 50 (0 4)	0.10 (0.0)	
$C_{d+a}$	2.17(1.5)	3.56(2.4)	3.18 (2.3)	ns
$D_{d+a}$		1.33(1.2)	1.31(1.2)	ns
$S_{d+a}$		0.83 (0.4)	2.31(2.2)	< 0.03
$C_d$		0.17(0.4)	0.69 (1.1)	ns
$D_d$		-	0.19 (0.4)	ns
$S_d$		0.17 (0.4)	0.50(1.0)	ns
Č,a		2.00(1.3)	2.94(1.8)	ns
$D_a^{\prime a}$		1.33(1.2)	1.13(1.2)	ns
$S_{a}^{-a}$		0.67 (0.5)	1.81 (1.5)	ns
		0.01 (0.0)	1.01 (1.0)	115
Age group 5	2 22 (1 7)	198 (14)	2 75 (1 7)	
C <sub>d+a</sub>	3.33 (1.7)	4.38 (1.4)	3.75(1.7)	ns
$D_{d+a}$		1.25(1.1)	2.38(1.9)	ns
$S_{d+a}$		2.08(1.2)	2.00(1.3)	ns
$C_d$		0.25 (0.5)	1.00(1.7)	ns
$D_d$		0.08 (0.3)	0.50(1.1)	ns
$\mathbf{S}_{\mathbf{d}}$		0.17 (0.4)	0.50(0.8)	ns
C,a		3.08 (1.7)	3.38(1.8)	ns
$D_a^{\prime a}$		1.17(1.2)	1.88(1.9)	ns
$\mathbf{S}_{a}^{-a}$		1.92 (1.2)	1.50 (1.2)	ns
Age group 6		()		
C <sub>d+a</sub>		7.67 (2.5)	5.88 (3.07)	ns
		3.33 (0.6)	3.00 (1.9)	
D <sub>d+a</sub>				ns
$S_{d+a}$		4.33 (2.5)	2.88 (1.9)	ns
$C_d$		0.67(1.2)	2.12(1.7)	ns
$D_d$		-	0.92(1.1)	ns
$S_d$		0.67(1.2)	1.20(1.0)	ns
C,a		7.00 (1.7)	3.76(2.4)	< 0.03
Da		3.33 (0.6)	1.88 (1.3)	< 0.05

## TABLE 2 COMPARISON OF REPRODUCTIVE PARAMETERS IN MALES (WILCOXON TEST)

who nurse up to five years, briefly and very frequently up to several times per hour<sup>27,28</sup>. In our sample the mean number of births exceeded the observations of Nancy Howell<sup>25</sup>: San women of age group 4, 5 and 6 gave birth to more than 5 children on average however, the number of surviving children was lower. However, all !Kung San women of the present sample had temporary contact to westernized life style and to westernized food products such as milk from cattle posts and farms. In comparison to the !Kung San women, rural Kavango women following a traditional lifestyle of horticultural pastoralists had given birth to a higher number of children, and these children had a better chance to survive. The improved living conditions of the sedentary Kavango especially the more stable food supply seems to lead to earlier sexual maturation and to an earlier start of reproductive life among traditional Kavango girls in comparison to their !Kung San counterparts. This may be the cause of the extraordinarily higher number of child birth among Kavango women of age group 1 (< 20a). Kavango females of this age group had given birth to 1.67 children on average, while!Kung San women of this age group reported 0.82 births on average. According to Nancy Howell<sup>25</sup>, !Kung San girls reach menarche relatively late. The average age of menarche was between sixteen and seventeen and the first child birth takes place at an average age of nineteen<sup>25</sup>. On the other hand the last child birth took place relatively early at about thirty-five years. Thus, the whole reproductive span of !Kung San women seems to be relatively short. This may explain the lower number of offspring among !Kung San women even in the higher age groups. The results of the comparison between temporarily nomadic !Kung San women following more or less forager subsistence patterns and the traditional Kavango women living in rural areas following a horticultural and pastoral subsistence are in accordance with the results of Bentley et al.<sup>10</sup>. On the other hand, the comparison between the two Kavango subsamples yielded a markedly reduced number of offspring among the Kavango women living in urban areas following a predominantly westernized life style. With the exception of age group 3, urban Kavango women had reported a markedly lower number of births and surviving children. This fact may be due to the general effects of modernization and first of all to the access of useful contraceptives. It is a world wide trend that urbanization and modernization leads to a reduction of offspring<sup>11,22</sup>.

Concerning the fertility outcome of the male probands, no differences between the various subsistence groups were found. This may be due to the fact that the male reproductive system is less influenced by environmental factors<sup>2,3</sup>. Energy imbalance, workload or food shortages may effect androgen secretion, however, a disturbance of spermatogenesis as a result of such stress factors has not been described up to today. On the other hand, it can be assumed that males are not completely aware of the total number of their offspring, in contrast to women. Therefore the association between reproductive function and socioecological parameters is more clearly visible within the female sex.

Regarding the hypothesis tested in the present paper, we can conclude that subsistence patterns seems to effect fertility outcome in women even in present times.

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### SOCIO-EKONOMSKI VIDOVI HUMANE REPRODUKCIJE U SUB-SAHARSKOJ AFRICI

## SAŽETAK

Cilj studije bio je usporediti fertilitet u dvije populacije sjevernih Namibija koji se razlikuju u strategijama preživljavanja. Ukupan broj potomaka, uključujući i broj umrle i žive djece uspoređen je kod 236 pripadnika !Kung San (91 žena, 145 muškaraca) lovaca-sakupljača te kod 248 Kavango (87 žena, 161 muškaraca) poljoprivrednika-stočara te malog broja pripadnika plemena Kavango koji žive u urbanom centru Rundu. Između dviju populaciju nije pronađena razlika u fertilitetu muškaraca, međutim kod žena ona je bila znatna. Kao što se i očekivalo, u usporedbi sa ženama plemena !Kung San, tradicionalna Kavango žena rađa veći broj djece i ta djeca imaju veću šansu preživljenja. S druge strane Kavango žene koje žive u urbanizirano imaju značajno manji broj potomaka. Može se zaključiti da se čak i današnjim populacijama mogu uočiti razlike u fertilitetu koje su odraz načina života.