

Kipsigis women's preferences for wealthy men: evidence for female choice in mammals?

Monique Borgerhoff Mulder

Department of Anthropology, University of California, Davis, CA 95616, USA

Received August 9, 1989 / Accepted June 24, 1990

Summary. In contrast to studies of birds, in mammals there is no clear evidence that polygyny evolved through female choice for males with high quality resources. Among the Kipsigis people of Kenya, polygyny may be a consequence of women's preferences for wealthy men, because strong correlations exist between land ownership and the number of a man's wives (Borgerhoff Mulder 1987a), and the resources men hold are primary determinants of women's reproductive success (Borgerhoff Mulder 1987b). This paper has two aims: first, to test whether Kipsigis women prefer wealthy men by examining the sequence of marriages among a group of pioneers (Table 1) who established a settlement in the territory of their enemies (1930–1949); second, to determine whether women suffer reproductively as a result of polygynous marriage. Data show that Kipsigis women, or their parents on their behalf, preferentially chose men offering high quality breeding opportunities, with respect to the number of acres available on which to settle (Fig. 2); controlling for quality of breeding opportunity there is a preference for bachelors over monogamists over polygynists. Analyses of the full demographic sample show that there are reproductive costs associated with having a large number of cowives (Table 2), costs which women attempt to minimize through judicious marital choices. These results are discussed in relation to resource defence polygyny, female choice and, specifically, the polygyny threshold model.

Introduction

Where resources critical to female breeding success can be monopolised by males, polygynous mating is commonly attributed to the differential resource holding power of males (Emlen and Oring 1977). Female choice for males with high quality resources may contribute to the evolution of polygyny, if the difference in quality

between resources held by males are great enough that females raise as many or more offspring by mating with already-paired males on superior territories than with bachelors on inferior territories (Orians 1969). This difference in territory quality is called the "polygyny threshold" (Verner 1964, Verner and Willson 1966), and female decisions can be characterised as following an "ideal free" distribution (Fretwell 1972). The classic test of the polygyny threshold model is that the fitness of monogamously and polygynously mated females should be equal but, because this prediction is based on a number of assumptions that are difficult to substantiate (Davies 1989; Searcy and Yakusawa 1989, see Discussion), such evidence is weak support that females assort themselves as predicted by the model.

A more robust prediction from the model is that the quality of resources held by a male will influence his breeding success through enhanced access to females attracted to his territory. Studies of passerines birds provide consistent evidence that the number of females settling on a male territory is influenced by features favoured by females; these include shaded nest sites in lark buntings *Calamospiza melanocorys* (Pleszczynska 1978), cattail density in redwinged blackbirds *Agelaius phoeniceus* (Lenington 1980; see also Searcy 1979) and elevated nest sites in pied flycatchers *Ficedula hypoleuca* (Alatalo et al. 1986).

Correlational evidence, however, is always open to alternative explanations. The most conclusive demonstration (bar experimental manipulation) that females do actively chose males for the territories they hold is to examine whether females chose the best breeding option available to them at the time of their settlement (Lenington 1980; Davies 1989; Searcy and Yakusawa 1989); this can be done through the analysis of settlement sequences.

In mammals resource defence polygyny is far rarer than in birds; consequently female preference for males defending large territories or valued resources is not

prominent, even in territorial species (Owen-Smith 1977). However, among the Kipsigis people of Kenya, strong correlations between resource ownership and the number of a man's wives are found (Borgerhoff Mulder 1987a). Resource access is also a primary determinant of women's breeding success (Borgerhoff Mulder 1987b), so polygyny may be a consequence of the preferences of females (or their kin) for wealthy males.

This paper has two aims: to test whether Kipsigis women prefer wealthy men, by examining the sequence of marriages among a group of Kipsigis pioneers who, in the 1930s and 1940s, settled different sized plots of land in the territory of their neighbours and enemies, the Masai. Second, to determine whether women in the full demographic sample of post-menopausal women (Borgerhoff Mulder 1988a) suffer reproductively as a result of polygynous marriage choices. In short, can the marriages that occurred during a period of pioneer settlement be characterised as resource-defence polygyny mediated by adaptive female choice for men with large plots of land?

Ethnographic background

Resources and reproduction

The Kipsigis are a Southern Nilotic pastoralist group, now settled as agro-pastoralists in south western Kenya, between latitudes 0°9' and 1° south and longitude 35° and 35°30' east. Families derive their entire subsistence from the cultivation of maize and the herding of domestic stock. The primary capital resources for these activities are land and cattle which are owned exclusively by men. Men marry up to 12 wives, who almost invariably reside on their husband's property and are entirely dependent on his land and stock. Some men hold single land plots, others more than one in different locations. Ownership of land persists through life as plots are largely inalienable. Competition among men over land is prominent, and pervades all accounts of the Kipsigis during the Colonial period (Manners 1967; Saltman 1977), stimulating the incursions of Kipsigis into Masailand (see below). The bitterness of disputes over land among related and unrelated men in semi-sedentary East African pastoralists is vividly depicted by many ethnographers (e.g. Goldschmidt (1986) for the Sebei and Gulliver (1963) for the Arusha Masai, with accounts of physical violence and lifelong feuds).

Land is shared on an equal basis among a man's wives (Peristiany 1939; Orchardson 1961). Land access is correlated with women's reproductive success, and may be an important causal factor contributing to reproductive differentials, given the greater availability of food in the homes of "richer" women and the lower incidence of illness among them and their offspring (Borgerhoff Mulder 1987b).

Divorce is not formally recognised, but a severely maltreated wife can desert her husband for several years or even permanently and produce children fathered by other men.

Marriage

A Kipsigis girl spends several months in seclusion after reaching menarche. During this time the father of each of her prospective suitors visits her parents and makes a proposal of marriage, entailing a bridewealth offer (see Peristiany 1939, p 57; Orchardson 1961, p 69; Borgerhoff Mulder 1988b for details). Such payments are required at marriage and are high, constituting almost one third of an average man's wealth. The parents of the young woman chose from among competing suitors a potential son-in-law, by ascertaining the man's character, wealth and social connections; usually this information will already be known to them, or to neighbours or relatives. The final bridewealth is negotiated with the suitor's father. The wishes of bride and groom are not formally taken into consideration (Peristiany 1939, p 57), except in so far as they can influence their parents. Finally, certain relatives and associates are banned from marrying one another, such as members of the same patrilan (see Peristiany 1939, p 107), but these prohibitions do not appear severely to restrict the number of potential marriage partners (pers. obs. at marriage negotiations where up to 11 suitors may be considered).

Given parental involvement in the marriage process, Kipsigis women are not technically "free" to choose their own mates. The role of a girl's parents in choosing a son-in-law suggests that the unwieldy term "bride's parents' choice" is more appropriate. Does this undermine the assumption of free female choice? In societies where women are coerced into marriages that are in their *parents'* political interests, and possibly against their own personal reproductive interests (e.g. Dickemann 1979a, 1982), the female choice model is clearly inappropriate (Daly and Wilson 1983; Gray 1985; Flinn and Low 1986). However Kipsigis daughters are rarely forced into marriages with which they do not concur (for exceptions see Discussion), because a discontented wife will desert her husband, return to her natal home and continue to produce offspring who must be fed from the produce of the parental land plot; this can place severe economic stress on the rest of the family, particularly if the deserting bride had brothers who are already married. Consequently, a primary concern of Kipsigis parents in selecting a son-in-law is to find a man with whom they expect their daughter will remain contented. Scope for parental manipulation in this particular ethnographic context is therefore limited, and the term female choice is retained on the assumption that the interests of parents and daughters are largely coincident, at least with respect to the parameters measured in this study.

Settlement of the Abosi area

Two events occurred soon after the arrival (1906–1907) of the first Europeans in Kericho District (south-western Kenya) that led to a pioneer group of Kipsigis families settling in the vicinity of Abosi, part of the traditional land of the Masai (Fig. 1). First, almost 50% of the Kipsigis' traditional territory was forcibly alienated, for

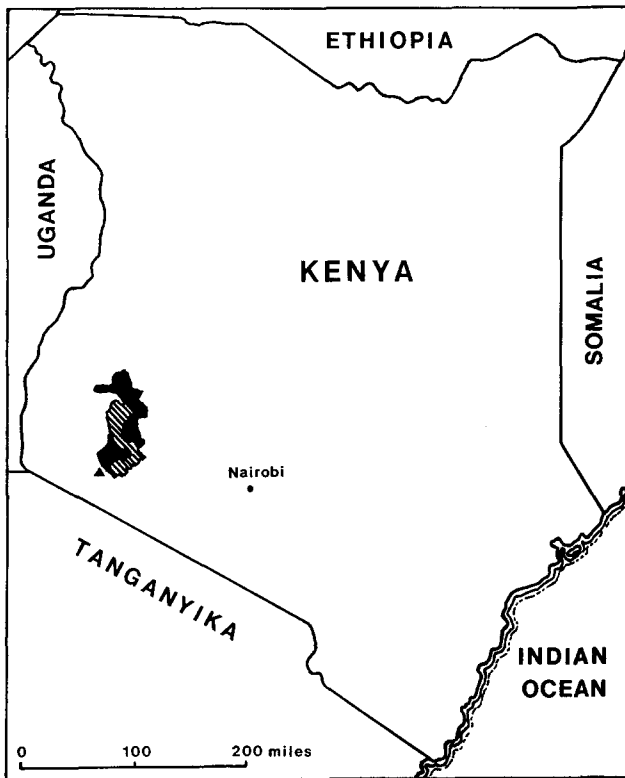


Fig. 1. Kenya, with its capital Nairobi, in 1960, after Manners (1967), showing the location of Kericho District; alienated land shown in black and the Kipsigis Reserve cross-hatched. The triangle indicates the location of the settlement at Abosi

both the founding of European dairy farms and the commercial production of tea and flax. This precipitated the establishment of Native Reserves in the central and south-eastern areas of the District. Second the Kipsigis, traditionally semi-nomadic pastoralists, were encouraged through market incentives to cultivate maize, leading to the development of individual rights over land (Saltman 1977). As a result of changed land use patterns in the geographically circumscribed Reserve, land shortages escalated and a number of families emigrated into the territory of the Masai, their traditional enemies. These events led to a number of migratory waves southwards in which individual Kipsigis men, pairs or trios broke away from their fathers and established new farms, rather than settling on small inherited plots in the Reserve (Manners 1967, pp 274–282). Abosi (see Fig. 1) was settled by 25 such pioneers between 1930 and 1949. Most of these men arrived with 1 (32%) or more (44%) wives but continued to marry young women who came largely from the overpopulated Reserve.

At Abosi, each pioneer staked out a plot of land, guided by the concept of individual ownership that predominated in the Reserve, forcing later arriving men to settle smaller plots deeper in Masai country. In interviews men stated that the size of the plot settled was influenced by the number of cattle and small stock requiring pasture. Land plots were fenced by laying cut thorn shrub branches on the ground. Skirmishes with Masai occurred quite frequently, but conflicts over land

with other Kipsigis were normally arbitrated in favour of the contender who was first to arrive in the area, although some brawls were reported.

Methods

Fieldwork. Between June 1982 and December 1983 a study area of 35 sq km was established on the border of Kericho and Narok Districts, Rift Valley Province, Kenya, incorporating a portion of the Native Reserve, the Abosi settlement area (see above) and other settlement areas. Interviews with men and women conducted in Kipsigis were used to determine land plot size, livestock holdings and marital histories; past events were dated to the year through the use of a calendar of local events such as circumcision ceremonies, droughts and administrative changes (see Borgerhoff Mulder 1987a for details).

Pioneer settlement study: variables, sample and analysis. Year of arrival in Abosi was determined for each pioneer. The ranking was then cross-checked with two of the earliest settlers, and no inconsistencies were found. The size of the plot settled was determined from the results of a land survey conducted by the Government Land Office in 1982 and 1983, the purpose of which was to register the current plots owned by different individuals which very closely reflect the original plots settled. After 1949 there was such an influx of families that it became difficult to determine a clear ranking of arrivals, so analyses were limited to the "Pioneer period" (1930–1949) during which 25 men settled. Age and marital history were available from reproductive interviews (Borgerhoff Mulder 1987a). The number of a man's surviving offspring was divided by the sum of the number of years he had spent married to each of his various wives (during the latter's reproductive years) to produce the measure "man's reproductive history".

Wives already married to pioneers at arrival were termed "previous wives", those married during the Pioneer period "pioneer wives", and those married after 1949 "subsequent wives"; these sum to a measure termed "total wives". Six men arrived at Abosi as bachelors, that is with no previous wives. The "breeding opportunity" offered by a pioneer at any one time was measured as the number of acres divided by the total number of his wives *plus 1*, so as to capture the resources potentially available to a *new* wife.

To examine whether men are chosen as husbands with respect to resources, the rank order in which women chose men should be compared to the rank order of breeding opportunities on offer (cf. Lenington 1980). However because some Kipsigis women chose mates before other men had arrived, comparisons of such rankings across years is inappropriate. Facing the same analytical difficulty Alatalo et al. (1984) resorted to within year comparisons, yielding small sample sizes with little potential for multivariate analysis.

In the present study a stratified Cox (1972) regression analysis was used to determine the effects of breeding opportunity on the probability of a man being selected. Cox's model offers two important features. First, it allows the risk set to vary between years, thus accommodating both the changing breeding opportunities on offer each year as a result of pioneers' marriages in a preceding year, and the arrival of new pioneers each year. Second, it permits assessment of the effects of a number of covariates on the probability of a man being selected, using a method analogous to multiple regression (BMDP 1985a). Where two or more men were chosen in one year, they were considered as ties, as month of marriage had not been recorded. The regression was run using a stepwise function; for each independently significant covariate the ratio of the beta coefficient to the standard error and its associated significance level is reported, together with the likelihood ratio chi-square improvement statistic. For all other variables tested the raw chi-square statistics are given. The analysis here is identical with Luce's choice model (Maddala 1983), except for the handling of ties; a similar type of survival analysis is presented in BMDP (1985b). Cox's model is particularly appropriate to the study of female

settlement patterns in which some males are chosen before others have arrived and where male mating status changes over time, as occurs in Kipsigis and several passerines.

Demographic study: variables, samples and analysis. All women of reproductive age in the study area were interviewed yielding reproductive histories that could be related to the economic and marital circumstances of their husbands. The analyses in this paper are based on two cohorts of women ("Maina" and "Chuma") who had entirely terminated their reproductive careers by 1983 and for whom lifetime reproductive success could be measured as numbers of surviving offspring (Borgerhoff Mulder 1988a).

Using information from men's marital interviews, two measures of polygyny could be calculated for each woman: the number of women married to her husband ("number of cowives") and her marital status (monogamous, primary polygynous, secondary polygynous, etc.; for further details, see Borgerhoff Mulder 1989a).

Husband's plot size ("husband's acres") was determined through interviews with men (Borgerhoff Mulder 1987a) in conjunction with the use of Land Office maps. The demographic sample is slightly smaller than that presented in Borgerhoff Mulder (1989a) because adequate wealth data were not available for the husbands of all women.

Analyses of variance, incorporating tests for deviation from linearity, were used to determine whether the number of surviving offspring produced by a woman is affected by polygyny; the effect of husband's acres was controlled using the Options subcommands available in SPSSx (1983). The effects of polygyny on number of surviving offspring was also examined within wealth categories.

Results

Settlement, wealth, age and mating success during the Pioneer period

For each of the pioneers his year of arrival, the size of the land plot he settled, and the number of his pre-

Table 1. Arrival date, wealth and number of wives of the 25 pioneers

Year of arrival	Husband	Size of plot settled	Previous wives	Pioneer wives	Husband's total wives
1930	O	150	3	1	4
1932	D	100	2	2	4
	A	160	3	1	4
1933	C	100	0	2	4
	B	300	0	6	8
1935	F	50	2	1	3
1936	E	30	0	2	3
1937	I	70	2	1	4
1938	S	100	4	0	4
1939	H	60	1	1	2
	G	120	0	3	3
1940	P	60	1	1	3
1942	L	40	1	1	4
1943	J	180	0	2	4
	K	32	2	1	3
1944	M	40	1	1	3
	T	20	2	0	3
1945	U	20	2	0	3
1946	V	8	1	0	2
	N	36	1	1	2
1947	W	20	4	0	4
	X	20	2	0	3
1949	Q	29	0	1	2
	R	20	1	1	3
	Y	10	1	0	1

vious wives, pioneer wives and total wives are shown in Table 1. Pioneer's year of arrival in Abosi was negatively associated with size of land plot he settled ($r=0.66$, $N=25$ and thereafter this paragraph, $P<0.001$); earlier arriving men established larger plots, as the Kipsigis themselves recognised. Plot size was strongly correlated with number of pioneer wives ($r=0.79$, $P<0.001$) and total wives ($r=0.81$, $P<0.001$), but not with number of previous wives ($r=-0.15$, NS), suggesting that the size of a man's plot was more a cause than a consequence of his marital history (Borgerhoff Mulder 1989b).

Some other correlated but unmeasured quality of the land, such as terrain, location or drainage, might be more important than the size of a man's plot in attracting a large number of wives; if such favourable plots were settled first, the number of pioneer and total wives would be more strongly correlated with a man's arrival date than with the size of the plot he settled. As anticipated, year of arrival was negatively associated with the number of pioneer and total wives ($r=-0.50$, $r=-0.57$, $N=25$, $P<0.01$), but partial correlations showed that both were still strongly correlated with plot size when the effects of arrival date were controlled ("pioneer wives" partial $r=0.71$, "total wives" partial $r=0.70$, both $N=22$, $P<0.001$); neither pioneer nor total wives were correlated with arrival date when plot size was controlled (partial $r=0.05$, partial $r=-0.09$, both $N=22$, NS). These results suggest that acreage (rather than other aspects of a man's plot) is a potentially important factor influencing polygyny.

There was no association between pioneers' age at arrival and the year of his arrival ($r=0.22$, $N=25$, N.S.), but men who were older unsurprisingly had more wives at settlement ($r=0.69$, $P<0.001$) and obtained fewer pioneer ($r=-0.58$, $P<0.01$) or subsequent wives ($r=-0.57$, $P<0.01$). Older settlers also established rather smaller land plots ($r=-0.43$, $P<0.05$). Despite these age effects, the associations between plot size and the number of both pioneer and total wives were independent of the effects of arrival age (partial $r=0.74$, partial $r=0.80$, both $N=22$, $P<0.001$).

Female choice of breeding opportunities during the Pioneer period

Men of 1st or 2nd rank with respect to breeding opportunities in acres were selected as husbands in 43% of the 29 marriages occurring during the Pioneer period (Fig. 2): a sign test (Siegel 1956) shows that marriages were preferentially made with men offering above the median ranked breeding opportunity ($X=2.16$, non-tied observations = 27, $P=0.05$).

Results of the Cox stepwise regression analysis showed independent effects of two covariates on the probability of being chosen: men were preferred if they were offering larger breeding opportunities (beta coefficient/standard error 2.7046, $P=0.01$); they were also more likely to be chosen if married to fewer wives (-2.2095 , $P<0.01$). The model yielded likelihood ratio

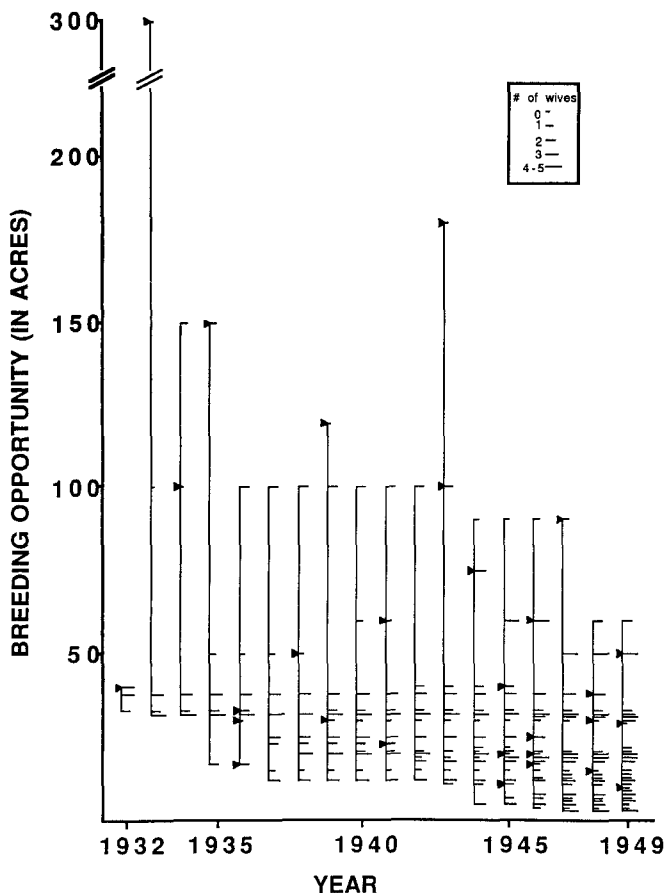


Fig. 2. Breeding opportunities selected by females arriving in the Abosi area between 1932 and 1949. Each horizontal bar indicates a breeding opportunity, with triangles denoting the breeding opportunities selected each year. The length of the horizontal bar shows the man's marital status (see key). Thus in 1934 (years denoted as a vertical bars) five men had already settled in Abosi. In that year one marriage occurred; the bachelor offering a breeding opportunity of 100 acres was chosen, in preference to the other four men offering 150 (monogamist), 37.5 (trigamist), 33 (bigamist) and 32 (tetragamist) acres. In 1935 the situation had changed: the bachelor who married in the preceding year has become a monogamist offering a breeding opportunity of 50 acres; in addition, a new pioneer bigamist arrives, with a breeding opportunity of 16.7 acres; the monogamist offering 150 acres obtains a second wife. Settlers were considered as offering a breeding opportunity the year they arrived and every subsequent year until 1949 (end of sampled period): settlers are therefore multiply represented in the Figure, although the breeding opportunity on offer and their marital status might change over the sampled period; for statistics, see text

chi-square improvement values that were significant for both covariates (breeding opportunity [step #1]: $X^2 = 14.94$, $P < 0.001$; number of wives [step #2]: $X^2 = 4.35$, $P < 0.05$). The effects of three further variables were examined. Men were more likely to be chosen if they had a high rate of production of surviving offspring with the women to whom they were already married ($X^2 = 7.71$, $P < 0.001$), whereas neither the overall size of the plot a man settled ($X^2 = 3.36$, $0.05 < P < 0.10$) nor his age ($X^2 = 2.02$, NS) was significantly associated with his probability of being selected. None of these three vari-

ables entered into the stepwise regression analysis reported above, for which tolerance levels for entry were set at $P < 0.10$.

To tackle the problem that the 232 breeding opportunities are not independent of each other (being offered by the same 25 men), each man was coded as a dummy variable, none of which entered into the stepwise regression at $P < 0.10$. It was not possible to enter the 25 dummy variables together with the covariates into a single simultaneous regression analysis, because of the small sample size.

Costs of polygyny

The number of surviving offspring produced by post-menopausal women is negatively affected by the number of cowives in 3 of the 4 wealth categories (Table 2) when the sample is split into lower, lower middle, upper middle and upper wealth divisions according to husband's ownership of land; note however that rather few women join large polygynous households in the poorest wealth categories.

The polygyny threshold model essentially predicts that women with perfect information and foresight (see Discussion) should minimize fitness differences by marrying judiciously. However number of cowives negatively affects lifetime reproductive success, even after husband's acres are controlled in an analysis of variance ($F_{3,253} = 8.72$, $P < 0.001$), suggesting that in this population there are costs associated with polygyny for which careful marriage choices do not entirely compensate. This may account for women's preferences for monogamous and bachelor pioneers even when breeding opportunity is controlled (see above).

Marital status, by contrast, has no overall statistically significant effect on lifetime reproductive success (Table 3), even after the effects of husband's acres are controlled ($F_{3,253} = 1.79$, NS; and see Borgerhoff Mulder 1989a). Nevertheless weak depressing effects of marital status are found in the poorer wealth categories where the lifetime reproductive success of secondary and tertiary wives is low.

Discussion

Resource defence polygyny

In several respects Kipsigis polygyny can be characterised as "resource defence" (Emlen and Oring 1977), resulting from both intra and intersexual selection. First, early arriving men established larger plots, and compete over retaining access to these plots. Second, men with larger plots were able to attract more wives, both during the Pioneer period and over their entire reproductive lifespans up to the present.

Acquisition of wives was more closely associated with a man's land plot size than his arrival date, suggesting that acreage itself is an important aspect of resource

Table 2. The effect of numbers of cowives on numbers of surviving offspring in 2 cohorts of post-reproductive women

Marital status	Full sample ^a	Husband's acres ^b				Total N
		0-14*	15-29	30-58*	59-300*	
0 cowife	7.05 (60)	7.27 (33)	6.75 (12)	7.86 (7)	7.33 (3)	(55)
1 cowife	6.82 (102)	5.96 (27)	6.54 (24)	8.00 (31)	8.80 (10)	(92)
2 cowives	5.58 (60)	3.00 (4)	5.18 (11)	5.24 (25)	6.46 (15)	(55)
3 cowives or more	5.81 (58)	4.00 (2)	5.00 (1)	5.25 (16)	6.32 (37)	(56)
Total N	(280)	(66)	(48)	(79)	(65)	(258)

^a The effects of numbers of cowives on the numbers of surviving offspring per woman. Difference between groups $F_{3,276}=4.37$, $P=0.005$; deviation from linearity $F_{1,276}=10.10$, $P<0.002$.

^b Husband's acres broken into four percentile ranges 0%–25%, 26%–50% etc. A slightly smaller sample ($N=258$) of women with husband's ownership of acres known was available for these analyses. Within each of these wealth categories the effects of marital status on number of surviving offspring were tested with analyses of variance. 0–14 acres: $F_{3,62}=5.00$, $P<0.005$; 15–29 acres: $F_{3,44}=0.93$, NS; 30–58 acres: $F_{3,75}=6.54$, $P<0.001$; 59–300 acres: $F_{3,61}=2.16$, $0.05<P<0.10$. Where F -values are $P<0.10$, deviations from linearity tests are also significant and indicated with * in the Table. 1–14 acres: $F_{1,62}=13.24$, $P<0.001$; 30–58 acres: $F_{1,75}=14.57$, $P<0.001$; 59–300 acres: $F_{1,61}=4.00$, $P<0.05$

Table 3. The effect of marital status on numbers of surviving offspring in 2 cohorts of post-reproductive women

Marital status	Full sample ^a	Husband's acres ^b				Total N
		0-14*	15-29*	30-58	59-300	
Mono-gamous	7.05 (60)	7.27 (33)	6.75 (12)	7.86 (7)	7.33 (3)	(55)
Poly-gynous (1st)	6.29 (122)	5.58 (24)	6.58 (24)	6.20 (46)	6.74 (23)	(117)
Poly-gynous (2nd)	6.02 (56)	5.14 (7)	6.13 (8)	6.58 (19)	6.77 (13)	(47)
Poly-gynous (>2nd)	6.29 (42)	5.50 (2)	3.00 (4)	7.57 (7)	6.77 (26)	(39)
Total N	(280)	(66)	(48)	(79)	(65)	(258)

^a The effects of marital status on number of surviving offspring per woman. Difference between groups $F_{3,276}=1.45$, NS; deviation from linearity $F_{1,276}=2.28$, NS

^b Statistics as in Table 2, note ^b. 1–14 acres: $F_{3,62}=2.79$, $P<0.05$; 15–29 acres: $F_{3,44}=2.58$, $0.05<P<0.10$; 30–58 acres: $F_{3,75}=0.92$, NS; 59–300 acres: $F_{3,61}=0.04$, NS. Where F -values are $P<0.10$, deviations from linearity are also significant and indicated with * in the Table. 1–14 acres: $F_{1,62}=6.65$, $P=0.01$; 15–29 acres: $F_{1,44}=4.91$, $P=0.03$

quality. The importance of plot size per se is also suggested by its correlation with the availability of food stuffs and milk in households (Borgerhoff Mulder 1987b). The significance of correlated factors such as drainage, terrain or location that might improve the productivity of land and livestock cannot be excluded as influences on female preference as they were not measured in this study. However, Kipsigis' parallel settlement patterns along hillsides ensure that plots are rather homogenous, with each family using well drained slopes for cultivation, lower-lying river flats for grazing cattle, and the stony hilltops for cattle and smallstock; in Abosi semi-permanent water is no further than a mile from any farm plot. For these reasons, then, size of plot itself, particularly the area suited to grazing and cultivation, is likely to be the critical component of territory quality. Small amounts of cash (up to \$150 per annum, not measured in this study), obtained by men through the sale of maize and expended largely in the restocking of herds, is also likely to enhance a man's chances of becoming polygynous, particularly through the purchase of cattle for bridewealth. This suggestion is supported by the very large number of wives married to men of the "Maina" cohort, many of whom as young men in the 1930s benefitted from employment opportunities on the farms of Colonial European settlers (Borgerhoff Mulder 1988a).

Consistent with this view of Kipsigis polygyny as "resource-defence" is the intense competition observed over land: this was the driving force behind the emigration of men to Abosi (see Ethnographic Background), and is a constant factor in hostilities and feuds within Kipsigis communities over, for example, incursions of livestock into a neighbour's property. There was one case during the 1982–83 field study when young men of one family attempted to "move" a neighbour's fence surreptitiously, and then argued that it got accidentally dragged in the tails of their cattle; this took over a year to arbitrate, using a traditional council of elders (Peristiany 1939). Finally, intense competition over resources, both within and between pastoralist groups, is key to the migration and expansion that characterises East African history (Waller 1986), hence this Kipsigis pioneer settlement cannot be considered as an isolated or unusual incident.

Men who control vast sources of wealth often acquire large numbers of mates in human societies (e.g. Betzig 1986; reviewed Flinn and Low 1986). Furthermore, in 63% of societies in Murdock's Ethnographic Atlas (Standard Half Sample $N=93$) property of economic value is exclusively or predominantly inherited by men (Whyte 1980). In addition, with increasing land limitation (as in the Kipsigis and many contemporary populations) the potential for men to control the resources critical to female productive activities (agriculture and husbandry) becomes critical (cf. White 1988, 1989; Borgerhoff Mulder 1989b). Therefore the potential for resource defence polygyny may be widespread across human societies, both traditional and those in transition.

Female choice

The fact that men who control vast sources of wealth often acquire large numbers of mates has led to the suggestion that female preferences for wealthy men may be an important factor in the evolution and current incidence of polygyny in humans (Dickemann 1979b; Hartung 1982; Irons 1983). Earlier interview data showing that Kipsigis parents place considerable emphasis on the wealth of a potential son-in-law pointed to the possible importance of such patterns of choice in contributing to polygyny in the Kipsigis (Borgerhoff Mulder 1988c). Several questions nevertheless remained unanswered.

First, are potential sons-in-law favoured for their overall wealth or for the resources they can offer an incoming wife? The finding that the size of the breeding opportunity on offer predicts whether or not a man would be chosen in any year whereas his total acreage does not suggests that parents are selecting a husband for their daughter on the basis of the specific resources he can provide for her and her offspring. This is the best documented and theoretically most straight forward form of female choice (Partridge and Halliday 1984), and provides some evidence for the importance of epigamic vis-a-vis intrasexual selection in this study.

Second, are men chosen as mates for the breeding opportunity they offer, or for genetic qualities or other phenotypic traits that might be correlated with (and hence masked by) breeding opportunity? This question has been tackled both experimentally (Alatalo et al. 1986) and analytically (Catchpole et al. 1985; Eckert and Weatherhead 1987) in non-human studies, and can only be addressed indirectly here. First, older men were not favoured over younger men, providing some evidence against the "good genes" argument, namely that females use prolonged survivorship as an indicator of genetic viability. Second, although men with successful reproductive histories (maintenance of a high rate of production of surviving offspring with their wives over their reproductive careers to date) were favoured over men with less distinguished reproductive histories, this was not an independently significant factor affecting female choice. Such an effect would however be much more precisely investigated with data on *fertility* rather than surviving offspring (itself correlated with wealth, Borgerhoff Mulder 1987b); unfortunately retrospectively dated livebirth records were not reliable for this early period. Third, it is plausible that, given the violent relations between Masai and Kipsigis (Orchardson 1961), brave, risk-taking Kipsigis men may have been the first to settle in pioneer communities such as Abosi, and may have been favoured for these traits. Partial correlations showing that the effects of plot size on polygyny were independent of arrival order provide some evidence against this hypothesis, at least insofar as these traits are uncorrelated with plot size. Furthermore, as mentioned above, men were chosen on the basis of their breeding opportunity on offer that year, not their overall plot size.

In sum, the importance of male qualities other than the resources they offer females cannot be discounted,

as they were not directly measured in this study. Nevertheless to demonstrate choice that has evolved solely because of *genetic* consequences it is necessary to rule out non-genetic benefits contingent on the choice (Partridge and Halliday 1984), benefits that are clearly in evidence in the Kipsigis.

Female settlement sequences

Only two other studies have determined female choice through an examination of settlement sequences. In redwinged blackbirds females arrive after all the males have established territories, allowing a comparison of the rank order in which females chose territories to the rank-ordered anticipated reproductive success from such nests (Lenington 1980). The correlation coefficient was rather low ($r_s = 0.15$, NS), although higher when only the number of young fledged from successful nests was considered ($r_s = 0.57$, $P < 0.01$). In pied flycatchers, where females begin choosing before all males have arrived (as in the Kipsigis settlement of Abosi), only comparisons within days could be conducted (Alatalo et al. 1984): females preferred early arriving males (paired $t = 3.71$, $N = 19$, $P < 0.01$), who offered better nest sites. In both studies, however, the tests reported give no indication of the number of incidences where females fail to chose the very best breeding opportunity. Thus, returning to the Kipsigis, although the breeding opportunity selected by women is not always the highest on offer, the strength of support for such preferences is similar to that shown in studies of passerines.

Factors that might contribute to the exceptions in this population include: (1) Negative consequences of polygyny other than reduced access to land. There is ample ethnographic evidence that polygynous (particularly junior status) cowives can suffer sexual neglect, reduced assistance from their husbands, increased exposure to venereal disease and tense family circumstances (e.g. Curley 1973; Brabin 1984; Borgerhoff Mulder 1989a). (2) The importance of the suitor's reputation. Sixty one percent of parents interviewed ($N = 94$) said "good reputation" was an important consideration in selecting a son-in-law (Borgerhoff Mulder 1988c). Because rich men can be notoriously unreliable and arrogant, a poor man with a good reputation is seen by some parents as a safer matrimonial option than a wealthy man with an unpredictable nature; this may represent some sort of bet hedging with respect to marriage choice. (3) Socio-economic ties. Marriage in many traditional populations, including Kipsigis, entails not just a mating relationship between two individuals, but social and economic ties between two sets of kin, such as acquiring access to political office (Comaroff and Comaroff 1981), settling disputes over land or cattle (Evans-Pritchard 1940) or reestablishing bonds of kinship (Stenning 1959). These reconsiderations may in some circumstances override the importance of wealth. (4) Bridewealth. A suitor's wealth does not correlate with his bridewealth payment (Borgerhoff Mulder 1988b). Three anecdotal cases (3%)

arose in my interviews ($N=94$) where parents reported having given their daughters to men who were patently poor because, they said, "the bridewealth offer was so good". These constitute cases where daughters' reproductive interests may have been sacrificed to parental manipulative interests (see Introduction), and indicate the potential for parent/offspring conflict in marriage systems such as this.

On account of these factors the size of breeding opportunity is unlikely to be the single determinant of the settlement sequence. The value of the present study is its application of a statistical technique that permits assessment of a number of independent covariates on patterns of female choice. Clearly for a Kipsigis woman, marital status is an important consideration *in addition* to the availability of land on which to raise her offspring; many other important considerations, such as status, reputation and longterm enduring friendships between families that may be consolidated through marriage alliances, remain unmeasured.

Polygyny and reproductive consequences

In proposing the polygyny threshold model, Orians (1969) predicted that the fitness of monogamously and polygynously mated females should be at least equal, because females will assort themselves optimally with respect to their fitness interests. Despite some supportive data (reviewed by Wittenberger 1981; Garson et al. 1981) there are problems with this prediction. First it ignores the possibility that a female's mating status during her reproductive period may be different from that she originally *chose*, because of subsequent females who may settle on the territory (Altmann et al. 1977). Second, it fails to consider factors (such as arrival or egg-laying dates) that may be responsible for differences among females in breeding success that are independent of mating status (Garson et al. 1981). Third, it assumes females have access to reliable information on territory quality and male mating status, (but see Alatalo et al. 1982 and Catchpole et al. 1985 for evidence of deception). Fourth, it assumes that the costs of assessing and choosing a mate are small, (as questioned by Slagsvold et al. 1988; see also Christie 1983). Fifth, the model assumes that females do not cooperate, that they cannot gain benefits from the presence of other females, and other specific patterns of cost-sharing among polygynously mated females (cf. Altmann et al. 1977; Davies 1989). Sixth, it assumes that female preferences are never thwarted by aggression from other females; detailed studies suggest female competition cannot be disregarded (e.g. redwinged blackbirds, Lenington 1980). Seventh, the model completely ignores the possibility that male and female interests may conflict (Davies and Houston 1986; Davies 1989), a situation which may prevent females from following their optimal strategy. Finally, it assumes females face identical options at settlement, rarely the case when arrival is not simultaneous, or at least that male territories are continuously distributed such that later-arriving females can make compensatory choices (Searcy and

Yakusawa 1989). Because the equal fitness prediction is based on a number of assumptions that are difficult to substantiate, evidence that the reproductive success of monogamous, primary polygynous, secondary polygynous and tertiary (plus) polygynous women is equal in six different cohorts (Borgerhoff Mulder 1989a) provides only very weak evidence that women assort themselves at marriage as predicted by the polygyny threshold model.

A more appropriate investigation of the reproductive costs of polygyny entails considering the original Verner-Willson-Orians model as one of a suite of alternative models that might explain the incidence of polygyny across mammals and birds (Searcy and Yakusawa 1989). They propose a hierarchical series of considerations that should be used to differentiate between alternative models: male coercion, whether polygyny is costly and whether these costs are compensated for, sex ratio biases, search costs, and possibilities for deception. The analyses presented above, in addition to the ethnographic background, suggest that polygynous marriage among Kipsigis women is not a result of coercion; furthermore coercion might be implicated if the reproductive costs were particularly high among women married to the wealthiest (most influential, and potentially most coercive) men in the sample, but this was not the case (Tables 2 and 3). Polygyny nevertheless entails a cost to women, a cost that is not entirely compensated for by women's preferences for large breeding opportunities, and which may result from lower rates of sexual intercourse, reduced direct paternal care or other male contributions unrelated to plot size. What may account for this tolerance of cost? Women are highly unlikely to be deceived as to the marital status of a suitor (marriage is a formal public event and always entails coresidence); indeed some women favour polygyny for the opportunity it gives them to assess what kind of a *husband* a man is. Search costs are likely to be low (in so far as grooms look for brides, whereas brides and their families assess the suitors' suitability using information from friends, neighbours and acquaintances). The default alternative, that females are behaving maladaptively seems unlikely given the marital choices reported in this paper. What seems most likely is that *partial* compensation (c.f. Searcy and Yakusawa 1989) is occurring; either some women make compensatory choices and others do not, or adequate compensation can rarely be attained by any woman. For example, it is possible that compensatory factors, such as cowife cooperation or marriage to a high status polygynous man, may have had positive fitness consequences for Kipsigis women living as pastoralists, but not nowadays; variations of Searcy and Yakusawa's models are now being tested with pure pastoralists (Borgerhoff Mulder, in prep). It is also possible that a form of delayed compensation through a sexy son effect is entailed.

Finally, although the sex ratio at independence is not skewed towards females (unpubl. data), competition over land leads to delayed marriage for men and to unsuccessful competitors leaving the area for tea planta-

tions and other forms of wage labour in the vicinity of Kericho and Sotik (Borgerhoff Mulder 1988a); this presents women with the choice of also leaving the Kipsigis area for a plantation (an option not favoured by many) or marrying polygynously. Although Searcy and Yakusawa would not classify this as a model based on sex-biased availability of mates, the discontinuous distribution of viable-sized territories among men is an important ecological factor underlying polygyny in the Kipsigis and perhaps many other persistently polygynous agricultural populations in Kenya, given the intense land shortages that exist in the highland areas.

Resource-defence polygyny and female choice in mammals

In contrast to birds, there is no clear evidence that polygyny has evolved through female choice for males with high quality resources in non-human mammals. The classic mammalian example of resource defence polygyny mediated by female choice, yellow-bellied marmots *Marmota flaviventris* (Emlen and Oring 1977; Krebs and Davies 1987), is now more accurately characterised as male defence of harems (Armitage 1986). More generally, evidence from ungulates that males tend to hold territories in areas favoured by females (e.g. waterbuck *Kobus defassa*, Spinage 1969) and that the number of females in a male's territory correlates with its forage quality (e.g. pronghorn *Antilocapra americana*, Kitchen 1974, and topi *Damuliscus korrigum*, Duncan 1975) are suggestive, but they provide no conclusive demonstration of female preferences for males with high quality territories; furthermore, the sequence of arrival of males and females in a particular area is often unknown and the extent of male coercion is often ambivalent. Without detailed longitudinal studies of known females, the settling options available to them, and their reproductive performance, the importance of female preferences for males with high quality resources is difficult to determine in non-human mammals. Studies of human societies such as the Kipsigis, where longitudinal data can be obtained retrospectively, are therefore of potential value to the study of mammalian breeding systems.

Acknowledgements. Critical comments and helpful suggestions on the manuscript were made by Richard Alexander, Nick Davies, Tim Caro, Warren Holmes, Magdalena Hurtado, Arne Lundberg, Alison Rosser, Dan Sellen, Daniela Sieff and Margo Wilson. John Warner offered generous statistical guidance; John Pepper and Andy Kerr drew the figures. The project was funded by the National Geographic Society, and permission to conduct research in Kenya granted by the Office of the President, Nairobi. Special thanks to the Kipsigis families for their friendship and cheerful cooperation throughout the study.

References

- Alatalo RV, Lundberg A, Stahlbrandt K (1982) Why do pied flycatchers mate with already-mated males? *Anim Behav* 30: 585–593
- Alatalo RV, Lundberg A, Stahlbrandt K (1984) Female mate choice in the pied flycatcher *Ficedula hypoleuca*. *Behav Ecol Sociobiol* 14: 253–261
- Alatalo RV, Lundberg A, Glynn C (1986) Female pied flycatchers chose territory quality and not male characteristics. *Nature* 323: 152–153
- Altmann SA, Wagner SF, Lenington S (1977) Two models for the evolution of polygyny. *Behav Ecol Sociobiol* 2: 397–410
- Armitage KB (1986) Marmot polygyny revisited: determinants of male and female reproductive strategies. In: Rubenstein RI, Wrangham RW (eds) *Ecological aspects of social evolution*. Princeton University Press, Princeton NJ, pp 303–331
- Betzig LL (1986) *Despotism and differential reproduction: a Darwinian view of history*. Aldine, New York
- BMDP (1985a) *Statistical software manual 1985*. University of California Press, Berkeley CA
- BMDP (1985b) *Technical report no. 80. Example 4*. University of California Press, Berkeley CA
- Borgerhoff Mulder M (1987a) On cultural and reproductive success: Kipsigis evidence. *Am Anthropol* 89: 617–634
- Borgerhoff Mulder M (1987b) Resources and reproductive success in women, with an example from the Kipsigis. *J Zool* 213: 489–505
- Borgerhoff Mulder M (1988a) Reproductive success in three Kipsigis cohorts. In Clutton-Brock TH (ed) *Reproductive success*. University of Chicago Press, Chicago, pp 419–435
- Borgerhoff Mulder M (1988b) Kipsigis bridewealth payments. In: Betzig L, Borgerhoff Mulder M, Turke P (eds) *Human reproductive behaviour*. University of Cambridge Press, Cambridge, pp 65–82
- Borgerhoff Mulder M (1988c) Is the polygyny threshold model relevant to humans? Kipsigis evidence. In: Mascie-Taylor CGN, Boyce AJ (eds) *Mating patterns*. Cambridge University Press, Cambridge, pp 209–230
- Borgerhoff Mulder M (1989a) The polygyny-fertility hypothesis: new evidence from the Kipsigis of Kenya. *Popul Stud (London)* 43: 285–304
- Borgerhoff Mulder M (1989b) Polygyny and the extent of women's contributions to subsistence: a reply to White. *Am Anthropol* 90: 179–181
- Brabin L (1984) Polygyny an indicator of nutritional slack in African agricultural societies. *Africa* 54: 31–45
- Catchpole C, Leisler B, Winkler H (1985) Polygyny in the great reed warbler, *Acrocephalus arundinaceus*: a possible case of deception. *Behav Ecol Sociobiol* 16: 285–291
- Christie JH (1983) Female choice in the resource-defence mating system of the sand fiddler crab, *Uca pugilator*. *Behav Ecol Sociobiol* 12: 169–180
- Comaroff JL, Comaroff J (1981) The management of marriage in a Tswana chiefdom. In: Krige EJ, Comaroff JL (eds) *Essays on African marriage in Southern Africa*. Juta, Capetown, pp 24–49
- Cox DR (1972) Regression model and life-tables (with Discussion). *J R Stat Soc* 34: 186–220
- Curley RT (1973) *Elders, shades and women: ceremonial change in Lango, Uganda*. University of California Press, Berkeley
- Daly M, Wilson M (1983) *Sex, evolution and behavior*, 2nd edn. Willard Grant Press, Boston
- Davies NB (1989) Sexual conflict and the polygyny threshold. *Anim Behav* 38: 226–234
- Davies NB, Houston AI (1986) Reproductive success of dunnocks, *prunella modularis*, in a variable mating system. II. Conflicts of interest among breeding adults. *J Anim Ecol* 55: 139–154
- Dickemann M (1979a) Female infanticide, reproductive strategies and social stratification: a preliminary model. In: Chagnon NA, Irons W (eds) *Evolutionary biology and human social behavior: an anthropological perspective*. Duxbury Press, North Scituate MA, pp 321–367
- Dickemann M (1979b) The ecology of mating systems in hypergynous dowry systems. *Soc Sci Inform* 18: 163–195
- Dickemann M (1982) Commentary on Hartung. *Curr Anthropol* 23: 1–12

- Duncan P (1975) Topi and their food supply. University of Nairobi, Ph. D. Diss.
- Eckert CG, Weatherhead PJ (1987) Male characteristics, parental quality and the study of mate choice in the red-winged blackbird (*Agelaius phoeniceus*). *Behav Ecol Sociobiol* 20:35–42
- Emlen ST, Oring LW (1977) Ecology, sexual selection and the evolution of mating systems. *Science* 197:215–223
- Evans-Pritchard EE (1940) The Nuer. Oxford University Press, London
- Flinn MV, Low BS (1986) Resource distribution, social competition and mating patterns in human societies. In: Rubenstein RI, Wrangham RW (eds) *Ecological aspects of social evolution*. Princeton University Press, Princeton NJ, pp 217–243
- Fretwell SD (1972) *Populations in a seasonal environment*. Princeton University Press, Princeton
- Garson PJ, Plezyczynska WK, Holm CH (1981) The “polygyny threshold” model: a reassessment. *Can J Zool* 59:902–910
- Goldschmidt W (1986) *The Sebei: a study in adaptation*. Holt, Rinehart and Winston, New York
- Gray PJ (1985) *Primate sociobiology*. HRAF Press, New Haven, CT
- Gulliver PA (1963) *Social control in an African society*. New York University Press, New York
- Hartung J (1982) Polygyny and inheritance of wealth. *Curr Anthropol* 23:1–12
- Irons W (1983) Human female reproductive strategies. In: Wasser SK (ed) *Social behavior of female vertebrates*. Academic Press, New York, pp 169–213
- Kitchen DW (1974) Social behavior and ecology of the pronghorn. *Wildl Monogr* 38:1–96
- Krebs JR, Davies NB (1987) *Introduction to behavioural ecology*. Sinauer, Sunderland MA
- Lenington S (1980) Female choice and polygyny in red-winged blackbirds. *Anim Behav* 28:347–361
- Maddala GS (1983) *Limited dependent and qualitative variables in econometrics*. Cambridge University Press, Cambridge
- Manners RA (1967) The Kipsigis of Kenya: culture change in a “model” East African Tribe. In: Steward J (ed) *Contemporary change in traditional societies*, (vol 1) Introduction and African tribes. University of Illinois Press, Urbana, pp 207–359
- Orchardson IQ (1961) *The Kipsigis*. Kenya Literature Bureau, Nairobi
- Orians GH (1969) On the evolution of mating systems in birds and mammals. *Am Natural* 103:589–603
- Owen-Smith N (1977) On territoriality in ungulates and an evolutionary model. *Q Rev Biol* 52:1–52
- Partridge L, Halliday T (1984) Mating patterns and mate choice. In: Krebs J, Davies NB (eds) *Behavioural ecology*. Blackwell Scientific Press, Oxford, pp 222–250
- Peristiany JG (1939) *The social institutions of the Kipsigis*. Routledge and Kegan Paul, London
- Plezyczynska WK (1978) Microgeographic prediction of polygyny in the lark bunting. *Science* 201:935–937
- Saltman M (1977) *The Kipsigis: a case study in changing law*. Shehkman Publishing Company, MA
- Searcy WA (1979) Female choice of mates: a general model for birds and its application to red winged blackbirds. *Am Nat* 114:77–100
- Searcy WA, Yakusawa K (1989) Alternative models of territorial polygyny in birds. *Am Natural* 134:323–343
- Siegel S (1956) *Nonparametric statistics of the behavioral sciences*. McGraw-Hill, New York
- Slagsvold T, Lijfield JT, Stenmark G, Breihagen T (1988) On the costs of searching for a male in female pied flycatchers *Ficedula hypoleuca*. *Anim Behav* 36:433–442
- Spinage CA (1969) Territoriality and social organisation of the Uganda defassa waterbuck *Kobus defassa ugandae* Neumann. In: Geist V, Walther F (eds) *The behaviour of ungulates and its relation to management*. IUCN New Series, No. 24, Morges, pp 635–643
- SPSSx User’s guide (1983) McGraw Hill, Chicago
- Stenning DJ (1959) *Savanna nomads*. Oxford University Press, London
- Verner J (1964) Evolution of polygamy in the long-billed marsh wren. *Evolution* 18:252–261
- Verner J, Willson MF (1966) The influence of habitats on mating systems of north American passerine birds. *Ecology* 47:143–147
- Waller R (1986) Ecology, migration, and expansion in East Africa. *Afr Affairs* 85:347–370
- White DR (1988) Rethinking polygyny: co-wives, codes, and cultural systems. *Curr Anthropol* 29:529–572
- White DF (1989) *Am Anthropol* 90:177–179
- Whyte MK (1980) Cross-cultural codes dealing with the relative status of women. In: Barry H, Schlegel A (eds) *Cross-cultural samples and codes*. University of Pittsburgh Press, Pittsburgh PA, pp 335–361
- Wittenberger JF (1981) Male quality and polygyny: the “sexy son” hypothesis revisited. *Am Natural* 117:329–342