

# Human Behaviour and Adaptation

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## **TESTING ADAPTIVENESS OF CULTURALLY DETERMINED BEHAVIOUR: DO BUSHMAN WOMEN MAXIMIZE THEIR REPRODUCTIVE SUCCESS BY SPACING BIRTHS WIDELY AND FORAGING SELDOM?**

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MANY recent writings in ecological anthropology or cultural ecology use the term adaptation and are based on the assumption that one can show that cultures are in various senses adaptive and that one way of behaving is "better" (in some economic or ecological sense) than another. Contrary to early anecdotal studies the ecological anthropologists find that when one observes and measures the interaction between people and the material world even quite bizarre practices turn out to appear economically advantageous. But the nature of "advantage" and adaptation is unclear and often refers to energy budgets or to group survival, both of which would no longer be acceptable criteria to evolutionary biologists. We admire this school of anthropology and hope that by discussing the criterion of "adaptation" and "advantage" that comes first to the mind of the biologist we can provoke further research and thinking on the nature of human cultural adaptation.

Important and relevant criticisms of the application of the concept of adaptiveness to human culture (equally applicable to the concept of adaptation in biology) have been set out by Burnham (1973) and Alland (1975). Recent developments have gone far towards solving these problems in biology (Hamilton, 1964; Trivers, 1975; Tinbergen, 1965; Sibly and McFarland, 1976). The ecological approaches to culture seem too valuable to lose merely from isolation from the answers to these problems. Consequently

in this paper we aim to contribute to the development of ecological approaches to culture by provoking discussion of biologists' answers to (1) what is the criterion of adaptiveness? What is improved or increased by adaptive behaviour? and (2) how do we test whether behaviour is adaptive or not?

Our approach to the second question illustrates the development from Tinbergen's (1965) comparisons of the outcomes of different behaviour (also called for by Alland, 1975) via his idea of compromise in adaptation to current attempts to use optimization techniques to calculate the behaviour sequence that would maximize reproductive success, the result then being compared with the observed behaviour (Sibly and McFarland, 1976). This is a difficult but potentially extremely powerful approach.

Burnham (1973) raised a third criticism: what is the mechanism by which an adaptive change takes place? The mechanism is clearly not the same as in biological evolution. Many possibilities are conceivable and have been discussed in the literature. One might be able to derive and propose the most efficient but we regard this question as independent from the first two. If cultural change is demonstrably adaptive this is not disproved by our inability to describe the mechanism by which the change occurs. Furthermore, since cultural change is more rapid than biological change, the short-term mechanisms may be of much less practical importance than the pressures towards adaptation, whose effect will be more powerful and remarkably rapid.

Lee (1972) has described various quantitative aspects of birth-spacing and foraging in Kalahari hunter-gatherers. He has shown how the "cost" of having babies in terms of weight carried by mothers increases cumulatively with shortened birth-spacing, the increase in cost from giving birth every three years rather than every four is much greater than the increased cost of giving birth every four years rather than every five. This, and his demonstration and explanation of the changes as Bushmen become more settled, is an elegant example of what contemporary ecological anthropology can achieve. But as biologists we believe that the analysis is incomplete, a further important step is missing—the demonstration that the increased costs of closer birth-spacing are not worth paying. Our proposition is that people, at least in the ancient hunter-gatherer niche, might, like many non-human

species (Lack, 1954), tend to have as many babies as they can successfully raise.

Thus in this paper we try to show how one might test whether people in a foraging culture behave in ways which maximize their reproductive success (and perhaps ultimately their inclusive fitness, Hamilton, 1964). Our example is very limited and our approach may or may not be applicable to other hunter-gatherer cultures or post hunter-gatherer societies. In our preliminary analysis of the spacing between births of the !kung Bushmen we are using the ecological data and suggestions published by Lee (1968, 1969, 1972) (see Lee and DeVore, 1976 for reports of the recent series of studies on the Kalahari !kung Bushmen), and physiological data from many people (Durnin and Passmore, 1967, Weiner, 1977), including Bushmen (Wyndham, 1956, 1958, 1964). Bushman mothers average nearly four years between births. Both the mothers themselves and Lee (1972) agree that this is desirable because of the difficulty of carrying two children on their gathering excursions. But what does "desirable" mean? We rephrase this question as: are they, by spacing births so widely, likely to be rearing to maturity more children than they would if they gave birth more often?

By testing the applicability of natural selection theory to human behaviour in this context we are not making any implications of "innateness" in the behavioural mechanisms involved: (1) questions about adaptation are questions about consequences of behaviour (which act as *long-term* causes) and carry only framework-setting implications about the short-term mechanisms of individual development or motivation (Tinbergen, 1951; Harris, 1968; Gross, 1975); (2) we know that all the variables discussed here, even the physiological ones, are strongly modified by physical and cultural environments. Indeed the interest of this exercise is in applying it to culturally transmitted behaviour and individually variable performance. If culture is adaptive, does adaptive mean maximizing inclusive fitness, or maximizing something else (individual wealth, group survival—which biologists regard as unlikely), or not actually maximizing anything—in which case the propositions of cultural ecology become less easy to test. It would seem reasonable to expect hunter-gatherer cultures (particularly when as with the Bushmen, the archaeological

record (Yellen, 1976) reveals the great antiquity of their material culture and habitat) to show behaviour that maximizes inclusive fitness. But it would seem very unreasonable to expect this to apply very effectively to rapidly changing industrial cultures, unless culture is even more adaptive than we think. Detailed empirical studies of a variety of cultures have been undertaken in recent years and hopefully our ideas could be tested on several non hunter-gatherer cultures as well as by further analyses of Bushman data.

Thus in this paper we attempt to bring together ecological approaches to human behaviour with data from physical anthropology and environmental physiology and current developments in evolutionary biology, particularly studies in which the techniques of optimisation are applied to the question of compromise in adaptation. Tinbergen showed how any feature of an animal's behaviour is a result of a compromise between conflicting pressures. This line of thought has been elaborated by Sibly and McFarland (1976) and others. In an ideal optimization study, one would know the costs and benefits involved in performing or not performing each activity in an individual's repertoire, so that its optimal strategy could be calculated exactly. This is the strategy one would expect as the ultimate outcome of natural selection.

In practice consideration has to be given to five points: (1) what options are open to the animal and what courses of action is it able to perform? This is partly a matter of discovering what it cannot do, of finding or assuming constraints on its behaviour like some of the "givens" enumerated below; (2) what risks, to personal survivorship or to the survival of kin, and what benefits in terms of the potential production of offspring, are entailed by each course of action? (3) is it feasible to measure these risks and benefits? (4) can a mathematical model of the individual's situation be constructed, and if so, what optimal strategy does it suggest? (5) how does this optimal strategy compare with the animal's actual behaviour?

This approach can embody the normal scientific procedure of hypothesis, prediction and test. A more rigorous account of the method, together with examples, is given in Sibly and McFarland (1976) and McFarland (1976).

Lee has shown that many features of Zhun/twa Bushman society and individual behaviour are readily explicable as successful adaptations to surviving with a hunter-gatherer technology in the sparse habitat of Ngamiland. Most of these are clearly adaptive in almost any sense—personal survival or comfort, survival of children or group. But the observations that we argue need further “explanation” are two which are in some ways “counter-intuitive” and may provoke more precise consideration of the way in which they are adaptive: (1) the interval between births in non-settled traditionally foraging Bushmen is approximately 4 years (this declines markedly when people settle); (2) women (who provide 67% of the calorie “income”) only go gathering once every 2 or 3 days. Most of the time they spend talking and singing and visiting or being visited by friends and relatives.

There are several observed aspects of Bushman behaviour, some very important, whose adaptive value we have not questioned at this stage of the investigation: (1) mothers carry children of under 2 years old when they go gathering, and frequently carry children under 4 years old. We use Lee's figures on this and *for the time being* assume that a woman makes the maximum possible use of available babysitters; (2) men do not gather, but hunt, acquiring at unpredictable intervals an average 33% of the calorie “income” (but of course acquiring a wider range of proteins); (3) that the women walk quite fast on their journeys to and from the nut groves. We assume a figure of 3 m.p.h. The consequences of higher and, more important, lower speeds for our model can be tested; (4) that the dry season villages are 6 miles from the nut groves and one mile from water and that Lee is correct in calling this optimal for the energy or thermoregulatory budgets; (5) that mongongo nuts (*Ricinodendron rautanenii*) are the most useful plant food source and the main one to consider (other plant foods provide 8.9% of calorie income—Lee, 1968), although (6) they take a very long time to crack (Lee, 1969) which excludes daily gathering excursions; (7) start and end ages for having babies (19.5–45 years) (Howell, 1976); (8) that Lee is correct in arguing that although plant food is superabundant and the supply of mongongo nuts is not exhaustible by foraging, exhaustion of supplies near dry season camps is, as Konner (personal communication) and Lee (1969) suggest, a reason for the long “six mile” journeys

late in the dry season.

Some further "givens" will arise and be discussed later in this paper. Every given can also be seen as a gateway to a new area of quantitative study linking ever wider facets of Bushman life into one sharply specified system. Regardless of the eventual answer about what is optimised, this procedure of constructing a system that specifies the consequences of one variable upon each other variable is to our minds an attractive potential outcome of the approach that we are proposing.

### **Birth-spacing, Food Requirements and Back-loads**

If a Bushman mother has a baby more often than every 4 years (given that as she does, she carries children up to 4 years old on her foraging trips) she will spend some time carrying two small children when she goes gathering and more time carrying at least one of them. This will reduce the amount of food that she can bring back, if there is some limit to the total weight that she can carry. At the same time it will increase the amount of food her family needs; there are more children to feed then and subsequently. As her payload goes down so the food requirements go up. Obviously at some point shortening the birth interval will lead to a situation where the mother would have to carry extremely high loads to feed her family. But of course there is strong selective advantage in having more children, so long as you can feed them enough for them to grow up and reproduce. If reproductive success is the criterion it would be worth great costs to the extent of risking physical integrity to have just one more baby (provided this meant more babies growing up and reproducing). Since too great a level of risk cannot be worth taking there must be some optimal birth interval which maximizes reproductive success.

The first step in analysing this situation is to work out what maximum back-loads are required to support various sized families. If we treat the number of years for which the woman reproduces as a constant, then family size and birth interval are closely correlated. Much of the relevant data is available. Lee (1972) published weights of children of various ages, and of adults. He also calculated dietary requirements of adults (1968). We have recalculated these and those of children. We have used

data from the biological data handbooks for calorie cost of lactation and requirements for babies under one year. Lee (1968, 1969) published data on the food values of a given weight of both prepared and unshelled mongongo nuts. From this we have calculated the weight of nuts a mother would have to carry home to feed her family (given she provides 58.8% of the calories from nuts) for a range of birth intervals (2 to 6 years in steps of 0.1 year), for gathering one day in three and for gathering one day in two, for family sizes that do or do not assume the infant mortality reported by Howell (1976).

Our first objective was to calculate the load of food and children that on average a mother will carry if she spaces births at a particular interval. This load is derived from the probabilities that a child will survive to each age and estimates of weight and food requirements of Bushman children of different ages as given in Table 1. In the computer simulation estimates were made every tenth of a year by linear interpolation between the values shown.

The weight of nuts that a mother will have to carry for each child is calculated as (expected nut requirement/child of given age, kg) = (probability that a child survives to that age)  $\times$  (energy requirements of a child of that age, calories/day)  $\times$  (% of Western recommended daily dietary allowance that Bushman children eat)  $\times$  (% diet that is nuts)  $\times$  (weight of nut needed to supply 1 calorie, kg/cal)  $\times$  (number of days nuts must last). We suppose that Bushmen children require 76% of the Western standards for children of that age (based on comparison of Lee's figures for adults with figures in Spector, 1956); that 58.8% of the calories in their diet are from nuts (Lee, 1969), and that 0.00119 kg nuts provide 1 calorie (Lee, 1969; Wehmeyer *et al.*, 1969). Our conclusions are fairly insensitive to small errors in these figures.

Older children are carried progressively less, and we have followed Lee (1972) in supposing that the most important parameter is the average weight carried per journey. Lee's (1972) Table 14.2 is the source of our figure for this: weight of child is multiplied by proportion of mileage for which child is carried. Whether it is correct to consider only *average* weight carried depends on the relative dangers of the different catastrophes that may ensue. If the greatest risk is heat stress, or dehydration, or some consequence of fatigue, then our assumption will be at least approxi-

TABLE 1. Calculation of load of food and child that a mother must expect to carry for a child at each age

Age <sup>1</sup> of child (years)	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Survivorship to that age <sup>2</sup> (%)	100	80	74	70	68	67	66	65	64.2	63.4	62.6	61.9	61.2	60.6	60
Bodyweight carried <sup>3</sup> (kg)	0	4.8	8.1	8.7	6.8	1.2	0	0	0	0	0	0	0	0	0
Expected bodyweight to be carried <sup>4</sup> (kg)	0	3.84	5.99	6.09	4.62	0.80	0	0	0	0	0	0	0	0	0
Energy requirement (cal/day) <sup>5</sup>	0	550	850	1200	1330	1470	1600	1730	1870	2000	2170	2330	2400	2550	2700
Expected nut requirements <sup>6,7,8</sup> (kg)	0	1.27	1.82	2.43	2.61	2.11	1.68	1.79	1.91	2.02	2.16	2.30	2.34	2.46	2.58

## Notes

1. Age is given in years since conception
2. By interpolation from Howell (1976)
3. By interpolation from Lee (1969). Older children are carried for less of the journey and following Lee we used the average weight carried (see text)
4. Calculated as bodyweight carried times survivorship
5. By interpolation from figures for normal vigorous daily activity
6. We suppose that 45% of the energy content of nut is wasted in providing the energy requirements of children up to 4 years p.c. age, i.e. 3 1/4 years old, assuming much of their food to be milk at a high calorie cost to the mother
7. Derivation of nut from energy requirements is given in text
8. Assuming nuts have to last 3 days



mately true, especially if reciprocal sharing of loads between mothers functions to even out the load of individual mothers around the average they expect to have to carry. On the other hand, if the major risk is of back injury when positioning the load before carrying it, then our assumption would be invalid. Although there is a surprising lack of evidence on this second risk, we believe, as we shall argue later, that the former is the greater risk, and so we have chosen to use the first assumption rather than the second. Our conclusions are very sensitive to which assumption is made (and so is the applicability of our model to other cultures).

In addition to these variable loads a mother has to carry a constant load, being her contribution to the 3 (or 2) day food requirements for herself at 1750 calories/day (this does not allow for milk supply or growth of foetus which figure as child requirements, a procedure which, along with calculating age from conception, greatly simplifies the calculations), for her husband at 2250 calories/day, and possibly a contribution for a dependent relative (average requirements of, say, 400 calories/day) (Lee, 1969, 1972). Working as above we calculate 3-daily nut requirement for adults as  $4400 \times 0.588 \times 0.00119 \times 3 = 9.24$  kg.

The figures in Table 1 are point estimates of, for example, energy requirement at exactly 7 years since conception, whereas the data on which they are based are usually for intervals, giving for example energy requirements of children aged 4-6 years since birth. We have arrived at our figures by interpolation making *ad hoc* assumptions where necessary. We do not give our working in full firstly because the original data is itself sometimes only a "guesstimate" and secondly because our conclusions are insensitive to small errors in our calculations (with the exception of calculation of weight of child carried).

The weight carried by a mother for each child (Figure 1) was combined with the constant load of food for adults in order to calculate the total load carried by a mother in different years. This load is shown for five different birth-spacings that she might adopt in Figure 2. It is clear that for some birth-spacings she has to carry more in some years than in others, the maximum amounts ever carried are shown in Figures 3 and 4.

These calculations produced two unexpected results: (1) a

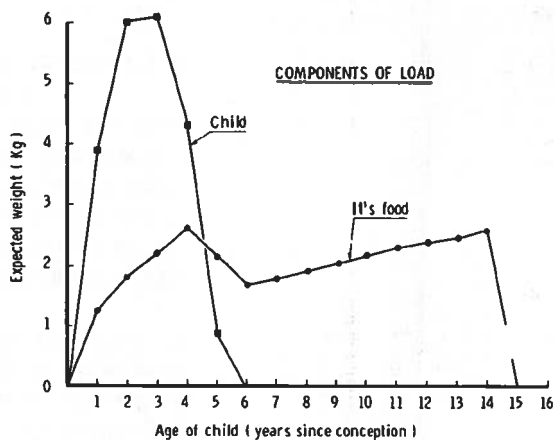


FIG. 1. The weight carried by a mother for each child as used in the computer simulation. (Data from Table 1.)

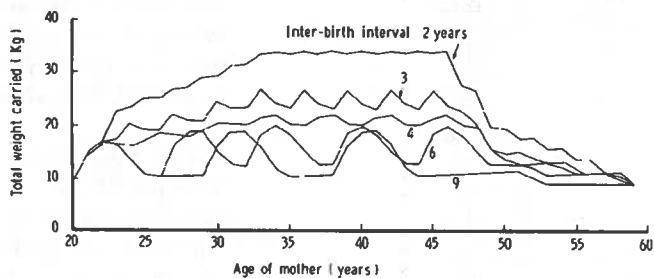


FIG. 2. Computer simulation of the total weight of children and food for her family, carried by a mother if she collects food every third day.

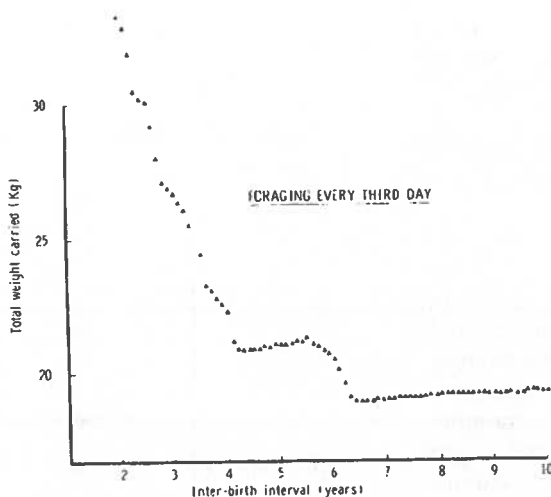


FIG. 3. The maximum weight ever carried by a mother who goes to collect food every third day in relation to different birth-spacings she might adopt.

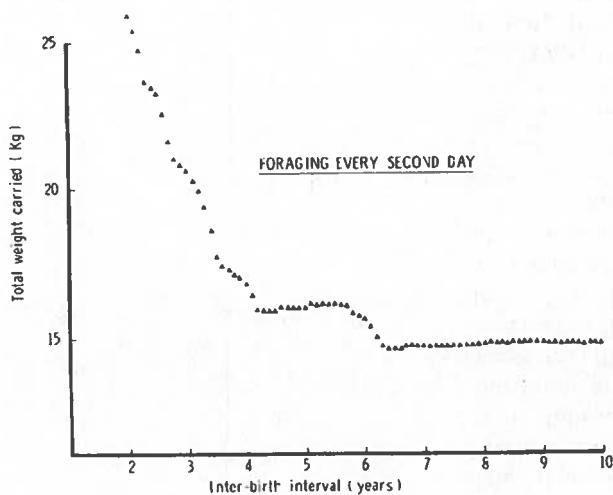


FIG. 4. As Fig. 3 except that food is collected on alternate days.

sharp upturn in the back-load of food plus babies when birth interval comes below 4 years (Figures 3 and 4); (2) a remarkably even level of back-load through a woman's reproductive career with birth intervals around four years (Figure 2). We had speculated that 4 years might allow a cycle of two easy years in which a woman could give away excess food to her friends or close relatives, followed by two years in which they reciprocated. We do not know any data on the amount of sharing of plant food between specified individuals but this contrasts with the frequent remarks in the literature on exchange of meat and the x'aro system of exchange of objects and so might suggest that the exchange of plant food between women of child-bearing age is minor and unimportant, as our model would predict.

However, the overall levels of back-load that one must expect is less clear. With no infant or child mortality, gathering one day in three, and a four year interval, some extremely high loads are predicted. Including mortality, and with gathering on alternate days, the back-loads decline to near the observations reported by Lee (1968, 1969) and DeVore and Konner (1974). It is important to note that Lee's original measurements of work and food income, although taken at a very hard time of year were, as far as we can judge from his published data, collected from a group of people with only two small children in the entire group. People with more children may indeed carry more or go gathering more often, or have husbands who contribute more calories than average. Thus we currently believe that either women with many children work harder than the literature suggests, that mortality in the first five years must be higher than reported, or birth-spacing wider, or that the population must be increasing. Future publications and analyses of their data by the Harvard team will undoubtedly clarify the situation.

### Limits to Back-load and Foraging Frequency

It now becomes clear that if we are to set any limit to family size and birth interval we must know about the limits to how much a woman can carry and how often she can go out foraging.

Bushmen are very small and we may wonder why big women do not manage to support more babies and thus why Bushmen

(women, anyway) are not bigger. We have considered several restrictions on back-load: the effect of exhaustion on your ability, even having shed the nut part of the load, to run away from a predator in the unlikely event of having to do so; load of water to be carried to replace sweat loss; and more probable: accidents to backs or ankles from lifting or carrying too much, which would make the mother unable to forage for a dangerously long time; and therefore badly in debt to her friends and relatives. The ergonomics literature (e.g. Davies, 1972) implies that safe limits for women are quite low, lower for smaller women, and that the observed 15–20 kg carried by Bushmen is likely to be about the safe limit. However, this evidence implies that it would be advantageous to Bushwomen to be larger and there is as yet no clear quantitative relation of risk of back injury to load (P. R. Davis, personal communication).

Finally and most promising, we have been considering the effect on the mother's heat balance of the energy liberated by carrying a load. Particularly in September and early October, the hardest months, the hot end of the dry season, there will be days when work of any kind is impossible. We can thus exclude daily gathering as a possibility on these grounds, in addition to the need to spend time processing the nuts that have been gathered, and in other domestic tasks. If we knew the number of days on which work of any kind was possible we would be able to say more about the maximum frequency of gathering excursions to which a woman can commit herself. There will be many days on which high loads cannot be carried without a good chance of collapse from heat imbalance. It is clear that there comes a point past which the more food the mother attempts to bring back the greater the risks she is taking.

A woman should not produce a family which requires her to carry heavier loads on a greater number of days than is safe. But within this limit there must always be an advantage in adjusting the back-load to the weather on any day, either by changing foraging strategies as the day warms up, or by predicting midday temperatures successfully from early morning conditions.

Environmental physiologists use a number of criteria for tolerable thermal conditions, the limit to conditions in which acclimatized people can expect to work without collapse. It is

important for the present discussion that once collapse has occurred the risks are severe. It would be very hard for people who collapsed from heat problems in the Kalahari in September–October to get home. If they could not get to shade their problems might worsen, and even if they did get to shade death occurs in a substantial proportion of untreated cases of heat stroke and other forms of heat collapse (Leithhead and Lind, 1964). Several ways of relating these criteria to work levels are available but one of the most appropriate and convenient, and one of the best regarded criteria of tolerable conditions is the Predicted Four Hour Sweat Rate (P4SR) (McArdle *et al.*, 1947). This gives an equation into which one can insert energy liberated by work. Carrying loads requires more energy than walking and thus liberates more heat. Empirically established equations relating energy liberated to body size, speed of walking and load carried, give the heat produced by 41 kg ladies walking at 3 or 4 m.p.h. carrying various loads (e.g. Durnin and Passmore, 1967, and others). Carried loads are, up to a point, similar to increased body weight. Thus although increased size might allow higher maximum loads it would also unhelpfully increase heat production (Robinson, 1942 and others show that large people are at a disadvantage when *working* in heat). The heat produced when carrying various loads can be fed into the P4SR equations and from these the environmental conditions under which it would be possible to carry each load could be ascertained. The P4SR depends on wet-bulb, dry-bulb and globe temperatures, air-speed, level of clothing worn, area of body surface and metabolic rate. In calculating metabolic rate we use the regression formula suggested by Datta, S. R., Chatterjee, B. B. and Roy, B. N. (1973), viz. (metabolic rate, kcal min<sup>-1</sup>) = 0.0943 × (body weight + load carried, kg) - 2.183. This was based on subjects of average surface area 1.62 m<sup>2</sup>, and for our purposes we prefer to express it as: (metabolic rate/unit surface area, kcal m<sup>-2</sup> h<sup>-1</sup>) = 3.493 × (body weight + load carried, kg) - 81. For Bushman mothers weighing 41 kg (metabolic rate/unit surface area, kcal m<sup>-2</sup> h<sup>-1</sup>) = 62 + 3.493 (load carried, kg).

Then P4SR is roughly: (P4SR, l/unit surface area) ≈ 0.014 × (metabolic rate, kcal m<sup>-2</sup> h<sup>-1</sup>) - 0.8 + B4SR where B4SR (Basic Four-hour Sweat Rate index) depends on wet-bulb, dry-bulb and

globe temperatures and air-speed. Therefore  $P4SR \approx 0.1 + 0.05 \times (\text{load carried, kg}) + B4SR$ .

The average daily maximum dry-bulb temperature in September and October at the nearest meteorological stations is around 90°F, but the relative humidity at midday is low (Met. Office, London). Globe temperature is probably about 30°F higher than dry-bulb temperature (Wyndham, 1956, 1958, 1964). At these temperatures B4SR is around 2.5 so that on an average day in these locations P4SR with a load approaching 30 kg would be around 4 in the critical region (Weiner, personal communication). Lee's published information on temperatures suggests that they are rather higher in the exact region with which we are concerned. He reports dry-bulb readings in September as 35–43°C (1972) and above 33°C on every day in September and October (Yellen and Lee, 1976). Thus it seems possible that in the Dobe area heat stress is a major hazard to anyone carrying heavy loads.

Daily readings of globe thermometer (which assess gain in heat from radiation) or wet-bulb thermometer (both required for P4SR) do not seem to have been taken in any part of !kung Bushman land so we cannot make precise predictions. However, Wyndham (1956, 1958, 1964) mentions that GT readings "of 140°F in the sun . . . were recorded. . . ." (1964) "as high as 50°C" at the cold time of year, and "up to 60°C in the Kalahari accompanying dry-bulb readings of 40°C" and "globe thermometer temperature exceeds air temperature by some 20°C at 2 pm". Lee (1972) gives September shade temperatures at Dobe (where he did his foraging measurements) as showing "highs ranging from 35–43°C". We can thus safely assume that there are many days with globe thermometer readings of 50°C and more. (Shade is negligible on journeys to the nut groves and we propose to leave it out of our calculations. In the habitats of other cultures it could be very important). The actual temperatures are rather critical but even a guess at the distribution of GT readings in September and the assumption of a very low wet-bulb reading (actually humidity rises steadily during September), suggests that there will be few days when 20 kg could be carried, rather more when 15 kg could be carried, very few when 30 kg could be carried. As load increases, number of safe days for foraging

decreases. The exact relationship will determine the maximum amount of food that can be brought home and thus the limits to IBI. But we can say that the fragmentary climatic information available suggests that carrying 15–20 kg on gathering excursions around one in two to three days is the best that can be done in the adverse climatic conditions of September and October. This is of the same order as Lee and others report that Bushman women in fact do. The increase in humidity might be expected to interact with family size in determining the date at which people change their strategy, and as Lee describes, cease gathering excursions and move from the dry season camp to the nut groves for periods of a few days, using water from roots.

### Discussion

Our basic argument is thus extremely simple. Our method consists merely of questioning each observation of behaviour (what else could they do, is this the right time to do it?) and of seeking measured consequences of each feature of behaviour or physiology. The consequences have all (if we use a criterion of reproductive success) to be reduced ultimately to a cost or benefit measured by number of offspring growing to maturity. Thus even the death of the mother must be costed as the reduction in the number of offspring she leaves due to her dying while needed to support those already born. The different options open to the mother can then be assessed in terms of the mother's reproductive success. It is interesting to note that there must exist some optimum strategy (or maybe a set of strategies) that maximizes reproductive success. Such a strategy can sometimes be found by analytic optimisation, but even if this is not possible it can be found by iteration using a computer. It will predict what the mother should do in order to leave the largest number of surviving offspring, and this can be compared with the observed behaviour of women.

In this study we have considered the different birth spacings and food gathering strategies that a mother might adopt. Under certain assumptions we have calculated the back-load she must carry for each inter-birth interval if her family is to be adequately nourished. As a first approximation it appeared that there would



be each day a critical limit below which load-carrying would be safe but above which death would be the probable result. Thus the problem was reduced to that of finding limits to back-load. Within these limits the optimal strategy is clear: to have the largest family that can be adequately fed during the dry season. What the mother should do on a particular day, however, depends critically on temperatures during the day, and without detailed climatic information we have only been able to make a limited assessment of the observed behaviour of the women.

It was our original intention at least to guess at the dependence of mortality on the variables we have calculated. Thus we wished to know how the daily risk (of death or serious accident) to the mother depended on the load that she carried. We recognize that she might suffer any of a number of calamities—heat stress, back injury etc., so that it is necessary not only to evaluate the more serious hazards but to estimate their cumulative consequences in terms of the one common currency, the risk of death. Similarly we hoped to assess the risks attendant on malnutrition (of parents and of children). Knowing these relationships a much more comprehensive study would be possible in which we could calculate the extent to which an extra baby slightly increases the hazards undertaken by each other person in the family. Such a study would still evaluate strategies in terms of the mother's reproductive success. We could however, investigate more of the options that in fact are open to her, for example, to decrease her load on especially hot days at the expense of the adequate nutrition of her family.

Obviously we have left many questions unasked. Besides the "givens" listed above we are assuming that physiological adaptation to heat has reached some limit; that dietary requirements cannot be substantially reduced below the level used in our calculations: that very inadequate nutrition for one or two months every year has a detrimental effect on the survival and reproductive career of the children comparable to the benefit to the mother of one extra child aged 0-4 (the reciprocal effects of nutrition and disease discussed by Morley, 1973, and Scrimshaw, Taylor and Gordon, 1968, is one argument for supposing that this is a reasonable supposition); that building up sufficient store of nuts before September to see the family through September (and until the

rains begin sometime in October) would have costs which outweigh the benefits in increased family size. It is obvious that in Bushman society as it is now this would incur intolerable social costs. But we feel we should regard this as an interim answer, for ultimately we must explain the social organisation that levies these costs; a very general ultimate explanation (reciprocal altruism) is possible (but the advantages of this have yet to be quantified, and we suggested they do not apply to plant resources); but our aim is for a detailed and quantitative argument that this social organisation arises from individuals maximizing their inclusive fitness and that a temporary breaking of the system (e.g. a seasonal holiday from reciprocal altruism, a Bushman *mardi gras*) would not increase the inclusive fitness of individuals partaking in it. We also assume that a woman will not be allowed indefinitely to go into "debt" to her friends and relatives.

Our toleration of "givens" might appear to weaken our argument. But at any step in our analysis the results could have differed from those obtained, and they could have differed in the direction of saying that Bushman mothers perform at a much lower level than possible. Quantitatively they tend in the opposite direction.

However, just as we took the mother's carrying capacity as a given in the first stage of our model, so any of these other givens can be the starting-point for a further investigation of the complex compromise which must be any adaptation. No scientific investigation is ever completed and we would feel it quite unjustified to use the incompleteness of any optimisation study as a reason for not pursuing this general approach. A much more important criticism would be that we fail to test our model against one in which a measure other than reproductive success or inclusive fitness is examined. We have to confess to some difficulty in thinking of an alternative, anything concerning, e.g. individual wealth precludes having any children at all. Inclusive fitness is the only measure for which it is not necessary to ask: why maximize that? But we feel that discussion and testing of different "target variables" is what is now required. The omission of any discussion of group advantage or even constancy of population may surprise the cultural ecologist reader. The omission is imposed on us by our choice of inclusive fitness as an ultimate criterion. But we do

have in due course to compare our model with for example one that supposes a restraint on over-exploitation of the habitat both for plant food and for animal food.

Ultimately one should be able to test our particular model against the known reproductive record of individual women. Those who give birth at the right time should raise more children than those who give birth at the wrong time. The analysis would have to be restricted to families that were dependent entirely on foraging and not using outside income (if a man finds some kind of work that reduces the need for his wife to forage by increasing his contribution to the family income, or which gives her greater access to babysitters, she should be able to give birth more often without detriment to her reproductive success, as they indeed do). Due account would also have to be taken of the value of giving birth quickly after the death of a child under 4 (still carried) and the costs of giving birth quickly after the death of a child over 4 whose successor survives and is still carried. It may be better to predict patterns of individual reproductive careers than the crude mean birth-spacing. But aside from these important points our basic prediction would be that women who gave birth substantially more often than once every four years (or whatever our eventual calculated optimum turns out to be), should raise fewer children than those who gave birth at around 4 year intervals (Lee, 1972 observes an average of 3.88 years). If this prediction is not borne out then wide birth-spacing and "part time" foraging are not maximizing reproductive success. They may be minimizing effort (in which case why have any babies!), or maximizing inclusive fitness (those who have more babies may be having a detrimental effect on the reproductive success of their relatives of a size which outweighs their own success, e.g. if they had one extra baby at a cost of two or more to their sisters). Or they actually may be adapted to extreme conditions as Lee suggests, with good evidence from several sources. The data for assessing some of these things may already exist.

While we have shown how we attempt to determine whether some culturally variable aspects of women's reproduction and foraging behaviour are adaptive for RS or inclusive fitness, we cannot claim to be showing anything about the classical core issues of social anthropology. Though we could make some pre-

dictions about male and female dress from work and climate, we have not shown whether all-night trance dances are good for inclusive fitness rather than something else, nor that "bird medicine" is good for the reproductive success of the mother who goes to the trouble of practising it (or alternatively for those who persuade her to practise it). But we do hope that we have raised a possibility that others will wish to follow further.

Many criticisms of our approach will be based on what to a biologist (and to cultural ecologists such as Harris, 1968, 1974 and Gross, 1975) would appear to be a confusion between function (long-term consequences, survival value, sometimes referred to as "ultimate causes") and development and causation (motivation or short-term "proximate causes"). We are talking about ultimate causes (i.e. remote causes) and make no statement about development or motivation. We would argue that the latter are the short-term mechanisms that ensure that functional behaviour is performed. It does not matter much for survival value exactly how the short-term mechanisms achieve the goals, so long as they do achieve them. In fact a good deal of work is now under way on the physiological mechanisms underlying the long birth-spacing of Bushman women and its rapid shortening when people settle.

In many animals, where long and short term are clearly separable, there is no problem here. Difficulties may indeed arise when long and short term come closer together, as they do when one proposes that rapidly changing cultural behaviour is adaptive. As biologists we would note that the propensity for culture evolved, that culture is clearly a major part of human adaptation, but that it can only have been adaptive by producing adaptive behaviour, in other words behaviour which maximizes inclusive fitness. Culture can have evolved only if individuals transmitted what it was in their inclusive fitness interests to pass on, and if individuals only acquired what it was in their interests to acquire (and the interests of transmitter and receiver can differ, even if they are parent and child, Trivers, 1974). Thus natural selection could have given rise to constraints on imitation; a little specificity about who an individual imitates, and under what circumstances, could have important consequences for cultural transmission. Beyond this we offer no suggestions as to how cultural transmission might maximize inclusive fitness. But we hope that our proposals will

help to unearth the most useful questions in this area, and help to allow cultural ecology to make even more use of its basic research strategy.

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