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Phil. Trans. R. Soc. Lond. B 1991 **334**, 243-251
doi: 10.1098/rstb.1991.0113

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Hunting income patterns among the Hadza: big game, common goods, foraging goals and the evolution of the human diet

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SUMMARY

The assumption that large mammal hunting and scavenging are economically advantageous to hominid foragers is examined in the light of data collected among the Hadza of northern Tanzania. Hadza hunters disregard small prey in favour of larger forms (mean adult mass ≥ 40 kg). Here we report experimental data showing that hunters would reduce their mean rates if they included small animals in the array they target. Still, daily variance in large animal hunting returns is high, and the risk of failure correspondingly great, significantly greater than that associated with small game hunting and trapping. Sharing large kills reduces the risk of meatless days for big game hunters, and obviates the problem of storing large amounts of meat. It may be unavoidable if large carcasses cannot be defended economically against the demands of other consumers. If so, then large prey are common goods. A hunter may gain no consumption advantage from his own big game acquisition efforts. We use Hadza data to model this 'collective action' problem, and find that an exclusive focus on large game with extensive sharing is not the optimal strategy for hunters concerned with maximizing their own chances of eating meat. Other explanations for the emergence and persistence of this practice must be considered.

1. INTRODUCTION

Many accounts of the early stages of human evolution assume that the practice of hunting and scavenging large animals arose and persisted because of the nutritional advantages hominid hunters earned for themselves and their families (Isaac 1978). The same assumption underlies conventional explanations for changes in human foraging strategies observed in many parts of the world at the end of the Pleistocene: widespread declines in the abundance of large game, previously favoured for nutritional reasons, forced a general increase in diet breadth, commonly involving increased use of small game and high-cost plant foods, and culminating in some places in the development of agriculture (Cohen 1989). Although argument about the timing of the first transition has recently been quite vigorous (Binford 1984), the underlying rationale for both remains unchallenged, apparently because it seems so self-evident.

Here we report data on hunting among the Hadza of northern Tanzania. The Hadza are especially interesting because, unlike other low-latitude foragers operating without firearms or dogs, they take big game to the virtual exclusion of small-bodied prey. Their hunting and scavenging incomes may reflect in the clearest way features associated with big game specialization. We report results of an experiment designed to

measure the income Hadza hunters could earn if they took small game. These data, combined with our observations of big game hunting, show that specialization in large animals maximizes mean daily rates measured in kilograms of meat. However, success rates for big game hunting, measured as the chance of acquiring a carcass on any day, are very low. The high average returns come at the expense of extreme variance. Big game hunting is a risky strategy in this habitat.

Sharing large carcasses is an effective way to reduce the risk. It is common among the Hadza, widely reported among other hunter-gatherers (Sahlins 1972), and generally considered to have a more or less ancient origin, crucial to human evolution (Isaac 1978; Lovejoy 1981; Binford 1984). Most anthropologists take it to be the likely outcome of an emphasis on big game hunting, arguing that everyone involved does better as a result.

The sharing of large carcasses solves two problems. It reduces the risk of meatless days for a hunter and his family, and obviates the problem of storing large amounts of meat. This consequence, however, may not explain the evolution and persistence of big game hunting and sharing. Among the Hadza, as among other hunter-gatherers (see, for example, Marshall 1961), meat from a large animal is taken and consumed by all, whether or not they paid the costs of capture.

Large carcasses are too big to defend against the demand for shares from other consumers. If sharing large game results from the economics of defence, these carcasses can be seen as 'common goods'. Given this, the evolutionary question is not why they are shared, but why anyone provides them in the first place. Ignoring the alternative of foraging for other resources, and assuming that animal tissue has special value (Hill 1989), a hunter's choice is between: (i) hunting and scavenging large game, which he will acquire at low frequency, and of which he will retain only a small portion; and (ii) hunting or trapping small animals, which he will take more often, and keep for himself and his family. We model this decision, using the Hadza data, to identify the evolutionarily stable strategy (ESS) for maximizing the number of days on which the hunters' children have meat to eat. The model shows that, although mean daily meat consumption would be much less, a hunter attempting to achieve this goal should take small game.

Clearly, hunters took big game in the past and continue to do so today. Among the Hadza, as among other well known modern hunter-gatherers, big game hunting is deemed to be the important activity of adult men. We infer that nutritional benefits may not account for the evolution and persistence of this practice. As for common or collective goods in general, 'selective incentives', benefits other than consumption of the goods themselves, may be necessary to motivate individuals to provide them (Olson 1965; Hawkes 1990, 1991). Like other cases in which individuals pursuing their own self-interest fail to serve the common good (Hardin 1968), hunters aiming to maximize their chances of eating meat would then be eating less.

2. THE EASTERN HADZA

The Eastern Hadza are a population of about 750 subsistence foragers who live in the rugged hill country south and east of Lake Eyasi. The climate of this region is warm and dry; the vegetation primarily savannah woodland. At the time of European contact, around the beginning of this century, the Hadza may have had this country largely to themselves. Since then (and especially over the past 30 years), they have been subjected to a series of government and church-sponsored settlement schemes intended to encourage them to abandon the foraging life in favour of full-time farming. None of these have been successful; in each instance, some Hadza have managed to avoid settlement entirely and continued to live as subsistence hunters. The most recent scheme, initiated in 1988, was in operation while the experiment described below was carried out.

3. HADZA HUNTING

Data on Hadza hunting were collected on 256 days of residence in Hadza camps during the period 1985–1989. Systematic observations enabled us to monitor the presence and absence of residents, and interviews helped establish the range of activities performed away from camp. 'Focal person follows'

provided quantitative data on the latter. Residents allowed us to identify and weigh all food brought back to camp, as well as food accumulated at various points during focal follows (see Blurton Jones *et al.* (1989); Hawkes *et al.* (1989); O'Connell *et al.* (1988a,b, 1990) for details).

Hadza hunting takes two forms, intercept and encounter. Intercept hunting is practised only in the late dry season (August–October). Men build blinds overlooking water sources and along heavily used game trails, sit in them overnight and shoot large animals with poisoned arrows as they pass within range. Since Hadza men are always armed, encounter hunting is effectively in progress most of the time they are away from camp. Hadza also scavenge large animals killed by other predators (O'Connell *et al.* 1988b).

4. HADZA HUNTING SUCCESS

Over the course of the study period, the Hadza hunters with whom we were living killed or scavenged 72 large animals, with an average of one animal every 3.6 days of observation. Species most commonly taken were giraffe (*Giraffa camelopardalis*), zebra (*Equus burchelli*), impala (*Aepyceros melampus*) and warthog (*Phaechoerus aethiopicus*). Table 1 shows the approximate number of hunters in the study camps, and the number of animals taken by intercept and encounter hunting and scavenging respectively. Table 2 shows the return rates gained per hunter-day overall, per hunter-day for encounter hunting and scavenging only, and per hunter-night for intercept hunting.

Return rates by mass are high. Overall, the Hadza took one large animal every 29 hunter-days, for an estimated return of 4.9 kg (live mass) per hunter-day. Intercept hunting was the most productive technique, yielding one animal every 18 hunter-nights, or about 7.5 kg per hunter-night. Encounter hunting and scavenging produced, on average, one animal every 45 hunter-days overall, one every 53 days in the late dry season, and one every 37 in the wet.

Small animals were rarely taken by Hadza hunters during the period covered by our fieldwork, and returns measured by mass were extremely low. When caught, they were usually consumed before the hunter returned to camp. This means that our record of small animal captures comes from focal follows of foraging men. During 45 follows in 1985–1986, on which a total of 75 hunter-days were monitored, men shot at small game (mainly guinea fowl (*Guttera* spp.) and francolin (*Francolinus* spp.)) about once or twice a day, but actually took only 14 individuals. Ten of these were immature hornbills snatched from the nest as the hunter walked by. The total mass of all small prey taken on these trips was about 4.65 kg, approximately 0.062 kg per hunter-day, nearly two orders of magnitude less edible tissue than the mean obtained from hunting and scavenging large animals (table 2). This implies that small game accounts for only about 1% of the animal tissue taken by the average adult hunter.

This pattern of prey selection differs sharply from that of other low-latitude hunter-gatherers operating

Table 1. *Kills by hunters in study camps, grouped by season and method of acquisition (256 days of observation, 1985–1989)*

(Encounter hunting and scavenging are daytime activities practised all year long. Intercept hunting is a night-time activity practised only in the late dry season.)

season	year	observation days	approximate number of hunters per camp	encounter		scavenge		intercept	
				animals	total/kg	animals	total/kg	animals	total/kg
late dry	1985	47	10	6	540	6	552	18	2465
wet	1985–1986	61	6	6	625	2	82	—	—
early dry	1986	36	6	3	440	2	1200	—	—
late dry	1986	44	10	4	150	2	48	7	877
late dry	1988	43	10	5	390	3	880	1	200
wet	1989	25	6	6	1666	—	—	—	—

Table 2. *Return rates in kilograms and numbers of prey, grouped by season and method*

	hunter-days	mean kg per		mean individual		mean kg h ^{-1a}
		hunter-day	s.d.	per hunter-day	s.d.	
all methods daily rate	2072	4.890	39.736	0.034	0.182	—
encounter/scavenger all seasons	2072	3.181	33.325	0.022	0.146	0.71
late dry ^b encounter/scavenger only	1340	1.923	21.080	0.019	0.138	0.45
late dry ^b night (intercept)	473	7.488	45.383	0.055	0.228	—
wet	516	4.599	41.999	0.027	0.163	1.02
late dry all methods	1340	4.566	34.249	0.039	0.193	—

^a For a sample of 80 observation days covering late dry and wet seasons in 1985–1986, mean number of hours spent by adult men in day-time foraging was about 4.5 hours (both seasons). We use this number to calculate an hourly rate.

^b In the late dry season of 1985 hunters spent, on average, every third night intercept hunting from blinds. We use these data to calculate rates for intercept hunting overall. For daytime late dry season rates, we exclude intercept kills.

on foot without dogs or firearms, many of whom take small animals often. For example, Lee's (1979) work diaries on !Kung hunters in the Dobe area show that, during a four week study period, all prey taxa taken without the use of dogs (an estimated 29% of total animal prey by mass) had adult body mass less than 20 kg. Yellen (1977), reporting data from the same population, shows that over several months, about 55% of total prey mass taken was derived from small game. For the Ache of Eastern Paraguay, Hill & Hawkes (1983) report that small animals account for more than 75% of prey mass acquired by bow hunters.

5. THE SMALL GAME HUNTING EXPERIMENT

The conventional wisdom on hunter-gatherer diets leads us to expect that the Hadza hunters specialize in taking large prey because they do better nutritionally than they would by taking smaller animals. We can test this hypothesis by means of the optimal diet model (Charnov 1976), which is designed to predict which resources a forager should select from among an available array (and which it should ignore), given the goal of maximizing mean nutrient acquisition rate. If we hypothesize that Hadza hunters seek this goal, the model helps us identify the suite of prey that best meets it. The model assumes random encounter with prey and knowledge of probable encounter rates with available prey types. Whether any particular prey item

falls in the optimal set, that which maximizes mean rates, depends on the net benefits associated with pursuing it, against ignoring it in favour of other resources. Our data suggest that, during the wet season, a Hadza hunter can expect to earn a long term average of about 4.6 kg per day, or about 1 kg h⁻¹, from encounter hunting and scavenging large animals. If his goal is to maximize that rate, he should ignore any potential prey item likely to yield a lower return. If the conventional wisdom on hominid prey choice and its determinants is correct, small animals should be among those resources yielding lower average returns. If, however, men hunt big game for other, non-nutritional reasons, we might find that small game hunting yields higher average returns than does the pursuit of larger prey.

During October–November 1990, we enlisted the assistance of several Hadza men, then living in a settlement, who agreed to accompany us back to the bush and participate in an experiment designed to provide quantitative data on foraging returns available from targeting small game to the exclusion of other animal prey. All the men had lived as subsistence hunters for most of their lives; all had been among the subjects of previous research on foraging in precisely the area in which the experiment was carried out. In return for their participation, all were provided daily rations and a wage. An observer followed a different hunter, or pair of hunters, each day. Men not followed presented all prey taken to be tallied and weighed. This produced two data sets, the smaller one consisting

Table 3. *Prey species pursued by focal men during small game hunting experiment and return rates post-encounter for those frequently pursued. Totals for 'all days' include prey taken by non-focal men*

prey species	number of pursuits	minutes in pursuit	kg taken on focals	kg all days	individual prey all days	kg h ⁻¹ after encounter
guinea fowl (<i>Guttera</i> sp.) or francolin (<i>Francolinus</i> sp.)	81	131	0.50	7.13	9	0.23 (0.90) ^a
hyrax (<i>Procavia capensis</i>)	52	819	9.52	11.57	9	0.66
dikdik (<i>Rhynchotragus</i> sp.)	21	35	0.90	0.90	1	< 1.54 (0.42) ^b
baboon (<i>Papio anubis</i>)	1	5	—	6.00	2	
tortoise	1	3	0.60	2.80 ^c	3 ^c	
impala (<i>Aepyceros melampus</i>)	14	26				
bird	6	4				
zebra (<i>Equus burchelli</i>)	2	13				
bat eared fox (<i>Otocyon megalitis</i>)	1	8				
buffalo (<i>Syncerus caffer</i>)	1	4				
giraffe (<i>Giraffa camelopardalis</i>)	1	4				
python	1	1				
kudu (<i>Tragelaphus strepsiceros</i>)	1	1				
small mammal	2	6				

^a Only one of the pursuits during focal follows was successful. We use the prey captured over all days, and assume the same pursuit times per hunter–day for non-focal hunters to estimate a total pursuit time, and so estimate an over-all post-encounter rate (in parentheses).

^b As only one (immature) dikdik was taken by encounter hunting during the experiment, (and that one during a focal follow) we consider the measured focal rate to be an extreme value. An overall post-encounter rate estimated as in ^a above is given in parentheses. It also depends on a single capture and may be high.

^c A 2.2 kg tortoise was brought to camp, then released, hunter unknown. This was not counted in tallying rates.

of detailed time allocation records for focal men, the larger of daily hunting incomes for all men.

6. RESULTS

The experimental period ran from 17 October–6 November 1990. Heavy rains, marking the beginning of the wet season, fell intermittently throughout. Data were collected on seven men over 16 days, for a total of 102 man–days. Income from hunting small prey averaged 0.225 ± 0.480 small animals per hunter–day, or about 0.252 ± 0.626 kg per hunter–day. Prey taken included francolin, guinea fowl, hyrax (*Procavia capensis*), dikdik (*Rhynchotragus* spp.), and baboon (*Papio anubis*) (see table 3).

Follows were conducted on 15 days. As men usually foraged in pairs, follows produced detailed records for 28 focal man–days. Most days included two foraging bouts, separated by a noon-time rest in camp. Focal men spent an average of 411 minutes per day foraging. Although each participant was asked to take as great a mass of small animals as possible, focal men spent time in other activities, mainly honey collecting. A daily average of 41.4 ± 29.6 min was invested in this, yielding a total of 21.89 kg of honey over 33 collecting events, for a mean daily rate of 0.78 kg per man–day. Focal men also pursued larger game on 19 occasions, never successfully.

Men were encouraged each day to apply themselves seriously to the assigned task. Focal men were actively encouraged to start hunting in the morning and after any mid-day break. The vigilant eye of the observer may have had an effect. Daily income was higher, although not significantly, for focal against non-focal men: 0.408 ± 0.750 kg per day and 0.429 ± 0.790 animals per day ($n = 28$), against 0.200 ± 0.593 kg per

day and 0.162 ± 0.362 animals per day ($n = 74$) (Mann–Whitney *U*-test, $p = 0.073$ for income measured by mass, $p = 0.140$ for number of animals).

Both small game encounter rates and return rates from subsequent pursuit can be estimated on the basis of data collected during the focal–person follows. Pursuits on 17 different species were observed, but only four (guinea fowl, francolin, hyrax and dikdik) were encountered often enough to provide useful samples (table 3). However, the number of encounters is not necessarily a measure of abundance. Some prey types may be so cryptic or elusive that actual encounters (defined as visual contacts in which pursuit was initiated) are low. Dikdik, for example, are seen many times in the course of an average day's foraging, but are so quick to flee that the encounter rate, marked by the fact that the hunter raised his bow, is only about one per day.

Encounters and return rates per small prey taxon are listed in table 3. Because most pursuits are unsuccessful, post-encounter return rates are low; for three of the four taxa for which useful samples are available, return rates are clearly lower (0.23–0.66 kg per hour) than the long term one kg per hour average for large mammal encounter hunting and scavenging in the wet season. We cannot reject the hypothesis that returns for the fourth taxon, dikdik, are also less than one kg per hour. According to the optimal diet model, a Hadza hunter does indeed maximize his average rate of meat acquisition by generally ignoring these taxa in favour of larger prey, at least in this season.

(a) Snaring

During the first day of the experimental period, hunters suggested that guinea fowl and dikdik could

be taken more effectively with snares. They were encouraged to pursue this or any other traditional strategy they thought might be more productive. None of them did so. Instead, they directed the two young men (later one) who accompanied the party as camp assistants to set and monitor snares.

About 16 snares were in operation for the duration of the experiment. All made use of a bent sapling, twine loop and a simple trigger. Twine for all snares was made by one of the hunters who participated in the experiment. It took about 15–20 minutes to set each snare the first time, but only a minute or so to reset it once it was sprung. Time spent on snares on any given day was always much less than the time focal men spent in encounter hunting. Attention paid to snares was inconstant. The young men assigned to monitor the snares were not themselves regularly monitored. On two occasions, hunters reported that dikdiks had been snared and were then stolen by leopards. Birds were also lost from the snares to other consumers. On one day, a guinea fowl foot, the only part remaining in the snare, was presented for weighing. On several occasions, an observer passed snares which were not set.

Two points should be underlined. First, the observed return rate for snares is unlikely to be the maximum that could be earned from this technique in this season in Hadza country. Second, snares in this environment require attentive monitoring because of wind and the density of competing predators. Unless they are actively watched, they may hang long unset or serve as a bonanza for others.

Seventeen individual prey (ten francolin, two guinea fowl, one dikdik and four small unidentified birds) were taken with snares, at least one on eight of the 14 days the experiment lasted. Daily income averaged 1.429 ± 2.174 animals per day, or about 0.781 ± 1.097 kg per day ($n = 14$). These figures are significantly higher than the average returns from small animal encounter hunting (Mann–Whitney U -test for daily income by number of animals, $p = 0.0008$; by mass, $p = 0.0029$). Income by mass from trapping is significantly lower than the long-term mean available from large mammal encounter hunting and scavenging in this season. Mean rate maximizers would therefore choose big game hunting and scavenging rather than snaring.

7. DISCUSSION

These data show that Hadza hunters who encounter hunt instead of monitoring snares, and who ignore small prey in favour of continued search for large prey, increase their long-term mean rate of acquiring meat. In doing so, they also increase their risks of failing to get anything at all. As our small game experiment was conducted in the wet season, we pay most attention to the wet-season data. The extreme risk of failure for big game hunters can be expressed in several ways. Hadza men take only 0.027 ± 0.305 individual large carcasses per hunter–day in the wet season, approximately one large animal every five weeks (37 days).

The chance of failure on any given day is just over 97%. In these circumstances, a man relying on his own work to get food for himself (let alone any dependants), and choosing big game hunting and scavenging as his procurement strategy, clearly has a very risky future.

By comparison, the daily success rate for !Kung hunters is 0.23 (about one animal every four man–days, on average; Lee 1979: 267); for Ache men it is 0.57–0.76 (2–3 successful days out of every four; Hill & Hawkes 1983: 176; Hawkes 1990: 151, respectively, using different samples). These hunters have a ‘failure rate’ that is an order of magnitude lower, largely because they include small game in the suite of prey they exploit. The Ache, and perhaps the !Kung, maximize their mean rate of meat acquisition by including small prey. The size and local abundance of large prey enable Hadza hunters to maximize their mean rates by specializing in big game; but in doing so, they accept an extremely high risk of failure.

Sharing can ameliorate this risk when large food packages are acquired asynchronously (Kaplan & Hill 1985; Cashdan 1985; Winterhalder 1986). The Hadza represent just such a case. If we assume that when any Hadza hunter kills a large animal every member of his residential group eats part of it, the probability of eating meat on any given day (in the wet season) is $1 - (0.973)^f$, where f is the number of active hunters. If that number is six (the typical figure for wet season study camps), the chance of eating meat from a large carcass is 0.15, (i.e. meat once a week). If meat from a single carcass may be available for more than one day (a reasonable assumption for animals the size of zebra (mean adult mass 200 kg) or larger), consumption frequency is increased. If meat lasts three days after a kill, and all eat on those three days, then the overall probability of eating meat on any given day is $1 - (0.973)^{3f}$. Where $f = 6$, this is 0.39. These are better odds.

In these circumstances, where all hunters specialize in big game and earn a daily average return of 4.6 kg (the observed wet season mean for the study period), the sharing pattern would give the members of each hunter’s household (assuming there are six) an average of 2.3 kg every third day on average. If any hunter and his household left the big game hunting and sharing group, and the hunter himself elected to target small game, he would probably take about one animal every other day, for a daily average return of 0.4 kg. Members of his household would receive 0.13 kg every other day. If he adopted a trapping strategy, his dependants would eat about twice as much meat, although only about one fifth as much as did the dependants of a big game hunter.

Big game hunting and sharing provides more meat for everyone, just as the conventional wisdom would have it. The variance for the big game hunters would be higher, which might have more deleterious effects on children than adults. This potentially important problem aside, all would do better if each hunter maximized his mean rate of meat acquisition and specialized in big game. Still, the question of how these practices could evolve and persist turns not on their consequence for the group, but on their consequences

Table 4. *Pay-off matrix*

(P = the probability of failure on any day for a big game hunter, f = the number of foragers, SG = the probability of not failing for a small game hunter, SN = the probability of not failing for a snarer.)

	others hunt or scavenge big game	others hunt small game	others snare
hunt or scavenge big game	$A = 1 - (P)^{3f}$	$B = 1 - (P)^3$	$C = 1 - (P)^3$
hunt small game	$D = [1 - (P)^{3(f-1)}] + SG$	$E = SG$	$F = SG$
snare	$G = [1 - (P)^{3(f-1)}] + SN$	$H = SN$	$I = SN$

for each individual hunter and the pay-off he could get from other choices.

8. THE COLLECTIVE ACTION PROBLEM

The advantages of sharing among specialized big game hunters hinge on what any hunter claims from the kills of others. A Hadza hunter earning the average 4.6 kg per day in the wet season and, sharing with five other hunters and their families, keeps for himself and his family only one sixth of his own income, 0.77 kg per day. If we count only what he and his family consume as his actual foraging income, he earns about what he would get by snaring, but with seven times the variance. In addition to what he brings in for his family, his big game hunting provides an equivalent amount for each co-resident hunter. As each of them does the same for him, it is the big game hunting of others that provides most (in this case five sixths) of what he and his family consume. This might be viewed as reciprocity; the shares he gives to others may be the price he pays for receiving in turn from them. The assumption that current contributions are the price of future benefits returned is central to models of reciprocal altruism (Trivers 1971). Some have argued that such contingent cooperation is extremely general (Axelrod 1984; but see Boyd & Lorberbaum 1987; Boyd & Richerson 1988; Hirshleifer & Martinez-Coll 1988).

Ethnographic characterizations of hunter-gatherer societies undercut this generalization, often emphasizing the non-contingent character of food sharing (Sahlins 1972), especially of meat (Kaplan & Hill 1985; Marshall 1961). Shares are distributed irrespective of contributions to the pot. Active hunters can neither sanction slackers nor refuse scroungers. In cases like the Hadza, high variance and skewed income distributions associated with large-animal procurement create additional problems of accounting. Large samples and long periods of monitoring would be required to distinguish between hunters who were out of camp but not investing time in hunting and scavenging big game, and those who were regularly seeking large animals but were either inept or unlucky.

Many forms of cooperation cannot be taken by the recipient, but must be initiated by the donor. Food is different, and its defence may be costly (Blurton Jones 1984, 1987). Observations among the Hadza suggest that small game are easily hidden and protected from the demands of others. With larger prey, defence becomes expensive. One way to view the sharing of large carcasses is to see them as common or collective

goods, i.e., goods which, like 'public goods', can be consumed by those who do not pay for them (Olson 1965; Hardin 1982). From this perspective, the question of why they are shared is not problematic: it follows from the prohibitive costs of exclusion. The question instead is whether a hunter in a group, knowing that most of any large carcass he captures will be consumed by others, finds it in his interest to specialize in acquiring them in the first place. If he does, he earns as much for others as for himself. Would he do better to take advantage of whatever other hunters earn from specializing on big game, but devote his own efforts to small animals for himself and his family?

We can model this decision as a game (Maynard Smith 1982) in which one forager chooses between big game hunting, small game hunting and snaring in a 'field' of other foragers; and evaluate whether any of these are stable strategies, given that the pay-offs are frequency dependent (i.e. one forager's chance of eating meat depends on what the others do). Assume that if any forager hunts or snares small game and is successful, he (and only he) eats his catch on that day. To include the assumption that a big game kill provides a large enough amount to cover several days, say three, assume: (i) that foragers cannot starve or suffer nutritional depletion for lack of animal tissue over the first two days; (ii) that they commit to a strategy for three days in sequence; and (iii) the crucial day of reckoning is the third.

Which of these strategies will be the best choice for a forager trying to maximize his chances of not starving for meat? In the matrix shown in table 4, the focal forager's choices are represented by the rows, and his pay-offs (his chances of getting meat) appear in the cells of the matrix. The columns are the strategies of the 'field' (the other foragers in the group). The simple assumption here, that members of the field all adopt the same strategy, allows us to see which strategy, if any is 'evolutionarily stable', i.e. once established, cannot be bettered by an alternative.

During the Hadza experiment focal hunters took small animals on nine of 28 days. The minimum take on a successful day was 0.5 kg. Assuming that 0.5 kg is a day's ration of meat, the chance of eating by hunting small game on any day (the value for SG in the matrix) is $\frac{9}{28}$, or 0.32. Snaring was successful on eight of 14 days, but yielded more than 0.5 kg on only seven of those days. If less than 0.5 kg is not enough, the chance of getting enough meat to eat on any snaring day (the value for SN in the matrix) is $\frac{7}{14}$, or 0.50. Given that the total number of hunters is six, the other values are:

$A = 0.39$, $B = C = 0.08$, $D = 0.69$, $E = F = 0.32$, $G = 0.87$, $H = I = 0.50$. Any hunter does better if others hunt big game: his highest pay-offs are all in the first column. But whatever the others do, he maximizes his chances of getting meat if he snares: the highest values in each column are all in the bottom row. If we assume snaring is not an option, and remove the last row and column, the hunter's best chance of eating meat requires taking small prey. If we use the overall rates for the small game experiment, rather than those for the focal hunters, the values of A and B remain the same, but those of D and E are lower. Incomes were greater than 0.5 kg on 19 of 102 hunter-days. The small game success rate is 0.19; thus $D = 0.56$, $E = 0.19$. Whether the others hunt big game or not, a forager increases his chances of eating meat by going for small animals.

This pay-off structure has the form familiar to game theorists and students of the evolution of cooperation as a 'prisoner's dilemma' (for example, see Hardin 1982). In some circumstances, cooperation can be evolutionarily stable in iterated prisoner's dilemmas (see, for example, Boyd 1989), but not so here. Strategies of cooperation which can persist are always contingent; they involve withholding benefits from those who fail to cooperate. Here, where the cooperation is the provision of common goods, individuals who do not themselves contribute cannot be prevented from consuming what has been provided by others. In these circumstances 'free riders' thrive, and a 'tragedy of the commons' follows (Hardin 1968). Although all would do better if only each contributed to the common or collective good, each does better for himself by maximizing his private benefits.

9. GENERALITY OF RESULTS

Our results are a function of values measured or calculated for the Hadza during the periods covered by our observations. Are they more broadly applicable, or do they depend on special features of this particular case? The small game rates from our experiment are very low, but results from the model are sufficiently robust that they would hold, even if lower still. Increasing them would further increase the relative advantages of small game hunting. The results depend most strongly on our assumption that large game are shared and small game are not. Given this, acquiring food for the consumption of the hunter or his offspring cannot be the adaptive function of big game specialization. Hunters pursuing that goal should take small game.

This does not mean that a forager should ignore opportunities to take large animals whenever they arise. Taking large carcasses when chance presented them would have little effect on the failure rates of small game hunters, in that chances to acquire large carcasses would necessarily be even rarer for small game hunters than for big game specialists. Occasional large carcasses would raise the long-term mean return rates of small game hunters; but they would still earn lower long-term means than they could by ignoring small animals. The resulting diet would include big

game, but in considerably smaller numbers than we see among the Hadza. In the circumstances we have described, hunters seeking to feed themselves and their families should not be mean-rate maximizers.

Just as the small game hunting and trapping rates we estimate for the Hadza may be unusually low, so the big game return rates may be high, especially in comparison with the prehistoric past. The poisoned, metal-tipped arrows used by Hadza men should increase their efficiency as competitive scavengers and big game hunters relative to that of hunters who lack this technology. Adjusting Hadza big game rates to compensate for this technology would make big game specialization even less successful at earning daily consumption requirements than we have calculated.

However, populations of large herbivores and their carnivore predators may be smaller in Hadza territory than elsewhere, especially in the past. Although the Hadza habitat has been characterized as unusually rich by comparison with the habitats of other modern hunter-gatherers, local game densities are lower than those in at least some other modern East African habitats (O'Connell *et al.* 1988*b*), and probably lower than those in many parts of the world during the marked fluctuations of the Pleistocene. If populations of large herbivores and their predators were more dense, big game hunting and scavenging rates might rise accordingly.

This caveat aside, we interpret our results to support scepticism that nutritional advantages to hunters and their families can account for the persistence of specialized big game hunting. We conclude that explanations for the practice here, and in different times and places where hunting incomes have similar patterns, may require us to investigate other benefits that serve as the 'selective incentives' to make big game hunting pay. As it pays for men but not women, mating advantages seem likely candidates.

This work was financed by the National Science Foundation, the Swan Fund, Ms B. Bancroft, the University of Utah, and the University of California at Los Angeles. We thank Utafiti (Tanzanian National Research Council) for permission to pursue fieldwork; we thank D. Bygott and J. Hanby for continued vital assistance, and the Hadza themselves for tolerance, advice and support. C. O'Brien, District Game Officer, A. Shanny, P. Shanalingigwa and associates provided assistance for the small game experiment. E. Cashdan, K. Hill, P. Lee, A. Rogers, A. Whiten and D. Zeanah provided useful comments on earlier drafts.

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Discussion

O. T. OFTEDAL (*Smithsonian Institution, Washington D.C., U.S.A.*). When the authors refer to kilograms of prey obtained, do they know or can they estimate the yield of edible flesh? Also it is important that the fat content of the edible portion be measured, if possible, as that will greatly influence the energetic return from hunting. Both factors may have a bearing on the relative advantages of large against small prey.

K. HAWKES. Yes they may, The numbers we used here are carcass masses of prey which include inedible fractions like bone and which ignore differences in fat and protein content. The nutritional value of what hunters earn depends on both the edible portions and their nutrient composition. These variables have not yet been measured for Hadza prey. Work is currently underway by our research group (O'Connell and Lupo) to do so, stimulated especially by systematic differences across species in the treatment at kill sites of carcasses in the same size class (e.g. zebra against alcelaphine antelope) which may be due to differences in body composition. The ranges measured and estimated for edible fractions of game animals elsewhere vary widely. Lee (1979) estimates this fraction for game taken by !Kung hunters in northern Botswana to be 50%. Hart (1978) calculated edible portions over 80% for game taken by Mbuti Pygmies in the Ituri Forest of Zaire. A few measurements of prey taken by Ache hunters in eastern Paraguay range between 69% and 88% edible (Hill *et al.* 1984). Body fat estimates vary widely by species, sex and season, and our experience suggests marked individual variation as well. If there is a systematic difference in edible fraction and fat composition by body size alone, it could affect the foraging choices discussed here. Hadza small prey may show the most extreme variance in these dimensions. Birds may be generally higher in edible fraction than mammals and lower in fat content. Hyraxes look like round packages of fat. I expect they have much higher fat fractions than the large ungulates. The big game animals are lean enough (Ledger 1968) that seasonal differences (and individual variation within season) of a few percent in fat can make a very large difference in nutritional value per edible kilogram. All of the potential sources of variability present opportunities for error in turning prey weights into nutritional values. More precise cost–benefit estimates would also include processing costs which have been ignored here. These costs might vary by prey size; for example, there may be some 'economy of scale' in that the cost per kilogram of skinning, butchering and cooking a giraffe may be less than the processing cost per kilogram of guinea fowl. But game animals differ substantially from many plant foods in that processing is such a small component of total cost that even a systematic difference by prey size may make a negligible difference in return rates.

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R. J. BLUMENSCHINE, (*Department of Anthropology, Rutgers University, New Brunswick, New Jersey, U.S.A.*). Might the currency optimized in large mammal acquisition not be meat (i.e. protein) but rather energy from fat deposits around organs and in marrow bones? As a corollary, does the hunter have preferential access to fat deposits from his kill?

K. HAWKES. Fat may be the component of greatest interest. People talk about carcasses in terms of their fat content. Woodburn surmised that Hadza men had greater access to meat than women, and that the parts reserved for adult men gave them greater access to fat. Certain parts of large animals are reserved as ‘men’s meat’ including, for example, the tongue, bellysheet, genitals, and foetuses. Speth (1990) follows Woodburn and uses an anecdote from Bunn *et al.* (1988) to illustrate discrimination against women in access to fat. Our data, covering a reasonable sample of cases, do not support this generalization. We do not have a quantitative answer to the question of preferential access to fat for the hunter, but men other than the

hunter, as well as women and children, regularly consume both meat and fat at kill sites, including notably heads and the marrow in metapodials and long bones of several species (see O’Connell *et al.* (1991) for a tabulation).

One could translate our treatment, which uses kilograms of game, to strictly fat by choosing edible portion estimates for Hadza prey species and combining these with estimates of fat fractions by species and season. It could be that such substitutions throughout would change our results, but it seems unlikely. As long as the fat in big game is eaten by many while the fat in small game is not, men (and their families) would eat fat more often by claiming shares from any large prey taken but not specializing in taking it themselves.

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