To kill a kangaroo: understanding the decision to pursue high-risk/high-gain resources

James Holland Jones, Rebecca Bliege Bird and Douglas W. Bird


References

This article cites 24 articles, 4 of which can be accessed free
http://rspb.royalsocietypublishing.org/content/280/1767/20131210.full.html#ref-list-1

Subject collections

Articles on similar topics can be found in the following collections

- behaviour (1023 articles)
- ecology (1431 articles)
- evolution (1565 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click here

To subscribe to Proc. R. Soc. B go to: http://rspb.royalsocietypublishing.org/subscriptions
To kill a kangaroo: understanding the decision to pursue high-risk/high-gain resources

James Holland Jones1,2, Rebecca Bliege Bird2 and Douglas W. Bird3

1Woods Institute for the Environment, and 2Department of Anthropology, Stanford University, Stanford, CA 94305-2034, USA
3Bill Lane Center for the American West, Stanford University, Stanford, CA 94305-4225, USA

In this paper, we attempt to understand hunter–gatherer foraging decisions about prey that vary in both the mean and variance of energy return using an expected utility framework. We show that for skewed distributions of energetic returns, the standard linear variance discounting (LVD) model for risk-sensitive foraging can produce quite misleading results. In addition to creating difficulties for the LVD model, the skewed distributions characteristic of hunting returns create challenges for estimating probability distribution functions required for expected utility. We present a solution using a two-component finite mixture model for foraging returns. We then use detailed foraging returns data based on focal follows of individual hunters in Western Australia hunting for high-risk/high-gain (hill kangaroo) and relatively low-risk/low-gain (sand monitor) prey. Using probability densities for the two resources estimated from the mixture models, combined with theoretically sensible utility curves characterized by diminishing marginal utility for the highest returns, we find that the expected utility of the sand monitors greatly exceeds that of kangaroos despite the fact that the mean energy return for kangaroos is nearly twice as large as that for sand monitors. We conclude that the decision to hunt hill kangaroos does not arise simply as part of an energetic utility-maximization strategy and that additional social, political or symbolic benefits must accrue to hunters of this highly variable prey.

1. Introduction

Recent work has proposed that gendered patterns of difference in human foraging decisions arise, at least in part, because women tend to be more averse than men to variance in energy returns. This perspective may explain why men often prefer to hunt prey associated with high rates of failure, and why women often do not hunt and, when they do, take mainly smaller, less mobile prey with lower rates of failure [1–4].

However, high-variance production choices are usually associated with higher mean returns, which might outweigh the utility of low mean returns. Thus, choosing a resource with higher variance may not imply risk proneness but may rather be the outcome of the optimization of long-term mean energy intake. Gurven & Hill [5] have made just such an argument based on mean foraging returns, suggesting that among Hiwi foragers of the Venezuelan savannahs, hunting (at a mean of 2700 kcal h−1) is more productive than gathering (at 1300–1600 kcal h−1), and that men must hunt in order to maximize their long-term average return rate, whereas women are kept from achieving such returns owing to their childcare constraints.

There are a number of problems associated with any attempt to compare the utility of high- and low-variance resources using mean energetic return. The first, most fundamental problem with using just energy is that it is not the energetic value of food per se that matters. What matters is what organisms can do with this energy to promote their fitness. Energy is a common fitness proxy in the study of complex foraging and reproductive behaviour in part because it is relatively easy to measure, but also because its acquisition is a
necessary predicate for both survival and reproduction. However, we do not know how fitness scales with energy. To survive, organisms need to have a certain baseline energy intake, averaged over some characteristic time scale, and this necessity will shape foraging preferences and observed decision-making in subsistence behaviour. But we do not know whether acquiring twice one’s daily energy requirement is twice as good for the individual’s fitness. If there is a nonlinear relationship between food and fitness, we could expect foragers to value surpluses differently: either preferring them if the marginal fitness of energy is increasing, or avoiding them if the marginal value is decreasing. While the marginal valuation of energetic resources plays heavily into some of the classic results of foraging theory [6], it has not contributed much to the debate over the sexual division of labour in foraging societies.

The second problem with using mean energy return lies in the reliance on the mean value itself as an estimator of expected utility/fitness. If there is a nonlinear relationship between food and the utility/fitness value of food, means do not accurately reflect the long-term expected utilities. When utility increases as a linear function of increases in harvest size, each unit of consumption has the same value no matter how large the harvest. This might occur where, for example, storage opportunities allow acquirers to defer consumption of surplus portions, allowing them to gain just as much from 100 kg of whale as they would from the sequential slaughter and consumption of 100 chickens weighing 1 kg each. Under a linear utility function, foragers should be indifferent to any of two foraging choices (chickens versus whales) regardless of variance in returns as long as the product of their harvest sizes and probabilities of harvest success are equal. However, if marginal utility declines with large harvest size, larger harvests may have less value than smaller harvests if there is a risk that pursuing larger harvests will lead to failure. Decreasing marginal utility is common where utility is a function of the consumption value of a resource—after a portion has been consumed, eating more benefits one less and less, as it might given a very large animal and limited storage opportunities for the surplus portion. In this case, given the choice between two resources, a forager will gain less value from the occasional bonanza of a more variable resource and should be risk-averse. A risk-averse forager benefits most from choosing harvests that minimize the probability of falling below some maintenance threshold. If marginal utility increases with harvest size, each additional unit of a harvest has more value than the previous unit. A forager will gain more value from a larger harvest and should benefit more from the more variable resource. This might occur (among humans) particularly where surplus portions of a large animal can be sold, or used as currency to acquire other goods and services. Utility is thus less a function of the consumption value of the resource and more dependent upon some socially negotiated value. Given this utility function, the best choice is one that maximizes harvest size. A risk-prone forager benefits most from choosing harvests that maximize the probability of a higher than average pay-off, in order to gain the big benefits associated with surplus production.

A third problem with using mean energy return is the relationship between the probability distribution of harvest sizes or return rates and an individual’s own utility threshold, which will differ from time to time and from individual to individual. A utility threshold is the minimum amount an individual needs in order to see a benefit from any resource. While utility thresholds can be set for any need (e.g. the minimum amount of deer needed to keep one alive over the winter, and the minimum number of rabbits to make a blanket), some of the most basic types of utility thresholds are those set for survival and/or reproduction. If a forager requires 60 kg of meat in the freezer in order to survive the winter and is faced with two choices, both of which will provide 40 kg on average but with different variance, the best strategy is to choose the more variable prey, gambling that the return will be bigger than average that year. The alternative is to take a more certain chance that will be less likely to reach the threshold. This was, in fact, determined to be the optimal solution for dryland agro-pastoralists in east Africa in the dynamic programming model of Milner-Gulland et al. [7]. While non-irrigated maize is almost certain to fail, and millet is almost certain to produce, the expected yield from millet is not sufficient for the most destitute farmers’ subsistence, so, paradoxically, their optimal strategy is to pursue the likely failure of a maize crop that, in the unlikely case of being successful, would be sufficient for subsistence needs.

If foragers have increasing marginal utility for resources, the more a forager exceeds the maintenance threshold, the greater the pay-off [8]. If marginal utility is decreasing, a forager gains less and less incremental benefit from exceeding the maintenance threshold. Following the pioneering work of Friedman & Savage [9], Winterhalder et al. [10] suggest that we may be able to accommodate both functions within a single sigmoid function in which foragers experience an increasing return for their investment in foraging as they pass the maintenance threshold, and ultimately declining marginal benefits as they accumulate more and more resources. Different strategies might thus push foragers towards different points on the utility function, thus affecting risk sensitivity. Individuals might be on the accelerating portion of the utility function, where success is contingent upon dynamic social competition, and increasing investment in resource acquisition nets increasing profits relative to other competitors. For example, the male nursery web spider (Pisaura mirabilis) gains increasing numbers of copulations as the size of its nuptial gift (a prey item wrapped in silk) increases [11]. The model would predict that male P. mirabilis, who targeted prey types with more variable body sizes as nuptial gifts, would gain bigger fitness benefits over the long term than those acquiring less variable prey types because of the disproportionate marginal contributions of infrequent large gifts. Individuals may be on the decelerating portion of the utility function if their strategies are limited more by parental investment and resource consumption rather than dynamic social competition. In this case, we would expect foragers to be willing to pay for increased certainty in returns (i.e. pay a certainty premium).

To account for these problems, we introduce an expected utility (fitness) maximization framework to the problem of human hunting decisions. This framework is well recognized in foraging theory [12] and has found its way into the human subsistence literature [10]. However, it has not played heavily in work on hunter–gatherer subsistence. Having introduced the framework, we proceed to analyse energetic return data from two different hunting activities—one characteristically male and one female—among Martu hunters of Western Australia. Here, patch returns for hill kangaroo hunting are twice as high as sand monitor hunting, but with six times
the variance. Much of this variance is due to the high risks of failure: more than 80% of all hunts fail to acquire anything, compared with less than 10% of sand monitor hunts [3]. Given the high variance and high risks of failure associated with (90% male) hill kangaroo hunting, we examine how well its expected utility fares against the lower return, but lower variance of (70% female) sand monitor hunting. Which activity should a rate-optimizing forager choose?

Before we turn towards an analysis of the data, we examine the standard linear variance-discounting model of Real [13], and try to address some of its shortcomings [10,14].

(a) Why does variance matter for understanding mean fitness?

Most work to date on risk-sensitive foraging decisions uses an approximation of the expected utility of resources, denoted by Real [13] as ‘linear variance discounting’. This is a powerful approximation that provides an intuitive sense of why variance matters for foraging and other decisions that entail risk. In this section, we briefly derive this approximation, whereas in the next section we note the weakness of this approximation for understanding many risk-sensitive foraging decisions.

Define some (evolutionary) utility function \( w(x) \), where \( x > 0 \) is the energetic value of a resource, which we assume to be described by a random variable \( X \). By definition of expected value, the mean utility is

\[
\bar{w} = \int_0^\infty w(x)f(x)\,dx,
\]

where \( f(x) \) is the probability density function (pdf) for \( x \).

In most applications, we do not know the pdf \( w(x) \), but we may know the moments. A standard approach to deal with this is to approximate the expected utility by means of a Taylor series expansion of \( w \) around the mean energy return, \( \bar{x} \). We can then take the expectation of this approximation to provide an estimate of expected utility. The Taylor series approximation for \( w(\bar{x}) \) is

\[
w(\bar{x}) \approx w(\bar{x}) + w' (x - \bar{x}) + \frac{w'' (x - \bar{x})^2}{2} + \cdots,
\]

where \( w' = \frac{dw}{dx} \) and \( w'' = \frac{d^2w}{dx^2} \). Now, taking the expectation of \( w \) with respect to \( x \) yields

\[
\bar{w} = \bar{w}(\bar{x}) + \frac{1}{2} \bar{w}'' \text{var}(X),
\]

where the second derivative is evaluated at \( \bar{x} \). This result follows from three facts about expectations: (i) the expectation of a constant is simply that constant \((\text{IE}(\bar{x}) = \bar{x})\), (ii) \( \text{IE}(x - \bar{x}) = 0 \) and (iii) \( \text{IE}(x - \bar{x})^2 = \text{var}(x) \), by definition of variance. The degree to which variance reduces expected utility from the utility of the average return is given by the curvature of the utility function. A concave utility function means that the second derivative is less than zero, implying risk aversion. The greater the concavity in the utility function, the more variance reduces the expected utility and the more risk-averse the forager is.

This relationship is well known in the decision-science literature [15]. It shows that expected utility is linear in variance of energy return. In behavioural ecology it is frequently known as linear variance discounting (LVD) [13]. Equation (1.2) clearly shows the importance of variance in energy supply and its intimate relationship to the concavity of the utility function. In particular, if \( w'' > 0 \), greater variance increases mean fitness. On the other hand, if \( w'' < 0 \), then increasing variance will reduce mean fitness. Note that by keeping only the first two terms of the Taylor series, this result is exact only for normally distributed \( X \). For a normal distribution, the mean and the variance are independent and sufficient to describe the distribution. For most other distributions, the mean and the variance are related in some complex way. For example, the mean of a lognormal distribution with parameters \( \sigma > 0 \) and \( -\infty < \mu < \infty \) is \( \exp(\mu + \sigma^2/2) \) while the variance is \( (e^{\sigma^2} - 1)\exp(2\mu + \sigma^2) \).

(b) On skewed resource distributions

The major difficulty with this approach for understanding human hunting decisions is that we (i) expand around the mean energy return \( \bar{x} \) and (ii) truncate our Taylor series expansion at the second-order term. Why should this be a problem? The great majority of resource-return distributions are right-skewed. This means that the mean of the return distribution could be quite far away (in the tail) from the most likely return. This is a common problem in population growth in variable environments (e.g. Tuljapurkar [16,17]) and means that the expectation based on the second-order Taylor series expansion will not be a very good approximation of the integral in equation (1.1).

To demonstrate this, consider a hypothetical expected utility calculation based on a normal (symmetric) versus a lognormal (skewed) resource distribution. Using a logistic utility curve, we can calculate expected utility (equation (1.1)) using numerical integration and compare this with the standard LVD result of equation (1.2). Figure 1 shows

Figure 1. Illustration of the difference in location of the mean (i.e. expected value) of (a) symmetric versus (b) skewed distribution.
Table 1. Comparison of LVD and exact utilities for the distributions plotted in figure 1. The difference between the LVD approximation and exact value of expected utility is 6% for the normal distribution and 30% in the lognormal case.

<table>
<thead>
<tr>
<th>resource distribution</th>
<th>LVD</th>
<th>exact</th>
</tr>
</thead>
<tbody>
<tr>
<td>normal</td>
<td>0.1371</td>
<td>0.1295</td>
</tr>
<tr>
<td>lognormal</td>
<td>0.1831</td>
<td>0.0800</td>
</tr>
</tbody>
</table>

normal and lognormal distributions with the same mean. Superimposed on these distributions is a logistic utility curve.

Table 1 presents the contrasting calculations of the LVD approximation to expected utility and the exact value based on direct integration.

(c) A solution

While it is possible to use more terms in the Taylor series approximation of the fitness function, there is no guarantee that a reasonable approximation of $u(x)$ will be achieved with a reasonable number of terms. Rather than using the linear variance discounting approximation, we can actually measure the underlying probability distribution for returns, $f(x)$, and calculate expected utility directly by integrating as in equation (1.1). Such an approach is possible when foraging data are drawn from focal follows of individual foragers, preferably over long periods of time, with sample sizes large enough to produce reasonably precise probability distributions. Data of this quality are available for Martu, contemporary part-time Aboriginal foragers living in the Western Desert of Australia.

(d) Foraging data from Martu

Martu hunt and gather for a wide variety of resources, but monitor lizards and kangaroo make up 58% of all foraged foods by energy value (see [3,18] for details). Monitor lizard hunting comprises 54% of all foraging time across all seasons, but is primarily a female activity among Martu. Resources from this hunt type account for 30% of all foraged calories. Varanids (*Varanus gouldii*, parnajarla) make up the bulk of this, but skink (*Tiliqua scincoides*, lungkuta) and python (*Aspidites ramsayi*, kanati) are also pursued on encounter. Monitor lizard hunters also sometimes take feral cats (*Felis silvestris*) and cossid moth larvae (*Endoxyla* spp., lunki; see below), and always stop to collect solanum fruit (*Solanum diversiflorum*, kampulpaja; *Solanum centrale*, jinyju-wirri) and nectar (wama) from *Hakea suberea* and *Grevillea eriostachya* flowers. To hunt sand monitors, foragers routinely establish temporary ‘dinner-time camps’ in the sandplains and dunes, near late successional spinifex grass habitat in the winter (Apr–Sep) and in patches of early successional habitat in the summer (Oct–Mar). In the winter, sand monitors brumate in the plains and swales between dunes. Hunting during this season requires first the choice of the right location where the lizards are denned, and then coordinating the use of fire to clear off vegetation in order to search the freshly burned area for the subtle cues that indicate an occupied den. The hunter then uses a long digging stick to probe around the entrance hole to locate the sleeping chamber, and quickly excavates the tunnel to locate the animal because when disturbed the lizards will attempt to escape through the tunnels to avoid the hunter. In the hot six months of the year, the animals are tracked on the surface, and hunters pursue them to capture in trees or shrubs, chasing them away from potential dens to avoid having to dig for them. The average hunter spends 3 h hunting and returns with between two and three animals, yielding a long-term mean of 650 kcal per hunter-hour of search, pursuit, capture and processing. Hunters can control to some extent the harvest size by foraging for longer: there is a significant correlation with time, which explains about 30% of the variation in harvest size [19]. In a given foraging party, there are usually four to five monitor hunters, more than half of dinner-time camp members who hunt. Most hunters on the sandplains are women between the ages of 40 and 80, who devote more than 70% of their foraging time to monitor hunting.

Hill kangaroo hunting accounts for 10% of all foraged calories, with the large euro (*Macropus robustus*, kirti-kirti) its sole target. Hill kangaroos are restricted to rocky ranges in the desert sandplains, using the range as refuge against coursing predators, such as humans and dingos. Hill kangaroo hunters make dinner-time camps around rocky hills and ranges, and are often accompanied by monitor hunters, who hunt on the sandplains nearby. Kangaroo are hunted on foot during the day by searching brush thickets in ravines and washes along the base of the range, moving upwind and looking for fresh track and scat. Hunters pursue prey by stalking along fresh track and smell until they are within range of a good shot using a small-calibre rifle. Some Martu have access to high-calibre firearms, but given the distances over which shots are taken and the length of many very rough pursuits, smaller-calibre, long-barrel rifles without scopes are preferred for their accuracy and durability. Even so, as kangaroos have tremendous escape speed, they elude the hunter on 70% of all encounters, and as a hunter averages only about two encounters per foraging trip, his success rate is very low, only 14% of encounters lead to a successful kill. On average, only one hunter in the dinner-time camp will hunt per day, providing a long-term mean of well over 1000 kcal per hunter-hour spent in search, pursuit, capture and processing. Most hunters in the rocky ranges are men between the ages of 20 and 60, who bring in 70% of all the kangaroo by kcals. Decisions to hunt kangaroo generally preclude any hunting of sand monitor as the two activities are spatially exclusive. Men spend less than 30% of their total foraging time in the search for sand monitors and more than 18% searching for kangaroos, whereas women spend 74% monitoring hunt and less than 2% kangaroo hunting. Given the high variance of kangaroo hunting, we next analyse which choice produces more utility, assuming that utility is derived through the consumption of the meat provided.

2. Material and methods

An appealing approach for estimating the pdf of the returns distribution for both hunt types is to use a non-parametric kernel-density estimator or related approach (e.g. log-splines). However, both distributions are highly skewed with a large number of observations that are exactly zero (i.e. failed hunts). This case leads to numerical difficulties in the estimation of the empirical densities and unreliable density estimates. There is a simple solution that has the additional, very appealing feature of being highly
interpretable. This involves fitting a two-component mixture model to the returns distribution. Such a model has the form
\[
    f(x) = \pi f_1(x) + (1-\pi)f_2(x),
\]
where \( f_1(x) \) is the pdf of the first component, \( f_2(x) \) is the pdf of the second component and \( \pi \) is a mixing parameter (i.e. the fraction of the total observations falling into the first component).

The two components can be generally thought of as ‘successful’ and ‘unsuccessful’ hunts. When the failure component is strictly zero, this mixture is essentially a zero-inflated model. For the zero-inflated model, there is a point mass at zero so \( f_1(x) = 1 \) and the first component is simply represented by the proportion of zeros in the data.

Even after accounting for the zero-inflation, which contributes to the skew of the distribution, the returns for each hunt type are still quite skewed. We use a lognormal distribution for \( f_2(x) \), the ‘successful’ component of hunting returns. Furthermore, ‘unsuccessful’ hunts do not necessarily yield zero energetic return. The primary decision that foragers make is to pursue a particular hunt type, which entails certain geographical, technological and social specifics. A hunter who fails to kill a kangaroo, for example, may nonetheless return to camp with material gathered (e.g. grubs, fruit or small game). As a consequence, we allow the first component distribution to follow a distribution such as a normal or another lognormal. Such models can be fitted in straightforward manner using maximum likelihood [20]. Furthermore, alternative formulations of mixture models can be compared using likelihood-based information criteria [21].

(a) Utility curves

One of the fundamental arguments of this paper is that what matters for understanding hunting or any other subsistence-related decision is not energy itself but what the organism does with it—its utility. Utility is here assumed to be a function of energy (although it may not always be). As such, we need to model the utility function of energy. A sensible model of the utility of energy is a Holling type III curve [22],
\[
    w(x) = \frac{ax^b}{b^x + x^2},
\]
where \( a \) is a scaling factor representing the saturation utility and \( b \) is the point at which half-saturation (i.e. \( a/2 \)) happens. This curve is S-shaped, like a logistic curve, but has the sensible property that \( w(0) = 0 \). It shows increasing utility to energy (approximately quadratic near \( x = 0 \)) at very low levels of energy return. At intermediate energy levels, there is an inflection point and the increasing marginal returns to energy become decreasing. At some point, a saturation utility is reached and the forager’s utility does not change with increasing energy.

Initially, we use a Holling type III curve that plateaus at the Food and Agriculture Organization (FAO) energy requirement [23] for a man engaged in heavy labour (3450 kcal day\(^{-1}\)), and we compare this with two curves with much higher plateaus. The three utility curves (with three different values of \( b \)) are plotted in figure 2.

With the utility function of energy along with the probability density functions of the energetic returns for the two resources, we can calculate expected utility according to equation (1.1) through numerical integration.

The empirical data on sand monitor and kangaroo hunting we use to test the variance discounting model come from a larger dataset consisting of focal follows on Martu hunters between June 2000 and September 2010. This dataset covers 345 camp-days, which include 1849 foraging bouts totalling 4343 forager-hours. Sand monitors were searched for on 175 of those days, kangaroos on 71. A total of 151 different individuals from Parrngurr, Parnmu and Kunwarritji communities are included in the total dataset. Sixty-six different individuals (21 men on 143 hunts, and 45 women on 610 hunts) contributed 2285 forager-hours of sand monitor hunting and acquired 1.392 587 kcal. Twenty-nine individuals (four women on six hunts, and 25 men on 135 hunts) contributed 404 forager-hours of kangaroo hunting and acquired 469 385 kcal. Data used in this analysis are archived at doi:10.5061/dryad.g1h6b.

3. Results

Table 2 presents the descriptive statistics of the two hunt types (sand monitor and hill kangaroo), and empirical distributions of hunting returns are plotted in figure 3. The mean energetic return of hill kangaroo hunts is higher, even though 85% of all hunts yield energetic returns of zero kcal. When conditioning on the 15% of hunts that are successful, the mean energetic return of hill kangaroo is enormous—in excess of 23 000 kcal, which is almost 10 times the FAO daily requirement for adult men engaged in heavy labour. The other two curves reach peak utility at higher energy levels with half-saturation levels at \( b = 1000 \) (dark grey) and \( b = 2000 \) (light grey).

Table 2. Descriptive statistics for the two hunt types. Unconditional mean is the mean across all hunts (kcal), conditional mean is the mean conditional on the return being greater than zero (kcal), variance is the variance in energetic return for the hunt type, proportion zero is the fraction of all observed hunts yielding zero kcal returns and CV is the coefficient of variation of energetic return for the hunt type.

<table>
<thead>
<tr>
<th></th>
<th>sand monitor</th>
<th>kangaroo</th>
</tr>
</thead>
<tbody>
<tr>
<td>unconditional mean</td>
<td>1868</td>
<td>3556</td>
</tr>
<tr>
<td>conditional mean</td>
<td>2083</td>
<td>23 947</td>
</tr>
<tr>
<td>variance</td>
<td>2.75 x 10^7</td>
<td>1.52 x 10^7</td>
</tr>
<tr>
<td>proportion zero</td>
<td>0.12</td>
<td>0.85</td>
</tr>
<tr>
<td>CV</td>
<td>0.89</td>
<td>3.47</td>
</tr>
</tbody>
</table>

Figure 2. Holling type III utility curves for three values of the half-saturation parameter \( b \). The black line (\( b = 500 \)) reaches a saturation at an energy level of 3450 kcal, the FAO requirement for adult men engaged in heavy labour. The other two curves reach peak utility at higher energy levels with half-saturation levels at \( b = 1000 \) (dark grey) and \( b = 2000 \) (light grey).
From these estimates of $f(x)$ and the assumed utility curve, we can calculate the expected utilities of the two sources.

4. Discussion

The framework of expected utility maximization has been used, at least implicitly, by means of the LVD model, in subsistence applications in human behavioural ecology [10,24]. We find that despite the higher mean energetic yield of hill kangaroo hunts, the expected utility of sand monitor hunts is over six times that of the hill kangaroo, assuming a sigmoidal utility function that plateaus at the daily energy requirement for an adult man working hard labour. While the mean return of hill kangaroo hunts is higher, even with the high fraction of zero-return hunts, the high returns of successful kangaroo hunts correspond to the plateau of the sigmoid utility curve. A person with such a utility curve should be indifferent between a return of 3500 kcal, one of 23 000 kcal or one of 80 000 kcal.

This result arises by integrating information on the non-linear preferences for different energetic returns with the distributional information about the likelihood of differing returns. The difference between the expected returns and expected utility highlights the importance of information on the distribution of returns. The approach we present to estimating the returns distributions in this paper is quite general and will work for any foraged resource. Two-component mixtures are a simple and flexible model for heterogeneity that has been used with great success in engineering [25], demography [26] and human biology [27]. Two contributing components are posited to underlie the distribution of observed energetic return. In the context of high-failure-rate hunts, the components can be thought of as representing returns associated with successful and failed hunts, respectively. In principle, there is no a priori limit of two components in the mixture model. We chose two components because of the straightforward interpretation in this application. Models with differing numbers of components can be evaluated using likelihood-based information criteria [21].

A clear inference from this exercise is that in ecological contexts where people target high-risk, very high-gain resources (such as hill kangaroo), they are doing this for reasons other than simple expected (energetic) utility maximization. This conclusion is predicated on individuals’ utility functions being concave (i.e. showing diminishing marginal utility). As noted by Winterhalder & Leslie [28], there are strong theoretical reasons to think that utility functions associated with resource acquisition are S-shaped, implying concavity at higher returns [9,29]. Nearly any sensible utility function that is concave at higher returns will yield results such as those presented in table 3. Note that the results for a utility curve corresponding to $b = 2000$ (last column of table 3, and the light grey curve in figure 2) approach maximum utility at an energetic return of approximately 20 000 kcal.

Nonetheless, we are faced with the empirical fact that people, especially men, often do pursue high-variability resources. If such resources are associated with high expected utility relative to other options—that is, when the mean is high and the variance is moderate to low, as is the case for

Figure 3. (a) Empirical distribution and best-fit probability density for sand monitor foraging returns. (b) Empirical distribution and best-fit probability density for hill kangaroo foraging returns. This curve is dominated by the 85% of unsuccessful returns, making visualization of the distribution difficult. (Online version in colour.)

Table 3. Means and expected utilities for the two resources. Mean energy return is in kcal, and expected utility is in arbitrary units scaled such that the peak utility is unity. Expected utilities are shown for three different values of the parameter $b$, which determines the half-saturation point of the utility function. $G/K$ is the ratio of sand monitor to kangaroo utility.

<table>
<thead>
<tr>
<th></th>
<th>mean return</th>
<th>$b = 500$</th>
<th>$b = 1000$</th>
<th>$b = 2000$</th>
</tr>
</thead>
<tbody>
<tr>
<td>hill kangaroo</td>
<td>3556</td>
<td>0.13</td>
<td>0.12</td>
<td>0.11</td>
</tr>
<tr>
<td>sand monitor</td>
<td>1868</td>
<td>0.84</td>
<td>0.66</td>
<td>0.42</td>
</tr>
<tr>
<td>$G/K$</td>
<td>0.53</td>
<td>6.45</td>
<td>5.35</td>
<td>3.76</td>
</tr>
</tbody>
</table>
prey such as nesting sea turtle or intercept hunting of animals with a high pursuit success rate—maintenance thresholds may expand when there are many other hungry people around, increasing the benefits for bigger harvests through the high value of sharing to others. Lower-variance resources have the potential to be responsive to hunger as they can more predictably be acquired, and larger harvests can feed more people. If such resources are associated with low expected utility relative to other options—when the mean is high but variance is also high, as for kangaroo—forces other than the expansion of the maintenance threshold may shift utility functions from the decreasing to the increasing segment of the utility function. The ability to gain multiple types of fitness-related benefits—survival and maintenance through consumption, plus the conversion of surplus into parental investment and competitive social strategies—could change the slope of the utility function itself, causing increasing returns to investment at a wider range of harvest sizes. This would be the case particularly where there is strong competition over the benefits gained through the acquisition or distribution of such a harvest, where one needs to look not just absolutely better but relatively better. The benefits in this case might be gained through a costly signalling mechanism, where there may indeed be increasing benefits for taking prey with higher variance relative to the mean, as hunters may be better able to distinguish their quality relative to other hunters [30]. Signalling through the acquisition or sharing of such a resource may also increase the survival or growth rate of a hunter’s offspring in addition to increasing his social standing among peers.

Acknowledgements. We thank, most of all, the Martu for many years of remarkable hospitality and patience, especially the Taylor, Biljabu, Morgan, Bidu, James and Chapman families. Brian Codding contributed greatly to field data collection and concept, and we thank Gabrielle Sullivan for support in and out of the field.

Funding statement. The Martu project is supported by the NSF (GRFP, DGE-0915380 and BCS-0127681,-0314406 and -0850664), an Environmental Ventures Project grant from the Woods Institute and Stanford University. J.H.J. was supported by an IRiSS faculty fellowship.

References
