Supporting Information

Venkataraman et al. 10.1073/pnas.1617542114

SI Text

Ethnohistory of the Batek. The Batek are categorized as Semang, a Malay exonym and subset of Orang Asli with differentiating phenotypic traits, such as short stature, curly hair, and dark skin (37). The Batek are also linguistically distinct, speaking a language in the Aslian branch of the Austroasiatic (Mon-Khmer) language family (38). Available evidence suggests that Semang peoples are united by a deep ancestry, dating to the initial dispersal of modern humans into Peninsular Malaysia >50 kya (39–41). Semang peoples have retained a foraging lifeway that has included trade with agricultural peoples for thousands of years (42).

Foraging Theory: Assumptions, Data, and Models. In this study, we use the framework of optimal foraging theory to analyze Batek mobility patterns. We assume that movement is costly in terms of both time and energy and that natural selection has favored behavioral variants that increase the efficiency of foraging. We treated the surrounding lowland dipterocarp rainforest as the habitat and the 11 campsites as patches that were consecutively occupied. This movement corresponds to residential (vs. logistical) mobility (5, 31). The various food and trade items (resource sets) found within the vicinity of these camps are considered as subpatches that were exploited on logistical forays. To our knowledge, there is no study that quantifies the gain function for a foraging human (or group of humans) to test whether patches are depleted and when patch depression occurs, what shape the function takes (15, 43, 44). The absence of such studies is problematic because tests of the marginal value theorem (MVT) should initially verify that the hypothesized gain function matches empirical reality (10). Our dataset enables us to evaluate how the gain functions of human foragers vary under naturalistic field circumstances. Environmental or other circumstances may create a situation where this is not the case. For the purposes of this study, we assume that Batek foragers have knowledge of the environmental average return rate for the resource sets examined and furthermore, that they know that gain functions within a patch are marginally decreasing.

Studies on humans that are consistent with the MVT include those by Winterhalder (11), Hames (12), and O'Connell and Hawkes (13, 14). Smith (15) writes that the "massive data requirements of the MVT ... make direct tests of its predictions so elusive." Associations between the time spent in patches and the return rates of those patches have been marshalled as support for the MVT. Smith's (15) study of the Inuit found no evidence for short-term patch depletion. He did find, however, that hunters remained longer in patches with higher profitability (kilocalories per hour). This finding conforms with predictions from the MVT given the following assumptions: (*i*) alternative patches evince smoothly decelerating return curves, (*ii*) the return curves run parallel (i.e., they do not cross), and (*iii*) all patch types are equally "available" (no external constraints that bias against particular patches) (15). Smith (15) acknowledges, however, that this does not make up a rigorous test of the MVT; the gain function was unknown in his case, because the data were "derived from reported rather than observed hunts" (15). Smith (15) further writes that, for a direct test of the MVT, "one would need detailed data on movement patterns, time budgets, and return rates sufficient to estimate both marginal capture rates at specific locales and concurrent average return rates at large."

Applying the MVT. When gain functions are not empirically measured, application of the MVT can lead to potential circulari-

ties. In particular, there may be a lack of independence between marginal gain rates within patches and the average return for all patches, including travel (10, 15). This problem can emerge when each patch type has characteristic gain functions and/or when the gain functions are assumed rather than empirically measured by the researcher. When patch and environmental averages are calculated from the gain function, the MVT can be tested only implicitly. Our dataset avoids this problem, because there is no necessary relationship between the gain function and the environmental averages. In other words, knowledge of the shape of the gain function does not predict the patch return rate. Camp residence times are predicted from the time at which the derivative of the gain functions (deterministic models fitted to the empirical data) declines to the environmental average.

One critique of the MVT is more specific to human behavioral ecology because of the targeted nature of human foraging. Several workers have noted that naturalistic observations of foraging behavior may result in gain curves that are skewed toward "good days," because foragers may respond to fluctuations in resource availability by not foraging on a particular day or avoiding particular patch types (15, 43, 44). These considerations have led to the suggestion that "naturalistic observations of foraging behavior will not provide an accurate measure of within patch gain functions" (44). To reduce such bias, ethnographers can ask foragers to alter foraging behavior (45). In the Batek case, we are applying the MVT at the level of the camp over the span of days to weeks, and the vast majority of items in the resource sets acquired by the Batek can hypothetically be exploited on any given day. It is important to note that a zero return on a day could result from failed search or no search at all. In either case, we assume that the resource had low availability on that day. Based on these considerations, we believe that the shape of the gain curves should be essentially unbiased.

Calculating the Energy Content of Foraging Returns. Endicott and Endicott (21) wrote that "the recorded weights of animals are the whole, unbutchered weights, and the weights of vegetable foods are the raw, unprocessed weights." To calculate the energetic content of these foods, the raw weights must first be modified to account for the fact that some of the food is inedible and that, for game, tissues vary in energetic content.

For game animals, converting raw weights to calories is somewhat complex and therefore, requires explanation. Fig. S2 presents a visual schematic of these calculations, which roughly follow those in the work by Hill et al. (46). The total weight of the animal is comprised of the inedible and edible portions (*I* and *E*, respectively). The edibility factor (*X*) varies between animals (e.g., turtles have lower edibility because of the shell). This relationship can be expressed as follows:

$$E = XT \tag{S1}$$

and

$$I = (1 - X)T. \tag{S2}$$

Some comments on the edibility of animal tissue are warranted. In many hunter-gatherer societies, virtually all of the edible carcass is consumed (47–49), although many modelers have assumed that muscle tissue was the primary animal tissue consumed by preagricultural humans (50–52). Studies have estimated the percentage of edible carcass as between 50 and 75% of the live animal weight (46, 53–55). The field measurements by Hill et al. (46) showed the edible portion of various game items to be between 68.9 and 88.1%, arriving at the value of 75% for their

study. Hart (56) calculated the edible portion of Mbuti game items as >80%. Bone is generally inedible, but fat from within the matrix of bone can be extracted by boiling, and indeed, the Batek sometimes boiled bones. In this study, edibility as a percentage of raw weight (X) was measured or based on values in the literature. When possible, we used data from the Endicotts' field study to calculate edibility and the proportional weights of component parts of the raw measured weights. Otherwise we typically referred to the study by Kuchikura (57) of Semaq Beri in Peninsular Malaysia for estimates. Kuchikura's (57) estimates were either directly measured in the field or derived from published food tables.

After edibility is calculated, it is possible to calculate the corrected weights of the carcass and organs. We follow Hill et al. (46) in assuming that, of the edible portion, 20% is organ, and 80% is carcass:

$$C = 0.8E \qquad \textbf{[S3]}$$

and

$$O = 0.2E. \qquad \textbf{[S4]}$$

It is crucial to note that the raw weights (W) of animals killed by the Batek during the study sometimes did not include organ meat or the tail (in the case of monkeys), which was often removed and consumed in the forest before weighing. As noted by Endicott and Endicott (21), "[i]f hunters made a kill early in the day, they might butcher and cook the animal and eat a bit of the meat before returning to camp with the remaining meat tied up in leaf bundles. Otherwise, they brought the unbutchered animal back to camp." Thus, the total weight of the animal (T) is not equivalent to the raw weight (W) measured by the Endicotts. Instead, W is a sum of the boxes highlighted in green in Fig. S1: the inedible portion (I) and the carcass (C). Thus, $W = I + C$. Given W and X, it is possible to use Eqs. **S1–S4** to solve for the other variables; in particular, writing E in terms of W yields

$$E = W/(1/X - 0.2). \qquad \textbf{[S5]}$$

Nutritional calculations were based on the values for the edible carcass and organs (C and O) only. Following the work by Hill et al. (46), the caloric value of internal organs was calculated at 138 kcal/100 g: this value is the mean of brain, heart, intestines, kidneys, liver, lungs, spleen, and tongue from the work by Leung (58). For the edible carcass, caloric values were estimated using several sources, usually Kuchikura (57) and Hill et al. (46) and occasionally, United States Department of Agriculture-based estimates. We generally preferred Kuchikura (57) as a source, because he provided estimates for specific East Asian foods. It seems that the caloric values of game items were approximated with domestic beef values in the works by both Kuchikura (57) and Hill et al. (46), despite the fact that domestic beef clearly differs from wild game in many respects (53). In the absence of data on wild game because of ethical and logistical constraints, however, we use these values and note that these estimates are similar to those of lean beef. Small animals (<10 kg) generally have body fat percentages below 5% (59), and therefore, 5% lean beef should be a reasonable approximation. The Batek do not hunt animals with body sizes >12 kg (the siamang is the largest). The caloric values of nonmeat food items were calculated in a more simple fashion. For tubers, vegetable items, fruit, fish, and trade-obtained foods, raw weights were corrected for edibility using a single multiplicative factor and subsequently converted to calories. As an example, unprocessed tubers are covered in dirt and may be toxic. Field notes indicate that after processing (cleaning, peeling, and slicing), 92.6% of the raw weight of takop tubers is edible. Similarly, the highly toxic gadong tuber is subject to complex processing, and only 63.8% of the raw weight is edible. For some food, edibility is virtually 100% (e.g., flour, rice, sugar, and oil).

Residential Mobility: Travel Times and the Costs of Search and Travel.
Data on how Batek moved between residential camps were extracted from the Endicotts' field notes. The moves occurred between the late morning hours and the early afternoon hours. The small thatch-roofed huts were not transported, and only a few belongings were carried, including sleeping mats, personal possessions in back baskets, bush knives, blowpipes and digging sticks, and perhaps, a little food (usually rice or slices of the gadong tuber). Camps were packed in the morning, a process that typically took about a half an hour. On arrival at a new camp, it took ∼3 h for a couple to set up their hut and fireplace. People were busy getting organized in the afternoon and evening after a move. Batek looked for signs of animals (e.g., bamboo rats) and edible plants as they walked along, either stopping to forage or making a point to come back and do it later. When they reached a new camp, some of the men might make a point of hunting in the vicinity right away on the theory that there might be game in an undisturbed location, game that would move away over the next few days because of the presence of people. Other men collected the poles and logs needed for the framework and bamboo for the floors of the huts, whereas the women gathered the palm leaves for thatch. Sometimes women immediately dug up any tubers in the vicinity of the new camp.

As noted earlier, the 93-d study by the Endicotts occurred across three seasons: fall, winter, and spring. During this time, the Batek moved camp 11 times, averaging 8.2 d (SD = 6.6) at each campsite (Table S1). The three field seasons were not continuous, because the Endicotts left the field during the rainy season (December and January) and again during the early spring (March). Therefore, the travel times to camps 8 and 10 are not known. We estimated these missing data by computing the mean travel time to the remaining nine camps (5.5 h) and using this value as an estimate for travel time to camps 8 and 10.

We used Google Earth to measure the distances traveled per residential move. We used two methods. First, we measured the linear distance between the camps. Second, we measured the distance by tracing the most efficient path along the river system. We traced the routes manually by assuming that the Batek moved in a straight line to the nearest river and on leaving the river near the new camp, moved in a straight line from the river to the camp. This approach is based on the Endicotts' field notes on how the Batek traveled to each camp. Most of the moves during the Endicotts' study consisted of foot travel. Some foot travel occurred along streams, where movement was faster because of more constant elevation and the lack of forest. Tables S2 and S3 summarize the circumstances of Batek movement between camps and the resulting travel times subsequently used in our analyses.

Travel times for the Batek were no more than a few hours. It is possible that the most relevant costs of camp movement may not be primarily with travel per se but may be with camp breakdown and setup and their attendant opportunity cost on foraging. One of the common assumptions of patch models in foraging theory is that searching and traveling are mutually exclusive. However, in the case of the Batek (and we suspect, most human foragers), moving does not entirely halt foraging, but foraging becomes less systematic (see description above).

We can use data from moves for which the distance and travel time are known to arrive at a general picture of travel costs for the Batek. The distance from camp 2 to camp 3 was 0.59 km (the shortest distance moved in the dataset) and took roughly 1 h, giving a travel speed of 1.69 km/h. The distance from camp 3 to camp 4 was 9.89 km in a straight line and 14.53 km via river. The latter is the most accurate quantity for our purposes. Via a trader's outboard motorboat, this trip took 2 h, resulting in a travel speed of 7.26 km/h. If the Batek walked this same route along the river and took 6 h, their travel speed was 2.42 km/h. If they traveled in a more or less straight line to camp 4, their speed was 1.65 km/h. Estimates for travel speed based on these

considerations are presented in Table S2. River travel via a boat with an outboard motor is, therefore, approximately three times more efficient than walking and presumably even more so than travel via river upstream on a bamboo raft.

Using these travel speeds as a guide, it is clear that most residential moves took little time, certainly no more than 6–7 h of travel time itself. From an optimal foraging perspective, for camp occupancies ranging from 3 to 24 d, altering the x intercept by several hours will make little difference to the perceived costs of moving and therefore, the marginal value of returns within a given patch. It may be more realistic to assume that the true cost of travel time is 1 d, regardless of distance, meaning that the Batek lost 1 d of foraging by moving, regardless of how far the move was. Regardless, because we have detailed data at a short timescale, we used the known values for travel time plus 3.5 h for camp breakdown and setup as the true travel times between the eight patches examined here. With these modifications,

the resulting median travel time is 0.23 d [$\pm$0.06 d (SD), range = 0.16–0.4 d].

The relative energetic costs of travel and search must also be considered, because they impact the shape of the net gain function. In this paper, we examine the gross gain function rather than the net gain function (i.e., gross gain subtracted by energetic costs of searching and traveling). However, under particular circumstances, the expectations of the MVT converge for the gross and net gain functions. As noted by Stephens and Krebs (10), "if search within a patch (including pursuit and handling) costs the same as travel (e.g., the predator walks both when traveling and searching), then incorporating energy costs does not alter the MVT's patch residence time predictions." Here, we assume that the energetic costs of travel and search are the same for the Batek, because both involve walking and few items are carried. As a result, the predictions of the MVT using the gross and net gain curves are identical.
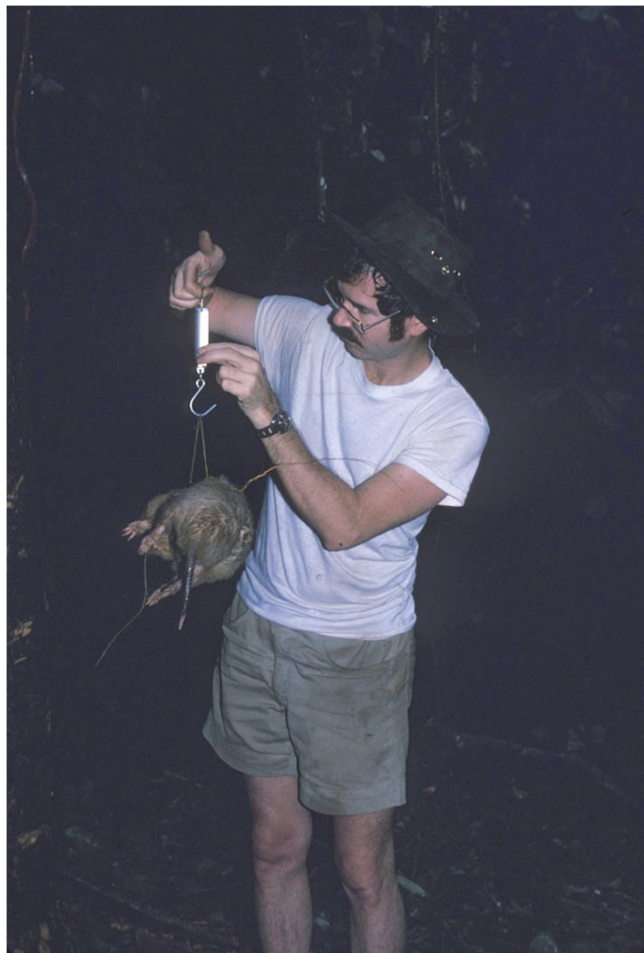

Fig. S1. Kirk Endicott uses a spring scale to weigh a bamboo rat (*Rhizomys sumatrensis*) acquired by the Batek before its processing and consumption. Photograph courtesy of Karen Endicott.
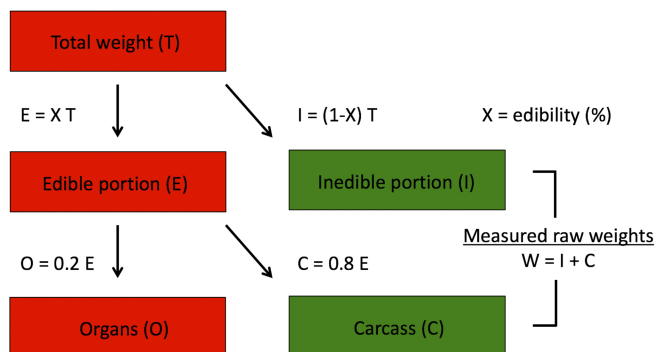
Fig. S2. Schematic diagram showing how edible organ and carcass weights were derived from the measured raw weights (*W*). The values for organs (*O*) and carcass (*C*) were then converted to kilocalories. Green indicates known variables *I* and *C*, the sum of which constitutes the measured field weight. Red indicates the calculated quantities *T*, *E*, and *O*.

Fig. S3. (*A*) Two men assembling some small-diameter rattan (*rotan barang*; foreground) and large-diameter rattan (*rotan manau*; background) to be picked up by Malay traders. (*B*) Malay traders assembling a consignment of rattan on bamboo rafts built by Batek. The traders will then pole the raft loads of rattan downstream to their villages. Photographs courtesy of Kirk Endicott and Karen Endicott.

Table S1. Information about Batek camp locations near the Upper Lebir River during the Endicotts' data collection period in 1975 and 1976

Camp	Dates	Latitude	Longitude	DD (km)	DR (km)
1	September 24–28	4.950947	102.412883	—	—
2	September 29–October 7	4.973600	102.397411	3.1	6.2
3	October 9–11	4.973701	102.402770	0.6	0.6
4	October 12–22	4.886830	102.421915	9.9	14.5
5	October 25–28	4.848432	102.434588	4.5	7.3
6	October 29–November 13	4.830557	102.429197	2.1	7.6
7	November 15–20	4.861484	102.439222	3.6	8.2
8	February 18–20	5.076645	102.352496	NA	NA
9	February 22–26	5.090737	102.375289	3.0	6.1
10	May 5–8	5.097099	102.367166	NA	NA
11	May 9–June 4	5.102913	102.370074	0.7	1.0

DD, linear distance from previous camp; DR, distance from previous camp via river; NA, not available.

Table S2. Estimated travel speeds for different methods of Batek movement

Method of travel	Speed (km/h)
Walking in forest	1.67
Walking near river	2.42
Outboard motor on river	7.26

Data were extracted from the Endicotts' field notes. Speeds were calculated using known travel times and geographic distances calculated from Google Earth (*Materials and Methods*).

Table S3.   Estimated travel times between Batek camps

Camp	Method (habitat)	Route	Total travel time (h)
1	NA	NA	4.0
2	Walk (river)	DR	6.1
3	Walk (forest)	DD	4.5
4	Walk	DR	9.5
5	Walk	DR	6.5
6	Walk (forest)	DD	4.8
7	Walk (forest)	DR	5.0
8	NA	NA	5.5
9	Walk (forest)	DD	5.3
10	NA	NA	5.5
11	Walk (forest)	DD	3.9

The speed of travel differs between dense rainforest and along the river. Some travel times are known from the Endicotts' notes, and the rest are calculated using travel speed estimates and distances between the camps, including information on the exact route taken. Total travel time represents time moving plus 3.5 h for camp breakdown and setup. Travel times for camps 3, 4, and 7 were extracted directly from field notes and used to calculate travel speed so that travel times to other camps could be indirectly calculated. Total travel times were unknown for camps 8 and 10, because the Endicotts were not present during travel to these camps. The value of 5.5 h was calculated as the mean total travel time to the other nine camps. DD, linear distance from previous camp; DR, distance via river from previous camp; NA, not available.

Table S4.   The environmental average (per capita return rates in units of kilocalories per person per day) after travel time has been taken into account for different resource sets acquired by the Batek

Resource set	Kilocalories per person per day
Meat	253.5
Tubers	963.6
Rattan	2,423.8
Wild food	1,323.3
Wild food and rattan	3,756.1