Hunter-gatherer residential mobility and the marginal value of rainforest patches

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The residential mobility patterns of modern hunter-gatherers broadly reflect local resource availability, but the proximate ecological and social forces that determine the timing of camp movements are poorly known. We tested the hypothesis that the timing of such moves maximizes foraging efficiency as hunter-gatherers move across the landscape. The marginal value theorem predicts when a group should depart a camp and its associated foraging area and move to another based on declining marginal return rates. This influential model has yet to be directly applied in a population of hunter-gatherers, primarily because the shape of gain curves (cumulative resource acquisition through time) and travel times between patches have been difficult to estimate in ethnographic settings. We tested the predictions of the marginal value theorem in the context of hunter-gatherer residential mobility using historical foraging data from nomadic, socially egalitarian Batek hunter-gatherers ($n = 93$ d across 11 residential camps) living in the tropical rainforests of Peninsular Malaysia. We characterized the gain functions for all resources acquired by the Batek at daily timescales and examined how patterns of individual foraging related to the emergent property of residential movements. Patterns of camp residence times conformed well with the predictions of the marginal value theorem, indicating that communal perceptions of resource depletion are closely linked to collective movement decisions. Despite (and perhaps because of) a protracted process of deliberation and argument about when to depart camps, Batek residential mobility seems to maximize group-level foraging efficiency.

foraging theory | marginal value theorem | hunter-gatherer | residential mobility | ethnoarchaeology

Humans have lived as hunter-gatherers for more than 95% of our species history, moving as individuals and groups in response to variation in the distribution of food in time and space. Food availability is, therefore, central to explaining the logistical and residential (i.e., camp) mobility patterns of hunter-gatherers (1, 2), a relationship that informs prevailing theories of hominin evolution and human uniqueness (3). Given that residential moves are costly, natural selection should minimize these costs within the bounds of local ecological constraints (4). Consistent with this notion, bioenergetic availability dictates the number of residential moves per year and the distance traveled per move, with foragers in warm, high-productivity environments moving shorter distances more frequently compared with foragers in cool, low-productivity environments (1, 4–6).

These group-level macroecological patterns necessarily emerge from the foraging behavior of individuals, but the proximate ecological and social factors that influence these collective movement decisions remain poorly understood (1, 5, 6). One prominent yet untested hypothesis is that selection should optimize the time at which hunter-gatherers abandon camps to maximize foraging efficiency. However, as social central-place foragers who depend on extensive cooperation for survival, hunter-gatherers may face collective action problems when it comes to moving camps, because individuals can have conflicting economic

goals. Accordingly, movement decisions are a major source of contention among hunter-gatherers, with arguments sometimes lasting for days or weeks (1).

At the heart of this issue is how individuals and groups perceive and respond to local resource depletion. Ethnographic reports (1) indicate that hunter-gatherers move camp residences in anticipation of the "imminence of diminishing returns" (7). Charnov's (8) marginal value theorem is a simple yet powerful theoretical model for formalizing these subjective impressions, and support for its predictive capabilities has been found for many species (9, 10). This model predicts that long-term return rate-maximizing foragers should leave a camp or patch (the foraging area associated with a camp) when the instantaneous return rate declines to the environmental average after travel time between patches is taken into account. One important assumption of the marginal value theorem is that the gain curves—describing cumulative resource acquisition across time in a patch—exhibit diminishing marginal returns. In reality, the gain curves may adopt different shapes that reflect the nature, abundance, and distribution of resources in the environment in addition to specific behavioral and technological capabilities of foragers (10).

Several studies of human foragers have found indirect evidence consistent with the marginal value theorem (11–15), but the framework remains underutilized in human behavioral ecology (16), in part because of its "daunting data requirements" (15): travel time between patches must be known, and return rates within patches should be measured at short timescales. Depleting gain functions have been empirically measured in carcass butchery experiments and applied to the ethnoarchaeological record (16–20), but gain functions have proven difficult to quantify in ethnographic settings. It is unknown whether

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groups of human foragers completely or only partially deplete local resources, because there has been no detailed quantitative assessment of camp-level mobility patterns in relation to foraging returns at short timescales.

Here, we directly test the predictions of the marginal value theorem in the context of hunter-gatherer residential mobility. We used historical data on the foraging economy of the Batek, a population of egalitarian, nomadic hunter-gatherers inhabiting the rainforests of north-central Peninsular Malaysia (21, 22). Using foraging return data collected at high temporal resolution in and around different camps between which travel times are known, we characterized gain functions (cumulative kilocalorie acquisition aggregated across all individuals) for several important resources. We then tested whether the marginal value theorem predicted camp residence times in concordance with empirical observations.

Materials and Methods

Study Site, Subjects, and Data Collection. In 1975 and 1976, anthropologists Kirk and Karen Endicott collected data among Batek hunter-gatherer-traders living in the Upper Lebir River watershed in Kelantan, Malaysia (Fig. 1 and Table S1). The environment in that area, which includes the northeastern section of Taman Negara National Park, consisted of tropical lowland dipterocarp rainforest interspersed with a series of rivers and tributaries. Annual rainfall currently averages 2,270 mm, and the temperature is 20 °C to 35 °C (23). Most of the area outside the park has now been logged and converted into oil palm plantations. The population then living in that area numbered about 90 Batek and was usually divided into two to four camps of varying sizes, averaging 34 individuals (20 adults and 14 children). During the period of study, September 16, 1975 to June 11, 1976, the Batek lived most of the time in forest camps, but after late January of 1976, they also participated intermittently in a Department of Aboriginal Affairs-sponsored swidden farming program at Gintah on the bank of the Lebir River.

The Batek are one of several indigenous groups living in Peninsular Malaysia, collectively termed Orang Asli ("original people" in Malay) (*SI Text*). The Batek economy revolved around a traditional nomadic hunter-gatherer lifestyle that included hunting, gathering, and fishing (21, 22). Common sources of meat included small game items, such as monkeys, gibbons, squirrels, civets, birds, bamboo rats, and porcupines. Honey and fruit were seasonal, appearing mainly between the months of April and August. The most common tubers available were wild yams in the genus *Dioscorea* (~10 species), which provide a stable carbohydrate source throughout the year. The rainforests of Malaysia may be more resource-rich for humans compared with other rainforests around the world (24).

The Batek were highly mobile during the study at both the group and individual levels. In addition to foraging, some Batek visited other camps during the day; individual families and young unmarried adults frequently moved residence from one camp to another, thus changing the size and composition of camps on an almost daily basis. There was a high premium on maintaining social proximity. The Batek did not stay in a camp if the population fell below two or three families out of fear of animal predators and because of a feeling of depression at the sight of empty shelters surrounding them. At some point, the entire group would abandon the location and move elsewhere, either as a group or subgroups, to new locations. Here, we address not individual decisions to leave but instead, how groups abandon patches based on communal perceptions of daily variation in per capita resource acquisition. Ethnographic notes suggest that there was minimal advance planning regarding the timing and destination of moves. Each new campsite was cleared and then, completely abandoned with each move. The Batek moved between camps on foot carrying minimal belongings, and food storage was negligible. Travel times were either recorded or indirectly calculated (Tables S2 and S3). The average duration of camps during the study period was 8.2 d (SD = 6.6; range = 3–24 d).

We studied the pattern of acquisition of food and rattan in 11 forest camps. Our analyses focus on those camps in which the Endicotts were present for the establishment and abandonment of the camps (camps 2, 3, 5, 6, 8, 10, and 11). Here, we briefly discuss the exceptions. The Endicotts were not present for the establishment or abandonment of camp 7, and therefore, the gain functions at this camp could not be investigated, but we did include camp 7 in the calculations of the environmental averages. The Endicotts joined two camps (1 and 4) several days after establishment (6 and 13 d, respectively), and they joined camp 8 after an unknown date of establishment. Because the Endicotts departed with the Batek when camps 1, 4, and 8 dissolved, it is still possible to fit gain curves and predict departure times for these camps, despite the shape of the gain functions being uninformative. The return rates for these camps were also used in the calculation of the environmental averages. To summarize, we investigated the shape of the gain functions for resources exploited at camps 2, 3, 5, 6, and 9–11, for which return rate data reflect the camp's occupation from establishment to abandonment. We tested the predictions of the marginal value theorem using return rate data from camps 1–6 and 8–11.

The Endicotts used spring scales to weigh all items acquired by the Batek on a daily basis (Fig. S1). During the study period, the Batek consumed 60% of total kilocalories from wild foods and 40% of total kilocalories from agricultural products (mainly rice, sugar, and flour) obtained by collecting and trading rattan. We excluded all trade-derived foods from these analyses, because they were not acquired from the rainforest. Caloric values were estimated using standard conversions (Fig. S2).

Rattan is a general term for all climbing palms in the tribe Calameae (Fig. S3). Rattan in the genus *Calamus* was and is a major component of the Batek economy because of its market value (*SI Text*). Rattan was either bartered for food or exchanged for cash, which was used immediately to purchase food (21). We, thus, converted rattan proceeds to the kilocalorie units of rice to establish comparability with wild food items. Batek acquisition and trade of rattan focused on two types: species with large diameters (Malay *rotan manau*) and those with small diameters (Malay *rotan barang*) (Fig. S3). We examined the energetic returns from five nonexclusive resource sets pursued by the Batek that were likely to impact their movement decisions: (*i*) meat, (*ii*) tubers, (*iii*) rattan, (*iv*) total wild food, and (*v*) total wild
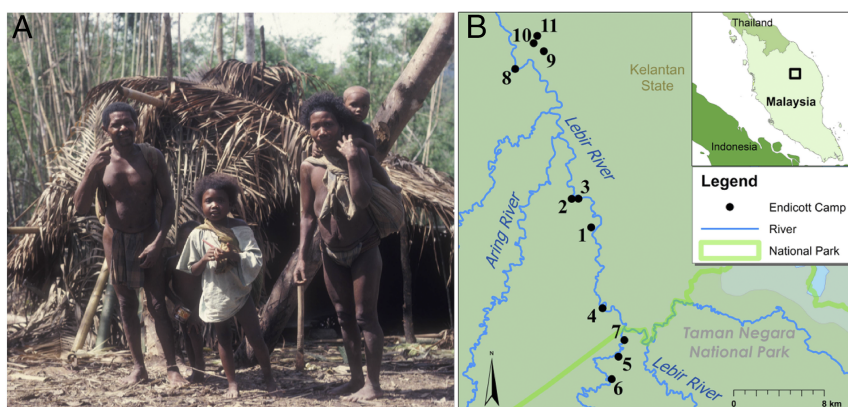
Fig. 1. Batek residential mobility from September of 1975 to June of 1976. (*A*) A Batek nuclear family prepares to move to the next camp. Batek individuals usually carried sleeping mats, digging sticks, blowpipes, and light food during the moves, which typically lasted a few hours. Photograph courtesy of Kirk Endicott and Karen Endicott. (*B*) The focal group of Batek foragers occupied 11 camps along the Upper Lebir River in the state of Kelantan, Peninsular Malaysia. Map courtesy of Thomas Overly.

food and rattan. Total wild food includes meat and tuber returns in addition to vegetables, fruit, honey, and other miscellaneous resources.

Testing the Predictions of the Marginal Value Theorem. The fine scale at which foraging returns were collected facilitated the construction of gain curves for each resource set at each of 11 Batek residential camps (patches). These gain curves represent gross gains rather than net gains (*SI Text*). Because our analysis used naturalistic foraging data rather than experimental data, it is possible that the full extent of the gain curves in each patch was not realized. For the analysis, we operated under the realistic assumption that the tail end of gain functions would follow from the shape of empirically measured data. We fitted a variety of predetermined deterministic models to the data and used information-theoretic model selection to choose the best-performing model. We chose asymptotic and sigmoidal (S-shaped) gain functions commonly used in applications of foraging theory that have several critical properties that satisfy the assumptions of the marginal value theorem (10): (*i*) net energy gain is zero when time spent in the patch is zero [$f(0) = 0$], (*ii*) the function $f(x)$ is at least initially increasing [$f'(0) > 0$], and (*iii*) the function eventually negatively accelerates [$f''(x) < 0$]. We opted to fit deterministic models rather than locally weighted regressions, because we assume that Batek foraging behavior can be adequately described by processes similar to those found in other organisms (10).

Deterministic models were generated for 50 camp–resource set combinations. We tested five competing models (two asymptotic, two sigmoidal, and one linear) for each resource set–camp combination.

i) Asymptotic Michaelis–Menton: $y = ax/(b + x)$, where a and b are constants.
ii) Asymptotic exponential: $y = a(1 - exp(-bx))$, where a and b are constants.
iii) Sigmoidal: Holling Type III curve: $y = ax^2/(b^2 + x^2)$, where a and b are constants.
iv) Sigmoidal: four-parameter logistic function: $y = a + (b - a)/(1 + exp((c - x)/d))$, where a, b, c, and d are constants.
v) Linear: $y = mx + b$, where m and b are constants.

For each resource set–camp combination, we used an information-theoretic criterion [the Akaike Information Criterion corrected for low sample sizes (AICc)] to quantify the strength of evidence for five alternative models.

Environmental average return rates are important quantities in optimal foraging models, because they characterize the quality of the environment "at-large" and represent the decision threshold for patch departure (8). We computed the energy acquired at each campsite for five resource sets and

divided by (number of days in the camp + travel time to camp) to calculate foraging efficiency in that camp in the units kilocalories per day. For per capita analyses, we then divided by the mean number of adults (individuals >14 y of age) occupying each camp throughout its duration. These 11 values for each resource set were then averaged to generate the environmental average (Table S4). We focused our analysis on the cumulative per capita measure of energy acquisition (kilocalories per person per day), because group size fluctuated between days at each camp.

We selected a single best model for each resource set–camp combination using AICc. For depleting deterministic functions, we used the marginal value theorem to estimate the predicted camp residence time (in days) by calculating when the instantaneous return rate (kilocalories per person per day) of the best-fit theoretical gain curve at each camp declined to the environmental average for that particular resource set. To do so, we took the first derivative of deterministic gain functions with respect to x (days in camp) and solved for the value of x when $f'(x)$ was equal to the environmental average for the corresponding resource. We refer to the resulting value as "predicted camp residence time," which represents the number of days that the marginal value theorem predicts that the Batek will stay in a given camp. We then compared these estimates with the observed camp residence times. For some camps, linear fits performed better than depleting functions, and thus, the marginal value theorem could not be used to generate predicted camp residence times.

As noted above, the Endicotts joined camps 1, 4, and 8 after they were established. Because there were no return rate data for the days before the Endicotts arrived, rather than fitting gain curves to the entire camp duration, we opted to construct curves that started when the Endicotts arrived. For the sake of completeness, we have plotted these gain curves in Fig. 2, but we do not further discuss the functional forms of curves for these camps.

All analyses were performed in R (version 3.1.3) (25). The data and associated code for this paper are available at https://github.com/ThomasKraft/HunterGathererMarginalValueTheorem.

Research was conducted with consenting adults under protocols approved by the Research School of Pacific Studies, Australian National University, Canberra, Australia, and the Jabatan Hal Ehwal Orang Asli (formerly Department of Aboriginal Affairs) and Ministry of National Unity, Malaysia (permit nos. VC/60050/70-045847, -581/70, -147485, -4227, and -674/90).

Results

Many resources acquired by the Batek conform to diminishing marginal return curves. Gain functions ($n = 34$) in this portion of the analysis (with camps 1, 4, 7, and 8 excluded) were depleting
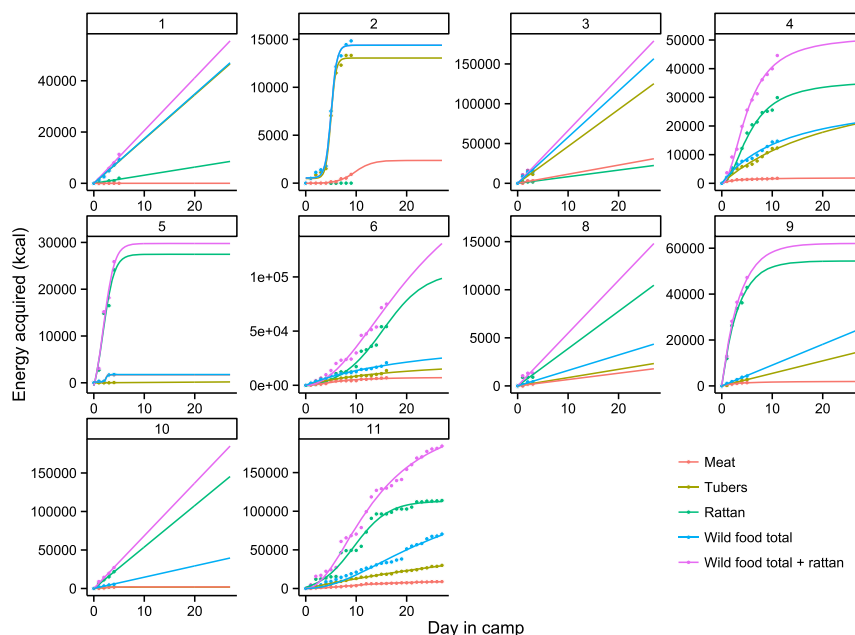
Fig. 2. The gain functions illustrating energy acquisition at each Batek camp (camps 1–11, excluding camp 7). Data are represented on a standardized 25-d *x* axis. Colors indicate different resource sets. Ethnographers were not present for the establishment of camps 1, 4, and 8. The gain curves for these camps are shown only for graphical purposes.

Table 1. Best-performing model types for deterministic gain functions of 34 camp–resource set combinations listed according to resource type (camps 1, 4, 7, and 8 were excluded from this portion of the analysis)

Resource set	Linear	4PL	H3	M-M	AE	% Depleting
Meat	1	3	2	1	0	86
Tubers	3	2	0	2	0	57
Rattan	2	3	0	0	1	67
Total wild food	3	2	1	1	0	57
Total wild food and rattan	2	2	2	0	1	71

Numbers represent counts of models that fall into each category. Depleting refers to models that are not linear. AE, asymptotic exponential; H3, Holling Type III; M-M, Michaelis–Menton; 4PL, four-parameter logistic.

in 68% of camp–resource set combinations, whereas linear functions were the best-performing models in 32% of cases. Importantly, 83.3% (five of six) of camps had at least one depleting resource, and "total wild food and rattan" (perhaps the best proxy for overall resource availability) was depleting in 71% of camp–resource combinations. For the depleting functions, the best-fitting curves in these cases evinced either asymptotic (26%) or sigmoidal (74%) shapes. Those camps with primarily linear gain curves were probably abandoned before deceleration in the rate of acquisition, because it is not likely that resources were replenished on the scale of days. For example, one camp with primarily linear gain curves (camp 10) was abandoned because of the danger of tree falls in the vicinity of the camp.

Although our sample sizes make it difficult to identify a characteristic functional form of gain curves for each resource type, the shape of Batek gain curves varied across time, space, and resource sets (Fig. 2 and Table 1). Asymptotic functions—the functional form most commonly assumed to characterize ethnographic and archaeological gain curves—performed poorly relative to sigmoidal functions for Batek foraging. One possibility is that gain curves for human foraging data derived from focal follows typically conform to asymptotic curves (20), whereas aggregated camp-level foraging data reflecting landscape-level bioenergetic constraints may evince more variation in gain curve shapes.

Previous studies of patch residence among foraging societies have implicitly or explicitly assumed diminishing marginal returns and tested an indirect correlate of the marginal value theorem, which states that foragers should occupy more productive patches for longer periods of time (15–19). The fine-grained foraging data

available for the Batek enables us to compare indirect tests of the marginal value theorem with direct tests using the gain curves established empirically from foraging data (Fig. 2). If the gain functions for the Batek were unknown, our results would suggest that Batek mobility patterns do not conform with the marginal value theorem, because camp productivity was not correlated with the length of camp occupation ($r = -0.25$, $P = 0.59$, and $df = 5$ for "total wild food"; $r = -0.49$, $P = 0.25$, and $df = 5$ for total wild food and rattan). When predictions of the marginal value theorem are generated using the empirical gain curves, however, observed camp occupation times are similar to those predicted by the model (Fig. 3). The data fall close to the 1:1 line (the expected relationship if the marginal value theorem was to perfectly predict camp residence time) plotted in Fig. 3A, which shows predicted vs. observed camp residence times. An ordinary least squares regression has a slope of 0.63 ($R^2 = 0.56$, $P < 0.001$, $n = 26$).

We also examined which resource sets produced the most accurate predicted camp residence times using the marginal value theorem. The resource set total wild food and rattan produced predicted camp residence times that were, on average, 0.4 d from observed residence times, an effect driven primarily by rattan (Fig. 3 and Table 2). The Batek generally stayed longer in patches than predicted by roughly 2 d (Fig. 3B).

Discussion

Here, we have established the proximate mechanisms that structure variability in the macroecological patterns of hunter-gatherer residential mobility (4, 5). As expected, central-place foraging in hunter-gatherers seems to be associated with diminishing marginal returns. Our results indicate that Batek residential mobility is associated with communal perceptions of declines in resource availability and that marginal rates of return at the times of camp departures were generally similar across patches.

These findings enable us to evaluate alternative hypotheses about the factors that influence collective movement decisions in hunter-gatherers. First, for example, nonsubsistence factors, such as religion or rituals, deaths, or a desire to visit others, are undoubtedly important, but these qualitative models make no a priori predictions about the patterning of camp residence times. Second, the accumulation of waste, which increases exposure to parasites and attracts predators, may also constrain the duration of camp occupation. This hypothesis predicts that the number of people in camp should be negatively associated with camp occupation time. However, these variables were uncorrelated for the Batek ($r = 0.3$, $P = 0.36$). Third, the Batek abandoned camps before resources in the surrounding areas were fully depleted. Taken together, our study supports the concept that
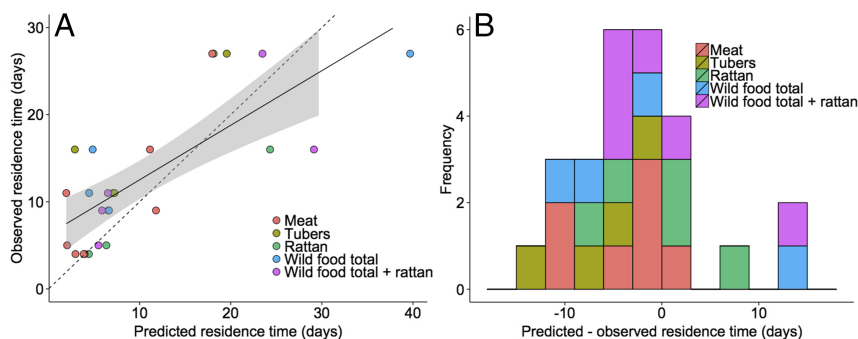
Fig. 3. (A) Predicted vs. observed camp residence time for camp–resource set combinations described by depleting functions. The regression line forced through the origin represents the one to one relationship predicted by the marginal value theorem. The marginal value theorem accounts for 56% (adjusted R^2) of the variance in Batek camp residence time. Gray shading indicates the 95% confidence interval. (B) Histogram of the differences between empirically observed camp residence times and those predicted based on the marginal value theorem. Each bar represents a camp–resource set combination best-described by a depleting deterministic function.

Table 2. The accuracy of the marginal value theorem for different resource sets relevant to Batek mobility decisions

Resource set	Mean difference (d)	SE
Meat	−3.5	1.7
Tubers	−6.7	2.4
Rattan	−0.5	2.9
Total wild food	−1.8	5.2
Total wild food and rattan	0.4	2.7

Means and SEs for predicted minus observed patch residence times are calculated across all camp–resource set combinations for which a predicted residence time could be generated.

diminishing marginal return rates are the primary driving factor behind hunter-gatherer residential mobility patterns.

Establishing an empirical connection between individual foraging and residential mobility in hunter-gatherers raises new questions about the social forces that enable group-level foraging efficiency to be maximized. Ethnographic evidence from our case study suggests several contributing factors. First, the Batek promote social norms that result in extensive cooperation and food sharing (21), resulting in common subsistence goals and mutual interdependence. Second, there is public knowledge about the foraging returns of other individuals and shared information about the locations of food sources. Third, collective camp movement decisions were not made by single individuals but instead, were made through a process of informal group discussion that involved most adults (21). We hypothesize that tensions between the economic goals of individuals, pair bonds, and kin groups, mediated through disagreement and eventual consensus, generate a self-correcting mechanism that maximizes group-level foraging efficiency.

Sex Egalitarianism and Hunter-Gatherer Mobility. Women's foraging for carbohydrates (often tubers) is thought to dictate hunter-gatherer camp movement decisions (1). Indeed, the Batek claimed that they generally move camps in response to tuber depletion (21). However, camps moved 6–7 d later than expected based on the tuber data (Table 2). These analyses thus reveal a subtle mismatch between what people said and what they did. Rattan performed far better than tubers in predicting camp residence times (Fig. 3B and Table 2). Men collected rattan, which was sold and converted to carbohydrates in the form of rice, thus creating a dynamic in which male carbohydrate contributions replaced those of women (i.e., rice consumption was inversely related to tuber consumption). The Batek case thus illustrates how access to agricultural carbohydrates could introduce elements of gender inequality into hunter-gatherer societies.

Resource Conservation in Small-Scale Societies. The so-called "ecologically noble savage" debate revolves around whether small-scale societies intentionally practice resource conservation or whether it is an epiphenomenon of other goals, such as maximizing foraging efficiency (26–29). Despite explicit mention of how the marginal value theorem may explain the sustainability (or lack thereof) of harvesting practices, to date there have been few data to bear on the question of whether and how small-scale societies deplete resources.

To show resource conservation, it must be shown that individuals reduce "the level of resource use below what would be fitness-maximizing in the short term in exchange for long-term sustainable benefits in the future" (28) and that there is intent on the part of the actors (27). Our data indicate that the Batek departed patches before completely depleting the resource base (Fig. 2) in a manner consistent with the maximization of

foraging efficiency. Although the Batek were fully aware that they could reserve or store resources for future use by leaving a patch before its resources were exhausted, interviews in 1975 and 1976 confirmed that residential moves were primarily motivated by resource depletion: "Eventually, after camp members used up the nearby resources of food and rattan, talk would turn to the possibility of moving on" (21).

These findings strongly suggest that Batek camp movements are inconsistent with resource conservation. However, certain Batek foraging practices and norms may qualify. In 1975, the Batek of the Upper Lebir River deliberately reserved some patches of resources for future use. They avoided exploiting some areas in the headwaters of side streams of the main river with the intention of retreating into them during the annual floods in December and January, which they did. They also harvested particular resources in a sustainable manner. For example, they replanted the growing tip of a yam vine if tubers were too immature to eat and made mental notes about the location, so that they could harvest them at a future time.

If the logic of the marginal value theorem applies broadly to group foraging decisions, it is important to consider how the subsistence behaviors of small-scale societies will respond to habitat degradation under this model. Under conditions of severe habitat degradation, foragers should make decisions based on profitability rather than abundance of prey, and market pressures (i.e., high profits for forest products) may make it optimal to engage in behaviors that conflict with conservation goals (27). The result would be extreme depletion of animal and plant resources that could otherwise be sustainably harvested.

Ethnoarchaeology. Empirical support for the predictions of the marginal value theorem in an ethnographic context bolsters the explanatory and predictive potential of human behavioral ecology in archaeological reconstructions (30–34). The key constraint identified here—that rapid resource depletion prompts frequent moves (every 1–3 wk) across short distances—has direct implications for archaeological inference. The marginal value theorem fundamentally concerns time allocation, and the time spent at a given location influences activity patterns and thus, the nature and quantity of archaeological remains (35). For example, tropical rainforests are notoriously poor taphonomic environments for preservation (36), but our study also suggests that reduced material accumulation is a direct result of short site occupation in tropical rainforests because of rapidly declining marginal returns.

Conclusion

The marginal value theorem has been influential and widely supported in studies of nonhuman organisms. This study shows that aggregated individual foraging behaviors in a small-scale nomadic society can result in optimized collective action. By investigating the factors affecting residential mobility at a proximate level, our study offers a framework for scaling up fine-scale foraging behavior to broad-scale macroecological mobility patterns.

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