Nahua mushroom gatherers use area-restricted search strategies that conform to marginal value theorem predictions

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We develop a method of analysis for testing the marginal value theorem (MVT) in natural settings that does not require an independent definition or mapping of patches. We draw on recent theoretical work on area-restricted search (ARS) that links turning-angle and step-size changes to geographically localized encounter-rates. These models allow us to estimate "giving-up times" using encounter-annotated GPS tracking data. Applied to a case study of Nahua mushroom foragers, these models identify distinct forms of intrapatch and interpatch search behavior, with intrapatch search transitioning to interpatch search after a predictable interval of time since the last encounter with a harvested mushroom. Our empirical estimate of giving-up time coincides with the theoretically optimal giving-up time derived under the MVT in the same environment. The MVT is currently underused in studies of human foraging and settlement patterns, due in large part to the difficulty of identifying discrete resource patches and quantifying their characteristics. Our methods mitigate the need to make such discrete maps of patches and thus have the potential to broaden the scope for empirical evaluations of the MVT and related theory in humans. Beyond studies of naturalistic foraging in humans and other animals, our approach has implications for optimization of search behavior in a range of applied fields where search dynamics must be adapted to shifting patterns of environmental heterogeneity affecting prey density and patchiness.

area-restricted search | marginal value theorem | tracking | GPS | Lévy flight

Foragers whose optimal search mode entails mobility (1) must invest some fraction of their limited energy budget in active search for randomly and often sparsely distributed (2) food items or natural resources. This active mode of search can require a substantial expenditure of energy (1, 3), increase exposure to environmental hazards and predators (4), and entail the opportunity costs of separation from a home base or social group. As such, understanding how mobile foragers increase resource encounter-rates has been central to a variety of foraging models in evolutionary biology, with applied consequences for fields as diverse as criminology (5), cognitive science (6), engineering (7), conservation biology (8, 9), and agricultural pest management (10). Early empirical work inspired by the marginal value theorem (MVT) (11) focused on models of patch choice (12, 13) and patch-residence times (14, 15). More recent work, drawing on increased computational resources, has focused on identifying efficient random walk search algorithms (16–19)—e.g., for Brownian walks, Lévy flights, and area-restricted search (ARS)—which can model a forager's movement patterns even in cases where patch choice and patch-residence times are hard to measure.

Brownian walk search patterns can be nonoriented and diffusive (e.g., dispersal), or oriented and superdiffusive (e.g., migration), while Lévy flight search patterns are scale-free, nonoriented, and superdiffusive (20). ARS search patterns, in contrast, are composites of intensive (low speed and high turning rate) and extensive (high speed and low turning rate) search periods (21). Simulation models suggest that encounter-conditional ARS can be more efficient than unconditional Lévy flights or Brownian walks with equal average movement velocities (e.g., ref. 22), but little work has explored how ARS parameters can be effectively tuned, or how the insights of the MVT literature can be applied to models of foraging in continuous rather than discrete environments.

Here, we use a model of adaptive, encounter-conditional search heuristics to link the MVT and ARS literatures. We demonstrate that the MVT provides numerical predictions for the optimal number of time-step lags for which a slow and tortuous ARS should be enacted following an encounter. We then draw on a database of encounter-annotated GPS data—GPS tracks paired with GPS waypoints on the time and location of food item encounters—recorded during focal follows of Nahua mushroom foragers searching in a natural setting. These data are used to fit a Bayesian model of encounter-conditional ARS

Significance

Using GPS trackers, we followed Nahua mushroom collectors to study how experienced foragers efficiently search for resources. Locating patchily distributed resources while reducing traveling costs requires a forager to balance time spent searching for new patches and searching within known patches. We present an analytical model of foraging behavior in which foragers can detect and change the way they search by adjusting direction and speed as a function of time since last resource encounter. This model can be used to test theoretical predictions concerning how long foragers should remain inside a given patch. Elucidating how organisms efficiently search is of widespread interest across academic disciplines: the potential applications of the method explained here range from conservation biology to robotic design.

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trajectories. The empirical estimates of "giving-up time" (GUT)—a measure of "intrapatch" search duration—from this model are numerically concordant with predictions of the same quantity derived from the MVT. More generally, we illustrate a method of analysis for testing the MVT in natural settings that does not require an independent definition or mapping of patches—expanding the empirical scope of the MVT to cases where quantitative data on patch boundaries and their respective food item densities are unavailable or impossible to obtain.

Theory on Search in Continuous Environments

ARS. A central focus in movement ecology is how mobile predators can most efficiently locate randomly distributed food items. A body of literature on the Lévy flight foraging hypothesis has suggested that foragers should search for randomly distributed food items using approximations to Lévy flights (18, 23, 24), since they are frequently more efficient than Brownian movement at encountering sparse, randomly distributed food items. More recent work on intermittent and two-stage search has examined how encounters with food items (22, 25, 26) can trigger ARS behavior (27–34) in which search velocity and turning-angle (35) are modified for some interval of time. This work demonstrates that foragers of patchily distributed resources can use a simple heuristic—*search with slower and more tortuous movement after a recent encounter with a food item* (intrapatch search) *and move with more rapid and linear movement otherwise* ("interpatch" search)—to improve search efficacy. These models demonstrate that ARS can outperform nonconditional Lévy or Brownian movement by minimizing search time (25), increasing encounter rate, and decreasing risk of starvation (22). However, it remains unclear how the parameters governing encounter-conditional ARS trajectories can be tuned to improve encounter rates in a given environment. In this paper, we draw on the MVT to provide some important—but partial—insights into the effective tuning of such parameters.

The MVT. Efficient foragers searching in a patch—a localized aggregation of resource items—face a declining rate of return as they continue to harvest (36). As resources are depleted or their availability is depressed, a forager faces the question of how long it should remain in its current patch before seeking out a fresh patch to harvest. Assuming a discrete set of patches, Charnov's MVT (11) predicts that a forager should transition into interpatch search when the marginal encounter rate in its current patch drops to the overall encounter rate averaged over interpatch search and intrapatch harvest.

Despite the sometimes "daunting" data requirements (37, p 257) involved in testing the MVT, studies of human (38–41) and nonhuman (14, 42, 43) foragers have found some evidence consistent with MVT predictions. Venkataraman et al. (41), for example, use extensive, daily records of Batek foraging returns to fit resource-depletion curves and show that camp-relocation events generally conform to MVT predictions.

Nonetheless, testing if a given group of foragers actually use MVT-predicted GUTs is complicated. The overall foraging encounter-rate is among the easier variables to observe and measure (11, 44, 45). It is considerably more difficult to produce the independent information required to delineate the key features of patches—their locations, boundaries, resource levels, and responses to exploitation. In controlled experimental designs, patch-specific data are not generally prohibitively difficult to acquire. However, food items growing in natural settings are seldom distributed in discrete, easily defined patches (46–49). Rather, they are typically distributed continuously and, even if clustering or spatial autocorrelation in their distribution is high, the "boundaries" between high- and low-density regions can be fuzzy. The difficulty associated with partitioning continuous environmental variation into discrete patches thus has been a key

impediment to empirical tests and technological applications of the MVT (41). Methods of analysis that mitigate the need to make a discrete map of patches have the potential to broaden the scope for empirical evaluations of the MVT and related theory (e.g., ref. 50).

Integrating ARS Models and the MVT to Explain the Search Patterns of Nahua Mushroom Foragers. To generalize the insights of the MVT to the case of sessile food items that are distributed continuously over an environment with spatial autocorrelation (i.e., patchiness), we use recent mathematical and statistical approaches developed in the ARS literature (19, 22, 26, 34) to estimate the number of time-step lags for which turning-angle and step-size changes are associated with encounters with food items. We use encounter-annotated GPS data to make these estimates. The number of time-step lags for which these effects are significant multiplied by the length of each time-step yields an estimate of the GUT (42, 51) for a local patch (22). Although GPS tracks annotated with behavioral observations on encounters with food items can themselves be difficult to acquire, such data have been collected in nonhuman animals using clever research designs (e.g., refs. 29 and 30), as well as in humans (e.g., ref. 34); increasingly powerful and simple-to-use GPS units will undoubtedly make production of such data easier.

In the following sections, we first introduce the field-site and foraging context. After this, we provide the mathematical details describing how theoretical GUTs are calculated and how empirical GUTs are estimated. We then demonstrate the main results that: (*i*) encounter-annotated GPS tracking data show that Nahua mushroom foragers respond adaptively to encounters with food items by increasing turning-angle between time-steps and decreasing search velocity, and (*ii*) this response leads to distinct forms of intrapatch and interpatch search behavior. Intrapatch search transitions to interpatch search after an average of 6 to 13 time steps, representing 3.0 to 6.5 min, since the last encounter with a harvested mushroom—an estimate that coincides closely with the theoretically derived GUT of 8 to 21 time-steps under the MVT. We conclude with a discussion of the relevance of our results for future studies of human and nonhuman foraging behavior and then comment on the applicability of our model to a range of applied problems.

Fieldwork

The database used here consists of focal follows conducted by authors L.P.-C. and C.C.-L. with mushroom foragers from a Nahua community in 2006 and 2007 within La Malinche National Park, Tlaxcala, Mexico (49, 52, 53). L.P.-C. and C.C.-L. maintained a position 1 to 2 m from the focal forager during slow movement or rest and 2 to 5 m during rapid movement. GPS positions were recorded at 30-s intervals using a Garmin GPS V Personal Navigator; the data are analyzed at this resolution. Table 1 provides descriptive statistics for each of the 34 foraging trips in the sample.

In total, L.P.-C. and C.C.-L. recorded 141.5 h of focal follows consisting of 16,979 GPS data points. Annotated points of interest were recorded on the GPS unit for each of the 1,485 mushroom encounters. Fig. 1*A* plots each recorded search path and encounter in the database. Fig. 1*B* plots a higher-resolution section of a single path. Focal foragers were selected opportunistically on each day of research with the constraint that the sample be balanced by sex. Informed consent was obtained from each forager before data collection.

Mushroom gathering is a rainy season (June–September) activity for families living in La Malinche. Foraging bouts are frequent (three to five per week) among the families that commercialize mushrooms. Our encounter-annotated GPS tracks reflect the behavioral patterns of single foragers on these trips; however, mushroom foraging is at least partially a social

Table 1. Descriptive statistics for 34 mushroom foraging trips

Trip	GPS pts.	Dist., km	Duration, h	Av. speed, km/h	Elev., m	Pts. w/enct.	Frac. enct.	Mushrooms collected
1	596	14.33	4.97	1.72	704.1	23	0.04	89
2	589	15.29	4.91	1.83	711.4	25	0.04	57
3	620	9.75	5.17	1.17	451.3	44	0.07	169
4	544	9.93	4.53	1.19	412.0	60	0.11	143
5	428	4.51	3.57	0.54	169.7	65	0.15	188
6	455	8.09	3.79	0.97	373.5	55	0.12	176
7	536	7.29	4.47	0.87	458.5	67	0.12	197
8	458	5.58	3.82	0.67	373.0	23	0.05	59
9	526	6.85	4.38	0.82	376.9	67	0.13	136
10	632	9.17	5.27	1.10	559.5	34	0.05	72
11	582	6.76	4.85	0.81	385.0	79	0.14	199
12	629	9.31	5.24	1.12	574.9	27	0.04	111
13	434	6.74	3.62	0.81	291.3	27	0.06	37
14	386	6.02	3.22	0.72	461.9	15	0.04	49
15	449	5.70	3.74	0.68	396.1	13	0.03	33
16	503	7.33	4.19	0.88	324.9	30	0.06	164
17	507	7.00	4.22	0.84	313.4	26	0.05	155
18	301	5.31	2.51	0.64	217.2	9	0.03	18
19	356	5.05	2.97	0.61	152.4	25	0.07	50
20	653	8.05	5.44	0.97	216.8	64	0.10	197
21	648	8.26	5.40	0.99	188.4	56	0.09	136
22	366	3.69	3.05	0.44	169.7	29	0.08	78
23	350	3.51	2.92	0.42	167.3	14	0.04	53
24	600	7.16	5.00	0.86	316.8	105	0.17	389
25	526	6.76	4.38	0.81	287.5	70	0.13	234
26	442	4.64	3.68	0.56	266.3	52	0.12	179
27	434	4.57	3.62	0.55	203.3	50	0.12	135
28	436	10.15	3.63	1.22	500.9	14	0.03	88
29	468	8.29	3.90	0.99	413.8	16	0.03	30
30	425	9.35	3.54	1.12	468.1	37	0.09	108
31	475	7.54	3.96	0.91	60.1	30	0.06	42
32	493	7.44	4.11	0.89	58.6	48	0.10	89
33	557	6.18	4.64	0.74	410.9	81	0.15	206
34	575	5.80	4.79	0.70	418.1	105	0.18	301
Sum	16,979	251.40	141.50	30.16	11,853.6	1,485	2.90	4,367
Mean	499	7.39	4.16	0.89	348.6	44	0.09	128
Minimum	301	3.51	2.51	0.42	58.6	9	0.03	18
Lower quartile	434	5.70	3.62	0.68	216.8	25	0.04	57
Median	498	7.08	4.15	0.85	373.2	36	0.08	123
Upper quartile	582	8.29	4.85	0.99	451.3	64	0.12	179
Maximum	653	10.15	5.44	1.22	711.4	105	0.18	301

For each trip, we describe the number of GPS data points (GPS pts.) recorded, the distance traveled (Dist.), the duration, the average speed (Av. speed), the change in elevation between lowest and highest points on the search path (Elev.), the number of GPS points with mushroom encounters (Pts. w/enct.), the fraction of GPS points with mushroom encounters (Frac. enct.), and the total number of mushrooms collected during the search. Summary statistics by column are given at the bottom of the table.

activity (54). On each trip, approximately 5 to 10 individuals forage together in a spatially dispersed group, and only 2 of these individual were tracked using GPS at any given time. Although mushroom foragers do not move completely independently, they typically spread out so that they are at least 15 to 50 m apart, and they often remain out of sight of each other, maintaining contact by calling or whistling throughout the search period (53). Foragers search in these loose groups so that lone individuals do not become lost in steep, trackless, and dangerous terrain, and so that there is help around in case of emergencies. Nevertheless, foragers keep their own harvests, giving them a personal incentive to forage independently without overtly signaling their encounters to other foragers.

Most trips occur in ecosystems predominated by fir trees (*Abies*), where edible mushroom diversity and abundance are high (55). Foragers typically alternate their visits among sites within La Malinche National Park, leaving time for mushrooms to fruit between visits. Foragers target *Ramaria*, *Boletus*,

Cantharellus, and *Amanita* mushrooms due to their high market value (56), as well as *Turbinellus floccosus*, which is highly appreciated for cultural reasons and also the most frequently harvested species. A detailed account of the diversity, abundance, and distribution of mushroom species in this region is provided elsewhere (52, 55). Multiple kinds of mushrooms were collected as encountered during each trip, and no single trip was dedicated to search for a single species. We, therefore, do not differentiate the analysis by target species.

The local value of wild mushrooms was around 3 USD per kg in 2006 (53). In the current sample, foragers gathered an average (±SD) of 3.7 ± 2.5 kg per trip, which would yield 11.1 ± 7.6 USD per trip if all collected mushrooms were sold. Taking into account that foragers visit the forest three or more times during the week, a single adult collector could obtain about 44.4 ± 30 kg/mo (133.2 ± 91.2 USD per month) from foraging during the 4-mo rainy season. Mushroom foraging thus provides an important source of cash income in rural areas. Knowing where
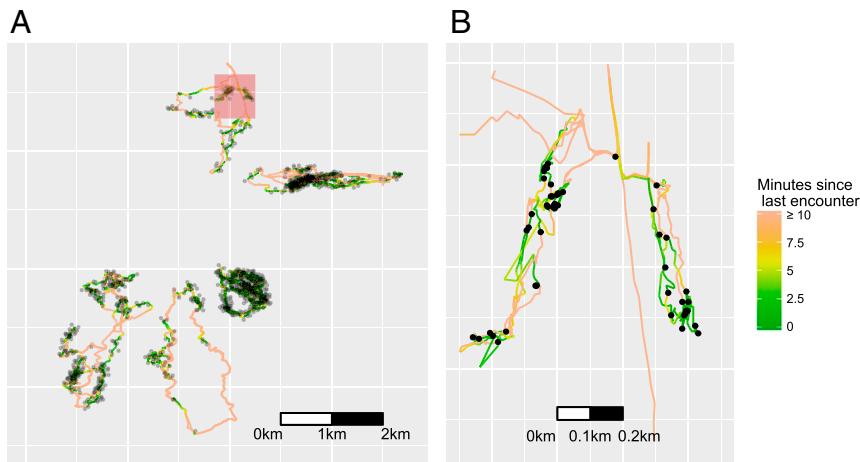
Fig. 1. Focal follow GPS recordings of Nahua mushroom foragers, 2006–2007. Shown in *A* are smoothed, low-resolution, and sometimes overlapping paths for all trips in the dataset. At this large scale, searches appear fairly linear. Shown in *B* is a high-resolution image of the red-shaded area in *A*. At this scale, it becomes evident that encounters with mushrooms (black dots) are associated with changes in search mode (shorter step-sizes and increased turning-angles). Note that the paths are colored by time since last encounter with a mushroom of interest. The orange regions, representing search periods of at least 10 min postencounter, are mostly linear. The green regions, representing search periods shortly after an encounter, are more tortuous (*B*).

and when to look for mushrooms, as well as how to modulate search mode upon encounter with a patch, is critical to optimizing the time and energy spent in the forest—as well as the cash income associated with foraging.

Modeling Forager Movement

Estimating Theoretical GUTs. The MVT predicts that foragers should make the switch between intrapatch search-and-harvest and interpatch search for an undepleted locale when the marginal encounter-rate within the current patch declines below the average encounter-rate inclusive of within and between patch costs (11). To test this prediction, we calculate the predicted number of time-steps with no encounters that would be required to decrease the intrapatch encounter-rate to or less than the overall mean encounter-rate. This value is known as the GUT and is a classic metric from the MVT literature used to measure patch leaving (14, 42). We then compare this value to the empirically estimated number of time-step lags of intrapatch search following an encounter before a forager fully resumes an interpatch search pattern.

To arrive at a numerical prediction for our case study, we first determine that the mean rate of encounters across foraging trips is 0.09 (interquartile range: 0.04, 0.12) encounters per time-step (Table 1). Then, we evaluate when a horizontal line with this value intersects the graph of $y = \frac{1}{x+1}$, where the value x indicates how many time-steps with no encounters have occurred after the most recent encounter, and the value y gives the encounter rate since last encounter, inclusive of that encounter. Given the average empirical encounter rate of 0.09 encounters per time-step and the interquartile range of 0.04 to 0.12 encounters per time-step, the MVT predicts that ∼8 to 21 time-steps without an encounter should cause mushroom foragers to transition from an intrapatch into an interpatch search mode (Fig. 2).

Estimating Empirical GUTs. To calculate an empirical estimate of GUT using encounter-annotated GPS tracks, we use a Bayesian model linking encounters and forager movement patterns (22). The data represent a forager's search path as a sequence of discrete points in space, $(x_{[t]}, y_{[t]})$, with a constant separation of 30 s. These data are easily converted into a more theoretically relevant form via Cartesian-to-polar mapping (57). We can parameterize the data so that $r_{[t]} \in \mathbb{R}^+$ gives the linear distance between

points $(x_{[t]}, y_{[t]})$ and $(x_{[t-1]}, y_{[t-1]})$, and $\theta_{[t]} \in (-\pi, \pi)$ gives the corresponding heading-angle:

$$r_{[t]} = \sqrt{(x_{[t]} - x_{[t-1]})^2 + (y_{[t]} - y_{[t-1]})^2} \qquad [1]$$

$$\theta_{[t]} = \arctan^\star \left| \frac{(y_{[t]} - y_{[t-1]})}{(x_{[t]} - x_{[t-1]})} \right|, \qquad [2]$$

where the $\arctan^\star$ function is the standard $\arctan$ function after adjusting the angle for the quadrant of the point in Cartesian space (57). Then, we transform heading-angle (an absolute direction) into turning-angle, by considering the difference in heading-angle between time-steps. The unit-scaled turning-angle, $\delta_{[t]}$, is:

$$\delta_{[t]} = \frac{\Delta(\theta_{[t]}, \theta_{[t-1]})}{\pi}, \qquad [3]$$

where the $\Delta(a, b)$ function returns the minimum of: $|a - b|$ and $2\pi - |a - b|$, since a 90° right turn is the same as a 270° left turn, for example. Division by π radians yields a value on the unit interval.

Since turning-angle is a unit-constrained variable, we can most effectively model its distribution using a Beta regression model (see ref. 58 for a formal justification):

$$\delta_{[t]} \sim \text{Beta}(\mu_{[t]}\nu, (1 - \mu_{[t]})\nu). \qquad [4]$$

The mean of the Beta distribution at time t is then given by $\mu_{[t]}$:

$$\mu_{[t]} = \text{logit}^{-1} \left(\psi_{[0]} + \sum_{s=1}^{S} \psi_{[s]} E_{[t-s]} \right), \qquad [5]$$

and the dispersion of the distribution for a fixed μ is controlled by $\nu \in \mathbb{R}^+$. $E_{[t]}$ is an indicator variable of whether a food item was encountered at time-step t, $\psi \in \mathbb{R}^{S+1}$ is a vector of unknown parameters estimating the effects of encounters on turning-angle over S time-step lags, and logit^{-1} is the inverse logit function. Eq. **5** allows us to estimate how encounters with mushrooms at lagged time-steps affect turning-angle in the current time-step.

Regarding the distribution of step-sizes, we use a log-normal model, as information theoretic model comparison of step-size
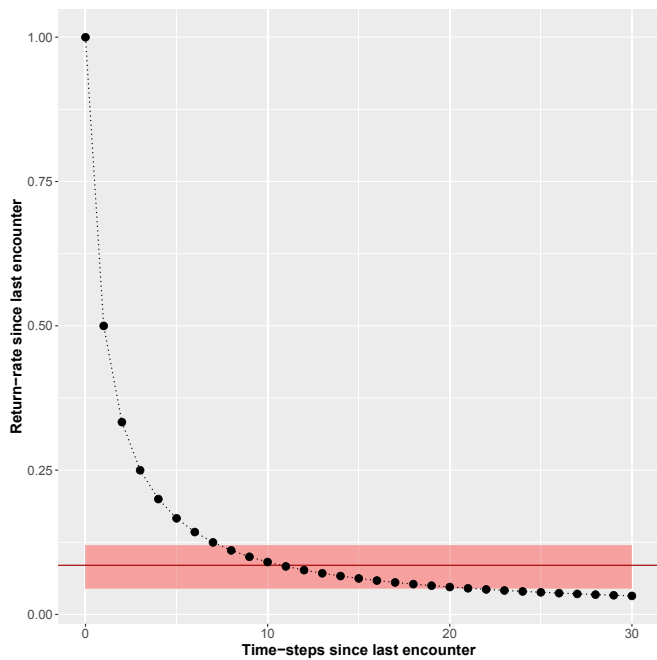
Fig. 2. MVT prediction of GUT for mushroom foragers. Assume that a forager has last encountered a food item at time-step zero, but then fails to encounter food items in subsequent time-steps. The declining encounter-rate since the last encounter, inclusive of that encounter, is given by the black points. The horizontal red line shows the mean encounter-rate over trips, inclusive of interpatch search costs. The shaded red zone shows the corresponding interquartile range of encounter-rate over trips (Table 1). The MVT predicts a transition from an intrapatch search-and-harvest mode to an interpatch search mode where the lines intersect—at 8 to 21 time-steps without an encounter. Note that there is a wide range of mean encounter-rates over trips (red shaded region) and that the exact location of the intersection point is sensitive to the value of mean encounter-rate for small values on the *y* axis. Since the mean encounter-rate is quite variable over trips, we acknowledge that the specific location of the intersection of the curve with the horizontal line representing the mean encounter-rate is consistent with a range of numerical predictions for optimal GUT—i.e., predictions of 8 to 21 time-step lags are all plausible.

in human movement (59) has shown that the log-normal distribution outperforms other commonly used distributions in predictive accuracy.

Specifically, we model the distribution of step-sizes as:

$$r_{[t]} \sim \text{Log-Normal}(\eta_{[t]}, \omega), \qquad \textbf{[6]}$$

where the mean of the log of the step-size at time t is given by $\eta_{[t]}$:

$$\eta_{[t]} = \left(\phi_{[0]} + \sum_{s=1}^{S} \phi_{[s]} E_{[t-s]} \right), \qquad \textbf{[7]}$$

and the dispersion of the distribution of the log of step-size for a fixed η is controlled by $\omega \in \mathbb{R}^+$. $E_{[t]}$ is the same indicator of whether a food item was encountered at time-step t, and $\phi \in \mathbb{R}^{S+1}$ is a vector of unknown parameters estimating the effects of encounters on step-size over S time-step lags. Eq. **7** allows us to estimate how encounters with mushrooms at lagged time-steps affect step-size in the current time-step.

In this empirical model, a measure of GUT can be usefully defined as the number of lags s for which there is a significant relationship between a mushroom encounter at time-step $t - s$ and the movement parameters at time-step t. In other words, the GUT is the maximum value of time-step lags, $\hat{s}$, such that

$\psi_{[\hat{s}]} > 0$ for turning-angle outcomes and $\phi_{[\hat{s}]} < 0$ for step-size outcomes, since these parameters measure the relationship between an encounter $\hat{s}$ lags in the past and one's choice of search mode at the present time-step. When more than $\hat{s}$ time-steps have passed without an encounter, the forager is operating in an inter-patch search mode, but when less than $\hat{s}$ time-steps have passed since the last encounter, the forager is operating in an intrapatch search mode. So long as $\hat{s} > 0$, these two search modes will have statistically distinguishable properties.

Results

The empirical model shows that mushroom foragers use encounter-conditional ARS heuristics to continually update their search mode. This is demonstrated by strong and reliable lagged effects of encounters on turning-angle and step-size (Fig. 3). Fig. 3*A* plots the distributions (medians and 90% credible intervals) of $\psi_{[s]}$, the lagged effect of encounters on turning-angle for each $s \in \{1, \dots, 30\}$. Fig. 3*B* shows the corresponding estimates of $\phi_{[s]}$, the lagged effects of encounters on step-size. Since each time-step lag, s, is taken at 30-s intervals, the graphs show estimates of lagged effects lasting up to 15 min postencounter.

We can compare these data on empirical GUT to the theoretical prediction of this value from MVT. The regression estimates of turning-angle, $\psi_{[s]}$, remain significantly greater than 0 for $s <$ 6 to 9, indicating that encounters are associated with increased turning-angle for about 3.0 to 4.5 min. Likewise, the regression estimates of step-size, $\phi_{[s]}$, remain significantly less than 0 for $s <$ 8 to 13, indicating that encounters are associated with decreased step-size (i.e., forager velocity) for about 4.0 to 6.5 min. These data-driven results imply a GUT of between 6 and 13 time-steps postencounter, closely matching the quantitative predictions of the MVT (8 to 21 time-steps).

In the *SI Appendix*, we show that these results are robust to analysis with a first-order autoregression (AR-1) model to control for temporal autocorrelation in outcomes and an analysis that includes vertical displacement between time-steps as a covariate to control for the effects of slope on search mode. Additionally, we conduct an analysis using sex-specific regression coefficients and find that male and female GUTs do not differ substantially.

It is apparent from Fig. 2 that: (*i*) the exact threshold prediction of the MVT is sensitive to small changes in average return-rate, and (*ii*) this average return-rate is fairly variable over trips in our database. Our results can be made more robust by showing that although the exact threshold is hard to measure precisely, foragers actually use a continuous mapping between encounter rate and search mode. Specifically, the mushroom foraging data reveal a strong, continuous correspondence between the parameters controlling the effects of encounters on forager movement dynamics (Fig. 3) and the theoretically defined encounter rate since last encounter (Fig. 2). The regression coefficient of the relationship between the log of the encounter rate since last encounter, $\log(\frac{1}{s+1})$, and the log of the parameters controlling the effects of encounters on turning-angle, $\log(\psi_{[s]})$, is 1.20 (95% credible interval: 0.81, 1.60; r^2: 0.88). Likewise, the regression coefficient of the relationship between the log of the encounter rate since last encounter, $\log(\frac{1}{s+1})$, and the log of the parameters controlling the effects of encounters on step-size, $\log(|\phi_{[s]}|)$, is 1.70 (95% credible interval: 1.40, 2.0; r^2: 0.93). In other words, mushroom foragers smoothly transition from a low-velocity, high-angle, intrapatch search mode to a higher-velocity, lower-angle, interpatch search mode, in response to the encounter-rate since last encounter (Fig. 4).

Our statistical results correspond qualitatively to what L.P.-C. observed during his ethnographic observations of the mushroom foragers. Foragers initially search for any hint of the presence of mushrooms—e.g., distinctive bright colors, bumps of displaced
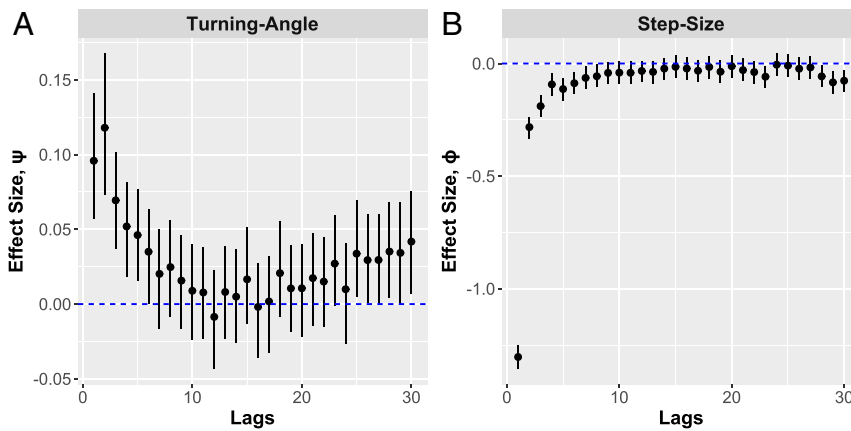
Fig. 3. Effects of encounters on turning-angle and step-size. Both *A* and *B* depict medians and 90% credible intervals. *A* shows $\psi_{[s]}$—the lagged effect of encounters on turning-angle—and *B* shows $\phi_{[s]}$—the lagged effect of encounters on step-size, for lags $s \in \{1, \ldots, 30\}$. Lagged encounters significantly affect both turning-angle and step-size, with effects lasting ∼6 to 9 time-steps (3.0 to 4.5 min) for turning angle, and ∼8 to 13 time-steps (4.0 to 6.5 min) for step-size. Each bar in the plot illustrates the value of the increment or decrement in turning-angle or step-size (*y* axis) as a function of the number of lags since last encounter (*x* axis). The number of lags for which the increment or decrement is significant is indicative of the length of time for which an encounter affects search mode.

soil or detritus from the growth of mushrooms below, or symbiotic trees or plants—using a linear and high-velocity interpatch search mode. Once they detect an edible mushroom, they quickly cut it off at its base and, then, using a slower and more tortuous intrapatch search mode, closely scan the surrounding area (1 to 5 m) to find the "brother" mushrooms. After depleting a local area of the easily located mushrooms, the foragers resume an interpatch search mode until they spot another mushroom or microhabitat clue signaling the presence of mushrooms.

Qualifications and Potential Issues. We note three potential issues affecting our model and analysis. First, since the mean encounter-rate is quite variable over trips in our data, we acknowledge that a fairly wide range of numerical predictions for optimal GUT—i.e., predictions of 8 to 21 time-step lags—are all plausible. More precise evaluations of the MVT using our methods could be conducted in systems where there is less variation in return-rate over trips. Alternatively, if mean return-rate is well explained by year, season, individual, or some other characteristic—and the dataset is large—predictions and statistical evaluations could be made more precise by structuring analyses by such variables.

Second, significant handling or processing time of resources might confound the interpretation of model parameters. If processing time after an encounter is large relative to the GPS sampling rate, then the parameters giving the effects of encounters on movement dynamics might reflect the behavioral response of item processing rather than intrapatch search over some range of lags. In the case of mushroom foraging, processing time is generally very brief, involving nothing more than the removal of attached soil or pine needles from the bottom of a harvested fruiting body, so it is unlikely to confound our inferences beyond a possible elevation of the effect sizes of parameters at a single lag. In some cases, foragers first place collected mushrooms into
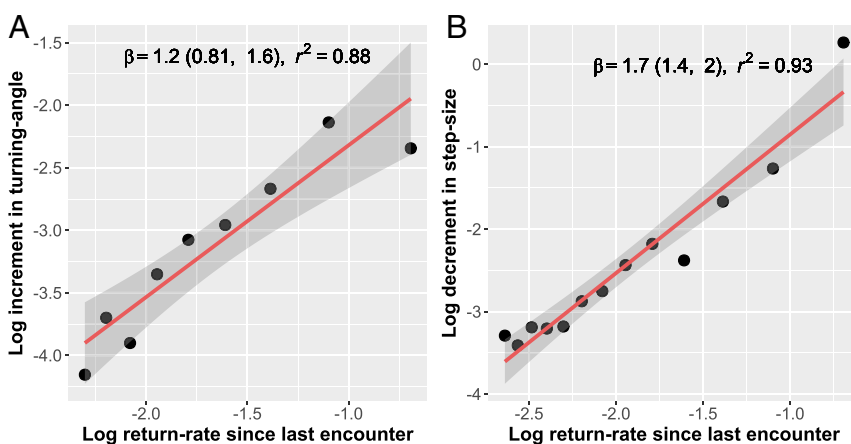

Fig. 4. Continuous relationship between search mode and encounter-rate since last encounter. *A* shows the relationship between the log encounter-rate since last encounter, $\log(\frac{1}{s+1})$, and the log of the regression coefficients giving the lagged effect of encounters on turning-angle, $\log(\psi_{[s]})$, for the lags with reliable effects, $s \in \{1, \ldots, 9\}$. *B* shows the relationship between the log encounter-rate since last encounter, $\log(\frac{1}{s+1})$, and the log of the absolute value of the regression coefficient giving the lagged effect of encounters on step-size, $\log(|\phi_{[s]}|)$, for the lags with reliable effects, $s \in \{1, \ldots, 13\}$. *A* and *B* show a strong continuous relationship between search mode *s* time-steps after encounter with a food item and the encounter-rate since that last encounter. *A* indicates that when the encounter-rate is relatively high, turning-angle changes are higher. This produces tortuous ARS when in a patch, and efficient, unidirectional movement when outside of a patch. *B* indicates that when the encounter rate is relatively high, step-size decrements are higher. This yields a slower search mode when in a patch and a higher velocity mode when outside of a patch.

hand-held plastic bags or buckets, and then, when a sufficient number of mushrooms have been gathered, they stop to clean and pack them into wicker baskets carried on their backs. These processing periods might lead to brief episodes of slow velocity on the GPS recordings that are not associated with encounters, leading to a downward shift in our estimates. Many of the foragers followed in this study, however, did not process items at all upon encounter, preferring to do it collectively with the rest of the group at the end of the day. In other cases of foraging, processing and handling time may not be negligible, and generalizations of our model that account for the effects of handling or processing time may be needed to appropriately examine search trajectories.

An additional concern about our results relates to the fact that mushroom hunting is a partly social activity. Foragers will sometimes spend time waiting for others before engaging in longer distance interpatch movement. These periods of waiting that are not triggered by mushroom encounters also have the potential to cause an underestimation of the extent to which encounters trigger ARS, since these waiting events lead to slower movement not associated with mushroom encounters. Nevertheless, we find strong and statistically reliable evidence of such an effect here, paralleling a similar study of Emberá Chamí blowgun hunters embarking on solitary hunts (34).

Discussion

The MVT has been widely influential in studies of nonhuman foraging (60, 61), especially in cases where resource patches can be easily defined or experimentally controlled. The MVT and related models have even been evaluated using archeological case studies (62). However, direct tests of the model in human foragers operating in natural environments have been hard to conduct (41). Here, we provide a quantitative test of the MVT using a database of high-resolution, encounter-annotated GPS tracks from mushroom foragers searching in a naturalistic setting.

As has been found in a study of artisanal fishers in the Commonwealth of Dominica (19) and a study of Emberá Chamí blowgun hunters pursuing small game in Colombia (34), we find evidence that Nahua mushroom foragers use encounter-conditional ARS heuristics when foraging. By extending the analysis to estimate both theoretical and empirical GUTs, we have been able to further demonstrate that these foragers use a form of ARS with a GUT that is parameterized close to the theoretical MVT optimum. Additionally, we provide a replicable statistical methodology that can be broadly applied to similar data obtained from the study of other human or nonhuman foragers.

We note here that a stochastic patch depletion and abandonment model developed by Oaten (50) generates predictions that can diverge from those of the deterministic MVT given by Charnov (11). Oaten's model is considerably more complicated than Charnov's but indicates that a forager might benefit from remaining in its current patch even if the marginal intrapatch encounter rate has declined below the average overall encounter-rate. This effect arises because the individual-level encounter history can provide the forager with information about the density of prey in the patch; an optimal forager can use this information strategically to increase returns. Future work might usefully explore if Oaten's model could be operationalized in such a way that it could be effectively tested using encounter-annotated GPS data like we have done here.

From Discrete Patches to Continuous Environments. To test the MVT with standard methods, the patches of an environment must be defined discretely. Such a classification of an environment is complicated by the fact that the relevant features of a resource distribution are often difficult to observe or measure, the patch boundaries diffuse, the patch locations ephemeral, and

the potential habitat range to be covered large (48). More generally, patches must normally be defined relative to the range of the foraging organism, its cognitive and other capacities, its needs for food and shelter, and its behavioral skills and proclivities (63). This entails the accumulation of a potentially daunting amount of species-specific information. At least in observational study of humans, the difficulty of identifying and characterizing discretely bounded environmental patches in a way that is independent of forager behavior has impeded, but not prevented, tests of the MVT (41). Although it may sometimes be necessary to define a discrete set of patches to test the MVT, our methodology for inferring GUTs from encounter-annotated GPS tracks mitigates the general need.

Our approach, however, could be improved by moving away from evaluations based solely on GUTs. While the length of time for which encounters affect search mode is an important part of ARS, so too is the overall magnitude of increments and decrements to step-size and turning-angle as a function of encounters. We have not yet explored how the magnitude of these changes relate to classic foraging models like the MVT.

Our approach here, though incomplete, is still a step toward extending the insights of early foraging theory models to contemporary algorithmic foraging models—for example, those based on encounter-contingent search strategies. Jointly, the MVT and encounter-contingent ARS models can lead to efficient search algorithms in cases where discrete patches are impractical or impossible to define, and behavioral outcomes must be generated in real-time. For example, robotic vacuum cleaners (64) can be programmed to use dust sensors in their intakes to vary their search speed as a function of the rate of dirt intake—with the units slowing their movement to more thoroughly vacuum areas with denser dirt deposits. By applying algorithms from foraging theory, like ARS heuristics and the MVT, engineers may be better able to optimize the design of such autonomous units.

Foraging Skill, Age, and Human Life History. Our focus on the proximate heuristics—sensu Tinbergen (65)—that shape successful foraging opens the possibility of studying how experience and socialization affect the acquisition of critical skills. Human life history is peculiar due to an extended period of juvenile dependence, which Kaplan et al. (66) argue was heavily shaped by a hominin commitment to exploiting a suite of high-quality, difficult-to-acquire resources; an enlarged brain, delayed adulthood, and significant investment in learning were entailed. González-Forero and coworkers (67, 68) use computational models to support the claim that human brain evolution is better explained by ecological factors, such as finding and catching food, rather than social challenges, such as formation of tactical coalitions. Providing empirical support for the argument that an extended period of learning is required to become a successful human forager, McElreath and Koster (69) examine a 20-y, longitudinal database of 147 Aché hunters, finding that peak hunting effectiveness is reached at about 40 y of age. Moreover, a large fraction of the variation in return-rates among human hunters arises from variation in encounter rates (70), demonstrating the importance of effective search heuristics in hunting success.

By combining the research methods presented here with the longitudinal, individual-level study design used by McElreath and Koster (69, 70), it should be possible to produce age-specific skill acquisition curves for search strategies, including an estimation of the time it takes to learn effective GUTs for a given resource type. Children start joining mushroom gathering trips when they are about 10 y old, and they continue foraging into adulthood. Foraging data collected over the developmental period paired with social network data (71) on teaching or coforaging could further test for evidence of social transmission of effective search behavior in a nonlaboratory setting (72).

Wider Importance of Search Optimization and Foraging Theory. The search behaviors analyzed here are ubiquitous and consequential in both ancient and modern times, for human and nonhuman foragers. While the MVT and foraging theory more broadly are instrumental to the analysis of hunter-gatherer adaptations, human life history, and our evolutionary origins (73), we all are foragers still. Software designers have looked to foraging models to aid in the design of internet search engines (7). Criminologists have used foraging decision models to investigate "prey" selection by automobile thieves (5) and the internet search behavior of sex offenders (74). Studies guided by models of search and prey selection can serve conservation biology by estimating the effects of current harvesting patterns on the middle- to long-term stability of prey populations (75–78). Environmental heterogeneity and the MVT are particularly important to studies of resource exploitation because they suggest that effective foragers will abandon a patch before fully depleting it of prey (8, 9, 79–82); our analysis illustrates that this same pattern should hold for continuous resource distributions as well as those clustered in discrete patches. Models of patch-residency times, like the MVT, combined with models of prey choice, are well poised to play a role in increasing the efficacy of integrated pest-management strategies (10), by illuminating how decoy crops can most efficiently be distributed and maintained. Cognitive scientists have even used foraging theory models to examine the ways in which our brains acquire and retrieve information (6, 83). It is easy to envision the application of high-efficiency search strategies in applied settings ranging from the design of robotic vacuum cleaners and product distribution warehouses to the implementation of search and rescue efforts. Greater understanding of the proximate heuristics underlying foraging decisions in patchy environments thus engages a broad array of scientific and practical endeavors that should benefit from greater understanding of how encounter-conditional search heuristics can be optimized.

Supporting Information. *SI Appendix* includes the results of robustness checks and provides statistical and modeling details.

Materials and Methods

Methods of data collection and analysis have been fully described in the main text. Additional methodological details and the results of robustness checks are included in *SI Appendix*. Analysis of data was conducted using R (84) and Rstan (85). The raw data and model code will be maintained at https://www.github.com/ctross/mushrooming (86).

The research protocol and consent process for this investigation were approved by the institutional committee at Posgrado Ciencias Biologicas at the National Autonomous University of Mexico. Respondents provided informed consent before participation.

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