Mobility-driven cultural transmission along the forager–collector continuum

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ABSTRACT

Hunter–gatherers mobility regimes are often treated as discrete adaptive strategies. Here we present a model of forager mobility which treats collectors and foragers as two ends of a continuous spectrum. We show that a mobility regime can be situated along this spectrum by specifying the number of foraging moves a group makes before returning to its home base. The model allows us to explore the behavioural space between forager (i.e. residential mobility) and collector (logistical mobility) adaptations. We discuss the heuristic value of the model by showing how it can be used to make testable predictions about the impact of mobility strategies on archaeological measures such as occupation intensity and raw-material transportation distance. We then use the model to investigate the impact of mobility on rates of cultural transmission. We show that mobility-driven cultural transmission may be equivalent to a Poisson process and that the time it takes for a cultural behaviour to be transmitted between two mobile groups is optimized when the mobility regime is somewhere between pure forager and pure collectors adaptations. In addition, we find that rates of cultural transmission decline in a very regular way, as the inverse of the square root of the number of moves made before returning to home base. This suggests that there is a mechanistic connection between the mean-squared displacement of hunter–gatherers in space and the transmission of cultural traits.

Introduction

Few ideas in hunter–gatherer archaeology have been as enduring as Binford's (1980) contrast between foragers and collectors. In this seminal paper, Binford described hunter–gatherer subsistence systems in terms of two organizational components, "mapping-on" and "logistic" strategies, and hunter–gatherer adaptations in terms of two idealized types. *Foragers* solve the adaptive challenge of acquiring resources by mapping-on, both spatially and temporally, to resource distributions. This is accomplished through residential moves, which bring the entire foraging group directly to targeted resource patches. By contrast, *collectors* occupy the same central place, or home base, for long periods of time and send small task groups to collect and bring back resources to camp. These two subsistence strategies have long been assumed to lead to predictable patterning of the archaeological record. For example, central place sites produced by collectors should be more intensively occupied and display a greater range of inter-site variability than those produced by foragers (Beck et al., 2002; Lieberman and Shea, 1994; Surovell, 2009; Zeanah, 2004). Binford has described the forager–collector model as a graded series of settlement system from simple to complex (Binford, 1980: 12). In practice, however, no attempt has ever

been made to develop a formal model to describe the whole spectrum of human mobility from central-based to free-wandering foraging. Given the fact that mobility is one of the main behavioural strategies by which human hunter–gatherers adapt to the temporal and spatial distribution of resource in their environment (Binford, 1980; Cashdan, 1992; Kelly, 1995; Marlowe, 2005), the risk of not exploring such model is that much of the potential variability in hunter–gatherer adaptations goes unrecognized.

The contributions of this paper are two fold. First, we develop a spatial model of mobility which fully describes the forager–collector continuum and allows us to explore the behavioural space between forager and collector adaptations. We discuss the archaeological relevance of the model by reviewing briefly how the different mobility regimes it generates impact typical archaeological measures such as lithic raw-material transport patterns and the intensity of site occupation (Brantingham, 2003; Surovell, 2009). Second, we focus on how mobility topologies affect rates of cultural transmission between groups. Specifically, we explore the simplest possible scenario of social transmission between two foragers occupying a bounded, but spatially continuous environment. Given different mobility strategies, ranging from collector to forager, we ask how long it takes for a cultural trait to be transmitted from one foraging group to the other. We are interested in specifying whether any particular mobility pattern maximizes rates of cultural transmission and, if so, what form does it take. Analyzing the distributions of the times before cultural

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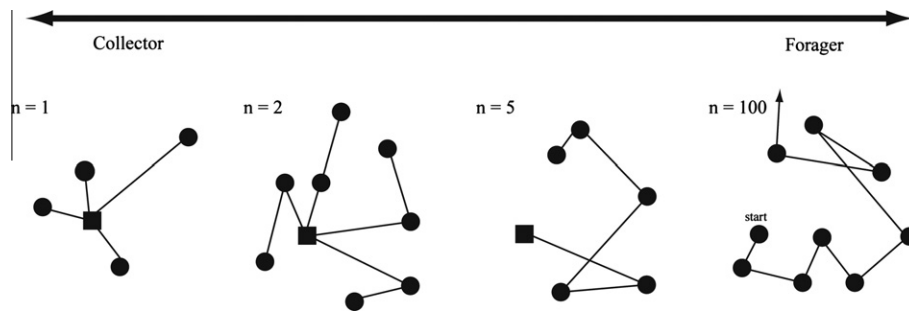
Fig. 1. Mobility regimes vary with the number of foraging moves *n* groups make before returning to home base (*black square*). When *n* = 1, groups make one move before returning to its home base. This situation is characteristic of extreme cases of central-place (*collector*) foraging. When *n* = 2, groups make two consecutive moves before returning to home base, when *n* = 5, they make five consecutive moves, etc. When *n* ≫ 1, groups multiply the number of residential moves over a long period of time and are unlikely to come back to their home base within this timeframe. This situation is characteristic of residential mobility (*forager*) foraging.

transmission occurs, we show that all mobility regimes distributed along the forager–collector continuum lead to transmission rates reminiscent of a Poisson process. We discuss the implications of this apparent mathematical regularity for understanding mobility-driven cultural transmission.

Modelling the forager–collector continuum

Hunter–gatherer mobility can be minimally described by the number of moves *n* a foraging group makes before returning to a central place. We are intentionally vague about the size and composition of the foraging group (e.g. solitary hunter, small group, band, etc.) noting only that mobility is necessary both for the generation of an archaeological record and for cultural transmission. When *n* = 1, a group makes one foraging trip and returns immediately to its home base (Fig. 1). This situation captures the essential properties of the *collector* mobility regime, specifically the frequent and deterministic reoccupation of a residential base and the infrequent occupation of locations where resources are extracted; the sites Binford (1980: 10) calls 'caches', 'field camps' and 'stations'. When *n* = 2, two foraging moves are made to two different activity sites before returning to the central place. As *n* increases, one approaches the forager end of the forager–collector spectrum. In the limit, *n* reaches infinity and hunter–gatherers only ever return to their starting point stochastically (Redner, 2001). In this last case, no one location acts as a central place or home base. This limit is a formal specification of "pure" residential mobility and is characteristic of the forager end of the forager–collector continuum. The impact of the variation along the forager–collector continuum on archaeological measures and behavioural processes of interest can be explored by varying the number *n* of consecutive moves groups make before returning to a home base.

So far our model is completely general. Decisions about where to move can take any number of forms. Movement choices can be modelled minimally with two variables: (1) the direction *β* in which to move; and (2) the distance *δ* to be moved (Brantingham, 2003, 2006; Turchin, 1998) (Fig. 2). It is thus possible to describe and explore a fully specified mode of the forager–collector continuum using only the three parameters *n*, *β* and *δ*.

We explore a simple model of foraging groups engaged in directionally unbiased random walks where each move is a Lévy flight. Let *β* be a uniformly distributed random variable ranging from 1° to 360°. The parameter *δ* is drawn from a Lévy distribution. The Lévy distribution has been widely used in physics and biology, notably to describe the foraging behaviours of animals (Bartumeus et al., 2003; Ramos-Fernández et al., 2004; Viswanathan et al., 1996, 1999) and modern human foragers (Brown et al., 2007, 2010). The Lévy distribution describes the probability that a forager makes a move of length *δ* as a negative power law:

$$p(\delta) = \delta^{-\mu}$$

where *μ* is a parameter ranging from 1 < *μ* ⩽ 3. As *μ* → 1, the distribution develops a 'fat tail' and longer moves become more common. At *μ* = 1 the distribution allows for infinitely long moves which are referred to as Cauchy flights (Desbois, 1992). When *μ* ⩾ 3, the majority of distances travelled will be short and the mobility pattern will approximate a simple random walk (Viswanathan et al., 1999). Animals and human movement distributions seem to lie somewhere between 1 < *μ* < 3 (Bartumeus et al., 2003; Brown et al., 2007; Viswanathan, 1996, 1999, 2010) and it has been shown mathematically that *μ* ≈ 2 optimizes search for randomly dispersed foraging target (Edwards et al., 2007; Turchin, 1998; Viswanathan et al., 1999). When *μ* ≈ 2, the Lévy distribution generates movement regimes which are dominated by short-distance moves but in which long-distance walks nonetheless occur (Fig. 3). It should be noted that our model is not dependent on the use of a Lévy distribution for determining distances. Other distributions could be used to test the robustness of our results. We suspect, however, that our qualitative results do not depend on the use of a Lévy distribution to determine move lengths. By contrast, as recognized in the conclusion, the assumption of unbiased movement directions likely has a significant impact on results (Turchin, 1996).

The forager–collector model and the archaeological record

With a mathematical specification of movement, our model of the forager–collector continuum is complete. It is now possible to use simulation to explore the region between *n* = 1 (collector) and *n* ≫ 1 (forager). The model has heuristic value because it can be used to generate testable predictions about how different mobility strategies impact archaeological measures which are
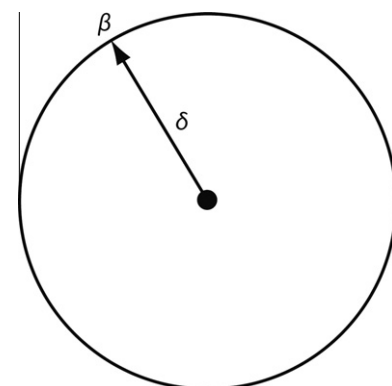

Fig. 2. Variables used to describe foraging movement during a single foraging move. Variable *β* denotes the direction of the movement and *δ* the distance moved.
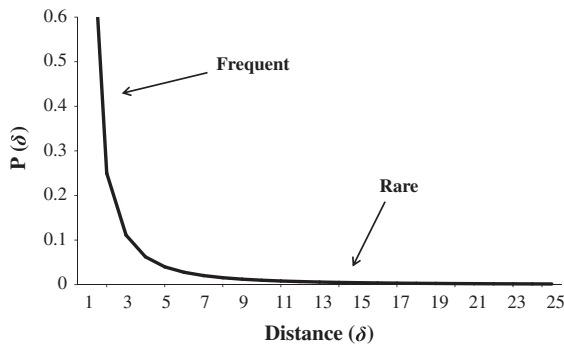
Fig. 3. Lévy probability distribution of move lengths δ when $\mu = 2$.

commonly used by archaeologists, such as the spatial distribution of archaeological sites and lithic-raw-material transport patterns.

Changes in n lead to quantitatively and qualitatively different foraging behaviours similar to how variation in μ affects the spatial density of foraging locations around a home base (see Brantingham and Tita, 2008). When n is small (i.e., collectors), movement is tightly tethered to the home base and, over many foraging trips, a dense area of repeated activity surrounding the home base develops. For a directionally unbiased system (i.e. β is a random variable drawn from a uniformly distribution ranging from 1° to 360°), the area of dense activity is disc-shaped (Fig. 4a) (Larralde et al., 1992). As n increases, a disc-like area of repeatedly exploited locations still develops around the home base, but a vast ring of sparsely occupied sites also appears on the periphery (Fig. 4b). In the forager limit ($n = \infty$) however, no particular location is favored and a disc-like region of intensive occupation does not develop. In a uniform environment with reflecting boundaries, all sites will eventually be exploited an equal number of times given infinite time (Redner, 2001). Therefore, our model predicts that the archaeological signature of a "pure" forager strategy is an even spatial distribution of sites all displaying equal occupation intensity.

The mobility strategies described by our model of the forager–collector continuum also affect raw-material transport distances (Brantingham, 2003, 2006). Assuming that raw material are transported and discarded at the endpoints of all moves, when $n = 1$, the distribution of the linear distances between home base and discard locations maps directly onto the Lévy distribution, with the most frequent raw-material transport distances being close to the home base. As n increases towards a forager adaptation, the mean transport distance increases and a prominent modal transport distance emerges (Fig. 5 and 6) (Denny and Gaines, 2002). For all mobility adaptations except pure collectors, our model predicts that the majority of raw materials will be transported some intermediate distance from their procurement point.

In sum, our formal model of the forager–collector continuum, though simple, is useful from the point of view of hunter–gatherer archaeology. The model allows us to link mobility patterns to the archaeological record. By exploring its parameter space, we can derive exhaustive quantitative descriptions of how various features of the archaeological record pattern under different mobility regimes.

Mobility and cultural transmission

We extend Binford's work on the archaeological implications of the forager–collector model to investigate how different mobility regimes impact cultural transmission. Theoretical models suggest that a capacity for cultural transmission is favored by natural selection under a wide range of environmental conditions (Boyd and Richerson, 1985, 1989, 1995; Henrich and Boyd, 1998; McElreath and Strimling, 2008; Whitehead, 2007). It is thus not surprising that social learning is being increasingly recognized as a potential determinant of human and animal foraging behaviour (Avital and Jablonka, 2000; Byrne, 2007; Fragasky and Perry, 2003; Galef and Giraldeau, 2001; Galef, 1996; Lefebvre, 2000; Lefebvre and Giraldeau, 1994; Lefebvre and Palameta, 1988; Richerson and Boyd, 2005). Formal models of cultural transmission have tended to deal mainly with within-group transmission dynamic and have rarely treated space explicitly (Boyd and Richerson, 1985; Cavalli-Sforza and Feldman, 1981; Durham, 1991; Feldman and Cavalli-Sforza, 1976; Henrich, 2001b; Laland et al., 1995). Given that human populations were exclusively composed of small and dispersed mobile groups until the advent of plant domestication around 10,000 years ago (Klein, 2009), mobility was almost certainly a prime factor influencing social transmission dynamics within a population of forager groups. Understanding how these small dispersed groups encountered one another is important if we are to understand the context in which reliance on social learning has evolved. Despite the fact that the dynamics of cultural transmission is a topic of growing importance in anthropology (Boyd and Richerson, 1985; Cavalli-Sforza and Feldman, 1981; Durham, 1991; Henrich, 2001a, 2004; McElreath et al., 2003; Mesoudi et al., 2006; Nettle and Dunbar, 1997; Richerson and Boyd, 2005; Shennan, 2001), and archaeology (Brantingham, 2007; Eerkens and Lipo, 2005, 2007; Hamilton and Buchanan, 2009; Mesoudi and O'Brien, 2008; Powell et al., 2009; Shennan, 2000, 2001; Shennan, 2008), we are not aware of any studies that address
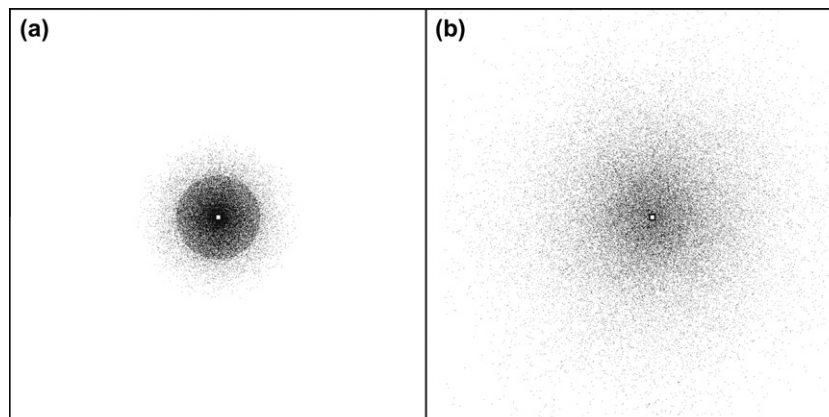

Fig. 4. Activity intensity around home base. (a) When n is small, the majority of the foraging trips are concentrated around the home base (white square); (b) When n is large, foraging sites are spread through space. Simulation consisted of 50,000 individual moves.
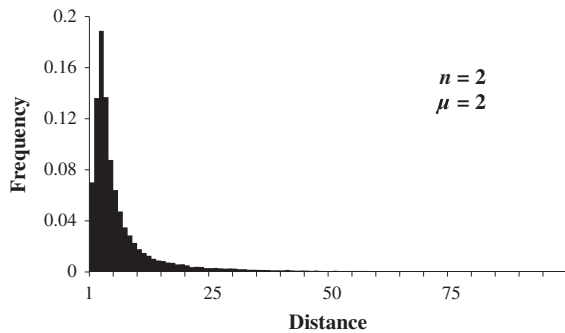
Fig. 5. Relative frequency distribution of raw-material transport distances from home base, $n = 2$ and $\mu = 2$. Total number of run = 45,000.
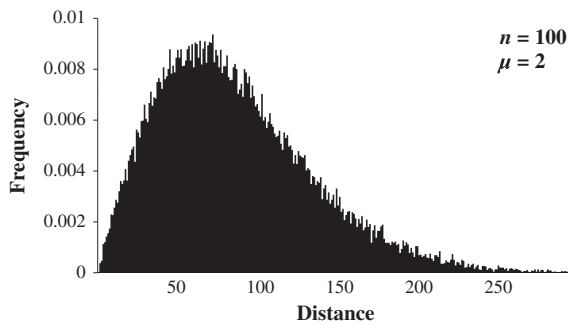

Fig. 6. Relative frequency distribution of raw-material transport distances from home base, $n = 100$ and $\mu = 2$. Total number of run = 45,000.

explicitly the relationship between mobility and cultural transmission. Deploying our mobility model in this context, we ask how changes in n affect the rate of transmission of a cultural trait. This research question is analogous to the studies that seek to understand how natural selection shapes the mobility patterns of a species in order to maximize currencies such as mate and prey encounters or predator avoidance (Bartumeus et al., 2008; Charnov, 1976; Gerritsen, 1980; Getty and Pulliam, 1991; Holling, 1959; Lee et al., 2006; Lewis, 2003; Lima and Dill, 1990; Nakajima, 2001; Shipley et al., 1996; Stephens and Krebs, 1986; Visser and Kiørboe, 2006; Viswanathan et al., 1996, 1999). Here we want to understand which part of the forager–collector continuum maximizes the rate at which cultural behaviours are transmitted.

Rates of cultural transmission vary non-linearly with the number of foraging moves

To control for other potentially important variables such as population size and density, we develop the simplest model possible that allows us to study the impact of mobility topology on rates of cultural transmission. Thus, our simulation contains only two foraging groups and focuses only on the transmission of a cultural behaviour between them. The environment is a spatially continuous environment (i.e., not a lattice) with reflecting boundary conditions. We only consider the case where the two foraging groups have starting locations (home bases) 10 arbitrary spatial units apart. The home bases are placed near the centre of a 10,000 by 10,000 unit box, thus ensuring that edge effects do not arise. We use a truncated Lévy distribution with $\mu = 2$, so that the minimum and maximum possible lengths for a single move is 1 and 100 spatial units, respectively. One of the foraging groups starts the simulation with a novel cultural trait. When the two groups encounter one another (i.e., when the distance between them is $\leqslant 1$ unit), cultural transmission occurs and the second

group acquires the novel trait. While the assumption that an encounter between the two groups necessarily results in cultural transmission might not be realistic, we found that relaxing it (for instance, by assuming that transmission happens during an encounter with fixed probability p) does not qualitatively affect our results. With both foragers making one move every time step, we tallied the number of time steps necessary for cultural transmission to occur. Simulations were repeated 2500 times for each selected values of n between 1 (i.e., collector) and 200 (i.e., forager).

The results show that n has a dramatic impact on the average number of time steps that are necessary for transmission to occur. Surprisingly, however, this impact is non-linear with a distinct minimum (Fig. 7). Time for cultural transmission appears to be optimized when $n \approx 6$; i.e., both the mean and the standard deviation of the number of time steps necessary for cultural transmission to take place are simultaneously minimized. It is important to note that the specific numerical results presented in this paper (such as the value $n \approx 6$ mentioned above) should not be over-interpreted, since they are dependent on the space between the home bases of foragers as well as the particular mechanisms that determine foraging moves. Nonetheless, the qualitative pattern holds for a wide array of initial conditions. For example, changing the distance between the home bases does not change the general shape of the relationship between n and transmission time. Our observations would likely break down, however, if biases in the directionality of movement were introduced (i.e., β was drawn from a non-uniform distribution) (Turchin, 1996). While an assumption of unbiased directionality is not entirely unrealistic, it is important to note that there are contexts in which forager movements is constrained by topographic or ecological structure.

Mobility-driven cultural transmission resembles a Poisson process

Histograms of the time to cultural transmission underscore a second interesting aspect of the impact of n on cultural transmission (Fig. 8). Higher values of n lead to flatter and longer distributions of time to cultural transmission. This means that as n increases, it typically takes more time before cultural transmission occurs. For example, when $n = 4$, the maximum time for transmission observed in the 2500 independent simulations is $t = 4923$. By contrast, when $n = 100$, the maximum increased to $t = 11,805$. But more interestingly, the distributions of time to transmission are exponential for all values of n. That the transmission times are exponentially distributed for all values of n suggests that
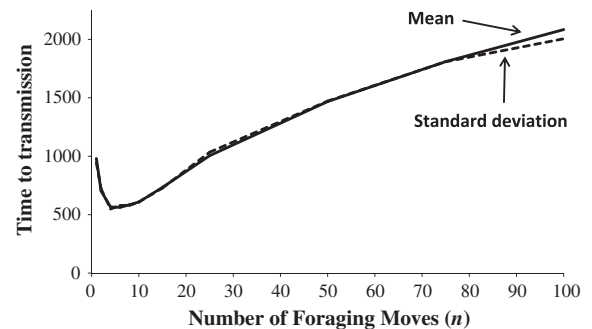

Fig. 7. Number of time steps before cultural transmission occurs as a function of the number of foraging moves (n). Shown are the mean and standard deviation of time to transmission. Transmission time initially declines as the number of foraging moves increases. A minimum is reached for mobility adaptations that string together a small number of moves before returning to a home base ($n \approx 6$) and then rises monotonically as mobility approach a pure forager strategy.
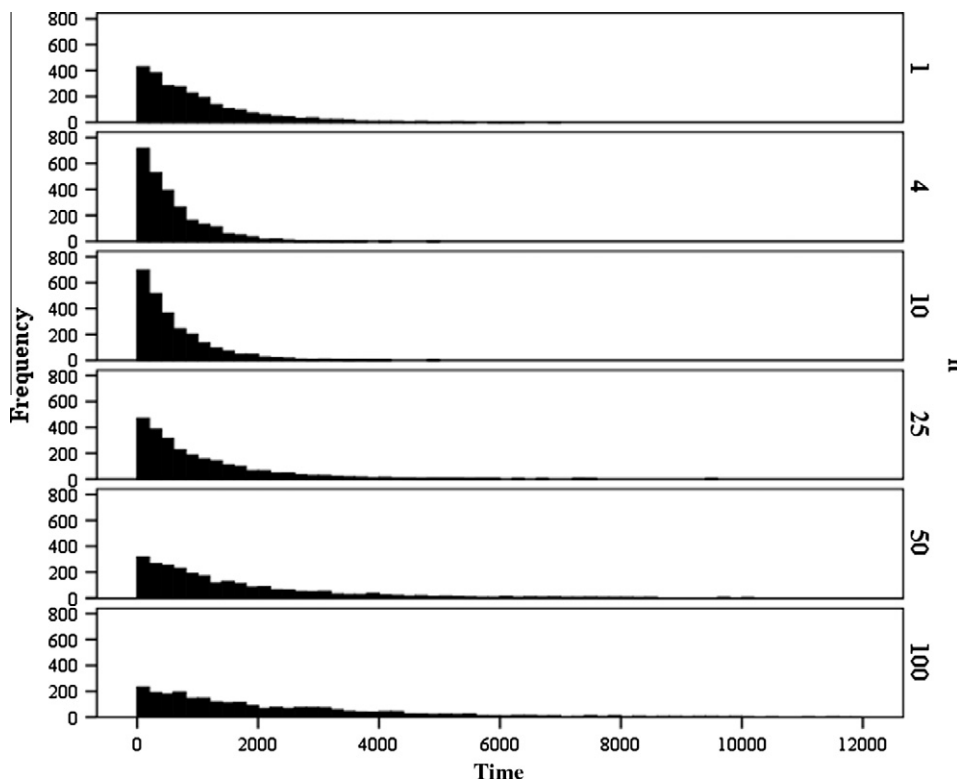
Fig. 8. Frequency histograms of number of time steps before cultural transmission occurs for different number of foraging moves n. Data in each case represent the results from 2500 separate simulations. Increases in n lead to flatter and longer distributions. The distributions are not significantly different than exponential distribution using one-sample Kolmogorov–Smirnov Z tests. For example, when $n = 4$, Kolmogorov–Smirnov $Z = 0.695$, $p = 0.720$, when $n = 100$, $Z = 1.153$, $p = 0.140$. The exponential regressions that best fit the histograms for $n = 4$ and $n = 100$ are respectively: $y = 160.57e^{-0.001x}$ and $y = 40.562e^{-0.0004x}$.

mobility-driven cultural transmission can be described as a Poisson process. A Poisson process is a continuous-time stochastic process where events occur in time at a constant rate λ and are statistically independent of one another. The waiting time *between* Poisson events is exponentially distributed with a mean equal to the standard deviation. Fig. 7 shows that the mean and standard deviation of transmission times are indeed strongly similar along the forager–collector continuum, suggesting that cultural transmission is Poisson-like for all types of mobility regimes.

The fact that mobility-driven cultural transmission appears to be equivalent to a Poisson process means that we can account for the impact of mobility on cultural transmission through the single parameter of the exponential function, λ:

$$p_n(\tau) = \alpha e^{-\lambda \tau}$$

where α is a constant related to sample size, τ is the time it takes to transmit the cultural trait, e is the base of the natural logarithm, and λ is the rate of cultural transmission. This equation describes the typical number of time steps that are necessary for cultural transmission to happen between two mobile groups. When $n = 4$, the exponential regression that best fits the histogram distribution of time to transmission yields $\lambda = 0.002$, or an average of one transmission event every 500 foraging moves (see Fig. 8). When $n = 100$, by contrast, $\lambda = 0.0004$, or an average of one transmission event per 2500 foraging moves. Thus, a 25 fold increase in the number of foraging moves (from $n = 4$ to $n = 100$) leads only to a five fold increase in the expected time it will take for cultural transmission to occur.

Extracting λ from the best fit exponential regressions of cultural transmission time against n, it is clear that the relationship between λ and n is non-linear (Fig. 9a). Values of λ peak between $2 \leqslant n \leqslant 15$ and appear to be constant over this range. We expect, however, the curve to be smooth with a well-defined maximum.

Indeed, the expected time to transmission seen in Fig. 9a should be simply the inverse of the pattern seen in Fig. 7, since the mean waiting time for a Poisson process is $1/\lambda$. Fig. 9b shows that the inverse of the mean time to transmission does follow the same path as that plotted in Fig. 9a. We attribute the plateau in values between $2 \leqslant n \leqslant 15$ in Fig. 9a to the error introduced by the least squares fitting of exponential curves to our simulation data.

Rates cultural transmission decrease as the inverse of the square root of the number of foraging moves

If we focus only the tail of the distribution for $n \geqslant 15$, a power function provides a good fit to the data (Fig. 9). It seems therefore possible to describe the impact of n on cultural transmission rate λ for mobility regimes at intermediate positions along the forager–collector continuum by the function:

$$\lambda(n) \approx \frac{k}{\sqrt{n}}$$

where k is a scaling constant that is linked to sample size. This result is strikingly similar to the well-known formula describing the mean-squared displacement of a random walker. Specifically, the mean distance travelled by a random walker *increases* as the square root of the number of steps taken (Denny and Gaines, 2002). Here, however, the mean cultural transmission rate *decreases* as the inverse of the square root of the number of foraging moves. Thus, cultural transmission tends to get slower as one moves towards the forager end of the forager–collector continuum. Overall, these results suggest that changes in mobility topology from collectors to foragers have a very regular impact on rates of cultural transmission.
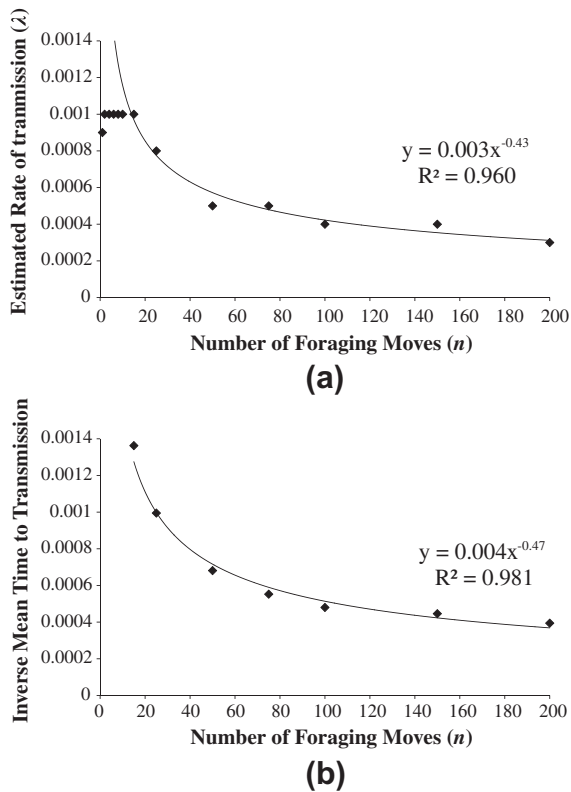
Fig. 9. (a) Estimated rate of transmission (λ), extracted from the exponential regressions that best fit the distribution of time to cultural transmission (see Fig. 8) as a function of the number of foraging moves (n); (b) The inverse of the mean time to transmission calculated from the simulations (see Fig. 7) as a function of the number of foraging moves (n). In both (a) and (b), a power law regression fits the data for $n \geqslant 15$ with an exponent of ≈ 0.5.

On a related point, we have noted that as one moves closer to a pure forager strategy, the decline in the rate of cultural transmission is very regular, and consistent with a model of mean transmission rates decreasing as the inverse of the square root of the number of foraging moves. This suggests that there is a mechanistic connection between the mean-squared displacement of foragers in their spatial environments and the transmission of cultural traits.

We have also shown that for any given mobility strategy, the time it takes for a cultural trait to be transmitted between two groups is exponentially distributed. This relationship is remarkably regular across all values of n and suggests that mobility-driven cultural transmission is equivalent to a Poisson process. We find this result to be particularly important because Poisson processes are the continuous-time equivalent of the discrete-time Bernoulli processes. Discrete-time Bernoulli processes lie at the heart of many non-spatial models of cultural transmission, where they are used to conceptualize random imitation (e.g. Boyd and Richerson, 1985). That mobility-driven cultural transmission in an explicitly defined spatial environment leads to a transmission dynamic that is equivalent to these discrete-time processes suggests that the assumption of random imitation is not necessarily invalid for spatially structured populations.

In sum, the mobility model presented here provides a starting point for a more comprehensive and quantitative approach to hunter–gatherer mobility and its impact on processes such as cultural transmission. By stripping the model to its key components and studying the simplest possible case of cultural transmission between two forager groups, we were able to untangle the fundamental dynamics of mobility-driven cultural transmission. We see this model as a springboard for many theoretical and empirical studies of cultural transmission in spatially structured environment. For instance, how important is mobility, as opposed to other variables such as population density, in explaining the rates of spread of cultural behaviours in a population of foraging groups? Also, because forager's mobility is influenced by numerous ecological factors such as the degree of seasonality and resource density (Kelly, 1995), our model provides us with a means to bridge cultural transmission processes with these ecological variables and make predictions about the way rates of cultural transmission should vary with them.

Discussion

We have shown in this paper that it is possible to describe the forager–collector continuum with a simple model composed of only three variables, n, β and δ, which describe, respectively, the number of foraging moves before returning to home base, the direction of movement, and the distance of movement. This model may seem unrealistic in some respects. We believe, however, that it is essential to understand the fundamental dynamics of such a simple model before adding in complexities that would bring it closer to real-world settings. For example, it is clearly desirable to investigate how directionally biased patterns of movement impact the results presented here. However, understanding the impact of directional biases would be difficult without a firm grasp of the baseline dynamic of forager–collector mobility. The model presented in this paper offers one attempt at understanding such baseline dynamics.

Our primary focus here has been on how various mobility strategies impact rates of cultural transmission. Several broad observations are worth making on the basis of our model. First, the relationship between the characteristic time it takes for a cultural trait to be transmitted between two groups, and the number of foraging moves n these two groups make before returning to their home base is non-linear. The average transmission time starts relatively high among collectors (i.e., logistical mobility strategy), declines towards some minimum where mobility strategies string together a small number of moves, and then rises again as mobility approaches a "pure" foraging (i.e., residential mobility strategy). The mobility strategy that optimizes rates of cultural transmission is thus neither at the collector, nor the forager end of the mobility spectrum, but rather somewhere in between.

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