Scaling of Hunter-Gatherer Camp Size and Human Sociality

José Lobo, Todd Whitelaw, Luís M. A. Bettencourt, Polly Wiessner, Michael E. Smith, and Scott Ortman

One of the most common tendencies of human settlements is for larger settlements to display higher population densities. Work in urban science and archaeology suggests that this densification pattern reflects an emergent spatial equilibrium where individuals balance movement costs with social interaction benefits, leading to increases in aggregate productivity and social interdependence. The temporary camps created by hunters and gatherers exhibit a tendency to become less dense with their population size. The different manner in which hunter-gatherer groups express their sociality in residential space suggests that they typically lack the social structures and material technologies necessary for humans to live at greater spatial densities in permanent settlements. Here we examine why this difference occurs and consider conditions under which hunter-gatherer groups may transition to sedentism and densification. We investigate the relationship between population and area in hunter-gatherer camps using a data set representing a large cross-cultural sample derived from the ethnographic literature. We present a model based on the interplay between social interactions and scalar stress that describes the observed patterns among mobile hunter-gatherers. We find that the transition to a densification scheme does not necessary involve domestic food production, only surpluses and storable resources.

A defining characteristic of *Homo sapiens* is ultrasociality, which involves interacting and cooperating with individuals far beyond the immediate family group. One of the most important physical manifestations of this behavior is the concentration of people in space and time. Growth in the population size of the largest communities in settlement systems is interpreted by many scholars as the result of the overall net advantages of social agglomeration over dispersion, whenever the former is feasible. Indeed, the outstanding spatial feature of contemporary urban areas is their high population densities, which are much greater than those of premodern settlements (Bloom, Canning, and Fink 2008; Lees 2015). Urban economists and economic geographers have long attempted to explain the origin and maintenance of high-density settlements as resulting from the net benefits of socioeconomic interactions facilitated by close proximity (Duranton and Puga 2004; Fujita, Krugman, and Venables 1999; Henderson 1988). Recent observations in sociology, archaeology, and anthropology suggest that these advantages are quite general and do not require formal markets, modern administrative or political structures, wage labor, or industrialization to be realized (Lobo et al. 2019; Ortman and Coffey 2017; Ortman et al. 2016; Smith 2019). These studies have shown that permanent settlements typically densify at consistent rates as their populations grow, in an open-ended way, in a wide range of societies past and present.

In contrast, several studies have found that the temporary camps created by many hunting and gathering groups generally become less dense as the number of people camping together increases (Fletcher 1990; Hamilton, Buchanan, and Walker 2018; Whitelaw 1991; Wiessner 1974). This strikingly different pattern raises several important questions regarding the cultural evolution of human spatial behavior, the differences in human social life implied by the densification versus de-densification regimes, and the conditions that enable a transition to sedentism. In this paper, we develop a framework for incorporating hunter-gatherers into the continuum of human spatial behavior, from temporary camps to permanent settlements, and we consider the conditions that must be met for the mobile scaling pattern characterized by de-densification to transition to the settled scaling pattern, in which densification is typical.

A wide array of hunting and gathering lifestyles has provided extraordinarily successful adaptations, deeply rooted in our evolutionary history, which have enabled humanity to spread across the globe (Bowles and Gintis 2011; Cavalli-Sforza,

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Menozzi, and Piazza 1994; Henrich 2015; Shennan 2002; Wilson 2002). This way of life is also remarkably stable and sustainable, exhibiting slow rates of social, environmental, and technological change in comparison with more settled and denser societies (Perreault 2012; Powell, Shennan, and Thomas 2009). Given these general observations, it is striking that over the past 10,000 years most human communities have transitioned to a type of social organization characterized by spatial agglomeration and the growth of regional urban systems (De Vries 2006; Fletcher 1995; Glaeser 2011; Jacobs 1969; Morris 2013; Ucko, Tringham, and Dimbleby 1972; Wrigley 2016).

Settlement scaling theory—the systematic study of how population size is related to other socioeconomic and physical characteristics of human aggregations—builds on the observations, long recognized in anthropology and related fields, that population size is both a determinant and a consequence of human social development, and that settlement size is a strong correlate of the rates and magnitudes of many social and ecological processes in human societies (Carneiro 2000; Chambelain 2006; Chick 1997; Johnson and Earle 2000; Turchin et al. 2018). Here we focus on how the areal extent of an agglomeration relates to its population. Although this is a simple and straightforward relationship, it is revealing of deeper dynamics because the area occupied by a human group relative to its population is itself indicative of the behaviors and social institutions that structure interactions among the individuals involved. The relevant theory has been explored widely with regard to sedentary agglomerations (Bettencourt 2013, 2014; Ortman et al. 2014). Here, we extend this framework to encompass short- and longer-term hunter-gatherer agglomerations.

In the following sections, we first review a series of factors that influence the size and density of hunter-gatherer camps. Then, we propose some simple quantitative theory that addresses conditions that favor mobility versus sedentism and the effects of interaction and social distance for camp density. Taken together, our results suggest that permanent settlements create opportunities for the intensification of human interactions, and associated socioeconomic and cultural outputs, in ways not characteristic of mobile hunter-gatherer adaptations. The manifestly different manner in which hunter-gatherer groups express their sociality in residential space suggests that they typically lack the social structures and material technologies necessary for humans to live at greater spatial densities in permanent settlements. In this way, sedentism would appear to be a key indicator of the appearance of these innovations.

Human Sociality and Physical Space

At the most fundamental level, we take human societies to be groups of people integrated by relationships, contacts, shared cultural traditions, and exchanges embedded in physical space (at least until very recently). As a consequence, the resulting spatial properties of human groups reflect the character of the interactions through which individuals accrue net benefits from others. There are of course many costs and disadvantages to agglomeration—disease, potential for conflicts to escalate, annoying neighbors, loud young children, etc.—but the fact of agglomeration indicates that benefits (or needs fulfilled) outweigh the disadvantages. In many small-scale societies there is a strong relationship between social distance and physical distance, such that friends and relatives reside nearer to each other than newcomers, strangers, or outcasts do (Wiseman 2014, 2016). So although proximity facilitates and implies more frequent contact (Hill et al. 2011, 2014), it may also signal a difference in the type of social interaction involved. All social interaction requires movement and communication across space and therefore entails an expenditure of time and effort; that is, it has an energetic cost. Physical distance also affects the senses, as vision, hearing, smell, and touch all decay with distance (Hall 1966; Moore 1996). As a result, one would expect the spatial organization of both temporary camps and permanent settlements to reflect patterns of communication, interaction, and residential group integration.

Among documented hunter-gatherers there is a great diversity of lifeways, from small and highly mobile groups following seasonal migratory patterns to large semisedentary and even sedentary groups that specialize in the management and storage of key resources as dietary staples (Ames 1994; Kelly 2013). This diversity of lifeways can be encapsulated in the different manners that hunter-gatherers deal with risk and uncertainty in their environments, that is, whether they use social techniques of risk sharing or rely heavily on storage (Wiessner 1977; Woodburn 1982). While conflating multiple characteristics, the literature broadly polarizes/dichotomizes these two modes of living as mobile versus sedentary hunter-gatherers, a simplified distinction followed here. The literature also emphasizes that hunter-gatherer settlement involves both residential and logistical mobility, with the former referring to the movement of residential base camps and the latter referring to the movements of specialized task groups for hunting or foraging activities (Binford 1980). Here, we focus primarily on the properties of residential base camps.

Gould and Yellen (1987) focus on the determinants of household spacing in residential base camps, a feature that ultimately determines the areal extent of camps. They identify the following factors: construction technology, resource endowments, climate, household interdependencies, degree of relatedness among members of different households, defense from predation, and group size. In addition to these, cooperative breeding and child-rearing also affect patterns of proximity (Hrdy 2009; Kramer 2010; Lee 2018). Some but not all of these factors have counterparts in permanent settlements, including in cities.

Although mobile hunter-gatherers do aggregate periodically, residential base camps typically consist of just a few families. Most camps are ephemeral, being occupied only for days or weeks and rarely for more than a season. The basal units of these camps are nuclear families that sleep in the same shelter (huts, tents, windbreaks, etc.) and associate strongly on a daily basis with other members of their extended family and with a small number of other families camping nearby. Small groups of extended families also regularly associate with one other, sharing access rights to a particular territory that they exploit for its plant and animal resources. Others can gain access to these areas if they maintain appropriate social ties. Accordingly, camps change in composition as visitors come and go. The resulting groups, often referred to as bands, usually contain 20–30 individuals (Hamilton, Buchanan, and Walker 2018; Kelly 2013).

In larger camps, extended families usually camp in a relatively dense cluster, with open space between additional extended-family clusters. If multiple bands come together for sharing, exchanging, socializing, and/or other activities, each band tends to stay distinct, camping somewhat apart from the others (Kelly 2013; Shott 2004). For example, in Plains Indian aggregation sites, the members of each individual band located their shelters in a cluster, spatially set off from other such clusters (Banks and Snortland 1995; Hassrick 1964). Each level of social group in a camp behaves essentially as a distinguishable module whose identity is represented and reinforced via spatial distancing from other modules (Hamilton et al. 2007). Thus, assembling a camp entails a process where modules are not simply added, but rather are placed more loosely together with extra spatial buffering between them. This pattern suggests that, in general, the population density of hunter-gatherer camps should decrease as the number of families (modules) who are camping together increases (Whitelaw 1991, 1994).

An additional factor that appears to influence the density of hunter-gatherer camps is the interface between subsistence and human psychological predispositions. In most hunter-gatherer societies there is a norm of food sharing, where camp mates can ask for food with the expectation of being given some, with only a general obligation to reciprocate in the future (Kaplan and Hill 1985; Kelly 2013; Woodburn 1982). This is especially true for foods that come in large packages. For close kin, a norm of generalized food sharing is consistent with the concept of "kin selection" in the evolutionary theory of cooperation (Hamilton 1963, 1964*a*, 1964*b*; Trivers 1971), but as the camp grows in population, the average relatedness and familiarity between individuals will decline. As a result, individuals often do not want to share with everybody, even when they could (Dyble et al. 2016; Schnegg 2016). The easiest way to regulate the frequency of solicitations from camp mates is through the insulation of physical distance (Whitelaw 1991, 1994). Willingness to share is also affected by other considerations, such as food risk, resource package size, and preservability. Still, other important aspects of human sharing, namely, cooperative child-rearing would have been facilitated by households' proximity within camps (Hrdy 2009; Kramer 2010; Lee 2018). These factors, in combination with the management of sharing as a social norm, should favor decreasing camp density as camp population increases.

Finally, as with any human society, hunter-gatherer groups must manage, minimize, and resolve conflict within the group. Mobile foraging societies have many social mechanisms for conflict avoidance, such as mediation or rules that structure relationships and specify with whom one may joke or to whom one must show deference. However, in the face of severe conflict, most hunter-gatherers disperse spatially until tempers cool. The most salient contrast with societies having permanent or semipermanent settlements is that these have a variety of social conventions or formal institutions to manage conflict without dispersal, as well as physical infrastructures (i.e., walls, enclosed dwellings, household compounds) that shield individuals and their property from others, thereby reducing potential conflicts (Bowles and Choi 2013; Kuijt 2000, 2008; Whitelaw 1991, 1994). These social institutions and physical infrastructures decrease the costs of close proximity and open up possibilities for other forms of interdependence and interaction between people who are not closely related.

Spatial Arrangements in Mobile Hunter-Gatherer Camps: A Model

We now turn to the quantitative consequences of the features of social relations and spatial arrangements in hunter-gatherer camps described above. We acknowledge debates concerning the use of recent hunter-gatherer groups as models for prehistoric foragers (Lee 1992; Lee and Guenther 1995; Marlowe 2005; Wilmsen 1989; Wobst 1978) but take it as uncontroversial that ethnographically documented mobile hunter-gatherers lived a nonsedentary lifestyle and thus present a clear contrast to more sedentary societies (past and present). In this context, we show that basic spatial properties of camps can be understood using simple considerations of (1) density-dependent costs (including energy requirements) and social interactions, (2) resource availability, and (3) the translation of social distance between groups and individuals, based on kinship and familiarity, into physical distance inside a camp. The resulting framework leads to several expectations regarding the relationship between camp population and area that we explore using ethnographic information in the remainder of the paper.

Anthropologists who have examined spatial arrangements within hunter-gatherer camps have generally not observed the in-filling of physical space—physical structures and the establishment of open communal space—characteristic of permanent settlements (Binford 1991; Gargett and Hayden 1991; Memmott 2002; O'Connell 1977; Turnbull 1961, 1966; Yellen 1977). Rather, households tend to arrange themselves spatially in ways that regulate interaction and permit some privacy. Rather than seeing residual organizations that adapt over the medium and longer term to already established physically defined spaces, the frequent reestablishment of the camps by mobile foragers makes it easier to see the mappings of social relations onto space.

A well-known arrangement, described by Wiessner (1974) for mid-twentieth-century San (Ju|'hoansi) camps, is a perimeter-area occupancy pattern. In this arrangement, households camp on the perimeter of the camp, typically an approximation to a circle, and may use the corresponding circumscribed area as social interaction space. In this circumstance, as noted by Wiessner, the population of the camp, N, will be distributed along the length of the perimeter, which can be approximated as the square root of the camp's area so that $N \sim A^{1/2}$. Thus, an expression for area as a function of population is $A(N) = aN^2$, with the constant a representing the average area taken up by a single shelter. The consequence of this spatial arrangement is that, as the group size increases, the area A grows proportionately to the square of the population, such that the population density ($n = N/A$) decreases rapidly: $N/A = N/aN^2 = a/N$. This de-densification helps to regulate potential conflicts while still allowing for some beneficial interactions. However, this area-perimeter spatial arrangement does not appear to characterize most (particularly smaller) hunter-gatherer camps and the empirically observed exponents for the population-area relationship are typically less than two, as we show below. It might be that such formalized interaction spaces are not required in small camps of an extended family (fig. 1).

There are three general features of mobile hunter-gatherer spatial behavior that we seek to capture in a more general model: (1) temporality, with a fission-fusion dynamic in camp size tailored to patterns of resource availability and use, (2) the general decrease in density of camps with increase in population size, and (3) a spatial arrangement within camps where more related groups (in biological and social terms) camp closer together than less related groups. We will see that, taken together, these three phenomena can be incorporated into a framework that highlights the conditions under which we might expect hunter-gatherer groups to transition from temporary camps to more permanent settlements. The ideas embedded in this model have been identified in previous studies, as described above. What we attempt to do here is put them together in a formal framework. The resulting model is not intended to predict the exact realized properties of individual camps, but rather the average relationships among properties across camps. We would expect additional contextual factors that are not included in this model to affect the extent to which average relationships are apparent in specific instances.

We first consider factors that encourage group camping versus dispersal. We begin by noting that, regardless of the detailed spatial arrangement of people in a foraging area, the average per capita rate of energy capture from foraging, r_E, and the average per capita rate of social production (mate selection, information sharing, knowledge creation, etc.), r_S, are both dependent on population density. It is important to note that several additional dimensions of hunter-gatherer settlements, including the frequency of residential mobility and the distance covered on logistical mobility, affect the likelihood and intensity of overall forager interactions within a regional population (Barton et al. 2011; Premo 2016). For the model presented here, we consider the residential base camp density as a key determinant of average local social interaction rates, acknowledging that these additional dimensions may affect the short-term incorporation of more socially distant individuals in camps. Overall, the social production rate r_S can be expected to increase with camp density, as social encounters become more frequent and probable.

However, with respect to the rate of energy capture, r_E, there is likely an initial increase with density (based on sharing information about the location of resources and the coordination of foraging activities) but then a rapid decline through competition as people exploit the same resources of the local environment. At higher densities one would expect this to happen more rapidly because the same mobility limits (effective daily foraging radius) apply to all, regardless of the population size.

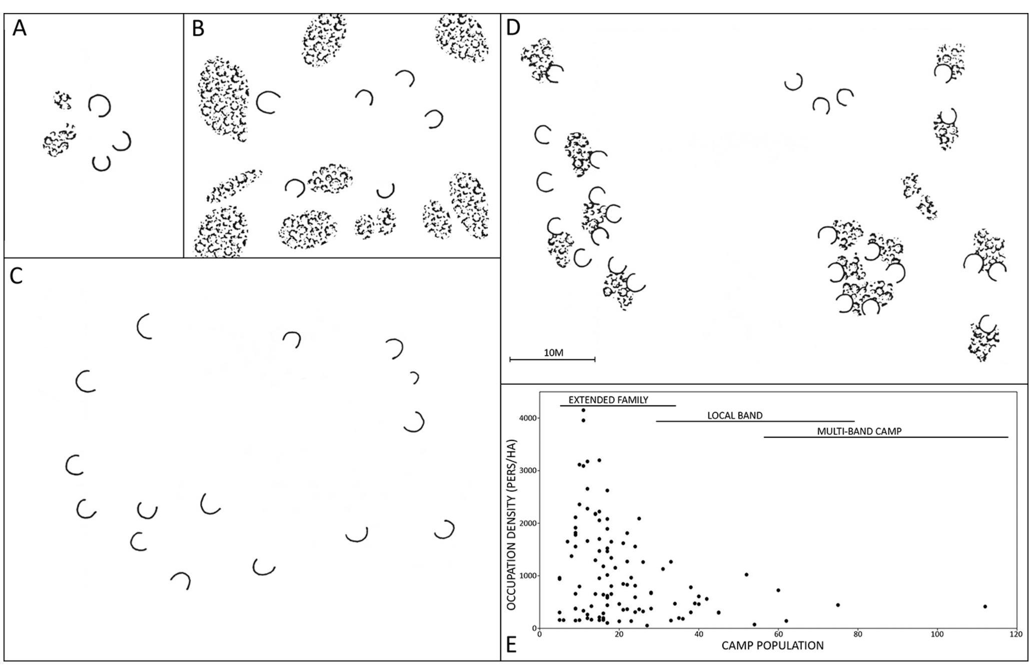

Figure 1. San camps. *A–C*, Ju|'hoansi. *A*, *B*, Extended family camps (Yellen 1977). *C*, Band camp (Brooks, Gelburd, and Yellen 1984:303). *D*, G/wi. Adjacent camps of hosts and visitors (Silberbauer 1981:197). *E*, Occupation density by camp population.

The per capita rates of energy capture and of social production can be described as the time derivatives of energy capture, E, and of the output, S, resulting from social interactions

$$\frac{dE}{dt} = r_E = r_0 - k\frac{N}{A}, \quad \frac{dS}{dt} = r_S = G\frac{N}{A} - r_c, \qquad (1)$$

where G denotes the (ultimately also energetically bound) benefits from social interactions, r_0 is a baseline rate of individual-level energy use, r_c is the limiting cost of engaging in social interactions, and k introduces a carrying capacity effect. (For the sake of tractability, r_0, r_c, k, and G are treated as constants with regard to the group size, N, but may depend on spatial distance interacting individuals, related to the area A.) The two rates express the simple accounting of the dynamics of accumulation of energy and social products, respectively. The dependence of both energy capture and social productivity on density is explicitly captured by the density term N/A: the kN/A term denotes the interaction between population density and environment carrying capacity, while the term GN/A connects the benefits of social interactions with density.

The rates in equation (1) are an instance of logistic growth (in which change is modulated by density). This can be seen more clearly by rewriting the equations in (1) as

$$r_E = k\left(n_E - \frac{N}{A}\right), \text{and } r_S = G\left(\frac{N}{A} - n_S\right), \qquad (2)$$

where $n_E = r_0/k$ is the population density at carrying capacity and $n_S = r_c/G$ is the analogous population density below which maintaining a stock of socially produced products becomes impossible. Note that in this framework the rates of social production (i.e., collective production, sharing and exchange of material goods, contracting marriages, the joint production of knowledge, the arts, festivities, and opportunities for cultural transmission) and rates of energy return from foraging have an opposite dependence on population density, such that increasing one decreases the other. These dynamics of social production and energy returns—which are opposed with respect to population density but not with respect to their direct effect on each other since increased social production requires more energy—lead to a set of scenarios that depend on the relative value of the two critical densities, n_E and n_S, representing, respectively, the maximum environmental carrying capacity and the minimum social carrying capacity.

Figure 2 illustrates the range of possible relationships between population density, energy production, and social production and their consequences for the temporal stability of settlements. Figure 2*A* shows the situation where the productivity of the environment is relatively low. In this scenario, increasing population density leads to even lower energetic productivity per capita so that individuals will enter a situation of energy production deficit at a density that is lower than the minimum needed for the accumulation of social products (resulting from social interactions). Under these circumstances, in order to obtain a beneficial balance between satisfying energy needs and engaging in social production, individuals must oscillate between situations of production of the first quantity and deficit of the other, and vice versa, as shown in figure 2*B*. This situation entails a pattern of periodic group fission and fusion typical of mobile hunter-gatherers. Figure 2*C*, on the other hand, shows the situation in a more productive environment, where a population density that supports both energetic sufficiency and positive net social production is possible. This situation, which can occur in productive ecotonal (e.g., coastal) environments or as a result of food production, makes longer-term camps or even multiyear settlements possible. For example, if the productivity of the environment varies seasonally, it may be possible to sustain larger camps during periods of higher productivity and then disperse during other seasons or provision through logistical mobility of resource-procuring task groups. Moreover, if food can be stored locally to bridge the population to the next productive season, year-round settlements become possible. Storage, logistical mobility, and trade are all potential strategies for offsetting resource shortfalls among sedentary groups, but for the sake of model simplicity, we do not include these details here. Even in this simple model, there is an echo of the observation that permanent settlements require not only energy sufficiency at a given population density but also a density sufficient to provide net benefits from social interaction and socially coordinated activity.

We next consider how camp area might be expected to vary with population size when hunter-gatherers camp together. We have seen already that mobile hunter-gatherer camps exist at population densities at or above which social production can occur, $n \geq n_S$; therefore, the dependence of camp density on its population will be at its extreme when the densities of energy consumption and social production are equal, $n_E = n_S$. The dependence of the average energy cost of interaction per unit time, r_c, on the physical size of the camp, can be characterized in terms of the camp's linear spatial dimension (camp radius) R. On purely dimensional grounds, $[R]^2 = [A]$, since R is a length and A is the camp's area. There are, of course, benefits of proximity since communication is more effective at close distances. Nevertheless, as Fletcher (1995) notes, the social stresses of interaction also become more acute with close proximity, depending on an individual's social relationships, the context in which interaction occurs, and so forth. The average cost of interaction can therefore be expected to be affected by camp population in two ways: through the energy cost incurred by moving within the camp and through the social stress generated by physical proximity to others within the camp. Equation (3) captures these two costs:

$$r_c(R) = \epsilon R + \rho\frac{\ell}{R}. \qquad (3)$$

The first term to the right of the equal sign in equation (3) denotes the physical cost of movement across the camp, where the parameter ϵ refers to the energy expended moving per unit distance. In small camps, this energy expenditure will be negligible, but in some ecological settings and in larger camps, such expenditures can be much larger. The second term to the left of

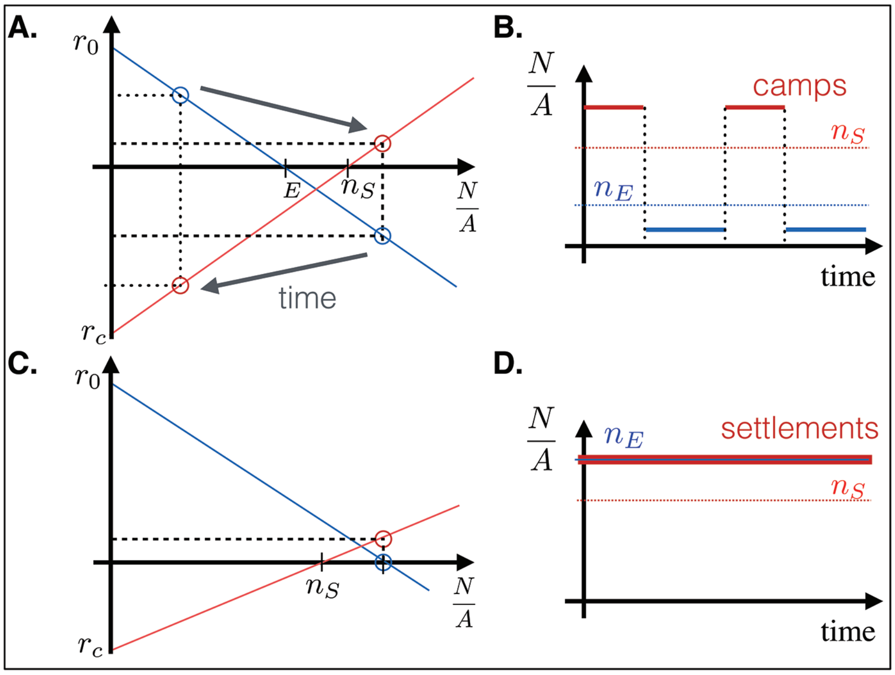

Figure 2. Schematic representation of rates of energy harvesting and socializing versus group density. Shown in *A* is the situation in a relatively unproductive environment. The blue solid line shows the population density dependence of energy production (logistic growth), while the red line shows the rate of social production. In this case, each rate can be positive only when the other is negative. As a consequence, there is no static arrangement of population in space (or corresponding fixed density). Instead, in *B*, the population must alternate periods of low density when energy harvesting is net positive, but social products decay, with other periods when the opposite is true, and the population experiences short periods of energy deficit in order to socialize. Shown in *C* is a different situation, when energy productivity (blue line) is higher. In this case, it is possible to find spatial population arrangements that break even in terms of energy and create a net production of social outputs. This makes possible permanent settlements for a group of a given size and spatial density, *D*. This situation may be seasonal, associated with higher productivity times and places while they last, or could be more permanent if any seasonal variations can be mitigated, for example, through logistical foraging or food storage. Thus, we conclude that longer-term camps and eventually permanent settlements require both energetically and socially favorable conditions, which can be realized in different ways in different physical environments and through cultural/social conventions/structures. Failure to realize break-even (or better) levels of energetic and social production simultaneously will lead to periods of alternating group fission and fusion.

the equal sign is a social stress–related cost, which declines with distance, capturing the (negative) effects of proximity (Fletcher 1995). This second term subsumes costs besides movement that reduce the benefits of proximity (communicable disease, food-sharing demands, conflict, noise, and more). The parameter ρ translates this net (negative) effect into an additional cost, and the parameter ρ represents the distance at which proximity costs become significant, which for this effect to be relevant should be in the range of meters, determined by the range of effective sensory perception.

From equation (3), a critical camp size, R_*, can be defined based on the ratio of the proximity costs and the transport costs entailed in interactions $R_* = \sqrt{(\rho\ell/\epsilon)}$. For a camp size (radius) larger than this critical size, such that $R > R_*$, the first effect in equation (3) dominates, and costs are driven primarily by the energetic cost of movement within a camp to participate in social life. In contrast, when $R > R_*$, proximity costs related to interaction stress dominate. The average relationship between area (which is proportional to camp size and thus to camp radius) and population for camps can now be estimated by equating the benefits of social interaction with the associated costs, that is,

$$G\frac{N}{R^2} = \epsilon R + \rho\frac{\ell}{R}. \tag{4}$$

Assuming that the benefits and costs of interactions within a camp need to balance, $\epsilon R + \rho(\ell/R) - G(N/R^2) = 0$. By performing some algebraic manipulations on the balanced equation—multiplying through by R^2, dividing each term by ϵ, and substituting $\rho(\ell/R)$ with R_*^2—we obtain an equation expressing the balancing of costs and benefits in terms of camp size and camp population:

$$R^3 + R_*^2 R - \frac{G}{\epsilon}N = 0. \tag{5}$$

The general solution of equation (5) is shown graphically in figure 3. It can be seen that when $R \ll R_*$, as one would expect in a small camp where proximity stress dominates, the role of R^3 is minimal, so we can solve for R and square both sides to obtain approximately

$$R \cong \frac{G}{\epsilon R_*^2} N \rightarrow A(N) = A_0 N^2, \tag{6}$$

with $A_0 = (G/\epsilon R_*^2)^2 = (G/\rho\ell)^2$. This is the perimeter-area scaling obtained by Wiessner (1974) for San camps. Conversely, when $R \gg R_*$, as occurs when family units are dispersed in separate camps across a foraging territory, the role of proximity stress $R_*^2 R$ becomes negligible, and we can follow the same procedure to obtain approximately

$$R^3 \cong \frac{G}{\epsilon} N \rightarrow A(N) = A_0 N^{2/3}, \tag{7}$$

with $A_0 = (G/\epsilon)^{2/3}$. This result is the typical densification pattern found in permanent settlements, from small villages to large cities, worldwide and throughout history, which has been characterized as the amorphous settlement model (Ortman et al. 2014, 2015).

One can consider equation (7) as resulting from a situation where $R_* \rightarrow 0$, which entails that proximity costs become much smaller than movement costs and which effectively removes the second term from equation (3). This would require the presence of social and physical structures, cultural institutions, and enforcement mechanisms that support privacy, property ownership, and more formal exchanges as a means of overcoming proximity stress (Fletcher 1995). The ethnographic literature described above indicates that proximity stress is relevant for mobile hunter-gatherers, and, as a result, the scaling of camp area with population size should not be scale invariant but instead should exhibit a gradual transition from an exponent of about 2 for situations where individuals reside in small camps to an exponent of about two-thirds in the extreme, or limiting case, where individuals are dispersed evenly across a foraging territory (again, the key point is that they are not socially associated/aggregated).

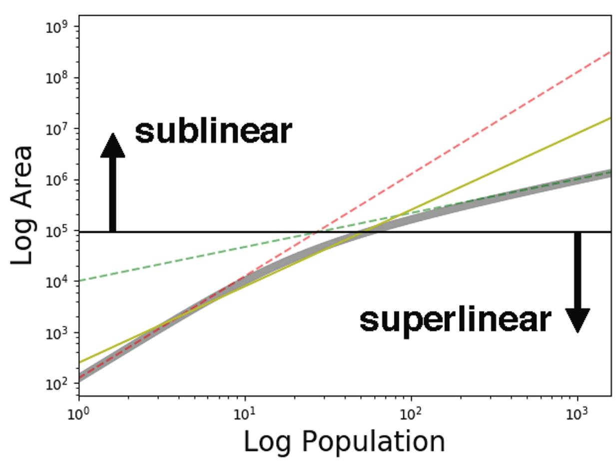

Figure 3. General solution of equation (5) for the relation between area and population. Camp area increases with the square of camp population (dashed red line) at scales where interaction stress dominates the costs of co-residence, and it increases with camp population to the two-thirds power (dashed green line) at scales where movement costs dominate. The horizontal black line represents the critical area AA_*=RR_*2 where these lines intersect. This, in turn, reflects the critical distance R_*, or area, (solid black line) at which the dominant cost shifts from interaction stress to movement costs. The solid gray line reflects the combined effect of both costs for the population-area relationship. The solid yellow line shows $A(N) \propto N^{1.5}$, which provides a reasonably close fit for small camps where interaction stress dominates.

The final ingredient for completing the modeling framework is the social distance between residents within camps and its relation to their level of kin relatedness. If, as argued previously by Whitelaw (1991), mobile hunter-gatherer camps are generally kin structured, with chains of households related by marriage and kin relationships that are generally reckoned back at most a few deceased generations, then the average coefficient of (genetic or fictive kin-based) relatedness between individuals in a camp should decline with group size (Whitelaw 1989, fig. 4.1). This decline in relatedness, and corresponding increase in social distance, leads to a population size dependence of the distance, $\ell(N)$, at which proximity costs become significant (eq. [3]). Walker and Hill (2014) compared group size and relatedness, r, across hunter-gatherer groups and found that relatedness does in fact decline with group size according to the expression

$$r(N) = r_0 N^{-\gamma}, \tag{8}$$

with an exponent $\gamma \simeq 1/4$, which can be understood as the inverse of the typical family group size (Hamilton et al. 2007). If we take as a given that there is a norm of generalized reciprocity, and we assume further that a version of Hamilton's rule ($rB > C$, where B is the reproductive benefit of sharing and C is the reproductive cost associated with sharing) also applies (Hamilton 1963, 1964*a*, 1964*b*), then for any given distribution of resources, the energetic (food) benefits of social contact will decline with group size, among other factors such as cooperation in resource acquisition and sharing patterns (Dyble et al. 2016). One would expect social distance to primarily affect the second (proximity) cost term of equation (3) by increasing the distance ℓ at which costs begin to be felt.

We are now in a position to describe the distance ℓ at which proximity costs begin to be felt in terms of the decay in relatedness with group size, $\ell(N) \sim (1/r(N)) = \ell_0 N^{\gamma}$. From here, one can substitute $\ell_0 N^{\gamma}$ for ℓ in the second term of equation (4), disregard the first term (reflecting the case where $R \ll R_*$ and movement costs are minimal), square both sides to turn the radius R into an area, and then solve for area to derive an expression that relates area to group size under these circumstances:

$$A(N) \simeq \left(\frac{G}{\rho\ell_0}\right)^2 N^{2-2\gamma} \rightarrow \left(\frac{G}{\rho\ell_0}\right)^2 N^{1.5} \text{ (when } \gamma \simeq 1/4). \tag{9}$$

This relation implies that the population density of mobile hunter-gatherer camps, $n(N) = N/A$, decreases rapidly with increasing group size. As a result, one can divide the group size N by equation (9) and simplify (in the case where $\gamma \simeq 1/4$) to yield:

$$n(N) = \frac{N}{A(N)} \simeq \left(\frac{\rho\ell_0}{G}\right)^2 N^{2\gamma-1} \sim N^{-\frac{1}{2}}. \tag{10}$$

According to equation (10), the rate of density decrease is strongest for populations that are less related (either biologically or through metaphorical extensions of the concept of kinship) and those that tend to camp more densely (such that $R \ll R_*$) in the first place. In addition, the baseline density is set by the proximity cost (ρ), the baseline distance at which proximity costs are felt regardless of relatedness (ℓ_0), and the energetic benefits of interaction (G), all of which may be context specific.

The modeling framework introduced here specifies a set of conditions that determine (1) when temporary versus more permanent camps are energetically possible, (2) the density of temporary camps deriving from the combined effects of movement costs and proximity costs, and (3) the effects of social/kinship distance in structuring the layout of camps and their overall area-population relationship. These arguments help us see that per capita energy capture and social productivity must both be above a certain level for the establishment of sedentary residence. Our models suggest that both quantities are characterized by finite thresholds, below which a society enters a situation of energetic or social deficit. These alternative patterns can, however, be managed over time, leading hunter-gatherer groups to oscillate between aggregation and dispersal. This framework also suggests that proximity costs related to social and biological distance are a primary impediment to densification of hunter-gatherer camps. We are led to conclude that such costs must be overcome through social or technological innovations (property rights, food production, group rituals, political institutions, substantial shelters, and more) for the open-ended densification regime that characterizes permanent settlements to emerge. Thus, the conditions implicit in sedentism, where the net benefits of interaction dominate even as the agglomeration is energetically and socially sustainable, are potentially latent in every hunter-gatherer society but manifest themselves only incipiently.

The framework developed here leads to several expectations regarding the average relationship between population and area in hunter-gatherer camps that we can now investigate empirically. First, while we would expect the exponent of the scaling relation to be between 1 and 2 in most situations, we would not expect it to have any particular value since this value should vary with scale, strength of proximity stress, and degree of relatedness across contexts. Second, we would expect this exponent to exhibit a curvilinear relationship with scale overall. It should be between about 1.5 and 2 for the regime where $R < R_*$ and proximity costs and social distance dominate, but it should decline as $R > R_*$ and mobility costs come to dominate over proximity costs (eq. [4]). Third, in cases where storable resources and storage technology provide a sustainable energetic return and sociocultural institutions (and potentially impermeable insulating/buffering structures) reduce the social stress between neighbors, one would expect the scaling exponent to decrease and approach the value of two-thirds that is typically observed in permanent settlements.

Empirical Analysis of Hunter-Gatherer Camps

To test these expectations, we use a database representing 1,760 hunter-gatherer camps from 112 different cultural groups and a variety of regional and ecological settings (Whitelaw 1989, 1991, 1994). Construction of this data set was possible because many ethnographic works include an example community plan, a normative camp sketch, or simply a description of the community where the ethnographer worked as part of the background documentation. These ethnographic reports were published throughout the twentieth century. While often not explicitly discussed in the text, such documentation allows the characterization of camp layout, habitation density, and group size. The information in the primary sources ranges from detailed ethno-archaeological plans of debris on occupation sites to small-scale sketch maps or written descriptions. In the case of aboriginal California, researchers calculated figures for normative seasonal village population size and areal extent based on archaeological data, explorers' accounts, and ethnohistoric data (Cook and Heizer 1968).

The groups represented reflect a variety of natural habitats, food-acquisition and storage technologies, and sociocultural behaviors. Community population estimates were ranked from the most to the least reliable based on the following scale: (1) a census made at the same time as the plan, (2) the ethnographer's rough estimate or an official census of about the same date as the plan, (3) an estimate usually based on the number of structures and average number of occupants per shelter for that culture, and (4) essentially an informed guess based on likely family size and the number of structures. The areas of camps (measured in square meters) were either directly reported or estimated from scaled maps. Ranked in terms of reliability, sources were (1) a detailed ethno-archaeological plan, (2) an ethnographer's rough plan, (3) a small-scale plan, (4) an unscaled sketch, and (5) verbal descriptions or tabled figures. The assembled data for each camp also include information on the cultural group represented (as noted in the original report) and the degree to which the community followed traditional social and economic behaviors, as well as an ecological classifications (arctic, subarctic, desert, savanna, temperate, and tropical forest) and regional classifications (Asia, equatorial Africa, southern Africa, Australia, Greenland, North America, and South America).

Site areas were based on the residential area of a camp, defined as a convex hull polygon connecting points 0.5 m beyond the perimeter of any residential structure. These areas were digitized using AutoCAD for all camps with plans. A minimum threshold size of two structures (or nuclear families) was imposed for including an observation in the analysis, on the argument that two would be the smallest number of nuclear families for which one might expect the balancing of costs and benefits to come into play in a camp's spatial arrangement. It is further assumed that a camp population of six individuals corresponds to two families, so the observations used in the study all have a population greater than or equal to six individuals. In addition, there was a concern that many of the communities in the original data set were nontraditional in the sense that their social and economic situation no longer represented a coherent indigenous, subsistence-oriented social and spatial adaptation. Some of the communities in the data set were actually permanent settlements, laid out by missions or government-settlement projects, so should not be used as examples of mobile communities (although members of these communities still forage or engage in limited hunting or foraging expeditions). Since all studied hunter-gatherer populations at the time of ethnographic documentation were living at the fringes of the world economy, interaction with the cash-based economy or a national welfare system erodes traditional (precontact) patterns of social and economic relationships. To avoid these confounding issues, we pruned the original data set by removing communities that were spatial subsegments of a larger settlement, those that were nontraditional aggregate groups, or those that relied significantly on nonsubsistence economic activities. These pruning exercises resulted in a data set with 1,209 observations, of which 748 denote mobile camps and 461 correspond to permanent or semi-permanent settlements. For a discussion of how traditional hunter-gatherer communities were identified, see Whitelaw (1989).

Summary statistics for camp area, population size, and camp area per person are shown in table 1 for the full and mobile data sets. The summary statistics convey the great diversity of camp life among the hunter-gatherer groups covered by the data. Figure 4 shows the relationship between the camp area (measured in square meters) and camp population for all of the observations (variables expressed in natural logarithmic form). The pattern of increasing area with increasing population is clearly visible, as is the gradual decline in the slope of the relationship with camp population (and thus length, R).

Table 1. Statistical summary of the ethnographic data set for all camps containing at least two shelters and a population equal to or greater than six individuals and for the subset of fully mobile communities

	Camp area (m^2)	Population	m^2/person
All observations:			
Mean	37,442	97	211
Median	1,694	34	42
Standard deviation	226,724	168	822
Coefficient of variation	6.06	1.73	3.90
Maximum	5,193,890	1,630	16,667
Minimum	7.3	6	.8
N	1,209	1,209	1,209
Mobile:			
Mean	9,024	42	128
Median	442	23	19
Standard deviation	47,495	87	669
Coefficient of variation	5.26	2.07	5.23
Maximum	436,162	1,630	16,667
Minimum	7.300	6	.8
N	748	748	748

Estimation Framework and Results

The average relationship between camp area (A) and population size (N) is represented using a power-function, $A = cN^{\beta}$ (Bettencourt 2013; Wiessner 1974). Estimates for the exponent β can be obtained via linear regression by first taking the natural logarithm of the power-function equation

$$\ln A = \ln c + \beta \ln N + \mathrm{e}, \tag{11}$$

and then using equation (11) as the basis for a regression estimation exercise, with the term "e" denoting fluctuations with a finite variance and zero mean over the population of observations. Under equation (11), a 1% increase in population is associated with an average β% increase in camp area. The basic estimation method used is ordinary least squares regression, augmented with controls for heteroscedasticity, and generalized least squares (GLS) to control for fixed effects. In all cases in which fixed effects estimation was used, the results were unchanged when using GLS with a large dummy-variable set (all estimations were carried out using the STATA SE ver. 14 software package). The scaling relationship is described as superlinear when β is greater than 1 (implying that an increase in population induces a greater than proportional increase in area), linear when it is equal (or almost equal) to 1, and sublinear when it is less than 1 (meaning that the increase in area induced by an increase in population is less than proportional).

Note that we investigate only the average relationship between camp population and area. There is obviously substantial variation in the density of individual camps because of a host of contextual factors, from cultural tradition to ecological and topographic context to the specific compositions of individual camps and other stochastic factors. The effects of these factors are summarized in the residual, e, for each camp away from the regression line.

Table 2 presents estimation results for several different models, which use all 1,209 observations. Model 1 includes all the observations, while models 2, 3, and 4 present regression results when using the ecological setting, continental location, and cultural affiliation as fixed effects controls. Models 2–4 attempt to account for the manner in which ecological setting, resource utilization, foraging and storage technology, and sociocultural practices specific to each group modulate the relationship between camp area and group size (for explorations of these variables, see Whitelaw 1989, 1991). Table 3 presents a series of additional models using observations only for the fully mobile hunter-gatherer communities. These observations correspond to communities that are highly mobile, rely on extensive sharing of resources, and form camps consisting of clusters of cooperating families. Model 5 uses all 748 observations for mobile groups with models 6 through 8 controlling for ecological and regional settings and cultural affiliation, respectively. The estimated scaling coefficient for both the full set of observations and the mobile groups are similar (and superlinear) and robust to the environmental, regional, and cultural affiliation controls.

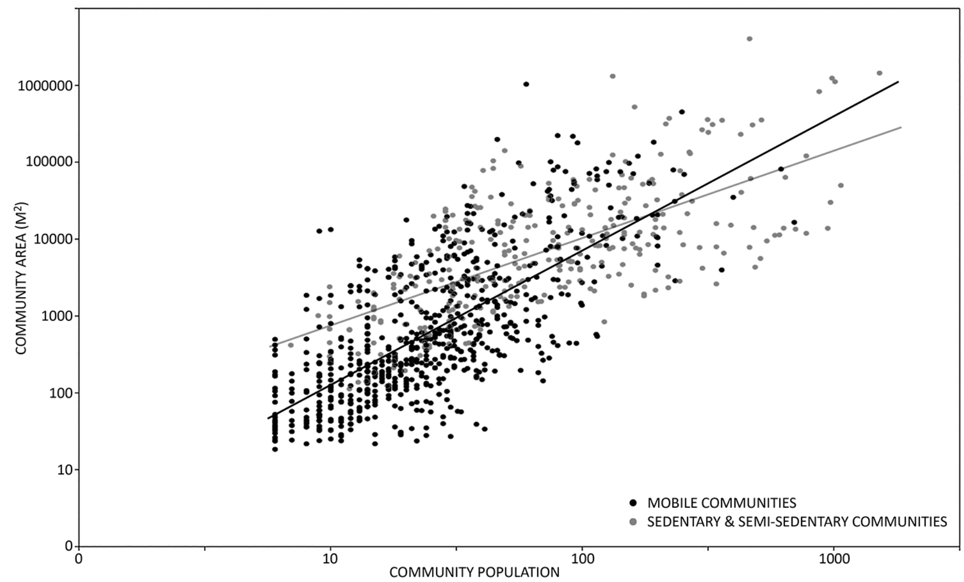

Figure 4. Relationship between population and occupation area for hunter-gatherer settlements included in the study ($\beta = 1.6698$, $R^2 = 0.68$).

Models 9 to 13 (in table 4) present the relationship between camp area and group size for distinct mobile hunter-gatherer lifestyles. Arctic and subarctic communities (Alaska, Canada, and Greenland) usually have wider inter-dwelling spacing and thus have lower densities than lower-latitude groups (notwithstanding how substantial Inuit winter dwellings can be). These are primarily hunters who rely on individual household hunting and storage rather than extensive sharing between families. The desert communities are mainly Australian desert groups, which are highly mobile, engage in limited sharing of subsistence resources, and maintain low-density communities. The savanna observations represent principally San groups from the central Kalahari and north Australian Aboriginal groups with extensive sharing. Tropical forest communities are mostly from central Africa and South America. These are also highly mobile, generally with a high degree of sharing of resources in the residential group, and some cooperative hunting (e.g., net-hunting, game drives). Temperate communities, predominantly in California and along the West Coast of the United States and Canada, are often larger and more permanent communities with more complex social organization.

Our first expectation receives widespread support from these analyses. The estimation results show a range of scaling relationships between residential camp area and group size; but in general, the relationship is very similar for the entire sample and for the subset of traditional communities. There are clearly superlinear scaling coefficients ($\beta > 1$) across the entire data set and for most controls examined. As expected, the actual value of the scaling coefficient varies across models, but most are in the vicinity of 1.5, as predicted by the model that includes proximity stress and kin selection, equation (8). These exponents ($\beta > 1$) indicate that it is not merely the case that the open space in hunter-gatherer camps increases with the number of shelters. Rather, the amount of open space per shelter increases as the number of shelters increases. If the open space within mobile hunter-gatherer camps were set aside to facilitate interaction

Table 2. Relationship between camp area (dependent variable) and population (independent variable) using all the observations in the data set for hunter-gatherer communities (dependent and independent variables in natural logarithmic form)

	Model 1	Model 2	Model 3	Model 4
	All observations	Controlling for ecology type	Controlling for regional group	Controlling for culture type
Constant	1.225	1.846	1.955	1.476
	(.132)	(.124)	(.132)	(.121)
β	1.698	1.533	1.505	1.631
	(.034)	(.031)	(.034)	(.031)
95% CI	[1.631, 1.766]	[1.471, 1.596]	[1.437, 1.572]	[1.571, 1.694]
R^2	.68	.78	.76	.89
N	1,209	1,209	1,209	1,209
Estimation method	OLS with a correction for heteroskedasticity	GLS with FE	GLS with FE	GLS with FE

Note. Standard errors are shown in parentheses. CI = confidence interval; FE = fixed effects; GLS = generalized least squares; OLS = ordinary least squares.

Table 3. Relationship between camp area (dependent variable) and population (independent variable) for mobile groups (dependent and independent variables in natural logarithmic form)

	Model 5	Model 6	Model 7	Model 8
	Mobile groups	Controlling for ecology type	Controlling for regional group	Controlling for culture type
Constant	.859	1.393	1.421	1.065
	(.198)	(.169)	(.171)	(.146)
β	1.742	1.576	1.567	1.678
	(.063)	(.051)	(.051)	(.044)
95% CI	[1.618, 1.866]	[1.476, 1.676]	[1.467, 1.667]	[1.591, 1.766]
R^2	.56	.71	.69	.86
N	748	748	748	748
Estimation method	OLS with a correction for heteroskedasticity	GLS with FE	GLS with FE	GLS with FE

Note. Standard errors are shown in parentheses. CI = confidence interval; FE = fixed effects; GLS = generalized least squares; OLS = ordinary least squares.

among the residents, one would expect it to be added no more than proportionately to the population. What actually happens is that open space is added more than proportionately to the population, in excess of what would be needed to facilitate interaction. This is why regulation of interaction through distance is a better interpretation of these population-area relationships.

The overall pattern we observe for mobile hunter-gatherers contrasts strongly with the densification regime that characterizes both ancient and contemporary permanent settlements, in which the scaling coefficient is in the range of 0.67–0.83 (Lobo et al. 2019). This result further suggests that, in contrast to settled societies, social interaction in mobile hunter-gatherer societies generally exhibits decreasing returns to scale (meaning that the average interaction frequency between two camp mates is greater in a less populous camp than it is in a more populous one). In turn, this suggests that the emergence of permanent settlements was a major watershed in human development that made possible the open-ended accumulation of social products, in the form of stocks of knowledge and goods.

Our second expectation for the overall relationship between population and area is supported by figure 4 (corresponding to model 1): the observations at the upper tail of the scatterplot are consistent with the hypothesis that as camp size increases, proximity costs will gradually give way to movement costs as the dominant factor behind the spatial arrangement of shelters. Finally, our third expectation for the relationship between population and area is supported by models 14 to 17 (table 5), which show results for the San from southern Africa (model 14) and several groups of sedentary hunter-gatherers from the North American Pacific Northwest (including the Haida, Kwakiutl, Nootka and Tlingit; model 15), a broad Northwest Coast behavioral group (covering the NW Coast, Northern California, and Western Coastal Alaskan groups and including the Ingalik, Koyoukon and Tanaina; model 16), and various groups from California (model 17). The California grouping includes communities living in coastal, inland, and riverine environments, predominantly in semisedentary winter villages that almost invariably had substantial timber houses that insulated each residential group and more complex social organizations that regulated interactions within communities. (These also regulated interactions between communities, but we are specifically concerned with intra-community interactions here.)

For the set of observations corresponding to the San of southern Africa, the estimated scaling coefficient is close in value to 2, as reported previously by Wiessner (1974) using a smaller sample, including only small camps. The scaling coefficients for

Table 4. Relationship between camp area (dependent variable) and population (independent variable) for mobile groups in distinct environmental settings (dependent and independent variables in natural logarithmic form)

	Model 9	Model 10	Model 11	Model 12	Model 13
	Arctic	Desert	Savanna	Temperate	Rain forest
Constant	1.867	2.123	.663	3.806	1.384
	(.326)	(.547)	(.284)	(.406)	(.212)
β	1.546	1.898	1.721	.951	1.236
	(.093)	(.143)	(.085)	(.085)	(.072)
95% CI	[1.362, 1.731]	[1.612, 2.184]	[1.552, 1.889]	[.771, 1.121]	[1.093, 1.378]
R^2	.49	.69	.68	.67	.65
N	222	95	192	104	225
Estimation method	OLS with a correction for heteroskedasticity	OLS with a correction for heteroskedasticity	OLS with a correction for heteroskedasticity	OLS with a correction for heteroskedasticity	OLS with a correction for heteroskedasticity

Note. Standard errors are shown in parentheses. CI = confidence interval; OLS = ordinary least squares.

Table 5. Relationship between camp area (dependent variable) and population (independent variable) for southern African San and North American Northwest Coast and California groups (dependent and independent variables in natural logarithmic form)

	Model 14	Model 15	Model 16	Model 17
	San	Northwest North American Coast	Extended Northwest North America	California
Constant	1.046	4.331	3.523	3.521
	(.551)	(.385)	(.407)	(.529)
β	1.955	.744	1.12	.99
	(.179)	(.084)	(.092)	(.125)
95% CI	[1.606, 2.304]	[.776, 1.113]	[.949, 1.313]	[.740, 1.242]
R^2	.52	.54	.59	.71
N	104	72	171	54
Estimation method	OLS with a correction for heteroskedasticity	OLS with a correction for heteroskedasticity	OLS with a correction for heteroskedasticity	OLS with a correction for heteroskedasticity

Note. Standard errors are shown in parentheses. CI = confidence interval; OLS = ordinary least squares.

the Northwest North American Coast and California are noteworthy in that the coefficient for groups living in California is nearly linear and the coefficient for the Northwest Coast is strongly sublinear, with a value close to that exhibited in other sedentary societies. These two groups represent sedentary hunter-gatherer societies in which aggregations are not properly referred to as base camps, but as semipermanent or permanent settlements (Bean and Blackburn 1976; Jorgensen 1980; McFeat 1989). Mollusk collecting, harvesting of salmon and acorn stocks, organized communal hunting of sea mammals or terrestrial large game, gathering of nuts and berries, developed storage technologies, and a variety of sociopolitical and ritual institutions enabled societies on the Pacific Coast of North America to support semipermanent or permanent settlements that were inhabited for multiple years (Ames 1994; Jorgensen 1980; Schalk 1981). The sublinear relationship between population and area observed in these settlements suggests that in larger settlements houses were spaced more closely together, contained more people per house, or both. Groups with larger communities correlate with greater frequency of warfare, so larger individual house groups and denser packing of houses may also be a response to intercommunity conflict.

The densification rates exhibited by sedentary hunter-gatherer communities of the Pacific Northwest and California are similar to those observed in agricultural and urban societies, suggesting that these groups used residential space in similar ways to sedentary agrarian groups. This, in turn, suggests that it is not agriculture, per se, but basic energetic and social factors (related to resource abundance and predictability, storage, and socioeconomic regulation of rights and obligations) that are likely most responsible for the shift from a decreasing density regime characteristic of mobile camps to an increasing density regime characteristic of permanent settlements.

Discussion

The empirical results presented here reinforce previous studies that have found that mobile hunter-gatherer camps generally become less dense as they grow in population (Fletcher 1990; Hamilton, Buchanan, and Walker 2018; Whitelaw 1991; Wiessner 1974). This general result implies that, among mobile hunter-gatherers, rates of some energetically relevant interactions between camp residents decline, on average, with camp size. The most important contribution of the present discussion is a modeling framework that places the social use of physical space at the center of explaining why mobile hunter-gatherer camps dedensify with increasing population, whereas sedentary hunter-gatherer communities and permanent settlements exhibit the opposite tendency. This analysis suggests that physical space (the spacing between residences and between socially coherent clusters of residences) is used in hunter-gatherer communities both to facilitate interaction among close relations and also to create privacy and regulate interaction with more socially distant persons, without incurring the cost of building more substantial housing and fencing in a highly mobile context (Whitelaw 1989, 1991, 1994).

What are the specific conditions that facilitate, drive, or allow mobile groups to coalesce into larger, denser, nonkin cooperating units and settle into permanent urban or proto-urban settlements? Our formal models indicate that the de-densification regime documented for mobile hunter-gatherers derives from a combination of proximity tensions in situations where the built environment provides only limited privacy. In addition, the carrying capacity of locally available resources is an important determinant of camp size and permanence, both of which may create more propitious conditions for social arrangements to develop and eventually sustain sedentary lifestyles. In this context, the critical conditions that support the transition from mobility to sedentism include (1) a sufficient energy density (via intrinsic resource properties in combination with technology) to support permanent agglomerations and (2) social institutions (especially with respect to property and group cohesion) that reduce proximity stress among more distant social relations. It is beyond the scope of this paper to identify the specific social institutions involved, which can be expected to vary substantially across societies. Our objective here is to develop an analytical framework for modeling variations in behavior on an axis between mobile and fully sedentary socio-spatial patterns.

The specific de-densification pattern that characterizes mobile hunter-gatherer camps is radically different from that documented for permanent, agriculture-based settlements across a wide range of sedentary societies. From small subsistence farming villages to contemporary cities, agriculture-based settlements tend to grow denser with population (i.e., area-population scaling coefficient <1), generally with scaling coefficients between 2 and 3 and between 5 and 6 (Bettencourt 2013; Nordbeck 1971; Ortman and Coffey 2017; Ortman et al. 2014, 2016). These qualitative and quantitative differences point to the existence of constraints that lead to increasing spacing between individuals in mobile hunter-gatherer camps. From this perspective, the de-densification in hunter-gatherer camps is a mechanism for foragers to experience the benefits of spatial agglomeration within the constraints of their social conventions, physical technologies, and economic (energetic) productivity.

But if this were the only barrier to agglomeration, one might expect agrarian settlements in a densification regime to expand exponentially, ad infinitum. That this does not occur demonstrates that there are additional factors that limit the scale of human agglomerations. Cross-cultural work by Carneiro (1967), Dumond (1965), Fletcher (1990, 1991, 1995), Forge (1972), and Narroll (1956) suggest some of the additional factors—technological, social and psychological—that constrain the advantages of density in small-scale agrarian and horticultural societies. This implies that several constraints, in addition to energetics, limit the scale of functionally interdependent social networks embedded in physical space. We also wish to emphasize that, although mobile and sedentary lifestyles may seem polarized, in reality the mobility strategies of hunting and gathering societies (and indeed even horticultural and pastoral societies) exhibit a continuum that suggests the transition from one to the other may not be best described using the concept of a "tipping point." Longitudinal studies of specific societies (or comparative studies of culturally related communities; Whitelaw 1991) will be needed to assess the character of the transition from mobility to sedentism. Whether pastoral societies follow patterns typical of mobile hunter-gatherers, sedentary societies, or a different pattern entirely is an important question for future research.

The theoretically derived scaling results reported here suggest that the social reactor process that characterizes permanent, agriculture-based settlements is not a universal feature of human sociality or an expression of some intrinsic set of evolved psychological predispositions, but rather a dynamic that emerged in tandem with the energetic and social conditions that made sedentism possible. The fact that sedentary hunter-gatherers create settlements that exhibit similar population-area scaling relationships as agrarian and industrial societies suggests that the key factors that enabled the transition from a de-densification to a densification regime do not necessarily involve domesticated food production, although they do involve surpluses and storable resources.

In making the arguments of this paper, we do not mean to suggest that hunter-gatherer societies do not possess any norms and rules (social infrastructure) that make it possible for individuals to live in close spatial proximity to biological nonkin or socially distant individuals. Indeed, many hunter-gatherer societies come together seasonally in relatively large, temporary gatherings to arrange marriages and to forge and maintain social networks that extend far beyond the typical camp (Wiessner 2014). In this context, the transition from mobility to sedentism is clearly built on foragers' experiences devising ways for more distant kin and nonkin to agglomerate. However, while both mobile and sedentary societies do have complex social and material networks, the agglomeration of networks in space in sedentary societies requires additional innovations in built infrastructure and social institutions that allow people to live together permanently in relative harmony. These innovations, in turn, may provide a foundation for developing increasing social complexity.

Our results align well with a tradition of research in anthropology and related disciplines that steers a course between claims of universality for common human social and cultural traits and claims of particularism and uniqueness for individual cases. In this tradition, advances flow from careful analyses of quantitative data, carried out in reference to appropriate theory and explicit research questions. Prominent examples include research in gene-culture coevolution (Boyd and Richerson 1985; Henrich 2015), cross-cultural research using standard databases (Ember and Ember 2009; Turchin et al. 2018), quantitative studies of wealth inequality (Kohler et al. 2017; Mattison et al. 2016), work in human behavioral ecology (Bettinger 2015; Smith 2013), and other related approaches. We propose that quantitative analyses of the spatial and demographic characteristics of settlements make a contribution to these and other works in anthropology that advance our understanding of patterns and regularities—not necessarily universals—in human societies around the globe and through history.

If an effort to model the social and technological correlates of spatial behavior is empirically supported, the model can then generate hypotheses about past social behaviors and institutions represented in the archaeological record, hypotheses that can be contextualized with other data sources. The theoretical and modeling frameworks presented here are intended to help clarify the social factors that lead some horticulturalists/agriculturalists to distribute residences widely within settlements and others to densify. For urban studies, there are certainly different spatial configurations of settlements, and the model presented may help identify the fundamental social factors and institutions behind the variations in social behavior as revealed in settlements.

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Comments

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I concur with the opinion of the authors that "quantitative analyses of the spatial and demographic characteristics of settlements makes a contribution to these and other works in anthropology that advances our understanding of patterns and regularities." I also concur that the transitions in many regions to what we habitually describe as sedentism were a major transformation in human behavior. There is, however, an issue. While some communities—especially agrarian-based communities that live in settlements of durable structures which have been occupied for decades or centuries—are habitually described as "sedentary," there is not in actuality a rigorous, generally agreed-on, systematically quantified specification of sedentism. What is clear over several decades of analysis from Muller-Wille (1954) through Kelly (1992) to Whittle's (1997) substantial appraisal to the present is that various durations of residency, ranging from 20 to 40 years to part of 1 year, amid a plethora of varied combinations of degrees of mobility, have been proposed.

The enduring establishment of what we habitually consider to be permanent sedentism appears to be a very recent phenomenon of the past 10,000 years—recent even within the 100,000-to-200,000-year existence of modern humans. That raises the conundrum of what appears to be a continuum but also involves a major and profound transformation. The value of recognizing the two differing density trends, one to increasing occupation density as community size increases in communities we habitually regard as sedentary and the other to decreasing density as community size increases in communities which habitually use mobility (Fletcher 1995:170–173), is that this offers a rigorous basis for beginning to specify what we mean by "sedentary." What is noticeable is that Whitelaw's impressive work in 1989 showed that Inuit and Northwest Coast Indian communities have a decreasing density pattern. This then poses a fundamental question that is decisive for the empirical analysis of transitions to sedentism. Is the difference between these two divergent trends an indicator that an abrupt phase change lies between them or that the initial change was gradual? That the Northwest Coast Indian communities have a shallower density decrease and a sample of UK villages (Fletcher 1995:173) have a shallower increase does not answer that question. We would need to seek cases of historically or ethnographically recorded communities that had or have flat density trends with increasing community size. What would be crucial is whether there are any and also whether any such communities were or are able to remain in that state for very long. If very rare and/or of short duration or else nonexistent, then a marked phase change is indicated, suggesting that a gradualist shift through increasing degrees of semimobility/sedentism is not an adequate description of the initial sedentizing.

Given that these two divergent trends do superficially appear to have a corollary in increasing density of material occupation markers relative to settlement area and decreasing density of material occupation markers relative to settlement size, respectively, we may be able to systematically extend the analysis to the archaeological record. This would require assessments to rigorously define the degree to which residential population density correlates with material occupation density, for example, as indicated by markers such as the density of occurrence of buildings. Definition of settlement area would also need rigorous quantified specification.

Because communities that definitely use mobility as a part of their seasonal operations can range from small hunter-gatherer communities up to the tens of thousands of the mobile capitals of literate states (e.g., the Ethiopian "ketema"; Fletcher 1991:405–410), we can observe a broad trend toward markedly lower overall residential densities for such communities as group size increases (Fletcher 1995:79–83). Mobile groups can carry much higher densities—more than 1,500 p/ha—in communities of up to a few hundred people than conventionally recognized sedentary communities. But larger mobile communities drop to substantially lower overall densities down to below 10–20 p/ha or less for communities of more than 10–20,000 people. Rather than mobile communities being limited to relatively small sizes beyond which sedentary communities are usual, there has instead been a continuing pattern of behavior that can produce mobile communities of considerable size. Just as there are varied settlement growth trajectories for conventionally sedentary communities, we should expect the same for mobility (Fletcher 2020).

Instead of a dominant trend toward compact, sedentary communities in the conventional sense, mobility may have been and also may be becoming a far more common mode of community operation operating on the markedly different interaction behavior that Draper's (1973) work presaged and Wiessner (1974) presented. The mobility of the communities of the European Neolithic (Leary and Kador 2016) strongly indicates that we should find it far more commonly. The Marind-Amin (Wirz 1922:25) show that mobility can operate agriculture. Perhaps we are not recognizing entire sets of settlements that used more mobility. The mobile capitals of literate administrations suggest that this behavior may be more common (see Sinopoli 1994) than we have supposed. And if decreasing density with increasing size does correlate with a habitual use of mobility, then seasonal movements in and out of Pre-Classic and Classic Maya cities (Smith et al. 2020) and Angkorian cities, for example, by construction labor and pilgrimage populations, may deserve further attention. And that may mean that a significant relationship exists between increased mobility and the decreasing overall densities of the vast megalopoli and *desakota* of the modern world. Jose Lobo and his coauthors deserve credit for presenting the quantified tools for investigating such issues.

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Lobo et al. have produced an intriguing paper that attempts to extend settlement scaling theory into hunter-gatherer ecology by considering the relative costs and benefits of social aggregation in foraging societies. Their model lays a foundation for modeling the transition from hunter-gatherer socioecology to the settlement scaling we observe in sedentary nonforaging societies. I admire the vision but would like to raise two sets of issues; the first is theoretical and the second concerns data.

Theory. For tractability, Lobo et al.'s model is essentially a zeroth-order model that assumes an energy cost to aggregation on the one hand and a social benefit on the other, both of which are density dependent. This is an axiomatic starting position, although there are nontrivial subtleties to consider as ethnographers have developed a detailed understanding of these costs and benefits. For example, studies show that foragers achieve higher long-term net returns by cooperating than they would alone, but as group size increases, these initial increasing returns to scale quickly turn negative as the risk of free riders increases (Gurven 2004, 2013; Jaeggi and Gurven 2013; Koster et al. 2020). Other important fitness-related benefits of sociality in foragers include alloparental care and intergenerational transfers of resources and information (Gurven et al. 2012; Hawkes, O'Connell, and Jones 2018; Hill and Hurtado 2009; Hooper et al. 2015).

Next we should consider larger-scale aspects of hunter-gatherer population ecology. Lobo et al.'s model focuses on flows of energy and information within camps. This is a common level of organization in hunter-gatherer societies to consider in the spirit of "Man the hunter," where bands were viewed as territorial, kin-based, autonomous units of hunter-gatherer social organization (Lee and DeVore 1968; Steward 1936). However, we now understand that bands can rarely be studied in isolation because a band only exists as long as the same families co-reside and band membership is fluid (Hamilton, Buchanan, and Walker 2018). Indeed, individuals and families relocate frequently and are networked into complex, multitiered metapopulations where individual costs and benefits flow through the network at all scales (Bird et al. 2019; Binford 2001; Hamilton et al. 2007). It would be interesting to consider how the model proposed here could consider this complex structure. Indeed, to successfully marry settlement scaling with hunter-gatherer ecology, the question to be answered is not how did hunter-gatherer camps become cities, but rather how did diffuse, low-density, mobile metapopulations of foraging groups become the nucleated, mega-dense, sedentary populations of cities; how did social diffusers become social reactors?

Given the above, I would like to raise three assumptions of Lobo et al.'s model for further consideration. (1) Are hunter-gatherer bands composed of extended families? This was often assumed to be the case in cultural ecology, but data analyzed by Hill et al. (2011) show that in mobile foraging societies families are no more likely to co-reside with kin than nonkin. (2) Are net return rates in foraging groups negatively density dependent? In ethnographic data, per capita net return rates are actually positively density dependent at small group sizes (i.e., Allee-like), hence the strong cross-cultural norm of reciprocal altruism (i.e., locally increasing returns to scale in productivity and system-wide economies of scale in space use [Hamilton et al. 2007]). (3) Do interaction rates among individuals vary in hunter-gatherer camps as a function of density? I am not sure whether we can assume more information flow in Ache forest camps than in Ju/'hoansi desert camps, for example, or whether dense Ju/'hoansi camps are more interactive than diffuse Ju/'hoansi camps. I would be surprised if the distance between individuals was a major constraint as the radius of interaction scales as the square root of area, so even in large camps distances are not great. Would the variation in these distances be significant enough to warrant evolutionary mediation through kinship? Moreover, within and across cultures camps will tend to have similar norms of cooperation, reciprocation, and sharing, which are more likely to mediate interaction than physical proximity.

Data. I am reasonably familiar with Todd Whitelaw's data set, having first worked with it in 2007 with James Steele at the Institute of Archaeology, University College London, and having discussed it at length with the lead author over the years. Although it is an impressive data set, I have two concerns here. The first is that these data do not record camp residence times. As correctly noted by the authors, there is considerable variance in residence times, from a few hours to a few months. Importantly, however, this variance is not random with respect to either camp area or the number of occupants. In Hamilton et al. (2018), we reported similar superlinear scaling between area and occupants in hunter-gatherer camps, but we also showed that once controlling for residence time, this superlinearity becomes linear. This is because a camp used by 10 people for a month will have a larger footprint than a camp used for a day simply because of increased activity levels accumulating in space over time. There is also a positive interaction between the number of occupants and residence time: longer-term camps tend to be larger and used by more people (Hamilton, Buchanan, and Walker 2018). My concern is that the superlinearity that Lobo et al. report is driven by the same latent variable of residence time.

The second issue is the extraordinary scale of variation in both camp area and the number of occupants in this data set. Figure 4 shows that the number of camp occupants is often more than 1,000 and that the camp area is often more than 1 million square meters (>1 km^2) for both mobile and sedentary groups. In ethnohistoric data, the total size of a regional hunter-gatherer population is often a few hundred (perhaps a few thousand at most), and the number of camp occupants is on the scale of a few dozen, even in the largest aggregations (Binford 2001; Kelly 2013). Similarly, in the ethnographic record, the largest, most-dispersed camps, such as those of the Alyawarra in central Australia, for example, are on the order of ~10,000 m^2 (O'Connell 1987). Perhaps these extremely large camps in the Whitelaw data are not single occupations, but networks of camps, and, if so, would require additional dynamics relating the spatial configuration of metapopulations to individual camps. This is an interesting and thought-provoking model that hopefully inspires much future work, although whether it currently captures the salient features of hunter-gatherer socioecology is unclear.

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Notions to Numbers: Comment on Lobo et al.

I have a somewhat mixed reaction to this impressive analysis. The sheer amount of data behind the analysis is unusual, and I am amazed that there are so many observations on camp characteristics. The framing of the problem in terms of physical space, interaction, and social space is laudable. The modeling in terms of equations seems very sophisticated, especially for those, like myself, who are untutored in such complexities. I also share many of the authors' assumptions and theoretical orientations concerning the fundamental variables at play in determining mobility, group size, and the importance of social or conflict management as a precondition for large aggregations. Given all the disadvantages of large agglomerations (provisioning and transport, diseases, conflicts, crime, poverty), there clearly must be some overriding benefits, or hoped-for benefits, to living this way, even if we can argue about what those benefits consist of. So overall I applaud their conclusions. And I like their provision for cultural-historical particularities creating variation within overall trends and constraints.

However, I also found the presentation difficult to follow in terms of the details of equations and in terms of what I consider the use of highly idiosyncratic or specialized jargon, especially for a general audience like the one that usually comprises the readership of *Current Anthropology*. "Proximity costs," "proximity stress," "de-densification," "social productivity," "social reactor processes," and "superlinear scaling coefficients" are all terms that are opaque and could be expressed more simply and clearly, for example, as "lower density," "conflicts," and so forth. Similarly, the three "expectations" and outcomes presented are unintelligible to people like myself who are not proficient with this type of equation modeling. As a technical note, it would have also been useful to have scatterplots for all the data in the tables. Standard deviations, ranges, means, and medians give only a very general idea of the data (especially when the density ranges vary from 0.8 to 16,667 with a mean of 211), whereas scatterplots show all the data and bivariate relationships.

After trying to decipher the key terms used and follow the logic of the model equations, the narrative conclusions seemed somewhat underwhelming, although gratifying in that they reasserted some of the more fundamental interpretations in the field. For example: that the key factors in sedentism are surpluses and storable resources which are, in turn, linked to rich resources, suitable technology, and suitable social features (largely to manage stresses of group living)—a point iterated at least four times. Another good point emphasized in recent years by a variety of researchers is that these features characterize more complex hunter-gatherers rather than being entirely dependent on agriculture.

Social costs and management were presented as being the most novel theoretical contribution of this article, but these have also been part and parcel of nonmathematical conceptual frameworks for some time, especially in terms of "political economies" (Earle 2019; Herskovits 1940). For instance, Rambo (1991, fig. 10.3) has depicted the exponential increase in energy consumption that occurs with increasing social complexity, much of which I argue is because of the social costs of motivating and managing people, for example, via feasts and prestige gifts. I have even tried to provide real cost estimates for at least some of these costs among some archaeological hunter-gatherers (Hayden 2020).

Tipping points for density reversals from mobile ring camps to amorphous sedentary settlements are very interesting but seem blurred and skirted around. Nevertheless, they should be more directly addressed. In fact, the scattergram in figure 4 seems to show different slopes for mobile versus sedentary groups, and it would have been informative to plot them separately. The reversal at issue is not very satisfyingly explained except by reference to the technological and social innovations necessary to live as agglomerated sedentary communities. This explanation for larger, more sedentary groups is really only a precondition and is hardly a new theoretical contribution (e.g., Ames 2004; Arnold 1996; Kelly 1995), but it is nice to see the concepts restated, even if in opaque jargon. The authors' model also seems predicated on an inherent desire for people to be social and aggregated, as expressed in their opening sentence, with platitudes offered about the benefits of social life. More explicit conceptual modeling would be welcome.

What was valuable for me was the highlighting of the ring structure of mobile hunter-gatherer camps versus the amorphous organization of sedentary hunter-gatherers (Northwest Coast linear settlements providing an exception to the amorphous generalization) together with a lowering of density (i.e., "de-densification") as population increased in mobile hunter-gatherer groups. The clumped settlement pattern of aggregated bands is something that I also observed in Western Desert settlements even when attached to government stations (e.g., Gargett and Hayden 1991).

A major issue that the authors avoid is whether the benefits of large permanent aggregations emerged because of pressures (circumscription, war, and so forth) or whether they emerged because of aggrandizer strategies developed to attract and bind people to aggrandizers (e.g., via feasting, debts, prospects of better or more marriages, defensive alliances, provision for compensation payments, sociopolitical and economic security, higher standards of living, opportunities to increase status or power, and more). And of course it is possible that large aggregations formed under both kinds of conditions. The issue is how to determine which was operative in specific past contexts. Although the authors did not address the formation of residential corporate groups as a subset of their settlement types, the same issues that they deal with apply (see Hayden 2012 and Hayden and Cannon 1982). Thus, it would be interesting to see their approach applied to residential corporate groups such as those on the Northwest Coast and Plateau as well as among many horticultural groups.

In sum, the authors have avoided key causal arguments but provided another descriptive level of analysis that reinforces previous conceptual models of mobility/sedentism, social costs, and hunter-gatherer complexity. There may be a bit of smoke and mirrors here, but not too much fire.

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In their article, Lobo et al. offer a challenging, yet rewarding, view on the scaling of camp size and human sociality, presenting this intriguing topic in a clear and accessible way. The authors examine why mobile hunter-gatherers tend to dedensify their camps as population increases, while sedentary groups, including pastoralists, farmers, and urban societies, generally do the opposite by congregating under denser living situations. They trace this difference to the mechanisms through which people balance the dual stressors of interaction and movement. For hunter-gatherers to change their settlement pattern, the social benefits of interacting with individuals outside their kin group must outweigh the stress created by living in closer proximity, including increased pressures on foraging and resource availability. On the other hand, sedentary groups have collectively "decided" that benefits gained through increased social contact, often aided by improved technological and storage solutions, outweigh the stresses created by living in the vicinity of an increasing number of unrelated individuals and groups.

The authors first discuss the basis of these concepts and then work through a series of equations to set up and refine the parameters of the model they propose. This model explains how two apparently opposite modes of living can actually coexist along a single continuum. The details are revealed through a series of assumptions and mathematical constructions, and take form as the equation for the model finally emerges. Last, to test the validity of the model, they apply it to ethnographic data using proxies for both hunter-gatherer and sedentary groups whose degree of sedentary living varies.

The model shows that at the mobile hunter-gatherer end of the spectrum, the observed trend is sublinear, which equates to the predominance of interaction stress. If they congregate, hunter-gatherer groups tend to space themselves out as the population of their camps grows. However, as the logarithms of both population and area increase, a critical point is reached, beyond which the costs of movement prevail. Sedentary populations employing a range of economic modes (e.g., herding, fishing, farming) tend to fall into the latter category. In these cases, the costs of living more closely together bestow greater benefits on their inhabitants, likely because of increased social interactions and the resulting improved economic perspectives. The stresses can, at least in part, be overcome through better regulation of the interactions, as well as the "accumulation of social products" through the transfer of knowledge and material goods. With this model, the authors integrate aspects of behavior that appear at odds with each other and propose a mechanism whereby a single model provides an explanation for two very different patterns of behavior.

Lobo et al. convincingly propose a set of circumstances under which such communal behavior could have begun. Of course, generating a model and testing its validity does not necessarily confirm it, but the authors lay out the necessary groundwork to make their arguments convincing. As a prehistorian, I was especially interested in the evolutionary and chronological ramifications of their work. Therefore, I draw attention to Kuhn and Stiner's (2019) publication, "Hearth and home in the Middle Pleistocene," as I think it has relevance to the concepts that Lobo et al. propose. Kuhn and Stiner examine the "emergence of true domestic spaces," as shown by the establishment of base camps by mobile hunter-gatherer starting about 450,000 years ago. Especially as evidence for the control of fire became more frequent, camps became places that gained a new significance for the people who used them. At this temporary central home, people conducted quotidian activities like stone knapping and animal butchering as well as socializing. Kuhn and Stiner cite the development of food sharing and cooperative child-rearing as likely outcomes of living together in a base camp. While they are careful to note that the first encampments probably did not work in the same way that later settlements did, they see in the structure of these early features the spark that ignited the evolution of such behaviors. Similar to Lobo et al., Kuhn and Stiner view the camp as a focal point for bringing together individuals and resources and as an important example of niche construction that altered the ways that people subsisted and interacted.

While it is essential to understand when this phenomenon began, the intensification of these kinds of behaviors started to become more apparent about 130,000 years ago. Evidence for increasingly complex behaviors spreads across Africa and

Eurasia, suggesting greater social interaction and the development of group identities. Such behaviors include the advent of new stone technologies (e.g., Henshilwood 2012), including the heat treatment of toolstone (e.g., Brown et al. 2009), the use of ochre for functional purposes (e.g., Villa et al. 2015) and ritual purposes (e.g., Watts, Chazan, and Wilkins 2016), geometric engravings (e.g., Texier et al. 2013) and drawings on various materials (e.g., Henshilwood et al. 2018), the appearance of personal ornaments on different carriers (e.g., Bouzouggar et al. 2007; Radovčić et al. 2015), the widening of the hunted resource spectrum especially through innovative technologies (e.g., Lombard and Wadley, 2016) and burials, among many other innovative examples that became ensconced within the behavioral repertoire of humans. Thus, while Lobo et al. establish a plausible explanation for the transition from purely hunter-gatherer settlement patterns to sedentism and its intrinsic denser settlement, their work, coupled with that of Kuhn and Stiner, provides a broad chronological framework and a deep evolutionary background.

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The strength of this article lies in the fact that it develops quantitative models that make clear predictions as to settlement area and settlement density under different demographic and environmental regimes. It does so with very simple yet also very explicit representations of the energetic and social costs and benefits associated with population aggregation versus dispersal. Its appeal especially to archaeologists should therefore be readily apparent: it quantifies the tenets of human ecology in ways that result in predictions that ought to be eminently testable using archaeological data. But it also tells us, for the most part, what we already knew: "complex" hunter-gatherers established many if not all of the prerequisites for agriculture, settled village life, and perhaps even urban living outside the purview of and likely before these other ways of living developed. They stored food, they generated surplus, they were often semi or fully sedentary, they actively managed the landscapes they lived in, and they embodied social structures that either facilitated or led directly to the evolution of these behavioral strategies (Morgan et al. 2020). Add to this list, per the research reported in the article, that they used space in their main residential sites in much the same manner as agriculturalists did. We also already knew, mainly via induction, that these types of behaviors ought to be found in productive, albeit seasonal, environments (Binford 2001). That said, the appeal of this modeling exercise is that it is deductive and predictive, rather than inductive or descriptive, and therefore of potentially considerable explanatory power.

Because of its prospective explanatory utility, it is worth looking at the basic model that Lobo and colleagues developed in a little more detail. First, it is very general and very simple, and therein lies a substantial part of its appeal. But it may also lack the precision and perhaps the realism (sensu Winterhalder 2002) necessary to capture important details of the processes at play in the evolution of settled, dense populations. In this vein, I doubt that rates of energetic or social production always increase or decrease linearly relative to population density (see fig. 2). Per the expectations of the ideal free distribution's Allee effect (Stephens and Sutherland 1999), for instance, it might be expected that rates of energy production increase logistically (rather than linearly) with increasing density at first (because of increased labor capacity and perhaps the greater efficiency afforded by collective action) and then decline toward marginal returns over time as population density comes to challenge carrying capacity. The difference may be of considerable consequence given that the steeply increased energetic benefits of initial aggregation might not only offset the costs of social proximity (as Lobo and colleagues model this relationship) but might also incentivize aggregation in the first place. Conversely, energetic and social production may not always be independent variables; it is very easy to imagine cases where social production might facilitate increased rates of energy capture. Prestige-oriented hunting (McGuire and Hildebrandt 2005), cooperation (Carballo, Roscoe, and Feinman 2014), and competitive feasting (Hayden 2001) are all ways that hunter-gatherers might increase both forms of production concomitantly, either because of increased efficiency related to scale, division of labor, or technological investment, among many other potential factors (Morgan 2015).

Although the authors briefly allude to its importance, the fact that there is pronounced variability in hunter-gatherer population size and site area is perhaps more salient than the general implications of the model, which is based on the average of these phenomena. These data make it clear, for one, that conceptualizing hunter-gatherers—mobile, settled, complex, or otherwise (typically in opposition to agriculturalists)—as a single analytic type misses the point entirely. In this light, the term "hunter-gatherer" is merely a convenient, and increasingly problematic, catch-all term that occludes the extremely wide range of technological, economic, social, political, and settlement behaviors embodied by people who do not (or did not) rely on domesticated plants and animals for subsistence. This distinction is more than semantic: if ethnographically reported hunter-gatherers reflect in any way preagricultural ones (i.e., late Pleistocene-early Holocene), then it would appear that some of the phenomena discussed in the article—scaling, storage, and social institutions—were part of the range of behaviors selected for in the evolutionary landscapes of the Pleistocene-Holocene transition, the ones that eventually gave rise to the first agriculturalists. Key to this idea is the range of behavioral variability either selected for or against, which is an essential component of any macroevolutionary scheme (Spencer 2019).

Finally, left unexplained (or, rather, unpredicted) by the model is the ultimate cause of scaling in hunter-gatherer camp size.

Although the authors appropriately note that this issue is beyond the scope of their research and that they eschew the notion of "tipping points," they do allude to those factors that might solve problems associated with densification, most notably increased energy capture, storage, and social institutions. The importance of economic intensification and storage is clear (Morgan 2012, 2015); what is less clear are those institutions (or norms) that allow people to store, to live in large groups, and to diffuse the tensions and conflicts endemic to tightly packed social groups. Privatization is of course one potential solution to this problem, where even large, densely packed, settled groups maintain considerable individual autonomy, as was apparently the case in pre-Columbian California (Bettinger 2015). Coercion, sanctions, hierarchy, and hegemonic relationships are other alternatives (Geiger 1988). The key point in all this is that some hunter-gatherer groups clearly solved these problems, likely repeatedly, in different contexts, and perhaps in very different manners. That means that if we want to understand how people resolved the problems of collective action, nonkin cooperation, and social aggregation in a general, evolutionary sense, we ought not only be doing much more modeling akin to that reported in this article, we should be testing predictions derived from these models using archaeological data sets recovered from more settled, dense hunter-gatherer occupations.

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Lobo et al. offer a provocative take on the spatial structure of mobile hunter-gatherer camps and by extension the development of dense aggregate settlements. In essence, they argue that mobile hunter-gatherers de-densify their camps as populations rise, which has the effect of enhancing privacy and constraining interactions between socially distant people. They then ask what would be required to favor higher density aggregates with closer spacing between nonimmediate kin groups. Lobo et al. cite three critical factors underlying this process, including access to abundant energetic resources, the development of social institutions associated with concepts of property and cohesion (cooperation), and the related capacity to invest in more substantial houses, walled compounds, and the like (e.g., Flannery 2002). They point to the need for more longitudinal studies to gain a better understanding of the transition.

I agree that expanded longitudinal study would be insightful for understanding variation, particularly if it includes pastoralist societies. Plains Indian societies should provide important data in this regard. As noted by Bethke (2020), the transition from "dog-days" to "horse-days" required a substantial reconfiguration of decision-making regarding mobility and coresidence. For groups such as the Blackfeet, residential moves during pre-horse times were conditioned by access to major game herds, especially bison. During the horse era, residential moves were predicated in part on access to horse pasturage and sources of water. Horses also provided the opportunity to possess and transport greater quantities of food and personal gear. The combination of horses as valued resources and accumulated materials required investment in defense against raiding and that was accomplished by higher-density settlements, among other things. Such high-density settlements were also structured by social demands, particularly in annual aggregations for ritual activities (Lowie 1954). Thus, examples from mobile bison hunting groups on the Great Plains appear to implicate seasonal high-density settlement, matching some predictions of the current model (high return energy source [bison] and social constructs structuring social proximity [e.g., Zedeño et al. 2014]), but not others (high annual rates of residential mobility and lack of permanent houses, compounds, or fences).

However, I think there is also a place for time-like studies in testing these hypotheses. Diachronic approaches permit us to invoke evolutionary concepts that are not possible in longitudinal studies within ecological frameworks. The author's concern with "tipping point" arguments is a good case in point. Tipping point arguments imply rapid transitions from one form to another or a punctuated process. We must take great care in addressing this question in individual case studies, as scale matters. Zeder (2009) notes that on the scale of tens of millennia, the Epipaleolithic to Neolithic transition in the Near East does resemble a single punctuational event. Yet when we examine it closely (decades to centuries), it is actually made up of many smaller-scale punctuations as associated with local innovations and associated socioeconomic changes. Groundstone and multicomponent tools requiring inset blades appear early, followed later by semisubterranean house structures and sedentary communities, social mechanisms for community cohesion, storage facilities, domesticated plants and animals, and ceramics. Thus, diversity in hunter-gatherer strategies preceded emergence of that integrated strategy we call the Neolithic.

We recognize a similar history during North America's Northwest Coast during the terminal Pleistocene and Early to Middle Holocene. Hunter-gatherers of the Old Cordilleran tradition innovated over time groundstone technologies, earth oven cooking, storage techniques, and pithouses, while developing an enhanced subsistence focus on marine resources and plant foods (Chatters et al. 2012). As with the Near Eastern Epipaleolithic, for thousands of years most of these traits rarely appeared simultaneously. Yet by about 5,000 years ago, the entire package emerged along with innovations in housing and resource management in the Lower Fraser Valley. The Charles Culture resembles the Neolithic given the presence of villages with permanent houses, wapato gardening, public ritual associated with large roasting ovens, mass production and distribution of stone beads, and elaborate burials (Coupland et al. 2016; Hoffman et al. 2016; Prentiss and Walsh 2016). From a long-term standpoint, this represents another major punctuational event, yet as elsewhere, it was preceded by multiple smaller-scale punctuations.

Evolutionary theory offers frameworks for enhanced understanding of these complex histories. I highlight two models associated with the extended evolutionary synthesis that should prove useful in providing insights into punctuated change on multiple scales. Nearly neutral theory when used in concert with advanced fitness landscapes predicts that long periods of apparent stasis are actually productive, leading to the evolution of new traits that at the time may be neutral, mildly maladaptive, or adaptive (Laue and Wright 2019). The persistence of such traits typically in low-population groups can provide the cultural variation necessary to fuel evolutionary events sometimes recognized as "tipping points." Evolution of development, or Evo-Devo, provides another potentially productive framework (Laland et al. 2015). Here, we might imagine cultural variants emerging as consequences of behavioral plasticity that are subsequently refined by selection under altered conditions. As noted by Zeder (2018), plasticity would be an essential element for human groups dropping old behaviors and adopting new ones during periods of significant niche construction, as might be associated with punctuated cultural evolution.

A potentially interesting implication of these case studies as viewed through evolutionary lenses is that aggregated sedentary existence may well be characterized by resource stability, social rules for coexistence at close proximities, and application of physical infrastructure to protect privacy. Yet these cultural developments might have accumulated under disparate conditions and not all as immediately adaptive innovations. Thus, while space-like models as derived from longitudinal studies should continue to provide us with generalities on the socioecological conditions underlying cultural patterns, time-like models remain critical for identifying specific evolutionary processes, whether adaptive, maladaptive, or neutral. As has been argued by Eldredge (1985), evolution requires action in the ecological and genealogical realms. I hope Lobo et al. will continue their productive efforts to understand hunter-gatherer adaptive variation and its implications for major cultural transitions.

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"Scaling of hunter-gatherer camp size and human sociality" by Lobo et. al. draws attention to a fascinating phenomenon regarding densification and de-densification regimes in human societies across space and through time. Their analyses help elucidate potential reasons how, and why, mobile populations tend to densify by increasing areal size as opposed to forming dense, more permanent, urban centers. Using quantitative formal modeling, the authors demonstrate that (1) sufficient energy density and (2) social institutions involved in relieving proximity stress are crucial factors supporting a transition from mobility to sedentism.

The question of why dense urban centers emerged at all is a fascinating one, and one that can be further elucidated by studying patterns in the African archaeological record. Hominins have adapted to dynamic environments for more than 6 million years, aided by manufactured sharp stone edges for ca. 3 million years (Braun et al. 2019; Harmand et al. 2015; McPherron et al. 2010). Major shifts in effective carrying capacity took place when hominins began gaining primary access to meat ca. 2 million years ago (Ferraro et al. 2013), and again with controlled fire ca. 1.5 Ma (Hlubik et al. 2017, 2019), altering the gastrointestinal system in profound ways, including a potential reorganization of tissues (Aiello and Wheeler 1995) and eventually enabling cooking, which had cascading effects on human energetics (Carmody and Wrangham 2009). Human-controlled fire also created new opportunities for social interaction, for example, via storytelling (Wiessner 2014), and may have served to eradicate pests, thereby enabling population densities to increase. Throughout the Early Pleistocene, hominins moved substantially, and their fossils were found in the Caucusus by 2 Ma at Dmanisi (Ferring et al. 2011). By half a million years ago, the ancestors of *Homo sapiens* had already diverged from their Neanderthal cousins (Gómez-Robles 2019).

What transgressed in the last 500,000 years is relevant to understanding how the two conditions that Lobo et al. reference—sufficient carrying capacity and social institutions—evolved. In terms of carrying capacity, the Middle and Late Pleistocene were dynamic times, with global temperatures varying across space and through time at rates hitherto unseen on earth (Sosdian and Rosenthal 2009). Important in terms of energy density was the human adaptation to marine resources, evidenced in South Africa by ca. 164 ka in the form of shell fishing (Marean et al. 2007). Aquatic resources are dense and highly predictable; they not only contribute fatty acids to the energetically costly human brain (Erlandson 2001 and references therein) but may also have required large-scale social cooperation to facilitate territorial defense (Marean 2016). The fact that the scaling coefficient of North American hunter-gatherers is the one most closely aligned with urban settlements, as Lobo et al. point out, is curious at least, and at most, may hint that aquatic resources were crucial for densification.

What about the social institutions that are needed to sufficiently relieve proximity stress for cities to emerge? Where, when, and how did humans develop social institutions needed to overcome the proximity stress brought on by increased population densities, and what did those social institutions look like? Again, we can turn to the African archaeological record for answers. A new kind of stone tool technology emerged sometime between 1.2 Ma and 400 ka (Li et al. 2017), in which toolmakers created sharp flakes of specific sizes and shapes (Boëda 1995), a process requiring multiple contingent steps within a system of physical constraints (Brantingham and Kuhn 2001), and possibly teaching with language (Lycett, Von Cramon-Taubadel, and Eren 2016). Levallois technology gave hominins a way to produce evenly thick, often triangular, armatures that could fit into a haft, and importantly for mobility, could be retouched and resharpened as needed. By 300 ka, there is evidence for increased movement of toolstone, possibly indicating long-distance exchange networks (Brooks et al. 2018).

Thus, by 100 ka human sociality as we know it was already emerging: it is easy to imagine a group of hominins (as illustrated on the cover of Gamble's (1999) *The Paleolithic societies of Europe*) around a fire of their own making, engraving eggshell for water vessels (Texier et al. 2013), or preparing bedding or other organic materials (Wadley et al. 2011). Indeed, such images with Neanderthals are gaining traction (Sykes 2020). The invention of backed stone tools provided another innovation, and a distinct trend can be seen in the miniaturization of stone tools in the Late Pleistocene (Pargeter and de la Peña 2016). Some argue that these microliths radically altered mobility strategy yet again, giving hominins a standardized weapon that was easier to manufacture than Levallois, could be replicated at a fast rate, and cost relatively little energy to replace (Ambrose 2002).

The proliferation of microlithic tools, and later of eggshell beads, seen in the thousands at archaeological sites like Kisese II (Tryon et al. 2018), both indicate economic reorganization of some kind. At Nasera, density of archaeological finds through the sequence suggests increased population density between 30 and 20 ka (Tryon and Faith 2016). In many respects, the diversification and intensification of tool manufacture in the Late Pleistocene point to the beginning of specialization, a pattern seen in complex societies from Mesoamerica (Clark 2003) to the Near East (Hartenberger, Rosen, and Matney 2000). The systematic manufacture of beads or arrow tips requires specialists who have the necessary *connaissance* and savoir faire (Pelegrin 1991) needed for scaled-up production, possibly creating divisions of labor (Kuhn and Stiner 2006).

In many ways, Lobo et al.'s work leads to new questions. How is mobile pastoralism conceived of in terms of densification and de-dedensification, and what mechanisms shape the use of space in these populations? How has forced resettlement and encroachment affected areal sizes inhabited today, and how do areal sizes for nonurban populations compare with those of the Late Pleistocene? Finally, how do the ways that nonurban populations use physical space to buffer and direct social interactions facilitate increased cooperation toward increased net benefits in their own right, in absence of "elaborate material or social institutions?" These are just some of the questions spurred by Lobo et al.'s important work.

Reply

We are thankful for this varied set of insightful comments, which allow us to further clarify our assumptions and methods and to discuss the implications of our results for future research. We agree that the main contribution of this work, as Morgan emphasizes, "lies in the fact that it develops quantitative models that make clear predictions as to settlement area and settlement density under different demographic and environmental regimes." We construct formal models that capture the dimensions and processes highlighted in the extensive literature on hunter-gatherers. As Hayden and Morgan note, we do not propose new variables or model parameters but focus instead on how these parameters are interrelated. Our main goals therefore are to provide a simple unifying quantitative and predictive framework for human settlement characteristics, and not so much in revealing new anthropological features unknown to experts.

The novelty of the study is not to be found in the explanatory narrative, which we assume is familiar to many in anthropology and archaeology. Instead, it is to be found in the way that we connect the forager and sedentary lifestyles through a common theoretical and modeling framework, opening up a new way for considering the emergence of sedentism as a continuous process. It is also to be found in our formalization of the common narrative and in the specification of quantitative predictions matchable with data. If the predictions from the variables used in the models do not survive an encounter with data, then we can ask: What other factors are at play? As Kandel and Ranhorn suggest, archaeologists can reach further back in time and find out whether the model constructed from present data holds beyond a certain period, say 150,000 years ago. Biological anthropologists might even ask whether this model applies to nonhuman primate communities. Such applications might help to identify when the characteristic socio-spatial behavior of mobile hunter-gatherers first emerged in our evolutionary history.

The central point of the paper is that variation in the socio-spatial arrangements of mobile hunter-gatherer camps with population size are fundamentally different from those of permanent settlements, which include a wide range of situations ranging from settled hunter-gatherer villages to towns and contemporary cities. We showed empirically that this fundamental difference has a clear quantitative signature in terms of the observed population-area scaling exponent. This expresses a systematic pattern of densification in permanent sites in contrast with a de-densification with population size for mobile hunter-gatherer camps. We also showed that a population dynamics model accounts for this range of patterns based on a small set of assumptions (not "axioms," as suggested by Hamilton), well supported by anthropological and ecological observations. The crux of the model is the tension between energetics and sociality, mediated by population distribution patterns in physical space. Equations for both these quantities are standard ecological dynamics, where density is not fundamental but appears as the result of competitive (energy) and synergistic (social products) population dynamics. These assumptions are in turn grounded on the idea that energy is a rival good, while information (culture, writ large) is nonrival, and both are subject to losses and depreciation in any social arrangement. (A rival good cannot be used by more than one individual and is expended in the process, whereas nonrival goods allow for multiple individuals using them repeatedly.) We also showed that the consideration of kinship and of the relationship between kinship and camping distances provides us with hunter-gatherer camp models that bridge the early ring model proposed by Wiessner (1974; where an exponent of 2 is observed for San camps) with what is observed more generally for other cultures, where the area-population exponent is closer to 1.5. The model suggests that a distance-based "repulsion" increases with social/kin distance, and this creates the characteristic "exploding" pattern of de-densification in hunter-gatherer camps. This repulsion disappears (presumably because it becomes very small, at the distance scale of the spatial footprint of the household) for permanent settlements, and on larger scales of foraging areas, as has been proposed by Hamilton et al. (2007).

Several of the commentators (Fletcher, Hayden, Morgan, and Prentiss) directed their attention toward the transition to sedentism, wanting more engagement with the actual dynamics of the transition. Our modeling framework suggests how changes in particular model parameters can shift a society from one regime to the other. In other words, the models presented in the study do predict circumstances under which the transition will occur. Of course, we readily acknowledge that many other salient factors behind the shift to sedentism are not included in the modeling framework developed in the paper. Predicting change to sedentism in specific circumstances would require a more complex model incorporating variables that are not systematically documented in a substantial cross-cultural sample of ethnographic data, such as time-series data for particular hunter-gatherer communities undergoing the transition to sedentism.

Additional comments (by Kandel, Morgan, and Prentiss) emphasize the importance of investigating the arguments put forth through an evolutionary perspective, and not just in the context of ethnographically documented hunter-gatherer societies. We agree and note that—in the usual sense of the relationship between ecology and evolution—the models express short time (seasonal) ecological dynamics and that evolution is incorporated in the change of their parameters. In this sense, though model elaborations will be necessary and welcome, we can already account for higher population carrying capacities (including through possible advantages of group foraging), higher or lower stock of "social products" (as a proxy for cultural complexity), and the relative importance of the regulation of conflict (across kin) and the strength of general social attraction through the specification of model parameters, which will vary across cultures, geography, and more. We showed how the combination of parameters involved in R_* predicts permanent densifying settlements versus temporary periodic camps, with consequences not only for the distribution of camping space but also considering the duration of occupations (Whitelaw 1991, 1994).

We agree with the need for future work that emphasizes this "evolutionary" approach via a comparative analysis of longitudinal behavior. Our framework proposes that the measurement and change of model parameters would provide a systematic, quantitative strategy to such an enterprise. As reflected by the set of comments, there is an excitingly large scope for such studies spanning human evolution and ethnography, across time and diverse ecologies and geographies. The hypothesis, arising from the present work, is that simultaneous ecological (energetic) and social (informational) innovations are necessary in the transition between mobile hunter-gatherer lifeways to permanent settlements. Furthermore, reversals are possible as parameters change. Social and political arrangements around collective energy storage and redistribution are likely key, as suggested by many authors in both anthropology and archaeology (Hegmon 1989; Kuijt 2008), even while kinship is preserved and expanded as a human universal (Fox 1983; Wiseman 2016). Any explanation therefore must encompass two phenomena. On the one hand, the historical stability of mobile hunter-gatherer lifeways in the presence of cultural evolution, while also accounting for the complexity and faster cumulation of culture and increases in population once sedentary settlements become possible. In this sense, as Hayden (and Kuhn and Stiner 2019) suggest, both mobile hunter-gatherer camps and permanent settlements should emerge as evolutionarily constructed niches, appropriate to different environmental and cultural situations.

We wish to respond to some specific points raised by the commentators. Fletcher raises a concern about the lack of a "a rigorous, generally agreed-on, systematically quantified specification of sedentism" in the paper. While we agree that such a definition would be worthwhile, we emphasize that such a definition is more central to data and modeling efforts than it is to our models themselves, which are agnostic with respect to what type of behavior should be labeled sedentary. He also points out that extensions of these ideas to the archaeological record will require attention to relationships between residential density and the density of artifacts and features at archaeological sites. We agree and would point out that initial studies have found strong correlations between house density and artifact density in the Basin of Mexico survey data, for example (Ortman, et al. 2014). Finally, he makes the important point that short-term mobility patterns vary even in sedentary societies. We agree and believe that more effort should be spent in characterizing patterns of human movement over various time scales. This tradition is most developed in hunter-gatherer archaeology (Binford 1980; Haas et al. 2015), and we acknowledge the importance of Fletcher's expansion of mobility concepts to state-level societies, as noted in his comment. A recent paper by Smith and others (2020) begins to illustrate how our modeling framework could be extended in this way.

Hamilton makes the important point that over time, individual foragers reside in groups of varying social scale, from microbands to tribal groups, and that the ethnographic literature does not always specify which type of group is represented by individual measured camps. Fortunately, our formal framework is agnostic regarding the level of social organization represented by a camp, but if one considers the social and spatial structures of larger camps, one can identify the nested clusters of social modules as documented by Whitelaw (1989, 1991) and highlighted by Hamilton and others (2007) as different levels of spatial clustering. Hamilton also asks whether the superlinear scaling we observe might be a by-product of the differential duration of camps. Whitelaw's data set includes an ordinal-scale variable that captures variation in camp duration, and in preliminary analyses we found that the relationship between camp duration and camp size is weak, and that population-area scaling parameters are insensitive to camp duration (with the notable exception of Northwest Coast settlements).

We thank Hayden for providing additional references to studies that consider the trade-offs between social benefits and energetic costs, and we appreciate his interest in specific factors behind the emergence of settlement aggregation, from environmental circumscription and warfare to aggrandizing leadership, socioeconomic opportunities, and political alliances. According to Hayden, "[t]he issue is how to determine which was operative in specific past contexts." Although such investigations are not without interest, our focus here is on developing productive generalizations as opposed to context-specific historical explanations. It seems to us that all the factors enumerated by Hayden have been involved in transitions to sedentary agglomeration in different settings, and that these are but surface expressions of a common underlying factor, which is the net benefits of social interaction.

Morgan points out that our model is very general and very simple, and that as a result it may lack the precision and realism needed to capture important details of the processes at play in the evolution of settled, dense populations. We do not doubt that more detailed studies of specific historical and/or archaeological sequences can provide additional insight. However, we do suggest that these more detailed studies will need to be consistent with the general processes captured by our model. A general model does not explain everything that could in principle be known about specific instances of a phenomenon. There is always a trade-off between generality and predictability versus specificity and uniqueness (Levins 1966). Our model focuses on the former. Morgan also asks whether rates of energetic or social production always increase or decrease linearly relative to population density, suggesting that a logistic relationship might be more realistic. We agree; in fact, our model does involve logistic growth in both forms of production, as is indicated by the change from positive to zero to negative rates in equations (1) and (2) and in figure 2.

Finally, in considering how one might expand the analysis in our paper, Prentiss points out the need for analyses of pastoral societies, which combine high mobility with domestication, individual property, and personal accumulation. Such societies, ranging from bison-hunting equestrian nomads of the North American Great Plains to cattle herders of East Africa and yak herders of Mongolia, may perhaps play a similar role to Northwest Coast societies in testing our theory, in that they combine elements of sedentary and mobile settlement strategies. Our framework predicts that such societies will produce camps with relatively larger areas because of the space needs of livestock but will nevertheless exhibit densification with population scale because of the benefits of social interaction.

In closing, we are grateful to the commentators, who have found our approach productive as a framework for considering transformations in human socio-spatial settlement behavior, and welcome their enthusiasm to extend our basic model in various ways to make it relevant to a wider range of societies in space and time, and their specific suggestions for ways that this research could be taken further.

—José Lobo, Todd Whitelaw, Luís M. A. Bettencourt, Polly Wiessner, Michael E. Smith, and Scott Ortman

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