The socioecology of hunter–gatherer territory size

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ABSTRACT

This paper contributes to understanding the socioecology of hunter–gatherer territorial dynamics. We develop and evaluate three hypotheses for the effects of corporate territorial ownership and the storage of food on the territory size of hunter–gatherer societies. We seek to initiate a more nuanced understanding of how social and technological organization cause and constrain the size of hunter–gatherer territories, in addition to the factors of population size and the productivity of ecosystems documented among primates and mammals in general. Our analysis suggests that the storage of food fundamentally alters population–territory size dynamics in hunter–gatherer societies. When societies store food, territory size is a sub-linear function of population. When societies do not store food, the function is approximately linear. The sub-linear scaling of population and territory size indicates that when societies store food, the social units that comprise ethno-linguistic groups produce more food per unit of area and share ever more over-lapping subsistence ranges in response to population growth. This non-linear population–territory size relationship signals that coevolutionary processes initiated by different ways of constructing a niche generate diversity in hunter–gatherer societies. We speculate that the storage of food, initiated to cope with the short-term risk of a short-fall of food, has long-term consequences on the trajectory of hunter–gatherer evolution in general.

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1. Introduction

The goal of our paper is to develop a model of hunter–gatherer territory size, and evaluate the consequences of corporate territorial ownership and storage on the population–territory size dynamics of hunter–gatherer social groups. Our purpose is to understand the processes that cause and constrain the ability of human foragers to harvest and distribute resources. We focus on the processes that determine the size of groups' territories because reductions in territory size are closely associated with major evolutionary changes in human societies, including the broad spectrum revolution (Yeshurun et al., 2014; Zeder, 2012; Stiner, 2001), the adoption of territorial ownership, (Kelly, 2013; Cashdan, 1983; Dyson-Hudson and Smith, 1978) and food production (Smith, 2011; Binford, 1999; Bar-Yosef and Belfer-Cohen, 1989), as well as storage (Testart, 1982). The model that we construct is a variation on the work of Hamilton et al. (2007b), who have developed and begun to evaluate a general model of hunter–gatherer territory size based on a deep intellectual tradition of production models drawn from animal ecology (and economics) (e.g., Jetz et al.,

2004; Kelt and Van Vuren, 2001; Nunn and Barton, 2000; Brown, 1995; Holling, 1992; McNab, 1963). Consistent with cross-species comparisons, Hamilton et al. (2007b) find that the size of hunter–gatherer territories is negatively correlated with temperature, and that foragers who primarily hunt use larger territories than foragers who primarily gather plants or fish for food (see also Alvard, 2006, Binford, 2001, p. 214, Kelly, 2013, p. 95). Hamilton and colleagues' most provocative observation is that the sizes of ethno-linguistic groups' territories are a sub-linear function of ethno-linguistic groups' populations (Hamilton et al., 2007b). By sub-linear function we mean that as population increases, territory size increases at a diminishing rate rather than in proportion to population increase. This pattern suggests that as modern hunter–gatherer ethno-linguistic groups increase in size, the social units that comprise such ethno-linguistic groups actually get better at harvesting and distributing energy and information from a territory and, thus, share more overlapping subsistence ranges (Hamilton et al., 2009, 2007b).

Hamilton et al. (2009, p. 12259) hypothesize that the sub-linear relationship between population and territory size is a net effect of the benefits of cooperation from diverse behaviors, such as: group defense, reproduction and sharing (see also Hamilton et al., 2007b, p. 4766). This argument suggests that the potential to move beyond a linear scaling to a sub-linear one is related to the capacity

of groups to sustain cooperation in the face of social dilemmas. Social dilemmas are situations in which group and individual interests conflict, and these often arise due to increases in group size. Groups who do not recognize norms that reward sustained cooperation might be, in a sense, restricted to a linear scaling and less able to capitalize on the increasing returns to scale generated by cooperatively managing the access, harvest, and distribution of resources.

One way to think about the above hypothesis is in terms of the costs of increases in the size of a social group. As a group increases in size, direct interference and depletion drive the costs of group living up (Clark and Mangel, 1986). One strategy to deal with these costs is for groups to fission into smaller foraging parties (with non-overlapping ranges) to extract resources and fuse at other times to facilitate activities like defense or finding mates (Grove, 2012; Grove et al., 2012; Roscoe, 2009). A second strategy is for groups or individuals to get better at the extraction of energy and information per unit of area. This option increases the availability of food in a territory per person by increasing output per unit area and, potentially, decreases competition for resources, leading to more over-lapping territories among foraging parties. However, this second option requires sustained cooperation as opposed to fissioning to deal with the costs of social dilemmas. Thus, Hamilton and colleagues' hypothesis suggests that sustained cooperation in the use of a territory is a critical process that allows human foragers to produce more food per unit area, which leads to derivatives such as population growth, larger group sizes, and increases in social complexity.

It is an open empirical question whether and how the net effects of cooperation generate the sub-linear scaling of population and territory size among ethnographically recorded hunter–gatherers. The scaling of population and territory size may systematically vary as population interacts with several dimensions of social and technological organization. In the rest of this paper, we use a simple model of territory size and the same data set analyzed by Hamilton et al. (2007b) to evaluate the consequences of corporate territorial ownership and storage on the population–territory size scaling relationship. Our analysis seeks to ascertain whether a single scaling coefficient characterizes the population–territory size relationship or whether this coefficient varies with social norms and technological traits. Our results indicate that the presence of storage technology but not norms of corporate ownership, generate a sub-linear scaling between population and territory size. Sub-linear scaling is observed among groups who store food, but the relationship is very close to linear among groups who do not store food. We hypothesize that the adoption of storage generates a positive feedback loop between social institutions that reward delayed versus immediate returns, group size, and storage. The long-term consequence of this emergent, positive feedback loop is that population growth puts different selection and copying pressures on foragers who store food relative to individuals in systems where storage is rare.

2. A model of energy flux and hypotheses

As we stated in the introduction, we begin with an energy production model applied to human foragers by Hamilton et al. (2007b). This model treats humans as equivalent to lions, wolves, or any other social animal. This statement is not necessarily meant as a critique, but to note that this model is a starting point. Our strategy is to start with the generalization that population and territory size scale in a sub-linear fashion and begin to identify potential boundary conditions on this generalization generated by social and technological process. Our results should, thereby, set future

studies up to continue this process and develop still more nuanced theory.

2.1. The model

We assume that the use of space by hunter–gatherers is determined by the flow of energy, materials and information between an ecosystem and the individuals that comprise a social group (e.g., Hamilton et al., 2007b; Brown, 1995; Holling, 1992). The group home range (i.e. territory size) is defined here as the area claimed by an ethno-linguistic population on an annual or greater time scale (Binford, 2001; Kelly, 2013). We formalize the size of a group's territory with a simple production function:

$$A = a(r, T, Q)N, \tag{1}$$

where A is the territory (km^2) of an ethnic group; a is the space (km^2) necessary to satisfy an individual's energetic wants that depends on rainfall (r), temperature (T) and search effectiveness (Q); and N is the population size of an ethnic group.

Assuming that a is a function of resource supply and demand, then, by definition,

$$a(r, T, Q) = \frac{E_d}{E_s} Q, \tag{2}$$

where E_d is the rate of energy demand (e.g., W) per person, and E_s is the energy production density (e.g., W/km^2) of a territory. Following Hamilton et al. (2007b), we treat E_d as constant for any given human population. This is a baseline assumption that future models can improve upon by taking into account variation in body size and the energy required for individuals to perform rituals and so forth as members of social groups. At a global scale, T and r largely determine variation in the productivity of an ecosystem (e.g., grams of biomass per unit area per unit time). Thus, we define the intrinsic energy supply of an environment as a function of rainfall and temperature. As a first approximation, we assume that the productivity of an ecosystem is an increasing, diminishing returns function of mean annual rainfall and that productivity increases exponentially as temperature increases from the poles to the equator. While a first approximation, analyses of the affects of rainfall and temperature on global patterns of net primary productivity are consistent with these assumptions (Del Grosso et al., 2008). Based on these assumptions, we write $E_s = c_1 r^{\beta_1} e^{\beta_2 T}$, where c_1 is a constant, $0 < \beta_1 < 1$ and e is the exponential.

Additionally, for omnivores, like human foragers, diet determines how effectively individuals locate resources. We assume, to start, that if individuals get enough food they also obtain a sufficient quantity of nutrients, fats and protein. The more that foragers hunt large bodied animals, the longer foragers must travel and search for food. This occurs because large bodied animals are both less dense than, say, grasses or tubers and animals move around over large territories, which makes them harder to find than stationary resources. We, thus, define the rate of energy production in an environment as the intrinsic supply of energy, E_s multiplied by how effectively foragers locate resources, Q. Search effectiveness is $Q = c_2 e^{-\beta_3 H}$, where e is the exponential, and H is the amount of diet that comes from hunting large animals. This assumes that individuals get exponentially better at locating food as they shift from large bodied, hunted game toward stationary resources. We can now write the area required per forager as:

$$a(r, T, Q) = \frac{E_d}{c_1 c_2 r^{\beta_1} e^{\beta_2 T} e^{-\beta_3 H}}. \tag{3}$$

If a group's territory depends solely on each individual's use of space to meet their demand for energy, as suggested by Eq. (1), then using Eq. (3) we can define a group's territory as