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Large mammal biomass predicts the changing distribution of hunter-gatherer settlements in mid-late Holocene Alaska

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ABSTRACT

This study provides an ecological explanation for the distribution of Arctic Small Tool tradition (ASTt) settlements in Alaska and the origin of their arctic maritime adaptation. Theoretically grounded in the ideal free distribution (IFD) model, which predicts that higher ranked habitats will be occupied first and most continuously, we contend that the location of large mammals was a major factor influencing human dispersal and settlement decisions in the arctic and subarctic ecosystems of Alaska. We rank habitat suitability based on historic mammal population densities from wildlife ecology reports across predefined ecological zones in Alaska; we multiply densities by average animal weights per species to determine suitability rankings. Coastal habitats in Alaska are higher ranked than adjacent tundra habitats, but the interior boreal forest may have been the highest ranked, considering technological constraints of hunting aquatic species. The ASTt migration into Alaska created population pressure that promoted the colonization of the unoccupied Arctic coast and development of the dual, terrestrial-maritime economy. When pan-Alaska human populations declined around 3200–2500 years ago low ranked tundra ecoregions were abandoned. As human populations recovered Alaska coasts became the most densely populated habitats. The adaptive logic entailed in the IFD provides a consistent evolutionary interpretation for settlement patterns documented in this region.

1. Introduction

Archaeologists routinely recognize relationships among resource distribution, adaptive strategies, and prehistoric settlement patterns (Bettinger and Baumhoff, 1982; Binford, 1980; Jochim, 1991; Winterhalder et al., 2010). Many have drawn on environmental and ecological variables to reconstruct settlement and subsistence patterns for prehistoric cultures of Alaska (Clark, 1984; Dumond, 1987a; Mason and Gerlach, 1995; Potter, 2008a; Yesner, 1981) and archaeological traditions have been linked to particular habitats (e.g., Dixon, 2013; Dumond, 1987b; Esdale, 2008). This work has demonstrated an uneven distribution of populations through time and delayed settlement of some ecological niches, including the arctic coast. This provokes two central questions: Why were some habitats chosen over others? And, what drove the settlement of previously uninhabited areas? The availability of resources almost certainly played a role in these processes. We have lacked, however, an explanatory framework that integrates considerations of resource availability, subsistence technology and economics, and human impacts. The goal of this study is to understand the ecological conditions that promoted the initial settlement of the Arctic and the development of maritime adaptations in northern Alaska in just those terms.

The first culture to make routine use of arctic coastal habitats in Alaska was the people of the Arctic Small Tool tradition (ASTt) (Ackerman, 1998). The ASTt are thought to be a colonizing population that arrived in Alaska from Siberia around 5000 years ago (Powers and Jordan, 1990; Prentiss et al., 2015; Raghavan et al., 2014; Tremayne and Rasic, 2016). They are widely recognized as the first to colonize the high Arctic of North America and Greenland (Dumond, 1987b; Friesen and Mason, 2016; Maxwell, 1980; McGhee, 1996). To understand the ASTt colonization of the Arctic and development of their novel economic system we require a method to compare between the qualities of habitats they were willing or able to settle. To do this we developed an ecological model that uses large mammal biomass to predict where newly immigrant ASTt people should have settled first, given the ecological constraints and opportunities facing them. In doing so we demonstrate the interpretive power of behavioral ecology for

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understanding complex archaeological problems at even the broadest scales.

2. Background

Alaskan researchers typically characterize the ASTt economy as terrestrially based caribou hunting with a secondary emphasis on hunting small marine mammals (Ackerman, 1998; Anderson, 1988; Dumond, 1982, 2001; Giddings, 1964; Workman and McCartney, 1998). Recent interpretations give greater emphasis to the importance of ASTt maritime adaptations (e.g., Dixon, 2013; Tremayne, 2015c), although uncertainty on the topic persists. In the eastern Arctic, the ASTt focus on marine resources is more apparent in the archaeological record, although caribou and musk ox were also important to their economy (Grønnow, 1994, 2016; McCartney and Helmer, 1989; Melgaard, 2004; Milne and Park, 2016; Møbjerg, 1999; Savelle and Dyke, 2002; Seersholm et al., 2016). At some stage along their migration from Siberia the ASTt became adept maritime hunters, their dual marine-terrestrial subsistence strategy helping to fuel their spread into Alaska and their migration east. One of the primary goals of this study is to explain why this adaptation emerged when it did and the role access to resources played in this process.

The ideal free distribution (IFD) model from behavioral ecology (Fretwell and Lucas, 1969; Sutherland, 1983) provides an excellent framework for analyzing regional settlement patterns of migratory populations such as the ASTt. Developed first to describe the dispersive behavior and distribution of birds (Fretwell and Lucas, 1969), the IFD has recently proved useful for explaining anthropological problems as well (Codding and Jones, 2013; Jazwa et al., 2013; Kennett et al., 2006; O'Connell and Codding, 2014; Winterhalder et al., 2010). The model posits that dispersive organisms will choose to locate first in the most suitable habitat available. Suitability includes such factors as access to resources, livability, and exposure to hazards (Winterhalder et al., 2010:471). Habitat suitability is typically assumed to be negative density dependent, meaning that suitability is reduced with increased population density and competition for resources. As suitability of the highest ranked habitat declines, it eventually equals the next highest ranked (Fig. 1). Once this threshold is crossed, new arrivals should distribute themselves into the highest ranking *and* next ranked habitat in a manner that keeps their suitabilities equal. The IFD model posits an equilibrium at which no organism has an incentive to relocate, providing us with several predictions: (1) higher ranked habitats should be occupied first and more continuously through time; (2) lower ranked habitats will be occupied in order of their suitability; (3) population density will be greatest in higher ranked habitats; (4) suitability will be equalized across occupied habitats; and (5) suitability declines across all occupied habitats as population grows.

In addition to these basic IFD predictions, the model allows us to take account of territorial or resource defense behavior of competing groups, economies of scale or Allee effects, technological capabilities and innovation, and environmental or other density-independent factors affecting suitability. The IFD model assumes that individuals are free to move to the highest-ranked habitat available. If mobility is constrained by the competitive or territorial behavior of conspecifics, resource defense induces the dynamics of ideal despotic distribution (IDD) (Codding and Jones, 2013:14569; Kennett et al., 2009). We follow evolutionary biologists in defining a despotic distribution narrowly as one in which one or more individuals or groups in the population is able to sequester and control a disproportionately large share of the factor or factors determining habitat suitability. Access to a territory and its resources would be an example. Subjugation of one class by another that limits

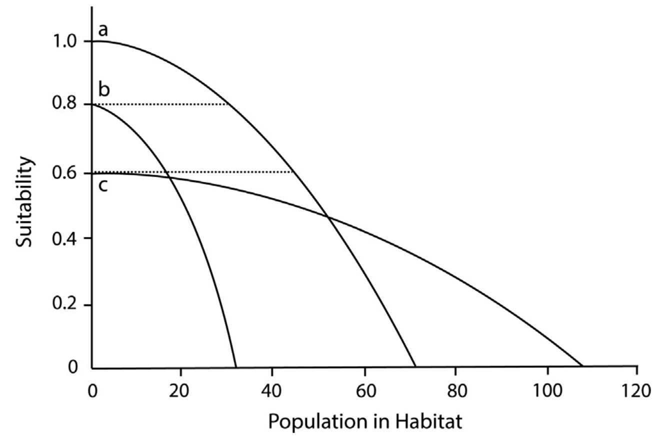

Fig. 1. An idealized depiction of three habitats with variable negative, density-dependent suitabilities. As population increases in habitat "a" suitability is reduced until it equals that of the uninhabited habitat "b", at which time new arrivals will distribute themselves between higher and lower ranked habitats (modified from Winterhalder et al., 2010:479). The gray-shade dotted line shows the relative distribution of population among habitats; the total population envisioned being the sum of the habitat specific populations. Note that IFD dynamics imply equalized suitabilities across habitats.

access to resources or the ability to relocate to an area with higher effective suitability (Bell and Winterhalder, 2014) also implies an IDD.

The Allee effect arises if suitability increases with population density over some range (Allee and Bowen, 1932; Kennett et al., 2006; Winterhalder et al., 2010). Population growth from small beginnings may engage economies of scale that raise per capita habitat suitability as it becomes easier to locate mates, coordinate complex social organization, implement demanding technologies, or gain efficiencies from the division of labor. Presumably there is a population density at which these benefits are exhausted.

A third factor that could affect basic IFD predictions is innovation in technological capability of the dispersing group. Habitat suitability rankings for subsistence are a function of harvesting and processing techniques; they will change if, for instance, an innovative technology transforms a marginally productive environment into a more attractive place to settle. Developments in projectile weaponry, plant processing techniques, fishing and other mass capturing equipment have altered the efficiency with which people have exploited particular habitats since the Upper Paleolithic (e.g., Stiner et al., 2000). Myriad factors affect technology development and the effectiveness of resource extraction (Bettinger et al., 2006; Tushingham and Bettinger, 2013; Ugan et al., 2003), but innovations are generally made to provide solutions to a resource imbalance.

Finally, density-independent environmental change can modify basic habitat suitabilities, perhaps altering the order in which they are ranked (Jazwa et al., 2013), a factor that potentially looms large in long-term studies such as this one. On a shorter time scale seasonal fluctuations in animal population densities and availability alter suitabilities on an annual cycle, adding short-term dynamics to IFD predictions.

We develop an IFD model that ranks major Alaskan habitats, holding technology and environmental change constant. Our first challenge is deciding which factors are most important for ranking habitat suitability. Other studies have used watershed size and resource base (Winterhalder et al., 2010), effective moisture (O'Connell and Codding, 2014), and environmental bioproductivity (Codding and Jones, 2013) as proxy measures for suitability. Here, we assess suitability by using large animal population densities. We contend that animal products—particularly meat for