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The Ideal Distribution Model and Archaeological Settlement Patterning

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ABSTRACT
Human populations distribute themselves across landscapes in clearly patterned ways, but accurate and theoretically informed predictions and explanations of that patterning in the archaeological record can prove difficult. Recently, archaeologists have begun applying a unifying theoretical framework derived from population and behavioural ecology to understand human population distribution and movement: the ideal distribution model (IDM). The three variants of this IDM - the ideal free distribution, the ideal free distribution with an Allee effect, and the ideal despotic distribution - are capable of generating testable hypotheses concerning the colonisation of landscapes, the spatial distribution of populations, cooperation and competition, social hierarchy and inequality, and the impacts of subsistence on settlement patterns. Their success in addressing such wide-ranging research questions demonstrates that IDMs are not only helpful for analysing settlement patterns in relation to environmental factors, but for better understanding the social forces that impact population distribution, as well. There seem to be no geographic or temporal bounds to the utility of IDMs, and we look forward to the application of these models in ever more diverse settings.

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Introduction

Where people choose to live is a central question in archaeological research that has been studied using wide-ranging theoretical approaches (e.g. Flannery 1976; Thomas 1973; Tilley 2010; Willey 1953). Human populations distribute themselves across landscapes in clearly patterned ways (e.g. Binford 1980; Hitchcock and Ebert 1989; Steward 1938), but accurately recording and explaining that patterning in the archaeological record can prove difficult (Parsons 1972). Commonly, archaeologists look for relationships between site locations and environmental and geographic variables such as elevation, soil fertility, modelled production capacity, or climatic patterns to explain site distribution (e.g. Contreras et al. 2018; Morgan 2009; Williams et al. 2015). Others have explored connections to demographic change, following longstanding hypotheses that describe the expansion of human settlements into new areas due to population density (Anderson 1990; Binford 1968). Occasionally, researchers have also examined the role of social factors in structuring the location and duration of human settlement (McDonald and Veth 2012; Thompson, Meredith, and Prufer 2018). Yet none of these approaches provide a single, unifying theoretical framework to deductively test how all of these factors shaped past settlement decisions and population distribution.

Recently, archaeologists have begun applying such a unifying theoretical framework. In 1969, Stephen Fretwell and Henry Lucas Jr. published a landmark paper entitled 'On Territorial Behavior and Other Factors Influencing Habitat Distribution in Birds' in *Acta Biotheoretica* (Fretwell and Lucas 1969). This seminal paper from the fields of ornithology and behavioural ecology has now been cited more than 5000 times. Fretwell and Lucas (1969) outline a model of habitat selection with three variants: the ideal free distribution, the ideal free distribution with an Allee effect, and the ideal dominance distribution (later known as the ideal despotic distribution). These three versions of ideal distribution models (IDMs) have been applied to many different species and circumstances to develop predictions for how non-human (Hendrickx, Palmer, and Travis 2013; McNickle and Brown 2014; Nicolai et al. 2014) and human (Disma, Sokolowski, and Tonneau 2011; Moritz et al. 2014a, 2015, 2014b; Morris and Kingston 2002) organisms should distribute themselves across a landscape. As we endeavour to establish in this editorial, and as the papers in this special issue demonstrate, IDMs continue to be useful in such conventional applications, but recently, these half-century-old models have inspired novel and exciting applications, particularly in the field of archaeology (see Codding and Bird 2015 for a recent review).

Ideal Distribution Model Dynamics

The foundation of ideal distribution models rests on the assumption that individuals will seek to maximise

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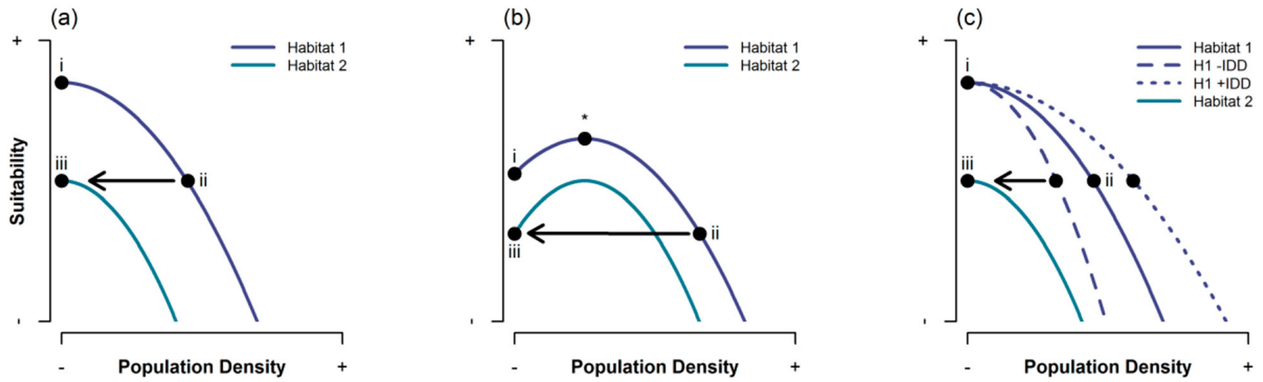

Figure 1. Graphical representation of an ideal distribution model for a simple two-habitat environment under (a) 'free' conditions with pure negative density dependence, (b) free conditions with Allee effects (initial positive or inverse density dependence followed by negative density dependence), and (c) negative density dependence with 'positive' and 'negative' despotism (ideal despotic distribution) in habitat 1. Suitability varies as a function of population density following Greene and Stamps (2001, eq. 1).

suitability. Suitability refers to the potential for a habitat to positively impact an individual's evolutionary fitness, whether by influencing reproductive success directly or, more likely, indirectly through somatic benefits in the form of economic efficiency or subsistence yields, for example. In the model, suitability declines as each new individual isadded to a habitat (a phenomenon termed negative density dependence) and by making optimal decisions individually, the population will distribute itself 'ideally' so that each individual obtains the same suitability value (i.e. is at equilibrium).

Under the Ideal 'Free' Distribution (IFD) with negative density dependence (Figure 1(a)), there are no restrictions to an individual's movement and no benefits to proximity to others. Thus individuals should settle in the most suitable habitat first (point i in Figure 1(a)) and should only begin settling in the less suitable habitat once population density depresses suitability in the better habitat to the point where the next individual added would experience equal suitability in either habitat (point ii to iii in Figure 1 (a)). From these dynamics, we can derive at least two qualitative predictions: (1) that individuals should always settle in the more suitable habitat first and (2) that as long as suitability declines at similar rates as a function of density across the two habitats, the more suitable habitat will always have higher population density.

One variant of this basic distribution model known as Allee's Principle or Effect emphasises that there can be benefits to conspecific co-occupation, at least up to some threshold (Allee 1931; 1949; see Courchamp, Clutton-Brock, and Grenfell 1999). These benefits may include inherently social factors such as shared defense or accessibility of mating partners, or relate to environmental modifications, such as increased resource abundance or productivity. That Allee Effects result in an increase in suitability with each individual added to the habitat (termed positive density dependence) up to some threshold also establishes an optimal group size (point * in Figure 1(b)), and illustrates how, in most circumstances, 'free' settlement will result in larger than optimal group sizes (i.e. the difference in population density between point * and point ii in Figure 1(b)).

IDMs may also take on a despotic form in which certain individuals control access to locations by excluding others and lowering their 'suitability' (Summers 2005; Vehrencamp 1983a, 1983b). This is sometimes called an ideal despotic (or dominance) distribution (IDD; Figure 1(c)). Two variants, 'negative' and 'positive' despotism, occur when individuals should leave a patch at lower or higher respective densities than a patch without despotism. Under 'negative' despotism, the early occupants of a habitat may find it worthwhile to defend semi-exclusive use of the patch by driving away newcomers who seek to cohabitate. Such territoriality reduces the suitability of the habitat to those who might settle there, resulting in lower population densities in higher suitability habitats, and more rapid dispersals to lower suitability habitats than would otherwise be expected. The 'positive' form of despotism is the opposite: the initial occupants of a habitat find it worthwhile to allow others to occupy their patch by relinquishing some of their control of the habitat's 'suitability', however that may manifest. Bell and Winterhalder (2014) mathematically demonstrated that instead of driving more rapid expansion, despots can lessen their monopoly on suitability by making concessions so that others find it more suitable to stay as a subordinate than to disperse to the next most suitable habitat as an autonomous individual. Serfdom would be an example of this kind of dynamic, in which a despot allows another to farm a portion of their land for a share of the harvest. Doing so provides incentives for others to remain in higher-suitability habitats under despotic control while granting despots some of the benefits of positive density dependence.

Archaeological Applications of IDMs

Since Kennett (2005), McClure, Jochim, and Barton (2006), and Kennett, Anderson, and Winterhalder (2006) first applied IDMs to archaeology, numerous applications have expanded their reach to a broad set of topics. Kennett (2005) examined the colonisation and subsequent resettlement dynamics in the northern Channel Islands of California. McClure, Jochim, and Barton (2006) employed the IFD (with and without Allee effects) to understand how climate change drove agricultural intensification which reduced the suitability of agricultural land in Neolithic Spain, leading people to move to new habitats and adopt new technologies (McClure, Barton, and Jochim 2009). In that same volume, Kennett, Anderson, and Winterhalder (2006) used the IFD to explain why the colonisation of Oceania was episodic: expansion was interrupted by pauses during which populations grew and subsistence intensified, thereby lowering habitat suitability and encouraging movement to lower-suitability islands. Since these pioneering studies, archaeological applications of IDMs have focused on five main areas of inquiry: the diachronic colonisation of regions, the synchronic distribution of sites and populations across a landscape, the origins or strengthening of cooperation, the origins of despotism and social hierarchies, and the relationship between subsistence and suitability.

Colonisation and Migration

Diachronic analyses of landscape colonisation lend themselves particularly well to the use of IDMs, as the models are fundamentally concerned with how increasing population density and declining suitability drive expansion into lower-suitability habitats. Allen and O'Connell (2008; O'Connell and Allen 2012) developed an ideal distribution framework to evaluate the Pleistocene colonisation of Sahul (modern day Australia and New Guinea), arguing that rapid colonisation was likely driven by negative density dependence, which led individuals to favour unoccupied habitats even when suitability declined only slightly. Winterhalder et al. (2010) showed that human settlement of the Northern Channel Islands of California conformed to an IFD using watershed attributes such as drainage size and beach length as suitability proxies. Giovas and Fitzpatrick (2014) explored the potential for the IFD to explain Ceramic Age colonisation of the Caribbean and found that island area and primary production were good proxies for suitability that predicted the order of island settlement reasonably well, and also helped to explain some interesting deviations from IFD predictions. Hanna and Giovas (this issue) continue to explore Caribbean settlement patterns in the southern Lesser Antilles, by using the IFD to inform a predictive model of site location over time. Miller (2018, 112–137) and Miller and Carmody (2016) use the IFD to demonstrate that population in-filling of Tennessee occurred through the Late Pleistocene and Holocene, creating population pressure that may have inspired the initial domestication of plants in the region. Miller and Carmody (this issue) follow up on this work by showing that settlement dynamics shift from being largely 'free' in the early Holocene, to more Allee-like in the middle Holocene, and finally more despotic in the late Holocene. Yaworsky and Codding (2018) showed that IDMs need not only be applied in prehistoric contexts by demonstrating that the Euro-American colonisation of Utah in the nineteenth and twentieth centuries conformed to predictions of the IFD, with settlers preferring areas with high moisture and agricultural potential. Given the common occurrence of human colonisation events and migrations throughout history, much opportunity exists to apply IDMs and future work could benefit from attention to population movements into already-occupied landscapes as well as the interplay between prey and patch choice dynamics and demographic expansion.

Population Distribution

Like diachronic analyses of colonisation and migration, IDMs are useful for modelling the synchronic distribution of populations across a landscape. According to the IDM, populations are assumed to be at equilibrium at any one time, meaning that even a single temporal snapshot can capture the underlying ecological dynamics that structure the relationship between suitability and population density. For example, Codding and Jones (2013) showed that ethno-historic population densities in California follow IDM predictions, with higher population densities occurring in more suitable habitats. This supports the second common qualitative prediction of the IFD discussed above: that more suitable habitats will have higher population densities. This predicted pattern holds across diverse modes of subsistence, both archaeologically and ethnographically, including hunter-gatherers (Tremayne and Winterhalder 2017), pastoralists (Moritz et al. 2015), and farmers (Yaworsky and Codding 2018), as well as across varied forms of sociopolitical structure, including relatively egalitarian societies (Allen and O'Connell 2008), emerging chiefdoms (Winterhalder et al. 2010), and monarchies (Jazwa and Jazwa 2017). Such predictions derived from the IDM can be incorporated into predictive site modelling, lending an element of theoretical robustness to such endeavours (Davis et al. 2020; Hanna and Giovas, this issue; Vernon et al. this issue).

Cooperation and Competition

Recent work has also demonstrated that IDMs are useful for understanding the dynamics of interpersonal cooperation and intergroup competition in the past. Codding, Parker, and Jones (2019) leveraged ethnohistoric data on early colonial period Native groups from western North America to show that the size of cooperative groups positively covaried with territoriality and rates of intergroup violence. Robinson et al. (2019) hypothesised that patterns of site aggregation and dispersion should relate to the presence and strength of Allee effects driven by cooperation. Their results show how site clustering co-varies with population density, revealing underlying Allee effects that structured settlement dynamics across Wyoming prehistory. Weitzel et al. (this issue) build on these findings by using site location data to explore how plant management and domestication in mid-Holocene eastern North America created a novel Allee effect that incentivised within-group cooperation while simultaneously inspiring intergroup violence. Work using IDMs to model within-group cooperation and between-group competition is still in its infancy, but these early results are promising and indicate potential for further investigation.

Despotism

While population expansion and distribution across landscapes are the patterns most commonly investigated using IDMs, these models, particularly the IDD, have occasionally been used to address the rise of social hierarchy, inequality, and territoriality. The IDD predicts that a despotic early-arriver in a habitat can monopolise the location's 'suitability' and force new arrivals to settle in lower suitability locations. Kennett and Winterhalder (2008) employed the model in this form to argue that while dispersion across Polynesia is consistent with IFD dynamics (Kennett, Anderson, and Winterhalder 2006), more rapid expansion after c. 1000 BP aligns better with an IDD. This is especially likelygiven that associated patterns of intensification, warfare, monument construction, and landscape modification co-occur with despotic social organisation. Einarsson (2015) explored despotism in the Viking-aged settlement of Iceland and finds that higher suitability habitats were defended with formal fencing while lower suitability habitats were not, indicating negative IDD dynamics followed the settlement of more suitable habitats. Harvey (2019) showed that late period archaeological sites in the Kern River watershed of California Sierra Nevada favoured lower suitability locations, which they interpret as a strategy to maintain access to key plant resources (acorns and pine nuts) while avoiding competition in more suitable locations.

In contrast, 'positive' despotism may occur when it is beneficial for individuals to settle on an already-occupied and despotically-controlled highly suitable patch in return for concessions. Prufer et al. (2017) argued that positive despotism – and with it, social hierarchy, inequality, and complexity – developed out of earlier ideal free dynamics in southern Belize during the Classic Maya Period. This occurred since the original highest suitability habitats supporting the greatest population density had thelongest population continuity, which benefitted those groupsin terms of lineal social organisation, cooperative defense, and food production. Kennett et al. (2009; Jazwa et al. 2019) made a similar argument for the Channel Islands in California, where earlier IFD dynamics gave way to despotism as increased population packing and subsistence intensification led to unequal access to resources. Individuals appear to have resisted settling in the most marginal habitats in favour of subordinating themselves to despotic control in higher-suitability locations.

Evaluating when settlement dynamics are more likely to take a negative or positive despotic form is a rich area for future theoretical and empirical research. Ecological theory suggests that individuals should only defend habitats from incoming settlers if the benefits of doing so are worth the costs (Brown 1969; Dyson-Hudson and Smith 1978). The same should be true for the costs of positive despotism where a despotic individual would only allow individuals to settle if the loss in suitability were worthwhile. Yet understanding how these trade-offs articulate within an IDM framework to produce varied outcomes remains under-explored.

Subsistence and Suitability

Defining suitability remains one of the greatest challenges to archaeological applications of IDMs, but it is also one of the greatest opportunities. To date, researchers have typically selected an environmental metric as a proxy for suitability and proceeded to evaluate whether settlement or population density conforms to predictions given that metric. Vernon et al. (this issue) take the opposite approach by assuming that populations will settle down following an IDM, and then using settlement patterns to identify which environmental variables were most important in determining settlement decisions. A middle-ground strategy that falls between these two approaches was undertaken by Winterhalder and colleagues (2010), who used a Bayesian model to iteratively evaluate the interaction between settlement and proxies of suitability. Still, archaeologists have not yet implemented a more comprehensive research strategy (Bird and O'Connell 2006; Codding and Bird 2015; O'Connell 1995) that first evaluates model predictions using ethnographic (or experimental) data and then links environmental proxies of suitability to actualised suitability (e.g. return rates) experienced by individuals across varying levels of population density. Such validation is required before any proxy of suitability can be considered robust. Codding et al. (this issue) make a move in this direction by using a proxy for agricultural suitability that predicts the historic distribution of farmers in the Colorado Plateau and Great Basin (Yaworsky and Codding 2018), but this measure of suitability still isn't sufficiently validated to truly assess model predictions. Given that such an approach requires extensive experimental or ethnoarchaeological research, it is not surprising that it has not yet been done.

Another complication of defining suitability is the fact that it changes over time. While IDMs fundamentally assume that population distribution is driven by the relationship between population density and habitat suitability, most studies have made the simplifying assumption that suitability remains constant over time, using static proxies extracted from modern environmental measurements. While this assumption has led to useful findings, and may be particularly appropriate for assessments of suitability based on predominately abiotic or geographically-fixed features of the environment (Winterhalder et al. 2010), habitat suitability can change for a variety of reasons and can impact the dynamics of IDMs (Kennett and Winterhalder 2008; McClure, Jochim, and Barton 2006). Bliege Bird et al. (2020) demonstrated that habitat suitability was elevated by anthropogenic fires set by Aboriginal Australians in the 1950s, impacting land use and settlement decisions, and such burning has likely impacted human settlement in Australia for many millennia (O'Connell 2020). Miller and Carmody (this issue) further illustrate that suitability is not constant by coupling paleoenvironmental records with settlement data to illustrate how changes in suitability throughout the Holocene may have structured settlement dynamics.

Recent work has explicitly recognised the difficulties of inconstant suitability and has sought to explore the relationship between suitability and subsistence economies. For example, changing agricultural and pastoralist subsistence strategies in Bronze Age Europe impacted habitat suitability and thus the distribution of human populations in many locations (Harper et al. 2019). Jazwa et al. (2016a) made another valuable contribution by modelling variation in streamflow across watersheds over wetter and drier periods of time. In this issue, four separate papers explore the relationship between subsistence economies and habitat suitability. Codding et al. (this issue) explore how the northward spread of maize farming in the southwestern United States occurred only when population density increased enough to make farming in lower suitability habitats profitable. Vernon et al. (this issue) use a variant of maximum entropy (MaxEnt) modelling to show that, assuming ideal distribution dynamics, suitability can be deconstructed into its constituent components based on where people chose to settle. These locations differed for Archaic foragers and Formative farmers in southern Utah. Collins-Elliot and Jazwa (this issue) model how suitability changes dynamically through time as a function of population density, site proximity, and environmental attributes in Morocco. Finally, Plekhov and Levine (this issue) use a large dataset of site locations from Afghanistan to argue that the land-use systems of agricultural and pastoralist populations were so different that the suitability of a habitat was not the same for both.

Another potentially fruitful area for future research is the exploration of the social and political aspects of suitability. Prufer et al. (2017) showed that the distance to important trade and exchange centres serves as an important predictor of settlement. Similarly, Jazwa and Jazwa (2017) used the distance to cultural and economic centres as important co-variates of suitability, while Collins-Elliot and Jazwa (this issue) also integrate such a distance measurement into their study. Theseattempts to include more historically particularistic attributes in IDMs show that such modelling exercises need not be regional in scope. Smaller-scale local (Jazwa, Kennett, and Winterhalder 2016b; 2019) and site-specific (Jazwa, Kennett, and Winterhalder 2013) analyses can easily be fit into broader regional frameworks informed by IDMs when other lines of evidence such as faunal data reveal habitat suitability changes that may or may not be density dependent.

Conclusions

That IDMs have been successfully applied to an increasingly wide variety of research questions suggests that these models are only beginning to realise their potential in archaeology. We fully expect the boundaries to be pushed even further through the application of these models in a more diverse array of settings. There seem to be no geographic or temporal bounds to the utility of IDMs, as successful analyses have been conducted across western and eastern North America, the Caribbean, western and eastern Europe, northern Africa, central Asia, and Oceania in time periods ranging from 50,000 years ago to the early twentieth century, not to mention contemporary ethnographic applications. Such models are capable of generating testable hypotheses concerning the colonisation of landscapes, the spatial distribution of populations, cooperation and competition, social hierarchy and inequality, and the impacts of subsistence on settlement patterns. Their success in addressing such wide-ranging research questions demonstrates that IDMs are not only helpful for analyzing settlement patterns in relation to environmental factors, but for better understanding social forces that impact population distribution, as well. These points are clearly demonstrated by the papers in this special issue. We look forward to the new knowledge that these models will unlock over the next fifty years.

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Disclosure Statement

No potential conflict of interest was reported by the author(s).

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Brian F. Codding is Associate Professor of Anthropology and Director of the Archaeological Center at the University of Utah. His research examines human-environment interactions in the past and present through the lens of behavioural ecology. Current research is focused on explaining the dynamics structuring subsistence and land use decisions, and the feedbacks these decisions have on social and ecological systems and across western North America.

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