



Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

The foraging potential of the Holocene Cape south coast of South Africa without the Palaeo-Agulhas Plain

Colin D. Wren^{a,*}, Susan Botha^b, Jan De Vynck^b, Marco A. Janssen^c, Kim Hill^d,
Eric Shook^e, Jacob A. Harris^d, Brian M. Wood^f, Jan Venter^{b,h}, Richard Cowling^b,
Janet Franklin^g, Erich C. Fisher^{b,d}, Curtis W. Marean^{b,d}

^a Department of Anthropology, University of Colorado Colorado Springs, 134 Centennial Hall, 1420 Austin Bluffs Parkway, 80918, USA

^b African Centre for Coastal Palaeoscience, Nelson Mandela University, PO Box 77000, Port Elizabeth, Eastern Cape 6031, South Africa

^c School of Sustainability, Arizona State University, PO Box 875502, Tempe, AZ 85287-5502, USA

^d Institute of Human Origins, School of Human Evolution and Social Change, PO Box 872402, Arizona State University, Tempe, AZ 85287-2402, USA

^e Department of Geography, Environment & Society, 414 Social Sciences Building, 267 19th Ave S, Minneapolis, MN 55455, USA

^f Department of Anthropology, University of California, Los Angeles, 375 Portola Plaza, Los Angeles, CA, 90095, USA

^g Department of Botany and Plant Sciences, University of California – Riverside, 900 University Ave, Riverside, CA 92521, USA

^h School of Natural Resource Management, George Campus, Nelson Mandela University, Madiba Drive, George, 6530, South Africa

ARTICLE INFO

Article history:

Received 4 December 2018

Received in revised form

10 May 2019

Accepted 9 June 2019

Available online xxx

Keywords:

Holocene

Paleogeography

Southern Africa

Data treatment

Data analysis

Agent-based modeling

ABSTRACT

The Palaeo-Agulhas Plain formed an important habitat exploited by Pleistocene hunter-gatherer populations during periods of lower sea level. This productive, grassy habitat would have supported numerous large-bodied ungulates accessible to a population of skilled hunters with the right hunting technology. It also provided a potentially rich location for plant food collection, and along its shores a coastline that moved with the rise and fall of sea levels. The rich archaeological and paleontological records of Pleistocene sites along the modern Cape south coast of South Africa, which would have overlooked the Palaeo-Agulhas Plain during Pleistocene times of lower sea level, provides a paleoarchive of this extinct ecosystem. In this paper, we present a first order illustration of the “*palaeoscape modeling*” approach advocated by Marean et al. (2015). We use a *resourcescape* model created from modern studies of habitat productivity without the Palaeo-Agulhas Plain. This is equivalent to predominant Holocene conditions before recent landscape modifications for farming. We then run an agent-based model of the human foraging system to investigate several research questions. Our agent-based approach uses the theoretical framework of optimal foraging theory to model human foraging decisions designed to optimize the net caloric gains within a complex landscape of spatially and temporally variable resources. We find that during the high sea-levels of MIS 5e (+5–6 m asl) and the Holocene, the absence of the Plain left a relatively poor food base supporting a much smaller population relying heavily on edible plant resources from the current Cape flora. Despite high species diversity of plants with edible storage organs, and marine invertebrates, encounter rates with highly profitable resources were low. We demonstrate that without the Palaeo-Agulhas Plain, human populations must have been small and low-density, and exploited plant, mammal, and marine resources with relatively low caloric returns. The exposure and contraction of the Palaeo-Agulhas Plain was likely the single biggest driver of behavioural change during periods of climate change through the Pleistocene and into the transition to the Holocene.

© 2019 Elsevier Ltd. All rights reserved.

1. Introduction

As palaeoanthropological and archaeological investigations have studied the Cape south coast of South Africa from the

perspective of past humans living on this landscape, we have become increasingly aware of the importance of the shifting sea-level and the repeated exposure and submerging of the Palaeo-Agulhas Plain (Van Andel, 1989; Fisher et al., 2010; Marean et al., 2014). While the modern landscape contains an impressive diversity of plant species (Cowling et al., 2003), there is a generally low density of mammal resources for hunting in the region during

* Corresponding author.

E-mail address: cwren@uccs.edu (C.D. Wren).

these high sea-level conditions compared to what was available on the Palaeo-Agulhas Plain during the low sea-level conditions that comprises the majority of the Pleistocene (Marean et al., 2014; Helm et al., this volume; Venter et al., this volume). In this paper, we ask how foragers would fare in the past during the high sea-level phases without the Palaeo-Agulhas Plain. We first developed a model for high sea-level conditions because the landscape would have been analogous to its present conditions (minus the effects of farming) and that can be observed in detail and modeled most easily. This allowed us to initially study one state, an interglacial, and build a strong foundation for applying the model to the less well-known low sea level (glacial) conditions in future work.

Here, we use modern studies of habitat productivity joined to an agent-based simulation approach to model a human hunter-gatherer foraging system situated on a reconstructed Cape south coast landscape. Marean et al. (2015) outlined a new research agenda where it was advocated that ancient *palaeoscapes* — organic computer models of past ecosystems — be constructed through a combination of modern studies of habitat productivity for human foragers (creating a *resourcescape*) that could then be projected for past conditions through a combination of paleoclimate and paleovegetation modeling (Franklin et al., 2015). Then, agent based modeling with human foragers as our agents would be used to create formal predictions of human behaviour for testing with archaeological data, test within the model hypotheses of changing parameters (resource change, cognitive evolution, social change, etc.), and conduct sensitivity analyses by changing resource productivity in the model (Fig. 1). This paper is a first order simulation using reconstructed Holocene conditions to probe the significance of the Palaeo-Agulhas Plain ecosystem to foragers inhabiting current coastal sites. The model will grow in complexity and utility as we add simulated palaeoclimate and palaeoenvironment information for glacial conditions with lower sea levels, and more resource-types are studied and built into the modeled *resourcescape*.

In this paper, we study a specific set of questions. We evaluate several aspects of the simulation to determine if the population functions as expected in terms of general foraging patterns, mobility, and group dynamics. We then evaluate the viable human population densities on this landscape under different scenarios. For the viable range of human population densities, we observed the simulated balance of their diet coming from the available food resources: terrestrial plants, mammals and coastal shellfish. The dietary balance of these different resources varies considerably among known ethnographic case studies, particularly with latitude

but also with other ecological and social contexts (Binford, 2001; Kelly, 2013; Hawkes et al., 1982). We also evaluate the effects of the same population density divided into different foraging group sizes. There are advantages and disadvantages to living in groups of various sizes when food sharing is an established practice. Larger groups may stabilise the daily availability of calories by averaging out high variance returns, however, each individual may derive less benefit from their own efforts if they are expected to share with a larger group (Dewar et al., 2006; Winterhalder, 1986; Hawkes et al., 2001). Finally, we also look at how the mobility patterns of simulated foraging groups respond to higher levels of population pressure and the differential stress on the resource base that those population densities exert.

2. Background to the model

2.1. General model assumptions and logic

The methodological approach taken in this paper is novel in several respects, including the level of detail we strive for in the modeled foraging system. A primary reason for this is our desire to bring archaeological and evolutionary anthropological approaches closer together (Marean et al., 2015). Archaeology has long had an interest in hunter-gatherer societies and the relationship between subsistence, mobility, and settlement. Evolutionary anthropology has brought a suite of tools within the broader optimal foraging theory approach that have not been fully embraced by archaeology (Coddington and Bird, 2015). Part of this previous lack of integration is due to the different scales of analysis of the two disciplines. A key strength of agent-based models is that they provide a framework for connecting fine scale human behaviour, which tends to be the scale of evolutionary anthropology and optimal foraging theory approaches, with the broad spatial and temporal scales of the aggregated archaeological record (Romanowska, 2015). Mithen (1988, 1990) first integrated optimal foraging theory's prey-choice model and an agent-based modeling approach in the MESO-SIM model of decision making during hunting although the model was not spatially explicit. Lake (2000, 2001) continued this work with the MAGICAL model focusing on a patch-choice model of hazelnut foraging and the effects of information sharing between foragers. In this paper, we also specifically develop our agent-based model of human foraging behaviour at the local scale using empirical and theoretical concepts derived from optimal foraging theory (Stephens and Krebs, 1986; Winterhalder, 1981) and use the model to derive patterns that can be compared to archaeological

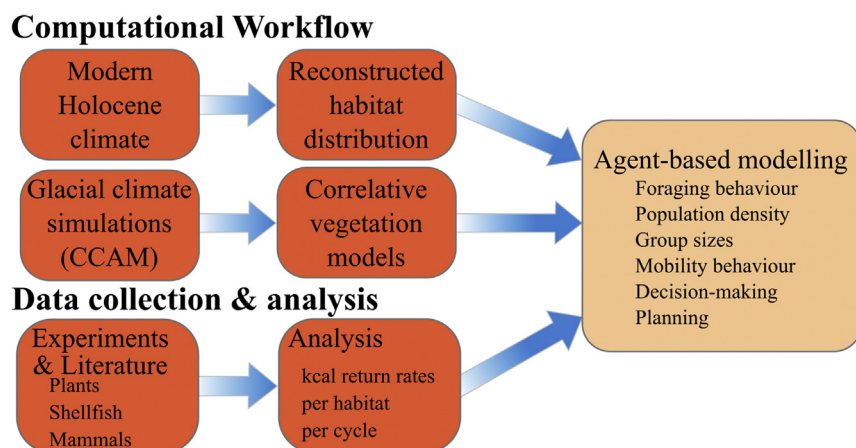


Fig. 1. Workflow diagram of the broader Palaeoscape research project. The current paper is the end point of a large amount of empirical and computational modeling studies that have contributed data to the agent-based model.

data. For example, our agents make mobility and foraging decisions with the goal of optimising their net caloric returns based on their current knowledge. We do not aim to precisely replicate the archaeological record, but instead to experiment with ecological, social, and behavioural characteristics to evaluate their impact on potential archaeological records and their implications for past human society (Barton, 2014). This allows us to evaluate a number of specific questions about how our understanding of human hunter-gatherer societies articulates with the Middle and Later Stone Age archaeological records of the Cape south coast. While the landscape and empirical values are particular to this region, the model's design allows it to be deployed for many time periods and regions provided sufficient data is available.

The use of optimal foraging theory principles as the underpinning of our agent-based modeling efforts also provides us with a well-studied theoretical foundation to give confidence in our approach and a concrete set of models to focus our data collection efforts. We use a patch-based model for plant and shellfish foraging and a sequential-encounter prey-based model for mammal hunting. These optimal foraging theory (OFT) models dictate which data we need in order to predict time allocation and daily caloric returns of a foraging society in the given landscape.

The model we designed makes a number of simple assumptions about hunter-gatherer societies. We assume that both individual foragers, and the collection of foragers who live together in a camp, will make reasoned decisions about their foraging and mobility to maximize long-term net caloric returns. These decisions will be based on their knowledge of their surroundings (whether resources are currently available), time lost while traveling, changes in caloric returns due to tidal cycles, and expected foraging returns moving across different habitats. We also assume that foragers share food among the people living together in each camp in order to ameliorate problems of high daily variance in individual food returns. We based the model on a model structure we developed for a study of contemporary hunter-gatherers, the Ache in Paraguay using a prey-based approach (Janssen and Hill, 2014). In this paper, we expand the model to including gathering using a patch-based approach as well as hunting. The landscape inhabited by the Ache is also a patchy mosaic of different habitat types, each with different densities of resources. Further, at least while on foraging excursions, they are residually mobile, share food, and hunt in relatively small groups, which are baseline assumptions for the present model. While the hunting weaponry may differ (the Ache use large bows) we use only the prey-based model structure while adjusting the per species parameters to be appropriate for the South African case study and hunting technology.

People first incorporated marine shellfish into their diet during the Middle Stone Age (Marean et al., 2007) and then further increased their reliance on the resource into the Later Stone Age (Klein and Steele, 2013; Marean et al., 2014). Shellfish contain valuable fats and proteins as well as calories and are relatively easy to collect from rocky intertidal areas under the right conditions. However, profitable resource patches are only available to foragers during the lowest spring tides, which occur for a couple short windows of time each month (De Vynck et al., 2016a). For this reason, Marean (2011) argued that humans required the abstract knowledge of the connection between lunar phases and tidal systems to successfully exploit the coastal ecosystem, linking shellfish exploitation to *Homo sapiens* cognition (see also Marean, 2010, 2014). In this paper, we assume that people had this knowledge and were able to anticipate the profitable low spring tides, hence, we build this knowledge into our agents by allowing them to forecast return rates five days in advance so that they may arrive at the start of the spring tides.

2.2. Specific model data and parameters

As discussed by Marean et al. (2015), in order to reconstruct the foraging system according to OFT principles, we needed several specific pieces of information to allow us to predict the net caloric returns from plant, mammal, and shellfish resources among several different habitat types on the Cape south coast. Our research group conducted studies to build this knowledge (De Vynck et al., 2016a,b,c; Singels et al., 2016; Botha, 2018) and those studies are ongoing and will be added to the model to grow its completeness. The data gathering methodology and empirical results are discussed in more depth elsewhere in this volume and in previous publications cited below. Here we will give a brief overview of our data sources and a summary of the per habitat and per resource category results.

Our study region is 550 km² of coastal (intertidal) and terrestrial habitats with the coastal site of Pinnacle Point and portions of Mossel Bay and Vleesbaai sitting on the southern edge (Fig. 2). We define the model's landscape with cell values representing fourteen specific terrestrial and coastal habitat types (De Vynck et al., 2016a,b,c).

For shellfish and plant resources, we take a patch-based approach to foraging that assumes prior knowledge of patch locations, sizes, and profitabilities and solves for optimal movement patterns and exploitation times. We use experimentally measured data concerning mean harvest rate (kcal/hr) per habitat type and the total number of foraging person-hours harvestable before no longer profitable (hr/ha) in each habitat type and assign these values to our modeled *resourcescape*. Note that we define "no longer profitable" in terms of the marginal value theorem, to be the point in time when it becomes more profitable to move on to the next patch than to stay, rather than when the patch has been completely depleted (Charnov 1976). Because one of our authors is a local resident (JDV), we were able to recruit knowledgeable informants by word of mouth for realistic foraging experiments to estimate relevant parameters. Informants self-reported themselves as descendants of Khoe-San populations and had knowledge of edible indigenous plant and shellfish species (see De Vynck et al., 2016a,c; Botha et al., this volume for further details on the methodology and Institutional Review Board approval).

For hunting, we take a sequential-encounter prey-based approach, which requires data on each species for: density per habitat, pursuit time, probability of success upon encounter, and average weight. From these, and assumed searching walk speed, plus detection distance we also derive probability of encounter. We then use measured nutrient composition or composition of similar species to estimate expected caloric return rate per unit foraging time (both search and pursuit).

It is important to note that at this stage we have not included all the resources potentially available and exploited in the past. We employ large mammals, a small mammal (hyrax), shellfish, and plant foods. We have not included animals such as snakes, lizards, and birds. This is largely because these species were not a significant component of Pleistocene human diet and so would not significantly affect the sustainable population density (Marean et al., 2014), probably because they were low ranked, and generally not targeted by subjects in our experimental studies of food returns. In the future, we hope to broaden our studies and build these resources into the model.

2.3. Shellfish data

We define five different coastal habitat types based on their underlying geology (Table 1). Habitat types were mapped along the



Fig. 2. Model landscape containing the Pinnacle Point site on the peninsula in the SE corner. Red house icons represent camp agents, here in a randomized starting location. The cells of this *resourcescape* are shaded according to the average return rates of the plant and shellfish resources with brighter green shades representing high caloric return rates. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

coastline of our study region using a combination of field survey and visual inspection of satellite imagery (De Vynck et al., 2016a). The collection experiments used 30-min foraging bouts along measured 100 m sections of coastline in each of the habitats. Collected shellfish were then identified to species level and weights recorded along with further details related to participant name, age, sex, weather condition, and tidal level. The most dominate species included *Turbo sarmiticus*, *Perna perna*, and *Haliotis spadi- cea*. Nutritional analyses per species allowed us to then convert these foraging bout data into estimates of kcal/hr.

Bi-monthly and bi-daily tidal cycles result in foraging returns from shellfish patches that are only highly profitable during the limited windows when the tide is lowest. This window of opportunity lasts for about 2 h per day (the second low tide is usually at night) on days immediately preceding or following the two monthly spring tides, giving about 10 total days (20 h) of profitable foraging, out of every 28-day lunar cycle. Accordingly, our model cycles the energetic harvest rate values available from intertidal foraging between the profitable spring low tides, and the unproductive high or non-spring tides (91% of the available foraging hours each lunar cycle).

De Vynck et al. (2016a) report mean intertidal foraging returns under best and worst conditions. Here we are interested instead in the average conditions, so we use simple averages of all bouts for spring lows (Table 1). Foragers were unwilling to collect shellfish during non-low and non-spring days, so we approximate their return rate using the poor conditions as a proxy. Collection bouts used teams of three individuals who worked together across the measured 100 m section of coastline over 30 min. In these

experiments, all three individuals maintained their return rate for the 30-min period, but had extremely low return rates if they afterward returned to the same plot to continue searching. We therefore assign 1.5 h as the total collection time per 100 m strip of coastline. We assume that there is no depletion over time due to repeated harvests as these harvests would still be separated by at least 10 non-spring days where few harvests would occur (though c.f. Klein and Steele, 2013).

2.4. Plant data

Today, the study region is dominated by farmland and other recent habitat modifications. Mucina and Rutherford (2006) published digital data on the reconstructed pre-modern distribution of terrestrial vegetation or habitat types for South Africa. This data represents the Holocene condition of the Palaeoscape, though we use this as a proxy for prior inter-glacial high sea-level phases as well. We define nine categorically different terrestrial habitat types within our study area (Table 2).

Foraging experiments for edible plants took place monthly from Nov. 2014 to Dec. 2016. Like the shellfish experiments, plant foraging bouts were stratified across habitat types. Bouts targeted all known edible plant species at a time for 30 min (averaging two species per bout). We weighed each participant's collection, recorded their distance travelled and, for some bouts, walking speed with GPS, and estimated the width of the area harvested during their transect. We sent the most productive species per habitat for nutritional analyses. Plant return rates vary seasonally depending on the available species' individual characteristics. We

Table 1
Shellfish return rates in coastal habitats.

Habitat type	Return rate (kcal/hr) spring low tides	Return rate (kcal/hr) non-spring or non-low tides	Harvestable time (hr/100 m)
Aeolionite	2019	250	1.5
Sandy beaches	87	87	1.5
TMS Boulders	1799	250	1.5
TMS Rocky headlands	1203	250	1.5
TMS Wave cut platforms	1867	250	1.5

Table 2
Edible plant return rates in terrestrial habitats.

Habitat type	Return rate (kcal/hr)				Harvestable time (hr/ha)			
	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring
Freshwater wetlands	270	223	164	233	1.54	1.47	1.22	1.47
Alluvial vegetation	179	240	122	240	2.18	2.95	3.58	0.97
Strandveld	219	231	211	248	0.62	1.26	1.20	0.67
Renosterveld	63	139	126	80	1.51	3.92	1.81	1.78
Sand fynbos	354	518	370	481	1.88	1.36	2.54	2.13
Albany thicket	241	176	66	62	0.58	0.70	0.44	2.24
Limestone fynbos	130	116	141	109	1.60	0.82	1.79	1.30

cycle the return rates per habitat on a quarterly seasonal basis. Any cell that is harvested is replenished at the beginning of the next season as there are often different plants to be harvested. For a more complete description of the plant foraging methodology and results refer to Botha et al. (this volume, also De Vynck et al., 2016b,c).

2.5. Mammal data

From the archaeological record of Later Stone Age and Middle Stone Age sites, we compiled a list of 28 key species that were commonly hunted in the past. However, only a small subset of five of these species were available and commonly exploited during the phases of high sea-level when the Palaeo-Agulhas Plain was submerged. Two of those are now extinct and we use related living species as proxies for those species (Table 3). We used available literature (Boshoff and Kerley, 2001; Boshoff et al., 2002; Skead, 1980; Skinner and Chimimba, 2005) and expert knowledge (Venter et al., this volume) to determine presence/absence and density (individuals per km²) of species in the different habitat types (Table 4). Because rock hyrax (*Procavia capensis*) is a habitat specialist, we added 'rocky outcrops' as a habitat in the model. While eland remains are present in Pleistocene assemblages, and figure prominently in rock art, its remains are rare in the Holocene assemblages that we use as a model for interglacial conditions, therefore we have excluded it from this model. However, it can be added in future model experiments.

Deriving estimates for prey profitability requires reliable estimates of two key parameters; pursuit time and the probability of a successful pursuit. Within optimal foraging theory, pursuit time is defined as the total time spent in pursuit of an encountered prey species, from initial encounter to either successful acquisition (carcass acquired) or failure (pursuit is broken) (Stephens and Krebs, 1986). We calculate the probability of successful pursuit as the number of successful pursuits of a particular prey species divided by the total pursuits of that species. To estimate the mean

pursuit time, published foraging data from modern hunter-gatherer groups from southern Africa (Marshall, 1976; Yellen, 1977) and eastern Africa (Bartram, 1993; Hawkes, 1991; Wood and Marlowe, 2014) were compiled to produce composite parameter estimates for each prey species included in this study. JAH provided additional data from his recent ethnographic work in Tanzania with Hadza hunters to supplement this dataset where required (Table 3; Harris, unpublished).

To account for inter-analyst differences in resolution (i.e. one ethnographer may record pursuit times at 1-min resolution and another at 1-day resolution), we only used published pursuit-time data recorded at 1-min resolution in calculating estimates of individual prey species pursuit time. Pursuit times used in this analysis include both the time invested in successful and failed pursuits. Both types can vary from a few minutes (animal shot well and killed, or clearly not shot well and abandoned) to several hours (tracking a wounded animal that appears likely to succumb). Therefore, rather than point estimates of pursuit time, we use distribution estimates, in order to account for high levels of inter-pursuit variation associated with certain prey species.

The majority of our mammal species variables do not vary by habitat (Table 3), however, probability of encounter does vary significantly by habitat based on the estimated density of animals (Table 4; Venter, this volume). We assume that all animals within a 20-m swath are encountered as a hunter walks from one side to the other of a given one-hectare cell. For example, a species distributed at 0.3 individuals/km² would have a 30% probability of being encountered in a particular square kilometer, and there would be a 0.06% probability of a hunter encountering an individual within a 100 × 20 m swath. While this is a narrow swath, it is a simpler approximation to assume 100% of mammals would be spotted within a small range, than to account for the per species and per habitat fall-off rates in probability of a mammal being observed. Given sufficient data, we could adjust the model in the future to account such an effect (e.g. by following methods in Buckland et al., 2015).

Table 3
Habitat independent prey parameters.

Species	Common name	Total pursuits	Average pursuit time (min) (SEM)	Probability of success upon encounter	Comment	References
<i>Tragelaphus scriptus</i>	Bushbuck	14	36.16 (4.78)	0.07	Greater Kudu as proxy	Yellen (1977); Hawkes (1991); Bartram (1993); Wood and Marlowe (2014); Harris (unpublished data)
<i>Potamochoerus porcus</i>	Bushpig	10	109.2 (64.19)	0.1		
<i>Sylvicapra grimmia</i>	Grey Duiker	6	6.33 (1.3)	0.5	Dik dik as proxy	Marshall (1976); Yellen (1977); Bartram (1993)
<i>Raphicerus melanotis</i>	Grysbok	71	1.93 (0.05)	0.042		Hawkes (1991); Wood and Marlowe (2014), Harris (unpublished data)
<i>Procavia capensis</i>	Hyrax (Rock)	78	13.21 (0.57)	0.22		Hawkes (1991); Wood and Marlowe (2014), Harris (unpublished data)

Table 4
Estimates of probability of encounter as a hunter passes through each habitat type derived from density.

Prob. of encounter/0.2 ha	Bushbuck	Bushpig	Grey Duiker	Grysbok	Rock hyrax
Freshwater	0.00003636	0.00004444	0.00004444	0.00000000	0.00000000
Alluvial	0.00003636	0.00005128	0.00000000	0.00000000	0.00000000
Strandveld	0.00000400	0.00002667	0.00006667	0.00000781	0.00000000
Renosterveld	0.00000400	0.00002667	0.00005714	0.00008696	0.00000000
Sand Fynbos	0.00000355	0.00002667	0.00006250	0.00009524	0.00000000
Thicket	0.00005714	0.00005128	0.00008333	0.00012500	0.00000000
Limestone Fynbos	0.00000294	0.00002667	0.00006061	0.00009091	0.00000000
Kopjes, Cliffs, Rocks	0.00000000	0.00000000	0.00000000	0.00000000	0.00100000

3. Modeling methods

The agent-based modeling approach we use in this study is becoming increasingly common in archaeological research, particularly in cases where the agents and the environment are heterogeneous (Barton, 2014; Romanowska, 2015; Lake, 2014). The ABM approach attempts to model the interaction between small units, in this case gatherers, foragers, camps, and hectare-sized patches of resources. From a simple set of rules governing those interactions, the model generates complex patterns of human behaviour from the bottom-up. Our model benefits from the experience of developing a detailed ABM of hunting of the contemporary Ache population in Paraguay (Janssen and Hill, 2014), which was tested successfully against actual foraging data and constitutes proof of concept for this modeling approach using a modern well-known hunter-gatherer system. Here we present a brief overview of our modeling approach, including the additional patch-choice gatherer section of the model (see the supplement for the full model description using the standardized Overview, Design concepts, & Details (ODD) Protocol). The full model code, written in NetLogo (Wilensky, 1999), is available online at comses.net (<http://doi.org/10.25937/y0z7-c733>).

Our goal in the Palaeoscape ABM is to model the day-to-day and minute-to-minute foraging decisions made by groups of knowledgeable local foragers under the conditions specified in the model. The model includes two types of agents: foragers and camps. Our model uses camp agents to represent collective decision making at the camp level (such as where to sleep each night). Every camp must pick a target destination for each day's move based on its estimation of the best net caloric returns for individual foragers after time lost due to travel, and inspired by OFT's marginal value theorem. In this decision, the camp members collectively anticipate the arrival of the spring tide by five days in order to maximize the possible returns from shellfish collection by moving to the coast. The individual gathering and hunting agents then disperse to forage, with the camp's expected new location as their target destination by the end of the day (they behave as central place foragers). Individual foragers perform fine scale sub-hourly mobility decisions about where to forage during the day in order to maximize their individual net caloric returns. All food is shared at the camp at the end of the day by summing all foragers collected kilocalories and dividing by the number of camp occupants.

3.1. Modeling the landscape

The model landscape is an imported raster map of 100×100 m (1 ha) cells each coded with a value from 1 to 14 corresponding to its vegetation or coastal type (detailed below). The study region is 30×20 km and includes the archaeological site of Pinnacle Point. About 8% of this area is ocean and is ignored by our model. There are 55,245 terrestrial 1-ha cells within the study area. A user-specified number of camps begin randomly scattered across the

landscape, with a population of hunters and gatherers randomly assigned to a camp. The overall forager population size, and the ratio of hunters to gathers, is also user-specified at the beginning of each run.

3.2. Modeling camp movement

At the beginning of each day, the camp looks back at the previous day to see whether the average per forager returns have dropped below a specified threshold. If so, the camp assesses the current state of all cells on the map (available or already harvested, and tidal state for coastal cells) using an algorithm that estimates the net expected returns for a day's foraging after the time lost due to travel to each cell (i.e. caloric return rate per hour * (foraging time – travel time)). For example, for two cells that are otherwise equal in expected kcal/hr, the algorithm would select the closer one since the net expected caloric return would be higher due to having more time to forage at that return rate. Similarly, if a high return rate cell would take a long time to walk to, the net return might be quite low due to only having a small amount of foraging time left once they arrived and thus not make the trip worthwhile. This calculation is done on a per-cell basis with the simplifying assumption that, in the highly “clumped” resource landscape, sufficient neighbouring patches will likely have the same value.

Since coastal shellfish harvesting can only take place for 2 h of the day in our model, the algorithm sums the returns expected from 2 h of harvesting with the returns expected in the adjacent vegetation patch for the remainder of the work day. In addition, camps consider up to five days into the future when considering their movement choices and net returns. This allows for camps to move towards the coast in advance of the spring tide and also allows camps to make better estimates of the pay off between travel to the coast (which only happens on the first day) and foraging (which continues for several days).

3.3. Modeling plant & shellfish gathering

Gatherers begin their day at the location of the previous day's campsite. The model allots each gatherer an amount of time to forage for the day. A looped series of steps then determines the gatherers' behaviour as they spend that time on different tasks. Each gatherer first determines if they are far enough away from the next night's camp that they need to start traveling towards camp. This is accomplished by comparing the forager walking speed (2 km/h) to the distance to camp. If foragers have sufficient time, they each use a knowledgeable search algorithm to independently assess their local surroundings and select the cell within a limited perceptual range (a 20-cell radius or 2 km plus coastal cells even if they are beyond that distance) with the best net caloric return (i.e. caloric return rate per hour * (foraging time – travel time)). Foragers then move to the chosen cell and gather resources, plants or shellfish. The limited perception improves computational efficiency

and is consistent with the minute-to-minute time-scale decisions of an individual forager. The model tracks the time foragers spend walking to cells and gathering resources in each cell entered. Some resources are extremely time intensive to harvest, underground storage organs (USOs) in rocky or clayey soils for example, while others like berries are harvested with little time investment.

3.4. Modeling hunting

Hunters also begin their day at the previous day's campsite. One randomly selected hunter chooses the most promising habitat for hunting in the area to head towards (hunters do not gather in the current version of the model). Promising habitats are defined at the start of the simulation as a per habitat type expected caloric return rate:

$$E = \sum_i^n \frac{s_i \cdot e_i}{t_i \cdot \epsilon_i}$$

Where i is each of the n number of prey species in that habitat type, s_i is probability of successful pursuit, e_i is the kilocalories, t_i is the pursuit time, and ϵ_i is the probability of encounter.

The other hunters belonging to the same camp face the same direction and begin to walk while fanning out slightly due to small turns in each of their headings. Each hunter loops through the set of procedures listed below until they run out of their daily allotment of foraging time.

First, they compare the distance to the campsite to their walking time to decide if they should head to camp or not. If there is time, they move forward one cell and subtract their walking time. They then run through an encounter procedure that determines, based on species densities in that cell's habitat type, if they have encountered a prey species. If they have, they expend a per species amount of time pursuing the target animal, and then have a per species probability of killing it. If killed, the hunter adds the energy content of one individual of that species to their daily tally and the cell is marked with a lower encounter rate for that species for one week. When the hunter has little time left in the day, they always move one cell in the direction of the expected campsite, but while moving hunters continue to hunt as specified above. Prey species in this model include bushbuck, bushpig, grey duiker, grysbok, and rock hyrax (Table 3).

3.5. Model accounting

Much of the model's code is dedicated to keeping track of how much time is left in the day, the schedule of the tides, the number of calories expected and acquired from each type of habitat, and the distances travelled. This data is then used to evaluate the success of each population of foragers, as a function of search and harvest strategy, population size, and resource density, among other variables.

3.6. Characteristics of the simulations

For the current paper, we held several aspects of the environment and forager behaviour constant, while mainly concentrating on the effects of population density and daily foraging hours on population viability and balance of food sources. In these models we assume that foragers have the capacity to predict the tidal cycle to take advantage of shellfish during the spring tides and that the number of hunters and gatherers are equal (agents are assigned their hunter or gatherer role with equal probability). We also hold the total resource base constant except for the cycling of seasons

and tides. Further research could explore these other modeling variables.

Our simulations here relate to variation in the total size of the population, as well as the division of that population into different sized camps. We assess their overall success in terms of the kilocalories per forager per day (calculated as the mean total calories acquired per camp/camp size/number of days simulated) to see if a given population would be able to sustain itself given the environmental and social constraints. Each run of the model represents ten years of foraging time for the population of foragers. This duration is sufficient to establish a stable overall average return rate that incorporates the fluctuations from the tidal cycle and seasonal plant cycle. Since the model does not include demographic dynamics (i.e. births and deaths), the population size and camp size remain constant within each run. For each combination of foraging hours, population, and camp sizes, we run the model five times to account for the effects of stochasticity (Table 5).

We assess the model results for several aspects related to basic hunter-gatherer foraging patterns to evaluate whether the model is performing as expected. With respect to foraging returns, we expect that average foraging returns per day will increase with more foraging hours but will decrease with increased population density. In terms of mobility, we expect that the frequency and/or distance of residential moves will increase as the resource base becomes over-exploited and that camps with fewer foragers each will move shorter distances per move. We evaluate the degree to which the model results conform to our expectations and then evaluate the results for our main research questions: what was the viable population density during high sea-level phases, and what was the composition of the diet given that viable population density?

Computational analysis is performed using R, including a number of specialized code packages (Clarke and Sherrill-Mix, 2017; Wickham, 2016; Wickham et al., 2018; Yutani, 2018), and all scripts necessary to allow for full replication of our results and figures is archived at SocArXiv.org (<http://doi.org/10.17605/OSF.IO/VDA2K>).

4. Results

4.1. Viable population density

The viable population size for our region varies depending on a number of input parameters including the number of hours spent foraging each day and the division of that population into different group sizes. Overall, the viable population size on the model's 552 ha, here defined as when the mean daily caloric input over the course of the run is above 2000 kcal/forager, is less than 10 people (Fig. 3). This population size corresponds to a population density of below 2 people per 100 km⁻² given the area of the modeled landscape. Even at this population density, the majority of the time the foragers do not meet their minimum daily requirement threshold of 2000 kcal. This variance reflects the other parameters we varied: number of foraging hours per day and number of camps.

Fig. 4 shows in more detail when the populations met their base 2000 kcal/day caloric needs (above the black horizontal line in the figure) as a function of time foraging and the number of groups into which the population was divided. With eight or fewer foraging hours each day, the foragers always go hungry. With a higher number of foraging hours per day allowed (greater than 8), it becomes more common for the foraging population to find enough food, at least at lower population densities.

The social effect of dividing the same population density into greater numbers of camps generally increases caloric returns by a small amount. For example, dividing the same population into 20

Table 5
Parameter values used in the experiments presented here. *For experiments with 10 foragers, only nrcamps = 5 was tested, and for 20 foragers, only nrcamps = 5 and 10 were tested to avoid there being camps with no foragers or only 1 forager.

Parameter	Description	Parameter value range in experiments
nrforgers	Total number of foragers	10*, 20*, 40, 60, 100, 200, 300, 400
pop_dens	Population density calculated in post-analysis as nrforgers/100 km ² (rounded here)	2, 4, 7, 11, 18, 36, 54, 72
nrcamps	Number of camps	5, 10, 15, 20
daily-time-budget	Number of foraging hours per day	4, 6, 8, 10, 12

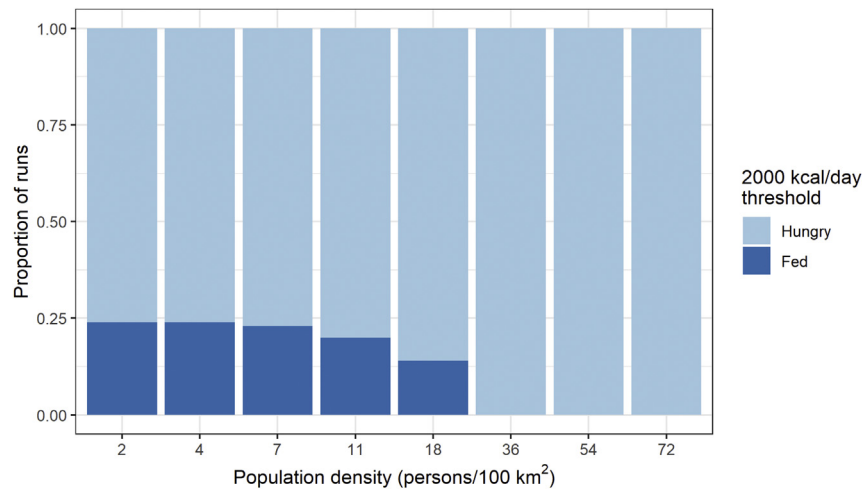


Fig. 3. Simplified fed or hungry variable **describes** whether the agents in a run of the simulation reached an average of 2000 kcal/day/forager after 10 years of the simulation. Y-axis frequency represents the proportion of runs for each population density tested. N.b. There are fewer runs at low population density due to having fewer camp size groupings.

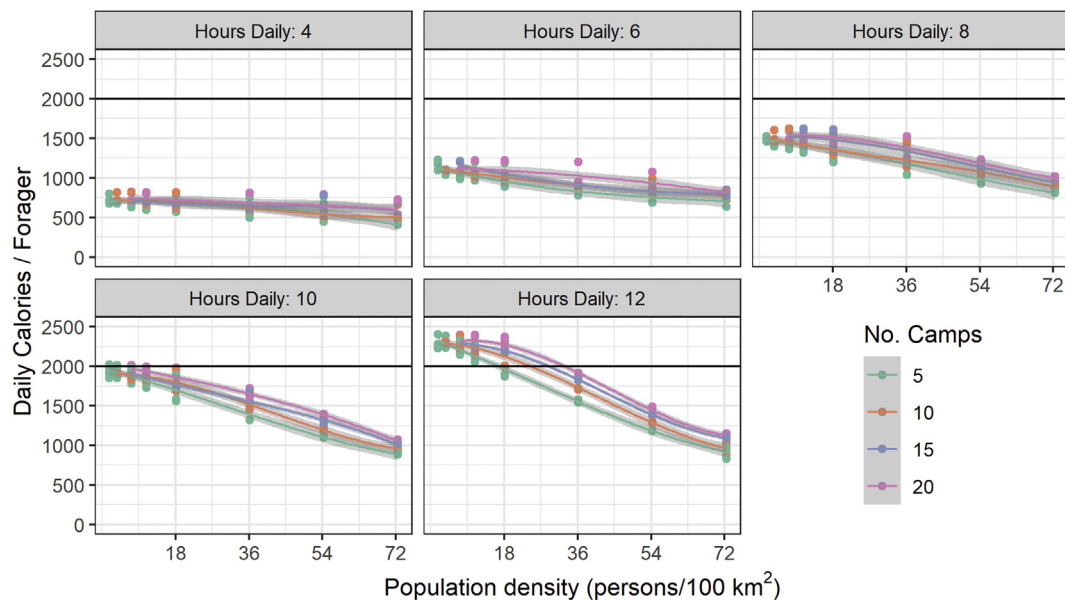


Fig. 4. More detailed visualization of the daily kcal per forager shows the effect of more foraging hours providing a higher daily caloric return. However, for any given population density, dividing that population into greater numbers of smaller camps generally increases their individual caloric returns despite food sharing. Points represent the final state of individual runs of the model. Coloured lines illustrate trends per number of camps with grey shading showing the 95% confidence interval of those trends (more camps means fewer foragers per camp).

small camps rather than 5 larger ones increases the average caloric returns by 5–25% depending on the population density and number of foraging hours. The effect is a little more mixed for four and six foraging hours and for lower population densities where the stochasticity of individual runs is larger and the amount of food to be shared is smaller (Fig. 4, coloured lines). This effect would have

to be weighed against the potential benefit of having fewer groups with more foragers per group to share daily harvest and cover shortcomings by individual camp members. The advantages of smaller group size are due to feeding competition and a product of the diet being primarily based on plant resources which are evenly distributed and widely available. Higher feeding competition when

resources are evenly dispersed, not clumped, is a well-documented ecological pattern for mammals when overall resource density is low (Clark and Mangel, 1986; Chapman et al., 1995).

4.2. Diet

During high sea-level periods when the Palaeo-Agulhas Plain was submerged, the South African coast's mammalian resources were quite limited. Only a small range of species were available and were exploited, and we estimate that these were in relatively low density. In Fig. 5, we see that the majority of the calories in our simulated forager diet are coming from plant resources (usually USOs, but also *Prionium serratum* in freshwater wetlands, *Schotia afra* in thicket, and *Carpobrotus* sp. in several habitats). Sand fynbos was the most intensively exploited habitat type, with strandveld and the coastally adjacent limestone fynbos being the second and third most exploited habitats respectively. Generally, under 15% of the daily calories came from mammalian prey and under 15% from intertidal resources. These resource types would still have made a nutritionally important contribution to the protein and fat requirements of the human population, though macronutrients are not explicitly modeled currently.

As the population density increases, the proportion of calories coming from plants decreases slightly as the population begins to over-exploit the seasonally available plant resources. Mammal resources become a slightly greater proportion of the diet as a result, but because they are not abundant enough to provide a sufficient offset to the lost plant calories at higher population densities, the foragers often fail to meet their caloric requirements as discussed above (Fig. 6). In contrast, the proportion of the diet coming from shellfish does not increase with diminishing plant resources although the higher population of foragers do more consistently harvest the coastal habitats to support the same proportion of the diet.

In Fig. 6, we can see that the proportion of shellfish resources in the foragers' diet don't increase with longer foraging hours per day, since they are temporally limited to both low tide hours and spring tide days. Proportion of the diet coming from mammal hunting

does increase with longer foraging hours at higher population densities because game encounter rates are a direct function of number of hunters and hours out searching for game. Note that in this figure we have coloured only those boxplots where the foragers were meeting their daily caloric minimum of 2000 kcal/day.

4.3. Mobility

Mobility levels increase as the resource base becomes over-exploited by higher population densities. In Fig. 7, we highlight only the runs where the population met their caloric requirements (others coloured grey) and then examine mobility pattern and proportion of the diet coming from mammal resources on these successful days. For successful days, less than 10% of the diet comes from hunting with decreasing proportions for lower population densities that allow the more distributed populations to acquire more valued plant resources. To exploit plant resources with a higher population density, camps move more frequently and farther as plant collectors work through a larger radius of plant resources around each camp location. The successful diet with the highest proportion of mammalian prey, just under 9%, comes from a run with high daily foraging hours and the highest viable population density. While plants are quickly depleted under those conditions, the generally low probability of a successful hunt is increased with greater search time, and food sharing of hunted meat means that all foragers benefit substantially from successful hunts. In this case, more frequent and longer distance moves help to bring the hunters to areas where animals have not been disturbed by previous hunts.

Dividing the population into more, but smaller, camps tends to decrease the distance per camp move slightly, though only minimally affecting the frequency of camp moves (Fig. 8). The distance between subsequent camps increases because camps with more agents exploit a larger local area around each camp location. The camp makes the decision to move based on whether or not it has met the specified threshold of caloric needs, so daily foraging hours allowed to agents have a larger effect on movement frequency than does camp size.

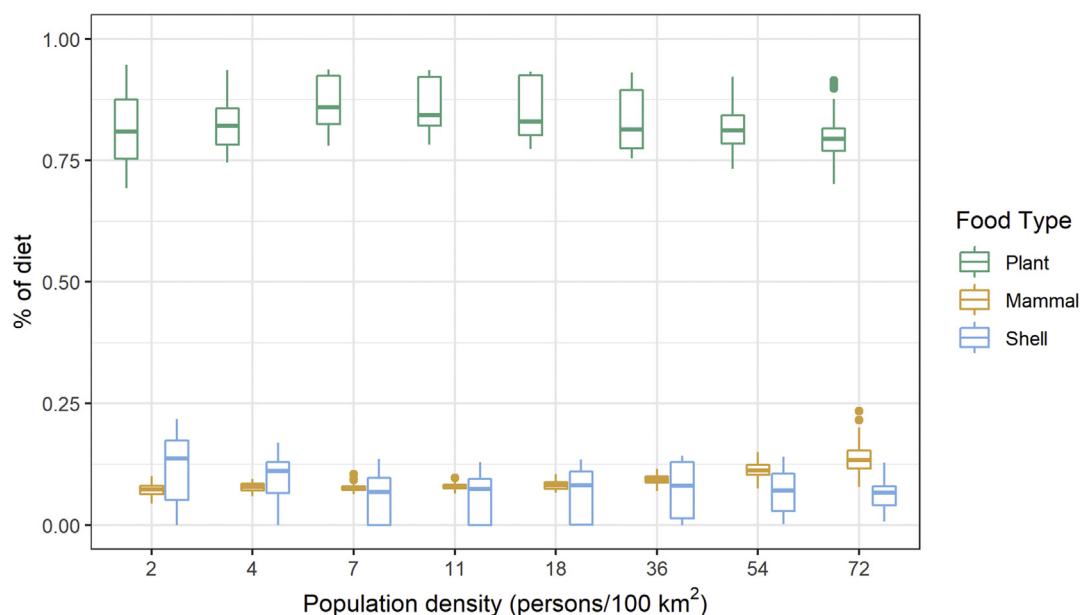


Fig. 5. Source of calories divided into three main food resources compared to population density per run. Note that while plants dominate in all runs, they decrease in proportion at the higher population densities. Boxplots represent the % of the total diet consumed by all agents during the runs of each population density tested (i.e. one boxplot per food type per run).

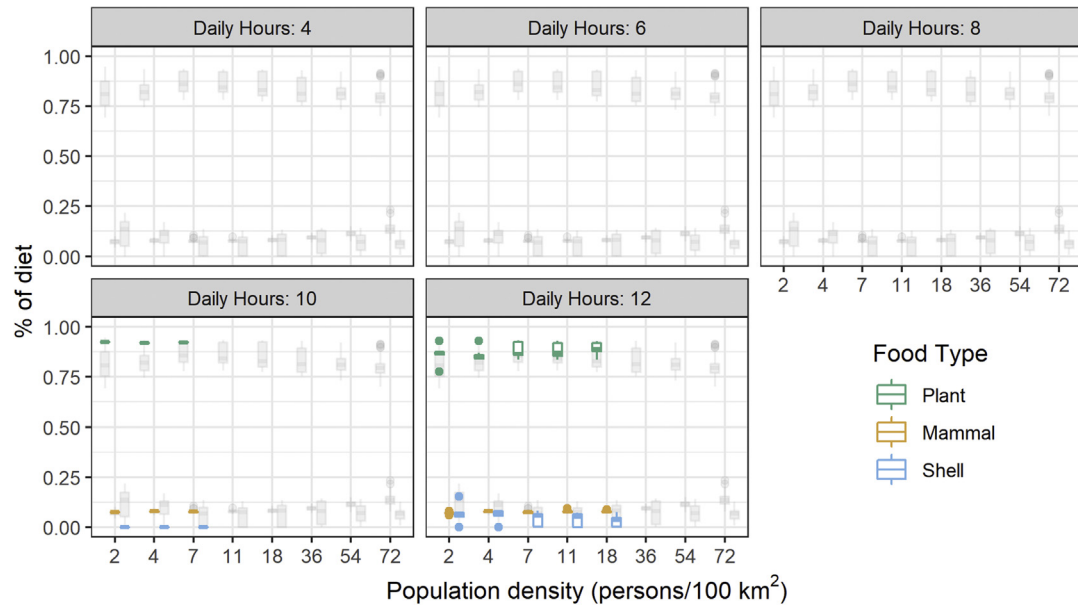


Fig. 6. Same data as previous figure but showing how diet is affected by number of daily foraging hours. Grey boxplots are runs in which foragers did not acquire sufficient kilocalories for survival (<2000 kcal/h/forager). Only the boxplots where the foragers acquired 2000 kcal/h/forager or greater are shown in colour. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

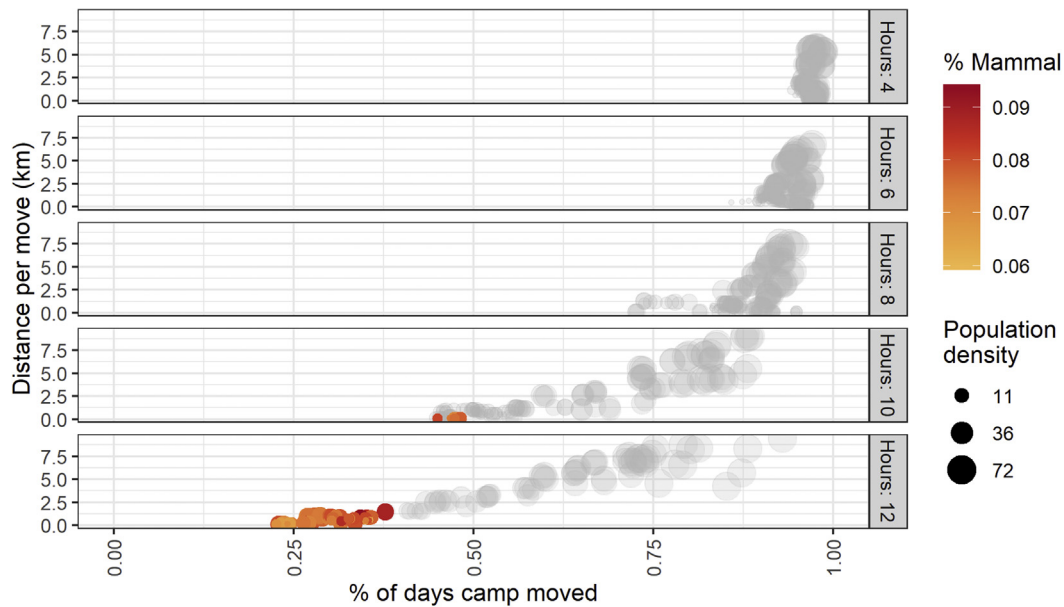


Fig. 7. Highest proportion of mammalian prey in the diet comes from 12 h foraging days with high residential mobility. Foraging runs with longer days moved less frequently and shorter distances. As in previous plots, population density is in persons/100 km² and only runs with greater than 2000 kcal/forager/day are shown in colour. See the supplementary information for a closer view of the “suivving” runs. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

In summary, the agent-based modeling results suggest that relatively low hunter-gatherer population density, under 20 individuals per 100 km² depending on assumptions about daily foraging amounts and group sizes, could be supported in the Pinnacle Point region during high sea-level periods. This population density would be supported by a diet in which plant resources contributed >75% of the daily energy and residential mobility would be relatively frequent and short-distance. Although mammalian resources from hunting remains a small portion of the overall calories, they are highest when foraging days are long giving more probability of prey encounters and when the plant resources

are exploited more heavily forcing higher levels of mobility.

5. Discussion

Our results suggest that while the Cape south coast has had the potential for greater population sizes during some periods in the past, in times of high sea levels, significant limits on the plant, mammal, and shellfish resources available would have resulted in a population density well under 20 individuals per 100 km², and moderately small residential groups along with reasonably high levels of mobility. This is consistent with ethnographic data from

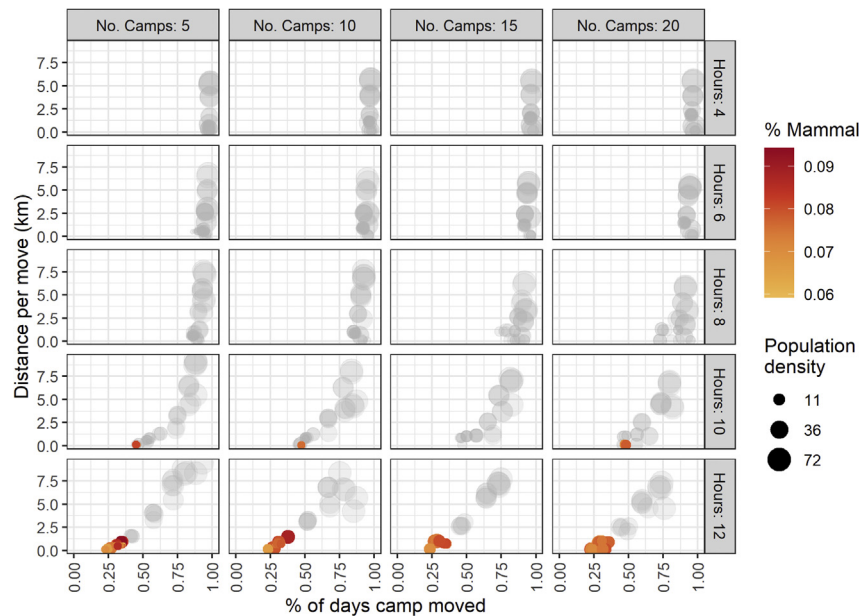


Fig. 8. Same data as previous figure but with addition of number of camps in the panel columns. With more camps of smaller size each, groups move just as often but for slightly shorter distances. See the supplementary information for a closer view of the “suivving” runs.

inland southern Africa which [Binford \(2001\)](#) reports to have a median density around three per 100 km². The predicted density is well below other global coastal regions (excluding the Arctic) which have a median density of 36 per 100 km² (digital database via [Marwick et al., 2016](#)).

During the high sea-level phases modeled here, human foragers struggle to find enough calories to sustain themselves even at low population densities unless they take the intensive strategy of spending 10 h or more on foraging per day. These are very long days compared to averages for hunter-gatherer societies although the variance is high among different groups. [Hill et al. \(1985\)](#) found that Ache men, for example, were actively hunting for an average of 7 h per day, which was the longest workday in their comparative sample ([Hill et al., 1985](#)). They also found that subsistence hours per day varied widely among individuals, among groups, among hunting technologies, and were not related to return rates in a predictable way. Plant resources in our data were highly diverse, but relatively low yield and provided a modest overall foraging rate of 115 kcal/h (including searching time). Shellfish resources were abundant and provided a high caloric return but were temporally limited by lunar-driven tidal cycles. Modern experiments show that stormy weather events could also add some limits to the return of inter-tidal shellfish ([De Vynck et al., 2016a](#)), an effect not included in our simulations. Holocene large mammals were low density and low diversity and so provided relatively large but rare influxes of calories. This suggests that foragers incorporated other, less desirable, lower ranked food sources into the diet during high sea-level phases in order to survive. Hunter-gatherers of the Cape south coast during the Holocene also exploited seal, marine birds, fish, and small animals that are not included in our model. In the majority of locations, seals would be procured as seasonally scavenged wash-ups, with the rare exception of some sites that were in close proximity to a seal haul-up (such as on the Robberg Peninsula) ([Marean, 1986a,b](#); [Parkington, 1976](#)). Holocene hunter-gatherers scavenged marine birds as seasonally punctuated wash-ups ([Avery, 1987, 2011](#)), and fished in the inter-tidal zone once fishing gear, and possibly inter-tidal traps, became part of the technology ([Deacon, 1978, 1984](#)). Small mammals like Cape dune mole rat and

springhare were exploited in both the MSA and LSA, though at PP all small mammals (including hyrax) are rare in the MSA and were primarily not predated by humans. In contrast, at Die Kelders Cave 1 to the west of our research region, small mammals are abundant and were accumulated by humans during the MSA ([Armstrong, 2016](#)). It is likely that scavenged seals and scavenged birds were rarely encountered and highly seasonally punctuated resources and would have not had a major influence on the gross caloric diet of Holocene foragers. Fishing represents labor intensification, and due to the costs of the technology production and maintenance, may or may not have been able to offset the caloric deficiency identified by our model. Small animals may very well have been low ranked prey species that came and went in the diet in response to the encounter rates with higher ranked prey, hence they might not change our picture of the diet very much. [Klein and Steele \(2013\)](#) argued that LSA foragers exploited shellfish so frequently and intensively that it led to an artificial selection towards smaller shellfish as the larger ones were systematically removed from the coastal zone. This would be consistent with our model results, since for a higher population density to maintain the same proportion of the diet coming from shellfish, a more intensive and frequent harvesting would be required. However, other climatically-driven processes can result in similar body size reductions ([Sealy and Galimberti, 2011](#)).

As noted, we have not collected experimental data on densities, pursuit times and success rates for procuring seal, birds, fish, and small animals, though we hope to do so in the future. We began the development of our model to investigate Pleistocene occupations at Pinnacle Point where these resources represent a minor component of the diet. We can make a few predictions as to the value and cost of other miscellaneous resources. For example, current information suggests that scavenged seals (and whales) would represent an occasional, seasonally punctuated, but large package of nutrition. We know that foragers harvested them upon encounter through both the MSA and LSA, as would be predicted from OFT, but this would not have been a significant component of the diet due to their extremely low encounter rates.

Scavenged marine birds are a small package of nutrition, and

studies of their availability show that they would be a predictable opportunity over the long run, but a rare and seasonally punctuated resource (Avery, 1990). They could have been collected while in route to other resources (such as shellfish), but to attain significant numbers would require regular, planned, and lengthy beach surveys that would significantly increase their search costs. We think their more regular occurrence in the Holocene record (Avery, 1990, 2011) signals a significant expansion of diet breadth to a very low productivity resource, and our model results suggest that the removal of the Palaeo-Agulhas Plain could have driven a diet breadth expansion.

Small animals such as tortoise, snakes, lizards, hyrax, dune mole rat, and springhare vary widely in their abundance in the MSA and LSA records in coastal South Africa. Overall, in the Holocene there is a greater representation of these small prey than in the Pleistocene, though this varies geographically. Tortoise and small mammals are abundant in the Pleistocene MSA record at Die Kelders Cave 1, but they are rare in the Pleistocene MSA record at Pinnacle Point. Tortoise are easily captured, hence we presume that these individuals are probably being captured while in route to other tasks and food resources. Snakes, lizards, and small mammals are much harder to procure due to their evasion speed or danger. When these small animals are abundant, like tortoise and small mammals at MSA Die Kelders Cave 1, this may represent a strategy of regular active search. Since small animals present a smaller food package size than large animals, regular and focused search in areas that contain such species represents an expansion of diet breadth to a low ranked item. Our model suggests that when the rich resources of the PAP were removed by high sea levels, struggling foragers might have expanded their diet to these items to compensate.

Our simulated caloric returns from Holocene mammal hunting (including all search and pursuit time) are so low, that it may have been advantageous for hunters to collect shellfish when available rather than hunt. De Vynck et al. (2016a) showed that males obtained significantly higher caloric returns during intertidal foraging, mostly because they took greater risks by descending lower into the inter-tidal zone known as the cochlear zone. In that study, a multivariate statistical model predicted that young men could obtain ~3400 kcal/h from shellfishing during optimal conditions. This is considerably higher than the ~1700 kcal/h average we used in this study and far higher than the ~200 kcal/h that our agent hunters managed in our simulations. De Vynck et al. (2016a) also found that modern foragers received higher returns during spring tides than during neap tides and from specific tidal habitats rather than other less productive habitats. We suggest that when the high return rates of hunting on the Palaeo-Agulhas Plain were lost to high sea levels, foragers would have expanded their shellfish collection to less productive habitats, worse tidal conditions and riskier intertidal zones (such as the Cochlear Zone). Given the low return rates of foraging for plants and animals on the Cape south coast Holocene landscape, foragers residing on the coast may have been forced to intensify, or specialize, on less productive and challenging intertidal habitats and even explore fishing with tackle and traps. This is consistent with findings that Holocene foragers with coastal territories in the Cape south coast consumed diets, indicated by isotopic analysis, to be rich in marine foods (Sealy, 2006; Sealy and Pfeiffer, 2000).

Our results suggest that a population divided into smaller residential groups (i.e. the same population density divided into a higher number of camps), would have acquired more energy per day given the limitations of the resource landscape. Smaller groups had higher caloric returns, all factors being equal, and moved shorter distances. This is consistent with Kelly's (2013) discussion of optimal group size maximizing the per forager return rate, in this case a small group since the resources are evenly dispersed, low

density, and the majority plant resources do not need cooperation to exploit successfully. This somewhat supports Wadley's (1993) claim, based on multiple dated assemblages across South Africa, that Holocene foragers were more numerous than earlier periods and occupied both large and small cave sites, rather than just the large caves occupied during earlier time periods. This is consistent with a pattern of small residential groups joining into periodic large aggregations. Sealy (2006) has also found evidence of small territorial Holocene populations on the south coast. However, a comparison of recent count and residential site size estimates to older phases of occupation with lower sea-levels, are most likely skewed by the archaeological invisibility of numerous sites on the Palaeo-Agulhas Plain itself.

One limitation of the current study is the relatively small area covered by our simulations. While the region is large enough to contain several independent foraging groups without impeding their foraging ranges, we chose the region for this study due to the presence of the Pinnacle Point site and its high-resolution archaeological record for comparison. This does somewhat limit the broader applicability of our results since each landscape of differentiated habitats will support a slightly different population density and dietary balance. Increasing the spatial extent to a larger area is beyond the current capacity of our computing hardware. For upcoming work simulating foraging during low sea-level phases, a larger spatial extent will be necessary and thus we have successfully experimented with running the model at a larger spatial extent on high-performance computing resources, i.e. supercomputers (Shook et al., 2015; Towns et al., 2014).

6. Conclusion

Just off the modern coast of South Africa is the Pleistocene Palaeo-Agulhas Plain that, when revealed by lower sea levels, provided a rich source of hunted game to the occupants of the many caves and rockshelters along the current coast that form essential paleoarchives for modern human evolution. This productive grassy habitat would have supported a large number of large- and medium-bodied ungulates accessible to Pleistocene hunters (Cawthra et al., this volume; Helm et al., this volume; Cowling et al., this volume; Venter et al., this volume). The archaeological record suggests that during the low sea-level phases, there was considerably greater diversity of mammal species and greater species abundance for foraging groups to hunt (Marean et al., 2014). However, during the high sea-level phases of MIS 5e (+5–6 m asl) and the Holocene, this rich foraging ground was closed and the remaining food would have been scarce. Fisher et al. (2010) highlighted the continual shifting of the position of the coastline and thus the available width of the Palaeo-Agulhas Plain over time. In this paper, we used an agent-based model of the human foraging system along the Cape south coast during higher sea level periods without the profitable Palaeo-Agulhas Plain (Botha et al., this volume; Singels et al., this volume; Rishworth et al., this volume; Venter et al., this volume). We demonstrated that under those conditions, human populations must have been small, low density, and subsisting mostly off the diverse plant resources available across the various terrestrial habitats. The limited mammalian prey and shellfish included in the diet would likely have been sufficient to meet the protein macro-nutrient requirements of this foraging population but without making as substantial a contribution to the overall caloric intake.

Our model results are consistent with the archaeological evidence from the well-studied sites along the South African coast where abundant shellfish and a relatively low diversity and low abundance terrestrial mammal assemblage are found compared to the lower sea-level phases between MIS 2 and MIS 5d. The large

area of grassy habitat and floodplains that exposed on the Palaeo-Agulhas Plain would likely have supported a much higher human population density with a much higher percentage of the diet coming from mammal hunting.

Acknowledgements

The authors recognize the support of a grant from the National Science Foundation (BCS-0524087, BCS-1138073 and BCS-1460376), Hyde Family Foundations, the Institute of Human Origins (IHO) at Arizona State University, and the John Templeton Foundation to the Institute of Human Origins at Arizona State University. The opinions expressed in this publication are those of the author(s) and do not necessarily reflect the views of any of these funding organizations. This work used the Extreme Science and Engineering Discovery Environment (XSEDE), which is supported by National Science Foundation grant number ACI-1548562. This work used the XSEDE Bridges and Stampede resources through XSEDE allocation DBS140003. We also wish to thank Ben Marwick and Matt Harris for advice with the R code and Alastair Potts for useful discussions regarding the vegetation habitats.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2019.06.012>.

References

- Andel, T.H. van, 1989. Late Pleistocene sea levels and the human exploitation of the shore and shelf of southern South Africa. *J. Field Archaeol.* 16, 133–155. <https://doi.org/10.1179/jfa.1989.16.2.133>.
- Armstrong, A., 2016. Small mammal utilization by Middle Stone age humans at Die Kelders cave 1 and Pinnacle point site 5-6, western Cape Province, South Africa. *J. Hum. Evol.* 101, 17–44.
- Avery, G., 2011. Holocene Avian remains, human behaviour and seasonality on the South African Coast. In: Jousse, H., Lesur, J. (Eds.), *People and Animals in Holocene Africa. Recent Advances in Archaeozoology*. Africa Magna Verlag, pp. 110–122.
- Avery, G., 1990. Avian Fauna, Palaeoenvironments and Palaeoecology in the Late Quaternary of the Western and Southern Cape, South Africa, *Archaeology*. University of Cape Town, Cape Town, South Africa.
- Avery, G., 1987. Coastal birds and prehistory in the western Cape. In: Parkington, J., Hall, M. (Eds.), *Papers in the Prehistory of the Western Cape, South Africa*. BAR International, pp. 164–191.
- Barton, C.M., 2014. Complexity, social complexity, and modeling. *J. Archaeol. Method Theory* 21, 306–324. <https://doi.org/10.1007/s10816-013-9187-2>.
- Bartram, L.E.J., 1993. *An Ethnoarchaeological Analysis of Kua San (Botswana) Bone Food Refuse*. University of Wisconsin, Madison, WI.
- Binford, L.R., 2001. *Constructing Frames of Reference: an Analytical Method for Archaeological Theory Building Using Hunter-Gatherer and Environmental Data Sets*. University of California Press, Berkeley.
- Boshoff, A.F., Kerley, G.I.H., Cowling, R.M., 2002. Estimated spatial requirements of the medium- to large-sized mammals, according to broad habitat units, in the Cape Floristic Region, South Africa. *Afr. J. Range Forage Sci.* 19, 29–44. <https://doi.org/10.2989/10220110209485772>.
- Boshoff, A.F., Kerley, L.J., 2001. Potential distributions of the medium- to large-sized mammals in the Cape Floristic Region, based on historical accounts and habitat requirements. *Afr. Zool.* 36, 245–273. <https://doi.org/10.1080/15627020.2001.11657142>.
- Botha, M.S., 2018. *A gatherer's paradise? Early Humans and Plant Foraging in the Cape South Coast, South Africa (PhD Thesis)*. Nelson Mandela University, George, South Africa.
- Botha, S., Cowling, R.M., Esler, K.J., De Vynck, J.C., Potts, A.J., 2019. Using the extant Cape Floristic region's flora to explore the foraging potential of the Palaeo-Agulhas plain. *Quat. Sci. Rev.* this volume.
- Buckland, S.T., Rexstad, E.A., Marques, T.A., Oedekoven, C.S., 2015. *Distance Sampling: Methods and Applications, Methods in Statistical Ecology*. Springer International Publishing, Switzerland.
- Cawthra, H.C., Cowling, R.M., Andò, S., Marean, C.W., 2019. Geological and soil maps of the Palaeo-Agulhas Plain for the Last Glacial Maximum. *Quat. Sci. Rev.* this volume.
- Chapman, C.A., Chapman, L.J., Wrangham, R.W., 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behav. Ecol. Sociobiol.* 36, 59–70.
- Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9, 129–136. [https://doi.org/10.1016/0040-5809\(76\)90040-X](https://doi.org/10.1016/0040-5809(76)90040-X).
- Clark, C.W., Mangel, M., 1986. The evolutionary advantages of group foraging. *Theor. Popul. Biol.* 30, 45–75. [https://doi.org/10.1016/0040-5809\(86\)90024-9](https://doi.org/10.1016/0040-5809(86)90024-9).
- Clarke, E., Sherrill-Mix, S., 2017. Ggbeeswarm: Categorical Scatter (Violin Point) Plots. <https://CRAN.R-project.org/package=ggbeeswarm>.
- Codding, B.F., Bird, D.W., 2015. Behavioral ecology and the future of archaeological science. *J. Archaeol. Sci. Scoping Future Archaeol. Sci. Pap. Honour Richard Klein* 56, 9–20. <https://doi.org/10.1016/j.jas.2015.02.027>.
- Cowling, R.M., Pressey, R.L., Rouget, M., Lombard, A.T., 2003. A conservation plan for a global biodiversity hotspot—the Cape Floristic Region, South Africa. *Biological Conservation. Conserv. Plan. Cape Florist. Reg.* 112, 191–216. [https://doi.org/10.1016/S0006-3207\(02\)00425-1](https://doi.org/10.1016/S0006-3207(02)00425-1).
- Cowling, R.M., Potts, A.J., Franklin, J., Marean, C.W., 2019. Describing a drowned ecosystem: Last Glacial Maximum vegetation reconstruction of the Palaeo-Agulhas Plain. *Quat. Sci. Rev.* this volume.
- De Vynck, J.C., Anderson, R., Atwater, C., Cowling, R.M., Fisher, E.C., Marean, C.W., Walker, R.S., Hill, K., 2016a. Return rates from intertidal foraging from Blombos Cave to Pinnacle Point: understanding early human economies. *J. Hum. Evol.* 92, 101–115. <https://doi.org/10.1016/j.jhevol.2016.01.008>.
- De Vynck, J.C., Cowling, R.M., Potts, A.J., Marean, C.W., 2016b. Seasonal availability of edible underground and aboveground carbohydrate resources to human foragers on the Cape south coast, South Africa. *PeerJ* 4, e1679. <https://doi.org/10.7717/peerj.1679>.
- De Vynck, J.C., Van Wyk, B.-E., Cowling, R.M., 2016c. Indigenous edible plant use by contemporary Khoe-San descendants of South Africa's Cape South Coast. *South Afr. J. Bot.* 102, 60–69. <https://doi.org/10.1016/j.sajb.2015.09.002>.
- Deacon, J., 1984. *Later Stone Age people and their descendants in southern Africa*. In: Klein, R.G. (Ed.), *Southern African Prehistory and Paleoenvironments*. Balkema, Rotterdam, pp. 221–328.
- Deacon, J., 1978. Changing patterns in the late Pleistocene/early Holocene prehistory of southern Africa as seen from the Nelson Bay cave Stone Artifact sequence. *Quat. Res.* 10, 84–111. [https://doi.org/10.1016/0033-5894\(78\)90015-7](https://doi.org/10.1016/0033-5894(78)90015-7).
- Dewar, G., Halkett, D., Hart, T., Orton, J., Sealy, J., 2006. Implications of a mass kill site of springbok (*Antidorcas marsupialis*) in South Africa: hunting practices, gender relations, and sharing in the Later Stone Age. *J. Archaeol. Sci.* 33, 1266–1275. <https://doi.org/10.1016/j.jas.2006.01.003>.
- Fisher, E.C., Bar-Matthews, M., Jerardino, A., Marean, C.W., 2010. Middle and Late Pleistocene paleoscape modeling along the southern coast of South Africa. *Quat. Sci. Rev.* 29, 1382–1398. <https://doi.org/10.1016/j.quascirev.2010.01.015>.
- Franklin, J., Potts, A.J., Fisher, E.C., Cowling, R.M., Marean, C.W., 2015. Paleodistribution modeling in archaeology and paleoanthropology. *Quat. Sci. Rev.* 110, 1–14. <https://doi.org/10.1016/j.quascirev.2014.12.015>.
- Hawkes, K., 1991. Showing off: tests of an hypothesis about men's foraging goals. *Ethol. Sociobiol.* 12, 29–54.
- Hawkes, K., Hill, K., O'Connell, J.F., 1982. Why hunters gather: optimal foraging and the Ache of eastern Paraguay. *Am. Ethnol.* 9, 379–398.
- Hawkes, K., O'Connell, J.F., Jones, N.B., 2001. Hadza meat sharing. *Evol. Hum. Behav.* 22, 113–142.
- Helm, C.W., Buckley, L.G., Cawthra, H.C., Cowling, R.M., De Vynck, J.C., Lockley, M.G., Marean, C.W., McCrea, R.T., Thesen, G.H.H., Venter, J., 2019. Pleistocene track-sites on the Cape south coast and their potential palaeoecological implications. *Quat. Sci. Rev.* this volume.
- Hill, K., Kaplan, H., Hawkes, K., Hurtado, A.M., 1985. Men's time allocation to subsistence work among the Ache of eastern Paraguay. *Hum. Ecol.* 13, 29–47.
- Janssen, M.A., Hill, K., 2014. Benefits of grouping and cooperative hunting among Ache hunter-gatherers: insights from an agent-based foraging model. *Hum. Ecol.* 42, 823–835. <https://doi.org/10.1007/s10745-014-9693-1>.
- Kelly, R.L., 2013. *The Lifeways of Hunter-Gatherers: the Foraging Spectrum*, second ed. Cambridge University Press, Cambridge.
- Klein, R.G., Steele, T.E., 2013. Archaeological shellfish size and later human evolution in Africa. *Proc. Natl. Acad. Sci. Unit. States Am.* 110, 10910–10915. <https://doi.org/10.1073/pnas.1304750110>.
- Lake, M.W., 2014. Trends in archaeological simulation. *J. Archaeol. Method Theory* 21, 258–287. <https://doi.org/10.1007/s10816-013-9188-1>.
- Lake, M.W., 2001. The use of pedestrian modelling in archaeology, with an example from the study of cultural learning. *Environ. Plan. B* 28, 385–404.
- Lake, M.W., 2000. *MAGICAL computer simulation of Mesolithic foraging*. In: Kohler, T.A., Gumerman, G.J. (Eds.), *Dynamics in Human and Primate Societies: Agent-Based Modeling of Social and Spatial Processes*. Oxford University Press, New York, pp. 107–143.
- Marean, C.W., 2014. The origins and significance of coastal resource use in Africa and Western Eurasia. *J. Hum. Evol.* 77, 17–40. <https://doi.org/10.1016/j.jhevol.2014.02.025>.
- Marean, C.W., 2011. Coastal South Africa and the coevolution of the modern human lineage and the coastal adaptation. In: Bicho, N., Haws, J.A., Davis, L.G. (Eds.), *Trekking the Shore*. Springer, New York, pp. 421–440.
- Marean, C.W., 2010. Pinnacle point cave 13B (western Cape Province, South Africa) in context: the Cape Florist kingdom, shellfish, and modern human origins. *J. Hum. Evol.* 59, 425–443. <https://doi.org/10.1016/j.jhevol.2010.07.011>.
- Marean, C.W., 1986a. Seasonality and seal exploitation in the southwestern Cape, South Africa. *Afr. Archaeol. Rev.* 4, 135–149. <https://doi.org/10.1007/BF01117038>.
- Marean, C.W., 1986b. On the seal remains from Klasies river mouth: an evaluation of binford's interpretations. *Curr. Anthropol.* 27, 365–368. <https://doi.org/10.1086/203449>.

- Marean, C.W., Anderson, R.J., Bar-Matthews, M., Braun, K., Cawthra, H.C., Cowling, R.M., Engelbrecht, F., Esler, K.J., Fisher, E., Franklin, J., Hill, K., Janssen, M., Potts, A.J., Zahn, R., 2015. A new research strategy for integrating studies of paleoclimate, paleoenvironment, and paleoanthropology. *Evol. Anthropol.* 24, 62–72. <https://doi.org/10.1002/evan.21443>.
- Marean, C.W., Bar-Matthews, M., Bernatchez, J., Fisher, E., Goldberg, P., Herries, A.I.R., Jacobs, Z., Jerardino, A., Karkanas, P., Minichillo, T., Nilssen, P.J., Thompson, E., Watts, I., Williams, H.M., 2007. Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. *Nature* 449, 905–908. <https://doi.org/10.1038/nature06204>.
- Marean, C.W., Cawthra, H.C., Cowling, R.M., Esler, K.J., Fisher, E., Milewski, A., Potts, A.J., Singels, E., De Vynck, J., 2014. Stone Age People in a Changing South African Greater Cape Floristic Region. *Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region*, pp. 164–199.
- Marshall, L., 1976. *The! Kung of Nyae Nyae*. Harvard University Press, London.
- Marwick, B., Johnson, A., White, D., Eff, E.A., 2016. Binford: Binford's Hunter-Gatherer Data. <https://CRAN.R-project.org/package=binford>.
- Mithen, S.J., 1990. *Thoughtful Foragers: A Study of Prehistoric Decision Making*. Cambridge University Press.
- Mithen, S.J., 1988. Modeling hunter-gatherer decision making: complementing optimal foraging theory. *Hum. Ecol.* 17, 59–83. <https://doi.org/10.1007/BF01047652>.
- Mucina, L., Rutherford, M.C. (Eds.), 2006. *The Vegetation of South Africa, Lesoto and Swaziland, Strelitzia*. South African National Biodiversity Institute, Pretoria.
- Parkington, J., 1976. Coastal settlement between the mouths of the Berg and Olifants Rivers, Cape Province. *S. Afr. Archaeol. Bull.* 31, 127–140. <https://doi.org/10.2307/3887733>.
- Rishworth, G.M., Cawthra, H.C., Dodd, C., Perissinotto, R., 2019. Peritidal stromatolites as indicators of stepping-stone freshwater resources on the Palaeo-Agulhas Plain landscape. *Quat. Sci. Rev.* this volume.
- Romanowska, I., 2015. So you think you can model? A guide to building and evaluating archaeological simulation models of dispersals. *Hum. Biol.* 87, 169–192. <https://doi.org/10.13110/humanbiology.87.3.0169>.
- Sealy, J., 2006. Diet, mobility, and settlement pattern among Holocene hunter-gatherers in southernmost Africa. *Curr. Anthropol.* 47, 569–595. <https://doi.org/10.1086/504163>.
- Sealy, J., Galimberti, M., 2011. Shellfishing and the interpretation of shellfish sizes in the Middle and later Stone ages of South Africa. In: Bicho, N.F., Haws, J.A., Davis, L.G. (Eds.), *Trekking the Shore: Changing Coastlines and the Antiquity of Coastal Settlement, Interdisciplinary Contributions to Archaeology*. Springer New York, New York, NY, pp. 405–419. https://doi.org/10.1007/978-1-4419-8219-3_17.
- Sealy, J., Pfeiffer, S., 2000. Diet, body size, and landscape use among Holocene people in the southern Cape, South Africa. *Curr. Anthropol.* 41, 642–655. <https://doi.org/10.1086/317392>.
- Shook, E., Wren, C.D., Marean, C.W., Potts, A.J., Franklin, J., Engelbrecht, F., O'Neal, D., Janssen, M.A., Fisher, E.C., Hill, K., Esler, K., Cowling, R.M., Scheiter, S., Moncrieff, G., 2015. Paleoscape model of coastal South Africa during modern human origins: progress in scaling and coupling climate, vegetation, and agent-based models on XSEDE. In: *Proceedings of the 2015 Annual Conference on Extreme Science and Engineering Discovery Environment*. Presented at the XSEDE15: Extreme Science and Engineering Discovery Environment 2015 Conference. ACM International Conference Proceeding Series, New York. <https://doi.org/10.1145/2792745.2792747>.
- Singels, E., Potts, A.J., Cowling, R.M., Marean, C.W., De Vynck, J., Esler, K.J., 2016. Foraging potential of underground storage organ plants in the southern Cape, South Africa. *J. Hum. Evol.* 101, 79–89. <https://doi.org/10.1016/j.jhevol.2016.09.008>.
- Singels, E., Difford, M., Cowling, R.M., Esler, K.J., 2019. Seasonal variation of geophyte resources across the Cape coastal lowlands: Implications for the available resources on the Palaeo-Agulhas Plain. *Quat. Sci. Rev.* this volume.
- Skead, C.J., 1980. *Historical Mammal Incidence in the Cape Province: Volume 1 - the Western and Northern Cape*. The Department of Nature Conservation and Environmental Conservation of the Provincial Administration of the Cape of Good Hope, Cape Town.
- Skinner, J.D., Chimimba, C.T., 2005. *The Mammals of the Southern African Sub-region*, third ed. Cambridge University Press, New York.
- Stephens, D.W., Krebs, J.R., 1986. *Foraging Theory*. Princeton University Press, New Jersey.
- Towns, J., Cockerill, T., Dahan, M., Foster, I., Gaither, K., Grimshaw, A., Hazlewood, V., Lathrop, S., Lifka, D., Peterson, G.D., Roskies, R., Scott, J.R., Wilkens-Diehr, N., 2014. XSEDE: accelerating scientific discovery. *Comput. Sci. Eng.* 16, 62–74. <https://doi.org/10.1109/MCSE.2014.80>.
- Venter, J.A., Brooke, C., Marean, C.W., Fritz, H., 2019. Large mammals of the Palaeo-Agulhas Plain: Conceptual reconstruction of large mammal assemblages and their habitats. *Quat. Sci. Rev.* this volume.
- Wadley, L., 1993. The Pleistocene later Stone age south of the Limpopo river. *J. World Prehist.* 7, 243–296. <https://doi.org/10.1007/BF00974721>.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York. <http://ggplot2.org>.
- Wickham, H., François, R., Henry, L., Müller, K., 2018. *Dplyr: A Grammar of Data Manipulation*. <https://CRAN.R-project.org/package=dplyr>.
- Wilensky, U., 1999. *NetLogo*. Center for Connected Learning and Computer-Based Modeling. Northwestern University, Evanston.
- Winterhalder, B., 1986. Diet choice, risk, and food sharing in a stochastic environment. *J. Anthropol. Archaeol.* 5, 369–392. [https://doi.org/10.1016/0278-4165\(86\)90017-6](https://doi.org/10.1016/0278-4165(86)90017-6).
- Winterhalder, B., 1981. Optimal foraging strategies and hunter-gatherer research in anthropology: theory and methods. In: *Hunter-gatherer Foraging Strategies: Ethnographic and Archaeological Analyses*. University of Chicago Press, Chicago, pp. 13–35.
- Wood, B.M., Marlowe, F.W., 2014. Toward a reality-based understanding of Hadza men's work. *Hum. Nat.* 25, 620–630.
- Yellen, J.E., 1977. *Archaeological Approaches to the Present: Models for Reconstructing the Past*. Academic Press, New York.
- Yutani, H., 2018. Gghighlight: highlight lines and points in "ggplot2". <https://CRAN.R-project.org/package=gghighlight>.