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Perception, Interaction, and Extinction: A Reply to Premo

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We respond here to L. Premo's commentary on our recent paper in *Human Ecology* (Barton *et al.* 2011; see also Barton and Riel-Salvatore 2012). His cavalier, one line dismissal of the archaeological evidence presented in the paper as "unconvincing" (Premo 2012, p. 647) indicates that he is unfamiliar with the many published supporting studies; we encourage him to give them a thorough read (e.g., Barton 1998; Clark 2008; Kuhn 2004; Meignen *et al.* 2006; Riel-Salvatore 2007, 2010; Riel-Salvatore *et al.* 2008; Riel-Salvatore and Barton 2004, 2007; Sandgathe 2006; Surovell 2009; Villaverde *et al.* 1998). In the remainder of his commentary, he uses a model of forager interaction as a basis for critiquing the computational modeling in our paper, and we turn to that work here.

Premo creates a simple agent-based model to examine interrelationships between resource density, length of stay at residential camps, distance foraged, and the interaction rates between two forager bands. He reports that this modeling experiment shows a positive relationship between length of stay and size of foraging territory, and a negative relationship between size of foraging territory and rates of interactions between different foraging groups. Premo also claims that his study calls into question the results of our modeling of biobehavioral evolution in the Late Pleistocene. It does nothing of the sort. To show why, it is useful to briefly recap the work we presented. First, using data from 167 Late

Pleistocene-age stone artifact assemblages across western Eurasia, we demonstrated how variability in retouch frequencies for Late Pleistocene assemblages serves as a proxy for variability in place provisioning (*sensu* Kuhn 1992) and length of stay at camps, which commonly is associated with variation between residential and logistical mobility in the ethnographic record. We did not then "...assume *a priori* that LMS [i.e., logistical mobility strategy] foragers tend to move over a greater geographic extent than RMS [i.e., residential mobility strategy] foragers during their lifetimes." (Premo 2012, p. 648). Rather, we noted that ethnographic data show that logistical mobility is generally associated with longer distance foraging forays than those associated with residential mobility. The fact that Premo's modeling results show a positive association between length of stay and distance foraged ultimately supports our observation that these are related on the basis of empirical ethnographic studies. Second, we proposed that "Hominin behavioral responses to changing Late Pleistocene climates and landscapes, particularly an increase in long distance forays to collect resources for provisioning base camps associated with LMS, would have altered the biological and social environment of Eurasian hominins by *increasing opportunities for social and biological interactions among hominins across broader geographic regions*. This would have had consequences for human biocultural variation and change." (Barton *et al.* 2011, p. 714) [emphasis added]. What our study explicitly tested with an agent-based model was the evolutionary consequences of foragers *moving longer distances*, not the impacts of interacting more frequently. By systematically varying foraging distance and assessing its impact on gene flow, we showed how shifting forager land-use can lead to the extinction of localized, endemic populations like the Neanderthals of western Eurasia. These conclusions are further supported in a subsequent paper that uses a more complex genome and tests the

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impact of other social and biological factors affecting bio-behavioral interaction (Barton and Riel-Salvatore 2012).

In other words, Premo has missed the point of what we were doing. Nevertheless, his work does raise some issues about how to model human interaction across space, although we demonstrate below that the frequency of interactions does not, in fact, have a significant impact on the evolutionary consequences of shifting land-use strategies modeled in our original study.

Perception and Interaction

Because Premo has not yet published the actual code used for his model, we can only assess how agents interact and interactions are measured from the brief description in his commentary. In his model world, there are only two forager agents, which establish residential base camps. Each forager agent moves out from the base camp to collect resources, within an area specified by an effective foraging radius (r_e , equivalent to our ‘maximum movement distance’) and then returns to the base camp. Periodically, each forager shifts its base camp to a new location at a distance of twice the effective foraging radius plus one grid cell from the previous base camp. (The virtual world is divided into grid cells on which agents move.) An agent moves its base camp when resources within the foraging radius are depleted (analogous to patch choice models of human behavioral ecology/optimal foraging theory). As Premo notes, small foraging territories are depleted more rapidly, leading to more frequent base camp shifts than are large territories. Although Premo states that “Rather than assume *a priori* that LMS foragers cover a greater geographic extent than RMS foragers, I allow for this to emerge from the dynamics of the simple foraging-radius model described above” (Premo 2012, p. 648). It is not at all clear what he means by this statement, since all foragers “... embark upon logistic forays to procure food resources from within their foraging areas...” (Premo 2012, p. 647) and foraging areas are fixed by the effective foraging radius at the start of each simulation run. That is, the geographic extent of movement within a foraging territory is controlled by setting r_e , and this determines the frequency of residential moves. This makes for a tightly controlled experimental design, but means that extent of movement is not an emergent property. The density of food resources (which also affects the rate at which a territory is depleted) also is fixed at the start of each simulation run, but is selected randomly (with food occurring on 0–100 % of the cells), adding a degree of stochasticity to each simulation run.

An interaction takes place if the two foragers are within a specified distance of each other. Premo’s Fig. 1 suggests that he examined interaction distances of 5 and 10 cells, though he does not discuss this. He also compared interactions

restricted to instances when base camps of the two agents were located within 5 or 10 cells of each other with interactions that occurred any time agents were within the specified interaction distance. He does not appear to measure the frequency of interactions directly; rather, he counts the number of simulation runs in which the two foragers had at least one interaction (caption of Premo’s Fig. 1). Movement is measured as mean residential moves per “year”. We assume that this refers to shifting base camp locations, and not logistical forays, but Premo does not describe how he defines a year in his virtual world. (There is a suggestion that a year is 365 “days”, but a virtual world day is not defined either). Premo claims that Fig. 1 demonstrates a positive relationship between the frequency of residential moves and frequency of interactions. This may be so, for reasons we discuss below, but we are uncomfortable about this assertion given the questions we note above about measurement of movement and interactions. Moreover, the points in Fig. 1 are means. No information about the variance of his many simulation runs is presented, nor is any statistical measure of the strength of the apparent relationships provided. While there are apparent trends, the lack of such basic statistical evaluations is worrisome. Conversely, Premo’s Fig. 2 shows that when interaction distances are larger, the relationship between interaction frequency and movement frequency is opposite that shown in his Fig. 1. It is not clear why Premo prefers relatively ‘myopic’ foragers over those more ‘far-sighted’ foragers who can sense others throughout their foraging territory, in spite of some discussion of this subject. Our original simulation, in contrast, allowed forager perception of the presence of others to vary with the size of the foraging territory, along the lines of what Premo presents in Fig. 2; those with small territories were ‘myopic’ while those with large territories were ‘far sighted’. There is some merit to representing foragers as either ‘myopic’ or ‘far-sighted’. On the one hand, prehistoric foragers did not have access to technological enhancements to their perception, like binoculars and satellites, and hence could only directly perceive others within the range of the human biological senses. On the other hand, ethnographic foragers often have reliable information about the presence of others within their territories, and can use a variety of clues—from patrolling territories, to knowledge of foreign material culture and tracking ability—to enhance the effective range of their perception (Kelly 1995; Whallon 2006; Wiessner 1983).

These results suggest that the way in which the perception of others is modeled has significant effects on interaction rate. To test this systematically, we revised our original model (see Barton et al. 2011 and associated online supplementary materials for details on the model and access to the code) to decouple the radius of perception of other agents (i.e., interaction distance as described above) from the effective foraging radius as Premo suggests. Then, we varied foraging radius and

Encounter Rates After 1500 Cycles with Varying Foraging Distances for Different Distances of Perception

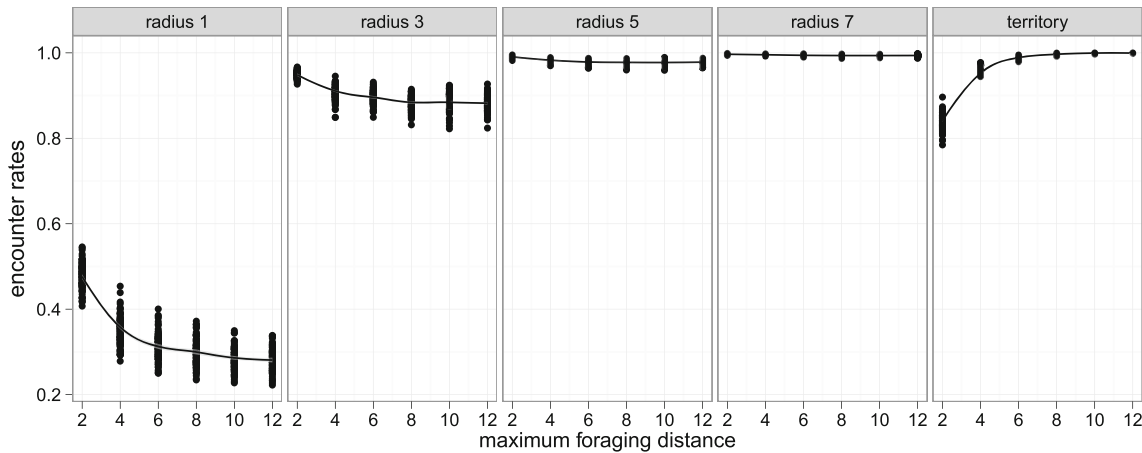


Fig. 1 Interaction rate (matings with non-self/all matings) with different foraging radii and different radii of perception (in cells beyond the cell occupied by an agent or over the entire territory). Solid line is a lowest curve fit of interaction rate vs. foraging radius and the (almost

invisibly narrow) grey shading is the 95 % confidence interval, for each radius of perception. Points indicate results of each experiment of 1,500 modeling cycles (100 repetitions for each combination of foraging radius and perception radius)

perception radius systematically, ran the simulation for 1,500 modeling cycles, repeated the simulation 100 times for each combination of foraging and perception radius, and measured interaction rate as the number of times an agent mated with a different agent divided by the total opportunities for mating for that agent. This is a more direct measure of interaction rate than Premo’s approach. The results of our updated modeling clearly confirm that the way in which ‘perception’ is modeled has a significant impact on interaction rates (Fig. 1). With very

‘myopic’ foragers, interaction rates start off low and decline rapidly with increasing foraging distance, agreeing with the main contention of Premo’s paper. However, as foragers become increasingly ‘far sighted,’ increasing foraging radius has less impact on interaction rates, with no apparent impact by the time perception radius reaches seven cells around the agent. And when an agent can perceive its entire territory, encounter rates climb rapidly with increasing distance instead of declining, (matching Premo’s Fig. 2) to level off at an

Population 1 After 1500 Cycles with Varying Foraging Distances for Different Distances of Perception

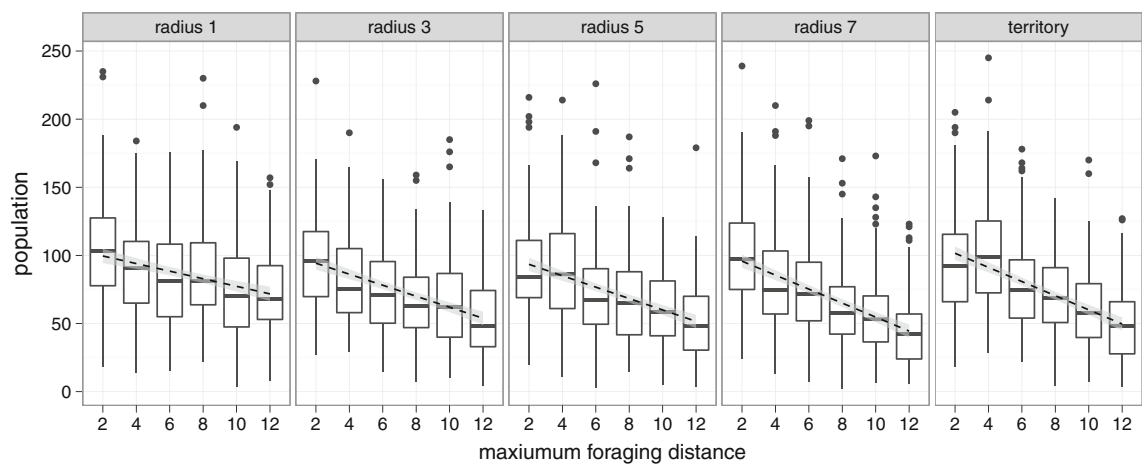


Fig. 2 Extinction trends for the smaller of two populations after 1,500 model cycles with different radii of perception (indirectly controlling for interaction rates) and foraging radii (see text and Fig. 1), with 100 repetitions of each experiment. Dashed line shows linear regression line for final population size vs. foraging radius and grey shading

shows the 95 % confidence interval, for each radius of perception. The final size of population 1 decreases for increasing foraging radius for all radii of perception/interaction rates and the negative correlations between population size and foraging radius are significant at $p < 0.01$ for all cases

interaction rate of 1.0. Although a shift in effects on interaction rate from myopic to far-sighted foragers is seen in both Premo's model and our revised simulation, it happens at smaller perception radii in our model for two likely reasons. First, Premo has only two forager agents, while we have many. Second, Premo's foragers shift their base camp with regularity, and its location jumps over twice the effective foraging radius each time it moves. Such common, relatively long-distance jumps, in random directions (within a 180° arc) would tend to add considerable noise to any relationships between interaction rates and effective foraging radius. Our foragers do not shift their camps (simulating different forms of residential movement was not our goal), although their offspring do establish new camps at a distance from their 'birth homes'.

There are two important points here. First, while there is no *a priori* reason to assume that hunter-gatherers should be especially myopic about perceiving others within their foraging territory, especially others who could serve as potential mates, assumptions about perception of others that are built into a model can condition the interaction rates of agents in the model. Second, while interaction rates are 'emergent' properties of agent (and human) behaviors and not parameters that can be directly varied in either Premo's or our model (as opposed to movement distances), changing the radius of perception allows us to control interaction rates indirectly and systematically examine their effects on the evolutionary dynamics that were the focus of our original paper.

Interaction Rates and Population Dynamics

A key finding of our original modeling was that for two populations of differing sizes, there is an increased tendency for the smaller one to trend toward extinction as foraging distances increase. Premo claims, but never tests, that this trend may not occur if interaction rates decrease as foraging radius increases. The relationship between perception and interaction demonstrated above allow us to test this proposition explicitly. Using the modified version of our original model, we repeated the experiments reported in our original paper while varying the radius of perception from highly 'myopic' to territory-wide. As seen in Fig. 2, the smaller of two populations trend toward extinction as foraging distance increases in all cases, *regardless of interaction rates*. The only effects of different interaction rates are that the trend toward extinction is slightly slower for the most 'myopic' forager agents (i.e., those with the lowest interaction rates), compared with the most 'far sighted' (i.e., those with the highest interaction rates). For all experiments, the strongly negative correlations between population size and foraging radius are significant at levels of $p \ll 0.01$.

Discussion

In summary, Premo has produced an interesting model that shows a relationship between interaction rates and foraging distance. However, further examination shows that this relationship is conditioned by the way in which agent perception is modeled. Moreover, while he suggests that differences in interaction rates may invalidate our original findings, he does not demonstrate this in his model. In fact, testing this proposition explicitly and quantitatively shows that varying interaction rates have minimal impacts on the trend toward extinction that is a consequence of increased foraging distance.

Model-based research in paleoanthropology (and indeed in the social sciences more broadly) is still in its infancy. Hence, it is important to carefully evaluate studies in this emerging domain of science (Bankes 2002). Like Premo, we consider the kind of computational modeling discussed here to be a form of experimental social science, providing a platform for carrying out controlled experiments on social dynamics that would be impossible in the real-world. One of the most robust scientific approaches for evaluating research results is that of replication; this holds true for modeling experiments as well (e.g., Janssen 2007).

The best way to test whether or not interaction rates impact the evolutionary dynamics in our original model is to replicate the model and alter part of the code to systematically alter interaction and monitor its effects. Premo did not do this, but we did. Providing for such replicative evaluation is the primary reason we placed our model in the publicly accessible Computational Model Library of CoMSES Net (<http://www.openabm.org>). We have also placed the modified version of that model that we used for the experiments reported in this reply in the CML. In order for model-based science to advance, it is imperative that the models themselves be as accessible as the written manuscripts that describe the experiments carried out with these new digital tools.

Our original model, the variant we describe here, and Premo's model as well illustrate the potentially valuable insights to be gained through model-based research in paleoanthropology. The main reason that his model fails to invalidate our prior work is because he is modeling different dimensions of human ecological behavior than we did. In the long run, this difference is more important than the failure of his model to invalidate our conclusions. While we are not yet convinced that the relationship between area of resource consumption and length of stay is key to understanding the shift between residential and logistical mobility, as Premo argues, his model is one of a number of reasonable starting places to begin to explore this. Both his model and ours are simple and abstract. While providing new insights not accessible through the paleoanthropological record alone, neither address a number of phenomena that, on the basis of empirical studies, are likely important to

fully understand the spatial and temporal dynamics of forager ecology, including: "...if food resources are strongly clustered in time and/or space or highly mobile and far ranging, if residential moves follow a pre-determined route rather than a correlated random walk, or if foragers possess perfect information concerning the presence of 'intruders.'" (Premo 2012, p. 649).

The preliminary nature of these and other model-based studies in paleoanthropology make it equally important that others be encouraged to build on our work to address increasing sophisticated questions about human biobehavioral evolution. This is the other reason that we strongly encourage Premo and others engaged in such research at the frontiers of social science to make their documented code accessible in the CML or other public repositories when they publish findings based on such models. While this carries the risk of revealing flaws in our models or even of our results being invalidated, such risks to one's pride is far outweighed by the longer-term benefits of robust research scaffolding in this new field (Barnes 2010). We want to close by thanking the editors of *Human Ecology* for giving us the opportunity to reply and, more generally, for supporting model-based science.

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