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## On Population, Foraging Efficiency, and Plant Domestication<sup>1</sup>

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In a recent paper on resource husbandry and the origins of agriculture, Layton, Foley, and Williams (CA 32:255–47) present a wide-ranging attempt to break free of models that presume an evolutionary progression. They focus on the material and political conditions that would have accompanied adaptive shifts among several subsistence strategies (especially pastoralism, foraging, and agriculture). They use the diet-breadth model to make predictions about the transition from foraging to plant cultivation, and they suggest that if—for any of a variety of reasons—the hunter-gatherers' preferred (high-ranking) foods diminish in abundance, then they should add foods of lower rank, foods previously not worth harvesting, to their diet. Ethnographic evidence on resource exploitation suggests that these typically are plant foods (e.g., seeds, tubers), which can be quite plentiful despite their low (net) return for the effort invested in harvesting and processing them.

Layton et al. suggest the possibility that increased mobility in search of lower-ranked resources added to the diet "should . . . lower the density of the hunter-gatherer population" (p. 256), but they focus on an alternative pathway in which "certain low-ranking food resources,

if husbanded, may contribute to population increase" (p. 260). They go on to suggest a mechanism for this predicted effect. In a favorable environment, stands of seed-bearing grasses and forbs might be sufficiently abundant and predictable to be defended (see Dyson-Hudson and Smith 1978). The possibility of reliable yield and exclusive use would lead to sedentism, husbandry to increase yield, and a diet increasingly rich in starch. By analogy with changes observed among the !Kung San (Lee 1980), the reduced nomadism and altered diet would produce population growth. This causal sequence makes "population growth . . . a consequence rather than a cause of intensive husbandry" (p. 262).

In a reply, Hawkes and O'Connell (CA 33:63–66) endorse the application of foraging models to analyses of agricultural origins, but they question several of Layton et al.'s conclusions on technical grounds and develop several additional insights from the models (see also Winterhalder and Goland n.d.). We will focus on one of their two points about population: "Layton et al. argue . . . that greater use of low-ranked but relatively abundant resources toward the end of the Pleistocene promoted population growth" (p. 64). According to Hawkes and O'Connell, this prediction is inconsistent with the assumptions and models of foraging theory: "Increases in diet breadth result from reduced foraging return rates and so lead to declines in population growth rates" (p. 64). In their follow-up, Layton and Foley (33:219) abandon their original hypothesis by noting their agreement with this assertion.

Layton et al. predict "population increase" and Hawkes and O'Connell "declines in population growth rates." Although both sets of researchers treat these as necessarily contradictory possibilities, they of course are not: a population can grow even as its rate of increase diminishes. Only if the growth rate becomes negative will the population decrease in size. Further, because of the possibility of dispersal, out-migration, or increasing range size, neither growth nor growth rate implies increasing density, the measure of importance to the ecological models cited in the two papers. Because it seems apparent in context that both sets of researchers mean to refer to an increase or decrease in population density, we will use this measure in the discussion to follow.

We will use a population ecology model to demonstrate that both sets of predictions need amendment. First, contrary to Hawkes and O'Connell, we show that a decline in foraging efficiency associated with expanding diet breadth may produce either an increase or a decrease (or conceivably no change at all) in the density of the foraging population. Second, unlike Layton et al., we show that changes in hunter-gatherer density do not necessarily require changes in mobility or territoriality. Such changes in forager population density can result solely from the characteristics of the newly adopted resources.

The diet-breadth model used by both sets of researchers has no population component. By contrast, our approach subsumes the diet-breadth formula within a simulation that incorporates population models for foragers

1. We thank Robert Foley, Sheryl Gerety, Abram Kaplan, Robert Layton, Eric Smith, and Richard Yarnell for useful comments and criticism on earlier drafts of this manuscript.

and their resources. The simulation will identify the conditions under which a foraging population will increase or decrease in density as a consequence of changes in diet breadth and foraging efficiency. We wish to make a simple point with some complex implications: the effect of a resource on the foraging population depends not only on its net return rate but also on its sustainable yield under exploitation. Sustainable yield is a function of a resource's density and its intrinsic rate of increase (hereafter  $r$ ). These parameters can vary independently of one another.

The relationships which rest at the heart of hypotheses about domestication and the origins of agriculture—relationships among subsistence choices, resource responses to exploitation, and human (population) responses to the tactics and efficiency of food procurement—are not easily grasped without formal models. Along with Layton et al. and Hawkes and O'Connell, we argue that evolutionary ecology offers unique insights into the microecological foundations of human subsistence economies in this and other contexts (Smith and Winterhalder 1992, Winterhalder 1993).

Our population ecology simulation (see Winterhalder et al. 1988) has three components: a forager population module, a resource choice module, and a resource population module. These submodels are linked by three functional relationships (fig. 1): forager population growth or decline is a function of overall foraging efficiency; foraging efficiency and resource choice are determined by the relationships specified in the diet-breadth model (especially, they are functions of resource density); and resource population density is a function of exploitation (what prey are harvested and in what amounts by a forager population of a given density, diet breadth, and energy requirements) and recovery potential. The forager population module is structured so that the population will grow if foraging efficiency is above a *maintenance requirement* (the caloric intake required for survival and reproduction at replacement rate) and shrinks if efficiency drops below that requirement. In each cycle of the model, prey populations are reduced by the magnitude of their harvest by foragers and then allowed to recover to a level set by the logistic equation of population growth (Wilson and Bossert 1974).

In the traditional diet-breadth analysis (Schoener 1974), resources are ranked by their decreasing net return for pursuit and handling. The forager's velocity and search radius determine the rate at which it searches (per unit area of habitat); the cost of search is measured in kcal/min. Each resource type has an energy value (kcal), a pursuit and handling time, pursuit and handling costs (kcal/min), and a density ( $\#/km^2$ ). The forager's rate of search combined with resource density determines encounter rates for each resource type. Assuming a search velocity of 0.75 km/hr., a search radius of 0.0175 km, a search cost of 4.0 kcal/min., a group range of 300.0  $km^2$ , and the ecological features of resource species given in table 1, optimal diet breadth is derived as in table 2. This analysis is static in that all variables are assumed to be constant.

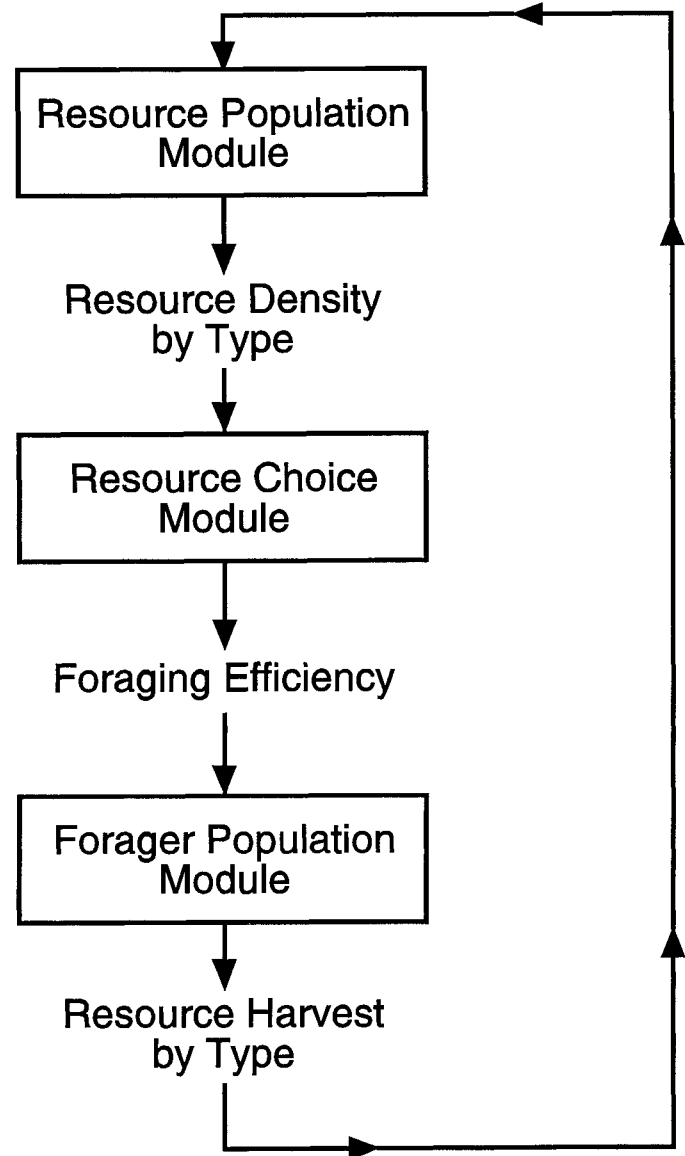


FIG. 1. Simulation model components and their interactions.

The forager that accepts only the top-ranked DPrey<sup>2</sup> (1,913.7 kcal/hr. pursuit and handling return) nonetheless has a relatively low overall foraging efficiency (212.5 kcal/hr.) because it encounters this one acceptable item infrequently. High search costs more than offset the high net return rate of DPrey once it is located. By adding BPrey to its diet the forager can increase overall efficiency to 705.8 kcal/hr. Not only is the net return rate of BPrey relatively high, but search costs decline as two encountered resource types are pursued. Pursuit of the third-ranked EPrey, however, returns fewer kcal/hr. (605.5) than a diet containing only the two higher-

2. Prey names and characteristics are taken from Winterhalder et al. (1988) to maintain consistency.

TABLE 1  
Ecological Characteristics of Resources for a Static Optimal-Diet-Breadth Analysis

Resource Type	Energy Value (kcal)	Pursuit Time (min)	Pursuit Cost (kcal/min)	Prey Density (#/km <sup>2</sup> )
BPrey	24,000.0	836.0	6.0	2.6
DPrey	3,600.0	95.0	6.0	6.4
EPrey	2,800.0	174.0	6.0	12.0
GPrey	240.0	21.0	6.0	300.0

TABLE 2  
Optimal-Diet-Breadth Analysis

	Net Return Pursuit and Handling (kcal/hr.)	Overall Efficiency (kcal/hr.)
DPrey	1,913.7	212.5
BPrey (Optimal Diet Breadth)	1,362.5	705.8
EPrey	605.5	676.5
GPrey	325.7	512.3

ranked items (705.8 kcal/hr.). EPrey is outside of the optimal diet. In fact, if the forager pursues EPrey its overall efficiency will drop to 676.5 kcal/hr. Pursuing GPrey, the resource with the lowest net return rate, has a like effect.

The optimal diet, then, consists of two items, DPrey and BPrey, and the forager should ignore EPrey and GPrey no matter how frequently they are encountered. However, if the density of DPrey and/or BPrey declines and search costs increase to the point that the overall efficiency of foraging for them alone drops below 605.5 kcal/hr., then EPrey will enter the optimal diet. Similarly, a drop below 325.7 kcal/hr. will bring GPrey into the diet as well. (If we imagine EPrey or GPrey to be potential plant domesticates, this is the type of scenario envisioned by Layton et al. and Hawkes and O'Connell.) Alternatively, an increase in the net return rate of EPrey to a value greater than 705.8 kcal/hr. will also move it into the optimal diet. If DPrey becomes sufficiently dense that foraging for it alone has an efficiency greater than 1,362.5 kcal/hr., even BPrey will drop from the diet.

To create a dynamic analysis of this situation, we assign the foragers an initial population of 2 (per 300 km<sup>2</sup>; density = 0.67/100 km<sup>2</sup>) and an *r* of 0.02. Their food maintenance requirement is 2,000 kcal/day; the foraging period is fixed at 5 hrs./day. For this duration a net efficiency of 400 kcal/hr. will just meet the mainte-

nance requirement. If actual efficiency is greater than the maintenance rate, the population grows (at a rate proportional to the difference); if less, it declines. If foraging efficiency drops to the point that it fails to provide the starvation threshold, the population declines at an augmented rate. Resource populations are assigned an *r*, a carrying capacity (#/km<sup>2</sup> and the total # in the 300-km<sup>2</sup> range on which the model is based), and an initial population (set equal in all simulations to the total carrying capacity as in table 3).

Figure 2 shows the results from 250 iterations of a simulation run for 500 iterations. It allows us to describe the basic structural properties of the model.

As in the static analysis, the two highest-ranked prey types (DPrey and BPrey) are in the initial diet (foraging efficiency 705.8 kcal/hr.). Foraging efficiency drops quickly in the first three iterations as the densities of DPrey and BPrey fall because of the impact of exploitation. Between the third and fourth iterations, efficiency falls from 625.0 kcal/hr. to 599.3 kcal/hr. and EPrey enters the diet. Forager population density has increased only slightly, from 2.01/300 km<sup>2</sup> to 2.10/300 km<sup>2</sup>. Because of its relatively high density and *r*, EPrey immediately moderates the steep decline in foraging efficiency and in the populations of the two higher-ranking resources. Following about 100 iterations, foraging efficiency approaches the maintenance rate (400 kcal/hr.) and growth of the foraging population slows. At iteration 129, foraging efficiency drops slightly below the maintenance rate, and forager population growth briefly becomes negative. All other variables likewise overshoot slightly and then approach their equilibrium values in a very shallow, damped oscillation. At equilibrium, foraging efficiency is 400 kcal/hr. (the maintenance rate). Forager population density stabilizes at 3.51/300 km<sup>2</sup>. This is an increase of 74.6%. The prey populations equilibrate at BPrey 386/300 km<sup>2</sup>, DPrey 122/300 km<sup>2</sup>, and EPrey 3,091/300 km<sup>2</sup>. None of the three prey types is depleted to extinction. GPrey (pursuit and handling efficiency 325.7 kcal/hr.) remains outside the diet throughout the simulation.

This time-course simulation depicts a population growing in parallel with decreasing foraging efficiency. However, this result is an artifact of the beginning values we assigned (foragers below their equilibrium val-

TABLE 3  
Resource Population Parameters for a Dynamic Optimal-Diet-Breadth Analysis

Resource Type	<i>r</i>	Carrying Capacity (#/km <sup>2</sup> )	Carrying Capacity (total #/300 km <sup>2</sup> )	Initial Population (total #)
BPrey	0.5	2.6	780.0	780.0
DPrey	0.3	6.4	1,920.0	1,920.0
EPrey	1.2	12.0	3,600.0	3,600.0
GPrey	2.0	300.0	90,000.0	90,000.0

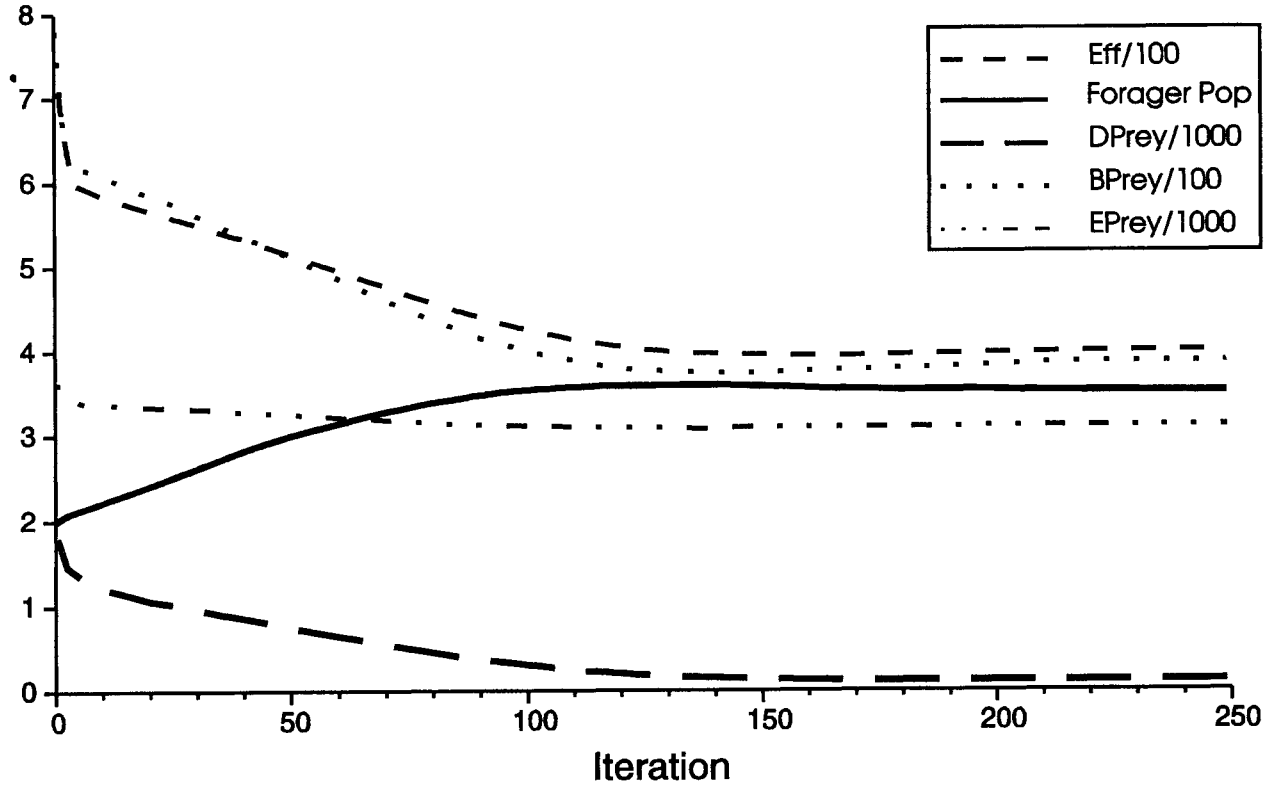


FIG. 2. Time course of the baseline simulation. All values greater than 10 (those for foraging efficiency and prey density) have been rescaled to the single-digit range; all population values are based on a 300-km<sup>2</sup> foraging range. GPrey is not shown because it is not harvested.

ues, prey types above). If we initially populate the foraging range with 4 foragers, efficiency declines and the forager population grows to a peak of 4.25 at iteration 11. Forager population density then begins to decline in parallel with efficiency. In general, forager-resource disequilibrium (which can include stable cycles, damped cycles, and lags in response) creates the possibility of positive or negative changes in forager density with declining foraging efficiency. Although any particular direction of disequilibrium is likely to be transient, disequilibrium itself may be common in prehistoric subsistence economies. More important, disequilibrium is implicit in the many domestication and agricultural origins scenarios that posit some kind of "disturbance" (e.g., climate change, migration to new habitat, or other destabilization).

To determine how equilibrium outcomes respond to a change of conditions, we change the foraging period to 8 hrs./day. This reduces the maintenance (or equilibrium) efficiency to 250 kcal/hr., which insures that GPrey—which we envision as the low-ranked but abundant plant resource of earlier discussion—will enter the diet. Comparison of the baseline equilibrium (5 hrs. foraging duration) with the new simulation again allows us to test the predictions of Layton et al. and Hawkes and O'Connell. How does forager population density respond to a decline in foraging efficiency and an increase in diet breadth?

In each of 32 variations on this new simulation, the ecological and population characteristics of the forager, DPrey, BPrey, and EPrey remain constant while two qualities of GPrey vary. Its density at carrying capacity (and initial density) takes on values of 6,000, 34,000, 62,000, and 90,000 (per 300 km<sup>2</sup>) and its *r* ranges from 1.0 to 8.0. We simulate each density at each *r* to produce the results shown in table 4 and graphed in figure 3. From examining the time course of these simulations

TABLE 4  
Equilibrium Density per 300 km<sup>2</sup> of the Forager Population for Different Values of GPrey Carrying Capacity and Intrinsic Rate of Increase (*r*)

GPrey <i>r</i>	GPrey Carrying Capacity per 300 km <sup>2</sup>			
	6,000	34,000	62,000	90,000
1.0	2.70	3.53	4.35	5.22
2.0	2.76	3.87	5.04	6.26
3.0	2.77	3.96	5.22	6.59
4.0	2.78	3.99	5.28	6.69
5.0	2.78	4.00	5.30	6.72
6.0	2.78	4.00	5.31	6.73
7.0	2.78	4.00	5.31	6.74
8.0	2.78	4.00	5.31	6.74

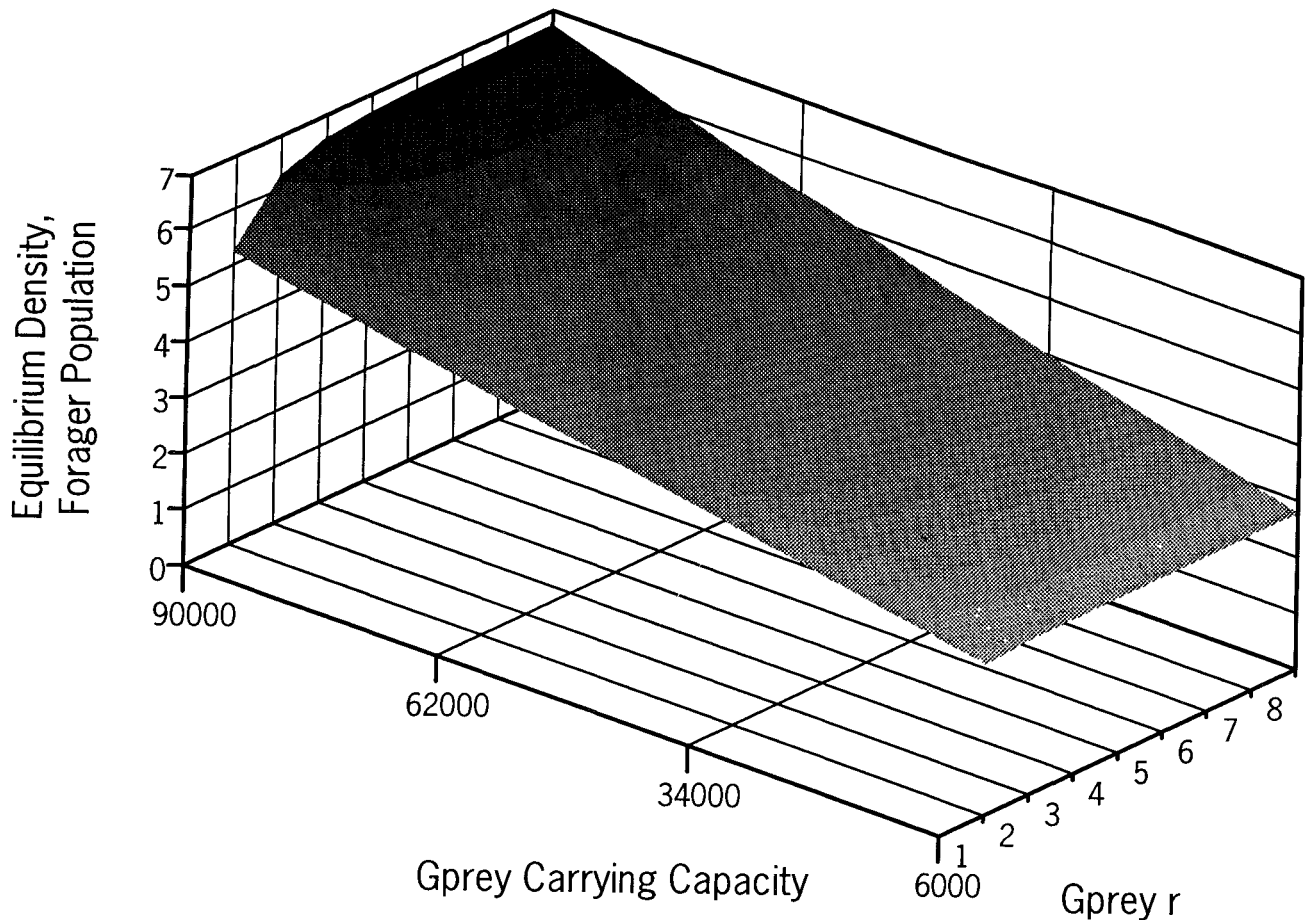


FIG. 3. Equilibrium density per 300 km<sup>2</sup> of the forager population for different values of GPrey carrying capacity (per 300 km<sup>2</sup>) and intrinsic rate of increase ( $r$ ).

(not shown here) we observe that EPrey always enters the diet at iteration 3, GPrey enters at iteration 20, and DPrey is exploited to extinction sometime between iterations 49 and 96.

The forager population at equilibrium ranges from 2.7/300 km<sup>2</sup> to 6.74/300 km<sup>2</sup>, compared with the baseline outcome of 3.51/300 km<sup>2</sup>. From this it is evident that forager population density will *drop* if declining foraging efficiencies bring into the diet a low-ranked (low-return-rate) GPrey that also has a low density and/or sufficiently low  $r$ ; however, forager population density will *rise* if the same diet-breadth change picks up the same low-ranked GPrey that happens to be dense and/or has a high  $r$ . The instances in which the forager population exceeds the baseline are especially striking given the extinction of the highest-ranking (highest-return-rate) resource, DPrey.

The impact of GPrey on the foraging population is sensitive to its density and  $r$  (sustainable yield) in spite of its low net return rate and the reduced overall foraging efficiency. Resource density appears to have a much greater effect on forager population than does  $r$ . Both factors vary (roughly) over a tenfold order of magnitude (i.e., 6,000 to 90,000 and 1.0 to 8.0, respectively), but

while resource density has an impact on forager population of increases ranging from 93% to 145%,<sup>3</sup> the impact of  $r$  is only between 3% and 29%.<sup>4</sup> The effect of GPrey density on forager population is roughly linear over the range of values we simulate while that of  $r$  is asymptotic. At higher values of  $r$ , the GPrey population rebounds from exploitation to a level at or near its carrying capacity in each iteration of the simulation. Thus further increases in  $r$  for this resource have little effect on the foraging population.

Whether we look at the time course of a simulation initiated from disequilibrium conditions or at shifts among equilibrium situations, declining foraging efficiency and expanding diet breadth may cause forager population density increase or decrease. Either outcome can be determined solely by the sustainable yield of the resource(s) being added to (or lost from) the diet. A population increase can be initiated by a low-net-return-rate

3. Holding  $r$  constant and comparing the extreme values for resource density.

4. Holding resource density constant and comparing the extreme values for  $r$ .



resource so long as it has a sufficiently high sustainable yield (due to high  $r$  and/or density). Such an increase can occur without or prior to sedentism, territorial defense, or husbandry (as in Layton et al.'s scenario).

In the process of domestication, coevolutionary pressures (Rindos 1984) may act on the net return rate, intrinsic rate of increase, or density of a resource. Our simulations hint that the type and magnitude of the impact on the subsistence economy will differ by variable. For instance, it appears that density changes are potentially more important than changes in intrinsic rate of increase. We suspect that both are more important than differences in net return rates. If this is the case, then opportunities for coevolutionary selection depend on which of these variables is being affected. Further analysis will be needed to disentangle these effects.

Intuition can be a hazardous guide to the workings of evolutionary processes, even those simplified for analytical purposes. Foraging models have illuminated many aspects of hunter-gatherer subsistence. Combined with population ecology approaches, they may provide key insights into the microecological processes by which foragers evolved into farmers or herders.

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## On the Search for (Truth) and Authority: A Reply to Lee and Guenther<sup>1</sup>

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In "Oxen or Onions? The Search for Trade (and Truth) in the Kalahari," Lee and Guenther (CA 32:592-601) call attention to an error in attribution of a map both in my book *Land Filled with Flies* (Wilmsen 1989:111, fig. 3.10) and in a subsequent article (Wilmsen and Denbow, CA 31:489-524).<sup>2</sup> They are correct in doing so; the map neither is by C. J. Andersson, as I wrongly said, nor traces his route to the Okavango River, which is accurately reproduced by Lee and Guenther (p. 593). But in setting off "Truth" in parentheses they imply that this was more than a mere mistake. They reinforce this implication by asking "Where, then, did the sketch map and mileage estimates come from?" (p. 539) and extend it by falsely attributing to me several other errors. This and the urging of colleagues prompt me to offer a short reply.

The map in question<sup>3</sup> comes from the National Archives of Namibia, Windhoek, where it is to be found in a microfilm copy of the Andersson Papers, requisition number A83; the original is pasted onto the inside of the back cover of volume 7 of Andersson's diaries (Davies n.d.) and appears in frame 669 of reel 2 of the film copy. Davies (n.d.:10) notes that the map, which he calls "the Okavango map," is initialed "F. G. (Frederick Green)"; a companion map of the Cunene River at its big bend, also by Green, who went there in July 1865, appears in frame 668 of the same reel. The two maps are rendered in identical format and delineated in the same style; there is no doubt that they are by Green, who was a close associate and friend of Andersson.

On December 7, 1865, Green wrote to Andersson from Ondongo reporting on the previous five months of his activities. His letter (A83, reel 2, frames 589-591), although it does not make direct reference to it, mentions a number of the places which appear on the Okavango map and seems to clarify it:

1. Support for my work has been provided by the University Research Council of the University of Witwatersrand in South Africa, by the Deutsche Forschungsgemeinschaft in Germany, and by the National Endowment for the Humanities, the National Science Foundation, the Social Sciences Research Council, the Wenner-Gren Foundation for Anthropological Research, and the National Geographic Society. James Denbow, Anne Griffiths, Tom Huffman, Gay Seidman, and Polly Wiessner made valuable suggestions after reading an early draft of this paper.

2. The error is entirely my own; Denbow played no role in its repetition.

3. Peter Reiner and Theo Karipi of the National Archives were instrumental in searching out documents for me. Brigitte Lau made my use of the archives as productive as possible.