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The Population Ecology of Hunter-Gatherers and Their Prey

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In this paper we combine foraging theory and population biology models to simulate dynamic relationships between hunter-gatherers and their prey resources. Hunter-gatherer population growth responds to the net marginal rate of foraging; prey population growth responds logistically to exploitation. Thus conceived, the relationship between forager and prey biomass is time-dependent and nonlinear. It changes from stable equilibrium to damped and stable cycles with modest adjustments of input parameters. And, it produces the largest sustainable human population at intermediate levels of individual work effort. At equilibrium the forager takes all prey types with a pursuit and handling rate greater than or equal to its maintenance foraging rate. The structural properties of the model compel us to reject standard anthropological interpretations of the carrying capacity concept; they provide new insights on old issues such as original affluence and intensification. Analysis of the interaction of human population, diet selection, and resource depletion requires microecological models in part because the relevant processes occur on time scales largely invisible to both ethnography and archaeology. © 1988 Academic Press, Inc.

INTRODUCTION

An analysis of the dynamic interplay between hunter-gatherers and their prey resources rests squarely at the juncture of population, economics, and ecology. At minimum it requires that we specify and bring together three processes: the effects of resource acquisition on the growth rate of the foraging group; the effects of changing prey densities on the resource selection of the foragers; and the effects of exploitation on the population densities of prey. The topic blurs distinctions between usually distinct areas of inquiry, in anthropology and biology and in economics and ecology. The need to find common ground among these subjects and the difficulties of direct empirical study of processes which encompass

multiple variables and long spans of time commend a modeling approach (Lowe 1985).

In this paper we develop a simulation model of the dynamic interaction between a group of foragers and their prey resources. The model encompasses each of the processes mentioned above. Experiments with it allow us to explore the population-level consequences of basic premises about ecologically adaptive behavior.

The Problem

Anthropological analyses of hunter-gatherer population ecology commonly begin with the concept of carrying capacity. This typically is interpreted as a quantity (biomass) of resources which is available for consumption and which determines the size of a human group of given resource requirements. In these analyses the methodological effort turns on estimating resource biomass and forager subsistence requirements. The theoretical dimension often takes a pro- or anti-Malthusian argument as its point of departure.

Because of its restricted conceptual apparatus, this approach must ignore the key dynamic interaction of any population-resource system: viz. the densities of the prey will change as a function of their exploitation by humans, and in turn, the resource selectivity and size of the foraging group will vary as a function of changing prey availability. Because the carrying capacity approach is developed in terms of a direct relationship between human and resource *biomass*, it cannot treat the economic side of food production. It gives us no information, for instance, on the effort required or the net productivity of various subsistence options.

At present, foraging theory is the only source of models which show systematically how hunter-gatherer resource selection might respond to relative prey densities. It likewise can tell us a great deal about the economics of the food quest, including its productivity (measured as net acquisition rate, NAR). However, to keep foraging models as simple as possible, it has been assumed that resource density is fixed, that the depletion of the species being exploited is accompanied by a perfectly balancing renewal of their numbers. For the single forager who harvests few prey relative to those available and for the short-term, nondynamic questions addressed by these models this approximation is a good one, although not fully realistic. In the first instance, modest exploitation is assumed to have a small or insignificant impact on effective densities. In the second, a long-term, dynamic view can be mimicked by iterating solutions to the static model, each iteration incorporating the density changes presumed to result from harvest or other factors.

In this analysis we relax the assumption of constant densities in order

to explore the long-term, dynamic consequences of optimal diet selection for foragers and their prey. In biological terms, we explore the population dynamics of a predator-prey system made up of a predator using optimal diet selection rules and one or more potential prey.¹ In anthropological terms, we are asking how hunter-gatherer population growth and food choice respond to prey exploitation and depletion. In both contexts, a goal is to add realism to microecological analyses of hunting and gathering by combining foraging and population biology models.

Approach and Outline

Foraging theory offers us a rough prediction about the effects of harvest: as highly ranked species (those within the optimal diet) diminish in numbers due to exploitation, the diet breadth should expand. Not revealed in this prediction are a series of basic issues: How rapidly and how far does the diet expand? How do the densities of the prey species respond? What is the effect of harvest and depletion on the NAR of foraging and the growth and size of the human group? How do economic factors such as the time available for foraging, or its marginal NAR (the net acquisition rate at the prevailing diet breadth and densities of prey), affect population ecology relationships? Is such a system stable or unstable? Does it have an equilibrium? What is the meaning of carrying capacity in such a system? The analysis that follows suggests answers to these questions.

The structure of the paper is as follows: We briefly introduce the relevant ideas of evolutionary ecology and population biology. We then describe the three components of the model—prey population, diet selection, and forager population—and the interactions among them. We note how values were assigned to model parameters and then follow with a series of simulations using one- or two-prey species. The results provide the basis for a discussion of hunter-gatherer population ecology, diet selection under dynamic conditions, modeling, and carrying capacity.

CONCEPTS AND THEORY

Evolutionary Ecology

The premises of evolutionary ecology and foraging theory are straightforward: With reference either to neo-Darwinian or neoclassical theory, we have good reason to presume that individuals make rational selections

¹ A paper in preparation will present and analyze the behavior of the model from the perspective of the classical (Lotka-Volterra) predator-prey population dynamics models and their derivatives.

among available alternatives with a tendency toward optimizing strategies. As a heuristic basis for inquiry, this claim is theoretically sound and entirely unexceptional in behavioral biology (Foley 1985). In the social sciences it currently is more controversial although widely adopted and defended (e.g., Elster 1985; Smith 1987; Winterhalder 1987). There are circumstances in which these premises must be discarded or qualified (Elster 1986), but they are not of immediate concern here. In general, optimality modeling in anthropology (or biology) attempts to place the study of behavioral adaptation and design on sounder methodological principles than previously have characterized functionalist (or adaptationist) analyses (Stephens and Krebs 1986).

The goal of foraging theory is to construct models based on these premises which show clearly how certain environmental features are expected to affect diet selection. The assumptions, mathematical form, hypotheses, and limitations of the diet selection model are published (Smith 1979, 1983; Stephens and Krebs 1986; Winterhalder 1986, 1987); the ensuing description will be correspondingly brief.

In searching for randomly located prey, any encounter poses this option to the forager: pursue this prey type or use the time and energy to continue searching in the expectation of finding and capturing a more desirable item. If encounter rates with more profitable items are high and search costs are low, it may be optimal to ignore the already found type. To adapt slightly an analogous piece of folk wisdom—a bird at hand may (or it may not) be worth two in the bush. The diet breadth model takes account of forager search and pursuit costs, relative prey densities, and the differing food values of the prey in order to offer a precise analysis of this issue.

To apply the model, prey are ranked by their NAR for energy (or some other “currency”) with respect to pursuit and handling costs. This is their net value to the predator making the decision to pursue. The highest ranked prey always is part of the diet. The model must ascertain how many additional prey types to add. It does so by determining whether the inclusive NAR of foraging (including search, as well as pursuit and handling) will be increased by addition of the prey type of next lower rank. This condition will be met if the next type has a pursuit and handling NAR greater than the inclusive NAR of the diet excluding it. The first prey type which reverses this condition is the first to fall outside of the optimal set.

The prediction most immediately relevant to the question of foraging and prey population dynamics is this: If the densities of the prey within the diet fall, due to exploitation or other factors, then search costs increase, inclusive NAR declines, and previously excluded prey types will be added to the diet in descending order of their pursuit and handling

NAR. Conversely, as prey densities increase, prey will be dropped from the optimal diet in an order reverse of their incorporation.

Population Biology

The prey populations in this model are affected by two factors: density-dependent processes such as crowding and depletion of food supply and exploitation by the human forager. In nature but not the model they also would grow or shrink in size from exploitation by other predators, and from the effects of density-independent variables such as climatic fluctuations or natural catastrophes.

The relevant models of population biology stem from the equations of Verhulst and Pearl (Hutchinson 1978). They begin with the exponential population growth equations, integral and differential form, respectively

$$P = P_0 e^{rt}, \quad dP/dt = rP, \quad (1, 2)$$

where P = number of organisms at time t ; P_0 = number of organisms at time zero; e = base of natural logarithms; r = intrinsic rate of increase; and t = time. Equation (1) produces the familiar j -shaped curve of runaway population increase; Eq. (2) the instantaneous rate of change of population size.

Such growth cannot of course be sustained for any length of time. If we define K to be the carrying capacity of the environment—the population size at which density-dependent factors bring further increases to a halt—then Eqs. (1) and (2) become the logistic equation by addition of a feedback term $[(K - P)/K]$ (Emlen 1973):

$$P = P_0 [(Ke^{rt}) / (K - P_0(1 - e^{rt}))] \quad (3)$$

$$dP/dt = rP[(K - P)/K]. \quad (4)$$

The feedback term steadily depresses the rate of population change (see Eq. (4)) to produce the familiar s -shaped curve which arises from the integral expression of the model (Eq. (3); Fig. 1). In the simulations below, we modify Eq. (3) to give the following difference equation;

$$P_{t+1} = P_t [(Ke^r) / (K - P_t(1 - e^r))], \quad (5)$$

which determines the size of a logistic population at time $t + 1$ as a function of its size at time t .

An unexploited population at carrying capacity exists in an equilibrium determined by density-dependent factors. Births are compensated by an equal number of deaths and any harvest (which exceeds compensatory mortality) necessarily diminishes the size of the population. As popula-

FIG. 1. Integral and differential form of the logistic equation ($K = 1000$; $r = 0.025$).

tion size is decreased below carrying capacity, births begin to exceed the density-dependent losses, generating recruitment. This recruitment represents the quantity of organisms which then can be harvested without the harvest itself causing a further change in numbers. The exploitable surplus associated with such an equilibrium density is greatest—the maximal sustainable yield, or MSY—when the population is one-half of its size at carrying capacity ($K/2$). Figure 2 shows the parabolic relationship between sustainable yield and population size. Although difficult to estimate in practice, game biologists routinely use the concept of sustainable yield when determining the ideal harvest of managed ecosystems such as fisheries.

Because MSY occurs at $P = K/2$, we can substitute $K/2$ for P in Eq. (4) to determine that recruitment and hence the exploitable yield at the maximum is $0.25rK$. The MSY is a direct function of the intrinsic rate of

FIG. 2. Harvest, sustained yield, and equilibrium population size ($K = 1000$; $r = 0.025$).

increase (r) and the carrying capacity (K). Note also that the fraction of the population which can be harvested at the MSY is $(0.25rK)/(K/2) = 0.5r$.

Of special interest are those cases in which there is a harvest, but less than the MSY: i.e., $0 < h \leq 0.25rk$ (Beddington and May 1977). To determine the outcome in this circumstance we set

$$h = dP/dt = rP[(K - P)/K] \quad (6)$$

(the point at which the harvest rate is equal to growth rate) and solve for P to derive the equilibrium population size. The result is a quadratic equation, with two solutions (roots):

$$P = K \pm [(K^2 - 4Kh/r)^{1/2}]/2. \quad (7)$$

This relationship is depicted in Fig. 2. The two solutions, the upper and lower equilibrium sizes (Eq. (7)), are designated P_u and P_l , respectively. Given an exploitation rate at a constant level h (and the corresponding P_u and P_l), the following relationships hold: If the initial prey population is greater than P_u ($P_{j=0} > P_u$), the population will decrease to P_u ; if the initial population lies between P_u and P_l , it will grow to P_u ; and, finally, if the initial population is less than P_l , it will decline to extinction. Note that P_u is a stable equilibrium; P_l is an unstable equilibrium. In sum, the initial size of a population is among the determinants of its response to exploitation.

THE MODEL

Components

Table 1 shows schematically the parameters and variables used in the three components of the model and their relationships. Table 2 gives the units and definitions. *State parameters* are assigned values at the beginning of a simulation and remain constant (i.e., they are not time dependent). All variables are time dependent. *Transfer variables* are passed from one component of the model to another, whereas *counter variables* track changes within a component. *File variables* are those saved for graphing and analysis. The subscript i refers to type and j refers to time (e.g., P_{ij} is the population of prey type i at time j).

The prey population. Prey populations are assumed to grow in a logistic, density-dependent manner in the absence of predation. For each prey type we specify its intrinsic rate of increase (r_i) and its initial population size ($P_{ij}, j = 0$) as state parameters. Its population size at carrying capacity ($K_i = Ad_i$) is derived from parameters specified in the diet selection component (see below). The number of prey harvested in a time interval

TABLE 1
PARAMETERS AND VARIABLES USED IN THE MODEL

Parameters	Variables		
	Transfer	Counter	File
Prey component $P_{ij}, j = 0$ r_i K_i	<pre>graph TD PP[Prey Population] -- d_ij --> DS[Diet Selection] DS -- db_j --> HP[Human Population] DS -- R_j --> HP DS -- f_ij --> HP HP -- h_ij --> PP</pre>	P_{ij}	P_{ij}
Diet selection component S_v s_r s_c A v_i t_i c_i $d_{ij}, j = 0$			R_j db_j
Forager component $N_{ij}, j = 0$ m θ w σ S		N_j	N_j

TABLE 2
SYMBOLS, UNITS, DEFINITIONS, AND ABBREVIATIONS

P_{ij}	No. of organisms	Population size of prey type i , time j
r_i	1/year	Intrinsic rate of increase, prey type i
K_i	No.	Carrying capacity, prey type i
d_{ij}	No./km ²	Density of prey type i , time j
s_v	km/hr	Forager search speed
s_r	km	Forager search radius
s_c	kcal/min	Forager search cost, in energy
A	km ²	Range of the foraging group
v_i	kcal	Value of prey type i
t_i	min/ind	Time to pursue and capture i
c_i	kcal/min	Cost of pursuit and capture, in energy
d_i	No./km ²	Density, prey type i
db_j	No. of prey types	Diet breadth, time j
R_j	kcal/hr	Inclusive net acquisition rate of energy, time j
f_{ij}	—	Proportion of prey type i in the diet at time j
N_j	No. persons	Number of foragers, time j
m	1/year	Malthusian parameter (intrinsic rate of increase) of foragers
θ	kcal/day	Forager maintenance energy requirement, for all nonforaging expenditures
w	hr	Daily time devoted to foraging
σ	kcal/hr	Maintenance foraging NAR
S	kcal/hr	Critical threshold foraging NAR
h_{ij}	No. of organisms	Harvest of prey type i , time j
MSY	No./yr	Maximum sustainable yield
NAR	kcal/hr	Net acquisition rate for energy or some other "currency"

(h_{ij}) and the number of prey in the population after harvest and growth (P_{ij+1}) are dynamic variables. If a prey population drops below 2, it is assumed to be extinct ($P_i = 0$).

For each prey type and foraging interval, the program takes the number of prey initially available (P_{ij}), it subtracts any harvest (h_{ij}), and it then calculates growth (Eq. (5)) to determine the prey population (P_{ij+1}) available to the forager in the subsequent round of foraging. This mathematical procedure envisions a prey species without age or sexual differentiation, which is harvested throughout the year but which reproduces seasonally at its conclusion. The mechanics of the harvest could be construed differently or with greater refinement, but this approach has the merit of mathematical simplicity and fair realism.

The size of each prey population (P_{ij} , for $j = 0$ to n) is saved for analysis; the density of each prey type d_{ij} is passed to the diet selection component as a transfer variable (Table 1).

Diet selection. For the forager, the speed (s_v) and radius (s_r) of its

search path determine the rate at which it will encounter prey of various types and densities. The forager also is assigned search costs (s_c), and the foraging group is assigned a range (A). State parameters for each prey species are as follows: its energy value (v_i ; edible portion), the average time required to pursue and capture it (t_i), the energy cost of pursuing it (c_i), and its density at carrying capacity (d_i). The number of each prey species at carrying capacity (K_i) is a product of its density (d_i) and the area (A) available to the foraging group.

This component of the program operates to determine which prey are in the optimal diet and thus harvested. It receives as dynamic input the density of each prey population (d_{ij}) at the conclusion of the preceding foraging interval. Its output to the human population component of the model consists of three transfer variables: the number of prey in the diet (db_j), foraging NAR (R_j) in the present interval, and the proportion of each prey type in the diet (f_{ij}). The diet breadth (db_j) and inclusive NAR (R_j) are saved for analysis.

The human population. The human population is characterized by an initial size ($N_j, j = 0$) and an intrinsic rate of growth (m = the Malthusian parameter). The individual foragers are characterized by a daily maintenance energy requirement (θ) and the number of hours they devote each day to foraging (w).

The equation describing human population growth expresses key analytic premises of the model. For the moment, we will understand all individuals counted in the model (that is, N_j) to be both producers and consumers. They are productive and reproductive adults. We define the daily maintenance energy requirement (θ) as that amount of energy which, over the long term, just enables an individual to survive and replace itself with one offspring. It is a figure exclusive of the energy costs of hunting and gathering (which are accounted for in the calculation of inclusive NAR). For any amount of time devoted to foraging, there is a NAR that will just meet this nonforaging maintenance requirement. We designate this value by σ (the maintenance foraging rate) and calculate it by dividing the maintenance requirement by the hours foraged ($\sigma = \theta/w$). We further assume that if the inclusive NAR of foraging is greater than the maintenance ($R_j > \sigma$) rate, then foraging produces extra energy which is available for individual reproduction above replacement, hence population growth. If $R_j < \sigma$, then individuals in the population are not meeting their maintenance needs and the population will decline in size. Finally, there is a critical threshold (S), which marks the point at which a falling NAR begins to have a more dramatic impact on the population.

Taking these considerations together gives us the following equations for growth of the human population:

$$\text{If } R_j > S, \quad \text{then } N_{t+1} = N_t + mN_t[(R_j - \sigma)/\sigma] \quad (8)$$

$$\text{If } R_j \leq S, \quad \text{then } N_{t+1} = N_t + mN_t[(R_j - \sigma)/\sigma][S/R_j] \quad (9)$$

$$\text{If } R_j \leq 0, \quad \text{then } N_j = 0. \quad (10)$$

Note that the last part of Eq. (8) is somewhat like the logistic (Eq. (4)), but that the feedback term $[(R_j - \sigma)/\sigma]$ is a *positive* function of the degree to which the net acquisition of energy exceeds the maintenance requirement, and a *negative* function of the degree to which it falls short of it. The foraging population grows when energy can be produced in abundance and declines when production falls below levels required to sustain and replace existing individuals. If net production falls precipitously, to and below the critical threshold ($R_j \leq S$), then Eq. (9) replaces (8). As R_j approaches zero the (S/R_j) term accelerates the impact of NAR shortfalls by producing very large negative growth rates and a rapid shrinkage of the foraging population. This would be expected, for instance, if they severely depleted their resource base. If R_j drops to or below zero (Eq. (10)), the foraging group is mathematically extinguished ($N_j = 0$).

These mathematical conventions can be interpreted as a three-stage response of members of the human population to their food gathering rate. In the first stage (Eq. (8)), deviations above or small deviations below maintenance requirements cause corresponding deviations above and below replacement reproductive levels. Birth rate moves with food availability to exceed or fall below levels which would match normal mortality. In the second stage (Eq. (9)), food shortfalls have become severe, perhaps suppressing reproduction and causing higher mortality among the individuals in the extant population. There is a more dramatic drop in the ratio of births to deaths. Finally if prey are depleted to such a degree that foraging NAR drops to or below zero, then the human population dies out immediately. This formulation simplifies and generalizes human demographic processes to the degree of realism desired for our analysis.

The simulation also must determine what prey and how much of each type are consumed by the foraging group. This calculation relies on the "contingency" property of the diet breadth model—prey within the optimal diet are presumed to be encountered and captured in proportion to their relative densities. Mathematically,

$$h_{ij} = f_{ij}[(N_j \times w \times 365)/((y + \sum f_{ij}c_i)/60)], \quad (11)$$

where y is the average time required to encounter an acceptable prey type at the prevailing densities and diet breadth. [More precisely, $y = 1/(s_v \times s_r \times 2 \times \sum d_i$, for all i in the diet]. The numerator of the bracketed ex-

pression is annual foraging time (hr); the denominator is the number of hours required to find and capture the average prey individual in the diet; f_{ij} is the proportional contribution of each type to the diet.

To demonstrate, assume that two foragers hunt and gather for 5 hr a day, for an annual effort of 3650 hr. Their average encounter rate is 120 min/prey, and they pursue two types (a and b) of equal density ($p_a = p_b = 0.5$) but differing pursuit and handling times ($c_a = 60$ min; $c_b = 90$ min). By this formula 561.54 of each will be harvested. The prey are encountered thus harvested in equal numbers and, as the reader can verify, the time required to locate and pursue this mix of prey sums to the annual total.

N_j , the size of the human group at time j , is a counter and a file variable. The number of each species harvested (h_{ij}) is a transfer variable which is passed to the prey population component, to complete a cycle of the simulation.

The Components Together

In summary, the dynamic model is built from three components (the logistic prey population model, the diet selection model, and the human population model), linked by four functional relationships. These are: (a) human population growth rate is a function of their inclusive foraging NAR; (b) diet selection by the human foragers is a function of resource density; (c) the absolute demand for resources is a function of the sizes of the human population; and (d) prey population density is a function of (b) and (c), that is, what prey are harvested and in what amounts.

CHOICE OF PARAMETERS

To activate the model we must set the relevant state parameters for forager and prey. In adopting certain values we do not mean to produce a universal hunter-gatherer. Still it will not do if our model forager is unrecognizable to his or her real counterpart, or is an analytical hybrid, eating small and hunting big. We wish to avoid anomalies of scale that might result, for instance, from endowing our forager with the appetite of an opossum and then giving it water buffalo to hunt. Hence, we have sought information on the ranges of values characteristic of hunter-gatherers and their environments (Tables 3–5), and have tried to set the model parameters within those ranges (Tables 6 and 7).

The characteristics of eight prey types (A through H) are listed in Table 6. Their "size," measured as edible kilocalories, ranges from 60,000 to 90 kcal, roughly a medium-sized ungulate through a small vertebrate, fruit, or tuber. The pursuit and handling times diminish roughly in parallel with size, and are meant to include all activities such as tracking, stalking,

TABLE 3
PARAMETERS RELATED TO DIET SELECTION AND ENERGY NAR IN HUMAN
FORAGING GROUPS

Property	Value	Source
Number of "staples" in diet	10-26	Hayden 1981: 400-401
Time spent obtaining food, daily	2-5 hr/day/working adult ^a	Hayden 1981: 407
	3.9-9.2 hr/day/working adult ^b	Hill 1982: Table 1
Energy costs of foraging activities	4 to 7.5 kcal/min ^c	Durnin and Passmore 1967: 84
Foraging net acquisition rate, NAR	-121 kcal/hr to 1894 kcal/hr ^d	Hill 1982: Table 1
Pursuit and handling, NAR		
Vegetable foods	-172 kcal/hr to 5952 kcal/hr ^e	Hill 1982: Table 2a
Game foods	915 kcal/hr to 64,700 kcal/hr ^e	Hill 1982: Table 2b
Ungulate biomass, various ecosystems	175 to 23556 kg/km ² ^f	Hassan 1981: 13-14.

^a Typically excludes equipment maintenance and food preparation; generally assumes between 60 and 100% of the adults are productive.

^b See notes to Table 1 in Hill 1982. Mean = 6.9 hr; $n = 9$. Some values given as "per hunt."

^c Combined range for male and female energy expenditure in moderately demanding recreational activities (e.g., gardening, cycling, and tennis).

^d See Table 1 and notes. Calculated as follows: [(Column 1 figures on kg meat/hour foraged) $\times$ (0.65, edible portion) $\times$ (2500 kcal/kg, energy value)] - 300 (kcal/hr, average foraging energy costs). The average value NAR for the human foragers listed by Hill is 428 kcal/hr.

^e Calculated as (returns for pursuit and handling, kcal/hr) - 300 (kcal/hr, energy expenditure). The mean for vegetable foods = 1707 kcal/hr ($n = 23$); the mean for game foods = 12,767 kcal/hr ($n = 10$). Note that the mean and average for game foods are heavily influenced by two exceptionally high values, those for peccaries (65,000 kcal/hr) and deer (27,000 kcal/hr).

^f Excludes deserts and dense rain forests; $n = 23$, mean = 6082 kg/km².

butchering, retrieving, peeling, grinding, and cooking, for each of the persons involved, with all activities up to butchering corrected to allow for those instances in which the pursuit is unsuccessful. Thus, assume that Aprey is located by two foragers, who take 2 min to decide to pursue it and require on average 3 hr either to track, stalk, and kill it, or to give up. Their success rate is 1 in 4. They also require 1 hr to butcher it, 1 to carry it to the camp, and 1½ to prepare and cook it for consumption. The total time for the decision, plus the remainder of the pursuit and handling gives 1864 min.

TABLE 4
DEMOGRAPHIC PARAMETERS OF HUMAN FORAGING POPULATIONS

Property	Value	Source
"Characteristic" group size	20–50 persons, or 4–8 families	Hayden 1981: 361, 374
	25–28 persons	Hassan 1981: 61
Maximum group range size	2500 km ²	Hayden 1981: 382
	314 km ² . ^a	Hassan 1981: 53
Population density	0.01 to 9.5 ^b ind/km ²	Hassan 1981: 8
	0.1 to 1 ind/km ² . ^c	Hassan 1981: 56
Individual energy requirements	2200 kcal/day ^d	Hassan 1981: 18
Intrinsic rate of increase	0.0052 ^e	Hassan 1981: 140
	0.0016 ^f	Howell 1979: 335

^a Based on a 10-km, maximum daily foraging radius around a (possibly temporary) home base.

^b $n = 40$; mean = 0.67; see Table 2.1 of Hassan (1981: 8).

^c Estimate for "most cases" of hunter-gatherer population density.

^d Estimate for temperate zone hunter/gatherers; 3000 to 3100 kcal/day is Hassan's figure for "colder regions."

^e Estimate of "the probable maximum growth rate for prehistoric groups" of hunter-gatherers.

^f General, "central tendency" value based on observations of !Kung demography, called a "low but plausible estimate for a population like the !Kung."

Pursuit and handling is moderately strenuous for either sex, costing 6 kcal/min in energy expenditure (Table 6). Prey densities range from 0.8 to 500/km² and intrinsic rate of increase (r_i) ranges from that 0.3 to 3.5 (Table 6), roughly characteristic of mammalian species in this size range (Table 5). Note that smaller prey are more quickly pursued and captured, they are more common, and they reproduce at a higher intrinsic rate. These are general but not invariable features of natural communities. The model environment has a biomass of roughly 300 kg/km².

Our forager likewise is a composite of generalities (Table 7). He or she searches for prey at 0.5 km/hr—a rate less than human walking speed but designed to allow for the cautious demeanor and tortuous pathways required of this activity, surveying a path 35 m wide ($= s_r \times 2$). The energy expenditure is 4 kcal/min, a light to moderate value for humans. The group has a range of 300 km², based roughly on the radius (10 km) of the area which can be encompassed by foraging trips which leave and return to a home base in the same day (Table 4).

The forager intrinsic rate of increase (m or the Malthusian parameter) is 0.02/year (Table 7). It is set above that estimated or observed by archaeologists and ethnographers (Table 4), because the intrinsic rate used in the logistic equation is meant to be $r_{\max}$, the rate under ideal conditions, early

TABLE 5
DEMOGRAPHIC PARAMETERS OF PREY POPULATIONS (REPRESENTATIVE VALUES OF
INTRINSIC RATE OF INCREASE)

Property	Value	Source
Intrinsic rate of increase		
Cottontail	11.51	Robinson and Redford 1986
Brown rat	5.4	Pianka 1983: 115
Vole	4.7	Pianka 1983: 115
Dog	3.3	Pianka 1983: 115
Peccary (<i>T. tajacu</i>)	1.25	Robinson and Redford 1986
Agouti	1.10	Robinson and Redford 1986
White-tailed deer	0.73	Robinson and Redford 1986
Armadillo	0.69	Robinson and Redford 1986
Raccoon	0.66	Robinson and Redford 1986
Anteater	0.35	Robinson and Redford 1986
Howler monkey (<i>A. seniculus</i>)	0.17	Robinson and Redford 1986
Sloth	0.14	Robinson and Redford 1986

in population growth and before any density-dependent factors take affect. The estimated or observed rates for prehistoric or extant foragers (Table 4) presumably more closely approximate the lower, realized values, which occur nearer to equilibrium. Finally, the foragers require 2000 kcal/day of energy, exclusive of that consumed during foraging, begin to starve if they drop below 1000 kcal/day, and they forage for five hr/day (see Tables 3 and 4).

Table 8 shows a static optimal diet breadth analysis for the full set of prey. Prey are ranked by decreasing pursuit and handling NAR. Inclusive or foraging NAR first increases and then diminishes as the diet expands to

TABLE 6
VALUES ASSIGNED TO PREY POPULATION PARAMETERS

Type (<i>i</i>)	Parameters ^a				
	v_i (kcal)	t_i (min)	c_i (kcal/min)	d_i (No./km ²)	r_i (No./year)
Aprey	60,000	1864	6	0.8	0.5
Bprey	24,000	836	6	2.6	0.5
Cprey	13,800	235	6	8.0	0.7
Dprey	3,600	95	6	6.4	0.3
Eprey	2,800	174	6	12.0	1.2
Fprey	1,500	67	6	40.0	1.5
Gprey	240	26	6	300.0	2.0
Hprey	90	7	6	500.0	3.5

^a Definitions in Table 2.

TABLE 7
FORAGER POPULATION STATE PARAMETERS

Characteristic ^a	Value	Units
Speed (s_v)	0.5	(km/hr)
Search radius (s_r)	0.0175	(km)
Search cost (s_c)	4.0	(kcal/min)
Group range (A)	300.0	(km ²)
Intrinsic rate of increase (m)	0.02	(1/year)
Daily energy requirement (θ)	2000.0	(kcal/day)
Critical threshold (S)	1000.0	(kcal/day)
Time spent foraging/day (w)	5.0	(hr)

^a Definitions in Table 2.

include additional types. The optimal diet is composed of the first four prey. Pursuit of any encountered type ranked below these returns fewer calories for the effort than could be expected if it were ignored in favor of items of higher rank. The net acquisition rates associated with this menagerie of invented prey are commensurate with those observed for actual hunter-gatherers, although it is fewer prey than would be staples in the diet of the typical forager and a somewhat lesser biomass than would be found in many environments (Table 3).

By defining our forager and environment so precisely and in so many respects, we recognize that we are inviting dispute from every hunter-gatherer specialist who prefers different or can defend more accurate values for these parameters. However, as long as the questions asked of the model are qualitative in nature, involving observations of relative magnitudes, directions of change, and basic structural properties of the population-ecology dynamic, the exact numbers used for any particular simulation are of minor significance. Indeed, a virtue of this type of ap-

TABLE 8
BASELINE OPTIMAL DIET ANALYSIS^a

Ranked prey types	Pursuit and handling NAR (kcal/hr)	Inclusive NAR, R (kcal/hr)
Cprey	3163.4	965.3
Dprey	1913.7	1062.8
Aprey	1571.3	1165.1
Bprey	1362.5	1209.9
Boundary of optimal diet		
Fprey	983.3	1160.4
Eprey	605.5	1079.6
Hprey	411.4	984.6
Gprey	193.8	719.1

^a A nondynamic analysis, with all prey at their carrying capacity density (see Table 6).

proach is its ability to accommodate and tell us the consequences of diverse premises about the input parameters.

RESULTS

Single-Prey Systems

Analysis using a single prey type will demonstrate the basic structural properties of the model. Strictly speaking, the one-prey case is not an optimal foraging analysis. With only one prey type our forager has no diet breadth selections to exercise, optimally or otherwise.

The foragers and resource (Cprey) are as described in Tables 6 and 7. The simulation begins with two hunter-gatherers ($N_{j=0} = 2$), and with the prey at its carrying capacity, as if the foraging pair had just migrated into an unharvested range. The initial inclusive NAR in this situation, with Cprey at its densest, is 965.3 kcal/hr (Table 8). For convenience, throughout we will deal with "populations" of only 2 to 12 foragers. Because it is the relative values which matter, the small numbers need not be disconcerting. In fact, if translated to densities, these are appropriate values for the number of hunter-gatherers that would occupy a range of 300 km² (Table 4).

The results of the first simulation are shown in Fig. 3. Initially, foraging NAR (R_j) declines, the human population (N_j) grows, and the prey population (P_c) shrinks. Each variable overshoots slightly and at about year

FIG. 3. Dynamics of a single-prey system, $d_c = 8/\text{km}^2$, $r_c = 0.7$, and $w = 5$ hr (see Table 9).

120 comes to a stable equilibrium at $R = 400.0$ kcal/hr, $N = 4.27$, and $P_c = 1013.7$. At equilibrium the NAR (R_j) is equal to σ , the maintenance rate. This is expected given the form of the feedback terms in Eqs. (8) and (9). Prey density and R_j have declined to the point that net production will maintain the population but not allow it to grow further.

The forager population itself has more than doubled in size (2 to 4.27 individuals) and the prey population decreased by 58% to 1013.7 organisms. The harvest (h_c) at equilibrium is 375 prey, providing 5,175,000 kcal. Of this 60% is used to meet the 2000 kcal/day maintenance requirement and 40% (or 1320 kcal/individual/day) is consumed in the foraging effort. The prey have been exploited to an equilibrium which is below $K/2$, hence less than the maximal sustainable yield (MSY). More precisely, once the system has stabilized, the foragers will receive a sustainable yield which is 89% of the maximal (375/420).

Several observations can be emphasized. First, forager biomass increases as prey biomass declines. The relationship is inverse, nonlinear, and time dependent. Second, the marginal NAR in relation to the maintenance rate is a crucial determinant of system dynamics and equilibrium values. Human population size stabilizes around $R_j = \sigma$. Third, the relationship between the harvest and the MSY is fairly close in this case, but coincidentally so. If the population growth of hunter-gatherers is determined by their marginal and maintenance NAR, it will be fortuitous if they exploit their environment at its MSY.

The effect of foraging time (w). Figure 4 shows a second simulation. The foraging time (w) has been increased to 8 hr, but all other parameters remain the same. As before, the foraging NAR and prey populations decline and the forager population grows, but they do so more rapidly than in the previous case and they overshoot more dramatically. Damped oscillations precede the equilibrium, at which $R = 250$ kcal/hr, $N = 2.83$, and $P_c = 736.1$.

A change in the number of hours (w) spend daily in hunting and gathering alters the structural properties of the forager-prey interaction. This occurs because increasing w reduces the foraging NAR which is required in order to meet maintenance needs. The initial foraging rates ($R = 965.3$ kcal/hr at $j = 0$) are quite high relative to maintenance requirements ($\sigma = 250$ kcal/hr at $w = 8$). Consequently, the feedback term in the foraging population growth equation is strongly positive [$(R_j - \sigma)/\sigma = 2.9$ at $j = 0$]. The net production and initial growth rates are large enough to cause the forager population to overshoot its equilibrium value in year 11 (Fig. 4). Due to overexploitation, prey densities decline so that the marginal NAR falls below maintenance in year 20 ($R_{20} < \sigma$). The forager population begins to decline in size. As the foraging population shrinks, exploitation

FIG. 4. Dynamics of a single-prey system, $d_c = 8/\text{km}^2$, $r_c = 0.7$, and $w = 8$ hr (see Table 9).

diminishes and by year 29 the prey population begins to recover. Each subsequent oscillation is of diminished amplitude.

Equally interesting is the effect of w on the equilibrium size of the human population. As w is increased from 5 to 8 hr, N falls from 4.27 to 2.83 individuals. The longer these hunter-gatherers forage, the fewer of them the environment will sustain. This result might appear odd on first reading, but it is a clear consequence of basic population ecology relationships. More hours foraging entails lower maintenance efficiencies (recall $\sigma = \theta/w$) and a greater potential to deplete prey to the low densities at which they produce small sustainable yields (Fig. 2). Put somewhat differently, the equilibrium density of the prey is determined by the maintenance NAR of the predator, irrespective of the yield of the prey and ultimately the number of predators that can be sustained at the equilibrium.

Table 9 presents the outcome of the simulation for daily foraging times ranging from $w = 2.2$ to $w = 10$ hr. It shows in more detail the effect of w on equilibrium numbers and stability properties of the foragers and their prey. Note the steady fall in P_c and R , and the quick rise and then slow decline in N as w grows (and the maintenance foraging rate, σ , shrinks). Parallel to this trend, system stability steadily diminishes, as overshoot and damped oscillations become more prominent. At $w = 10$, the foraging population initially grows rapidly but in the first downward phase of the

TABLE 9
EFFECT OF VARYING FORAGING TIME ON EQUILIBRIUM VALUES AND DYNAMICS OF A
SINGLE-PREY SYSTEM (CPREY AS IN TABLE 6; FORAGER AS IN TABLE 7)

	$w = 2.2^a$	$w = 2.4^a$	$w = 2.6^a$	$w = 2.8^a$	$w = 3^a$	$w = 4^a$
Gradual growth to stable equilibrium						
N	2.14	3.99	4.88	5.29	5.44	5.00
P_c	2231.8	2016.3	1845.0	1705.4	1589.4	1216.1
R	909.4	833.4	769.2	714.3	666.7	500.0
	$w = 5^b$	$w = 6^b$	$w = 7^b$	$w = 8^b$	$w = 9^b$	$w = 10^b$
Overshoot with damped oscillations						Overshoot and extinction
N	4.27	3.67	3.20	2.83	2.53	0.00
P_c	1013.7	886.7	799.6	736.1	687.8	2400.0
R	400.0	333.3	285.7	250.0	222.2	—

^a Value at $j = 2000$ (at low w the system approaches equilibrium very slowly).

^b Value at $j = 500$.

cycle it drops below 2 ($N_{24} = 1.998$) and becomes extinct. With minor quantitative differences, the same trends occur even if we adjust the maintenance requirements (θ) to allow for the diminished nonforaging energy expenditure that might occur as the number of foraging hours (w) expands.

Intermediate values of effort (w), then, are associated with the largest sustainable human population. Beyond a certain point [quickly reached (at $w = 3$ hr) in the present example] the longer individual foragers hunt and gather the fewer of them the environment will support. The Calvinist forager, it appears, is a lonely forager.

The effects of prey population parameters, K and r . As noted earlier, the sustainable yield of a prey population is a direct function of its carrying capacity (K_i) and intrinsic rate of increase (r_i). Increasing either of these parameters should generate a larger equilibrium foraging population, but in different manners. Elevating K_i increases density and with it foraging NAR. Elevating r_i has no effect on density and NAR but does enlarge the sustainable yield of the prey population at a given density. The following two simulations examine the effects of these parameters.

In the first simulation the Cprey carrying capacity is doubled to $d_c = 16/\text{km}^2$; all other parameters remain the same. For comparison w is manipulated as in the previous cases. Figure 5 and Table 10 present the results.

At $w = 4$ hr (Fig. 5), the foraging population grows quickly, overshoots slightly, and establishes a repeating oscillation. Biologists call this a stable

FIG. 5. Dynamics of a single-prey system, $d_c = 16/\text{km}^2$, $r_c = 0.7$, and $w = 4$ hr (see Table 10).

limit cycle. Foraging NAR and prey population size exhibit the inverse trends. The rapidly expanding human population peaks first in year 47, but reverses its growth in year 48, as R_{48} drops below the maintenance NAR of 500 kcal/hr. Exploitation is reduced sufficiently by year 59 that the prey population begins to recover. By year 67 P_{prey} is sufficiently dense that the foraging NAR rises above 500 kcal/hr and the human population again begins to grow. The period of the full cycle is 48 years; the peaks for the foraging population lag 31 years behind those of the prey and NAR, which are in phase.

The average hunter-gatherer population once the cycles are established (Table 10; $w = 4$ hr) is 6.31; the range is 5.29 to 7.33. As expected, doubling the prey carrying capacity has increased the average forager group size, but the small magnitude of the increase, 26% (5.00 to 6.31 individuals), and the cyclic nature of the equilibrium were unexpected.

Table 10 provides a more detailed portrait of the behavior of the system for $w = 3, 4$, and 5 hr; at $w = 6$ the prey go extinct on the first downward oscillation ($j = 30$). Note that the equilibrium group size again diminishes as w increases, and that the stability of the system diminishes in parallel, moving from damped to stable cycles and then to a crash, but that it does so over a much narrower range of foraging times. Although we have increased the resource density twofold, the foraging group has not grown in size by an equal, nor if we take into account the effect of varying w , by a constant degree (compare Tables 9 and 10). Doubling the prey carrying

TABLE 10
EFFECT OF VARYING PREY DENSITY (d_c) ON EQUILIBRIUM VALUES AND STABILITY OF A
SINGLE-PREY SYSTEM (CPREY AS IN TABLE 6, EXCEPT $d_c = 16/\text{km}^2$; PREDATOR AS IN
TABLE 7)

$w =$		3^a	4^b	5^b
		Damped cycles to equilibrium	Stable limit cycles	
N	Average	8.62	6.31	4.96
	Maximum		7.33	6.25
	Minimum		5.29	3.77
P	Average	1589.3	1429.3	1536.9
	Maximum		2445.4	2641.0
	Minimum		501.2	366.2
R	Average	666.6	562.8	597.3
	Maximum		979.9	1040.8
	Minimum		109.7	22.8

^a Equilibrium value at $j = 1000$.

^b Values derived from last six full cycles of the 400-year simulation.

capacity has increased the average size of the forager population at equilibrium by 58, 26, and 16% for $w = 3, 4$, and 5 hr, respectively.

For a second set of simulations we again set the density of Cprey to $d_c = 8/\text{km}^2$, but now double the intrinsic rate of increase, from $r_c = 0.7$ to 1.4. Table 11 gives the results of this simulation for $w = 3$ to 8 hr; beyond 8 hr the system crashes before completing one cycle. Note that the structural results are as in the other instances of varying foraging time. The equilibrium number of foragers and prey diminishes with more hours devoted to hunting and gathering. In parallel there is a diminishing stability in the relationship between predator and prey. As w grows from 3 to 8 hr, sigmoid growth to equilibrium is replaced by oscillations of greater magnitude and lessened damping. These eventually are replaced by a stable limit cycle.

If we compare Tables 9 and 11, keeping in mind that the only difference between them is a doubling of r_c , we see that the equilibrium foraging population is larger at the higher r_c value, but it is not higher by a proportional or constant amount. With 3 hr of hunting and gathering the foraging group size grows from 5.44 to 10.84 individuals (a 99% increase), but with 8 hr of effort it grows from 2.83 to only 4.64 individuals (a 64% increase). On the other hand, the density of the prey and foraging NAR at equilibrium are the same. This is expected. The human population grows,

TABLE 11
EFFECT OF VARYING PREY INTRINSIC RATE OF INCREASE (r_c) ON EQUILIBRIUM VALUES
AND DYNAMICS OF A SINGLE-PREY SYSTEM (CPREY AS IN TABLE 6, EXCEPT THAT
 $r_c = 1.4$; PREDATOR AS IN TABLE 7)

$w =$		3 ^a	4 ^a	5 ^a	6 ^a	7 ^b	8 ^c
		Gradual growth to equilibrium		Overshoot with damped oscillations		Stable limit cycle	
N	Average	10.84	9.02	7.38	6.20	5.32	4.64
	Maximum						4.86
	Minimum						4.43
P	Average	1589.7	1216.1	1013.7	886.7	799.8	742.8
	Maximum						986.1
	Minimum						515.1
R	Average	666.8	500.0	400.0	333.3	285.8	250.9
	Maximum						385.8
	Minimum						118.4

^a Value at $j = 500$.

^b Value at $j = 1000$.

^c Values derived from last six cycles of 500-year simulation.

expanding its harvest until prey are depleted to the densities at which $R = \sigma$. This key relationship is unaffected by r_i .

It is, however, less clear why the number of foragers departs from the expectation of a twofold increase. Refer to Eq. (7), and note that both P (the number of prey at equilibrium) and K are the same for the simulations represented in Tables 9 and 11. Therefore a change of one of the reciprocal terms (h/r) necessarily means a proportional change of the other. If r doubles so should h , and with it yield and the number of foragers at equilibrium. The solution to this seeming anomaly lies in the way in which prey are "harvested" in the present model. If indeed prey were harvested continuous with their production (each taken only as it was "born," so that the population density itself remained constant), then Eq. (7) would be applicable. However, in this model the harvest is not continuous with production. Instead it periodically depletes the prey population. In this circumstance, we must establish the prey population's capacity to recover from a reduced size. As it evident in Eq. 5, the latter is a function both of r and P .

To summarize, in these as in the earlier simulations, lowering σ (by increasing effort from $w = 3$ hr) reduces the equilibrium sizes of forager and prey population, and reduces their stability. By doubling the carrying capacity of the prey we have shown (a) that the range of foraging efforts

at which the system will persist diminishes, (b) that stable limit cycles are among the dynamic possibilities of the system, and (c) that the equilibrium number of foragers is not increased to an equal or, with respect to changing effort (w), invariant degree. Doubling the intrinsic rate of increase of the prey appears to have little effect on the persistence of the forager and its resources. Again, the equilibrium density of the foraging group does not increase to a proportional degree.

Effect of initial forager and prey population size (N , P). If we exclude values less than 2 or so large that they cause the system immediately to crash, the initial size of the foraging group has no effect on equilibrium values, although it does modify somewhat the trajectory followed by the population in reaching that equilibrium. In a simulation with $r_c = 1.4$ and $w = 6$ (comparable to that shown in Table 11), varying N_o from 2 to 8 produced the same pattern of damped oscillations to an equilibrium at $N = 6.20$. There is a slight tendency for the initial over- (or under-) shoot to be larger as N_o grows. At $N_o = 9$ or 10 the initial harvests are nearly equal to the prey density at carrying capacity and the prey are rapidly and completely depleted in the first 1 or 2 years, before sufficient compensatory adjustment in the forager population can occur.

Similarly, varying the initial prey population has no effect on the equilibrium and very little effect on the trajectory followed in reaching it. In a simulation, with $r_c = 1.4$ and $w = 7$ (again comparable to that depicted in Table 11), the initial prey population was varied from 800 to 2400 ($= P_c$ carrying capacity). The resulting curves for N_j virtually are superimposed; those for P_{cj} are dissimilar only in the first decade. In these first 10 years, predator numbers are small. Prey populations initially set below 2400 grow rapidly toward their carrying capacity. Whatever its starting point, due to its high intrinsic rate of increase the Cprey population trajectory rapidly converges with that which begins at its carrying capacity ($P_c = 2400$).

Two-Prey Systems

In an environment populated with two resource species, Cprey as before and now Eprey (Table 6), we can observe the effects of optimal diet selection on the population dynamics of predator and prey. This will show us how to extend the hypotheses of the diet selection model to incorporate dynamic depletion of resources.

As background, note in Table 8 that Cprey has a pursuit and handling NAR of 3163.4 kcal/hr. If it is the only resource in the diet, it can be harvested with an inclusive NAR of 965.3 kcal/hr when present at its carrying capacity density. By the diet breadth model cited earlier, when

Cprey is most abundant, Eprey (which has a pursuit and handling NAR of 605.5 kcal/hr; see Table 8) will be outside of the optimal diet. Indeed, the forager that harvests both types would suffer a drop in inclusive NAR, to 863.7 kcal/hr. Initially then, before significant depletion of Cprey, the forager will ignore Eprey.

Two prey and the effect of effort (w). This can be seen in Table 12, which shows the results of 10 simulations ($w = 3$ to $w = 12$). Look first at $w = 3$ hr. Foraging for this length of time entails a maintenance NAR of 667 kcal/hr. Although the foraging population grows and Cprey declines in numbers, Eprey remains outside of the equilibrium diet because its return on pursuit and handling time is always below the marginal NAR of foraging for Cprey alone. This result could be predicted by noting that the pursuit and handling NAR of Eprey is below the maintenance NAR of the forager (for $w = 3$ hr). Comparing Tables 9 and 12 at $w = 3$, it is evident that from the forager's perspective Eprey might as well not exist.

At $w = 4$ the situation is different (Fig. 6). As expected, in the early years N increases, both P_c and R decline, and P_e holds steady at its carrying capacity of 3600. In year 83 the NAR of foraging only for the dwindling Cprey has dropped to 605.4 kcal/hr, and Eprey, with a pursuit

TABLE 12
EFFECT OF VARYING EFFORT (w) ON EQUILIBRIUM VALUES AND DYNAMICS OF A
TWO-PREY SYSTEM (CPREY AND EPREY AS IN TABLE 6; FORAGER AS IN TABLE 7)

	$w = 3^a$	$w = 4^b$	$w = 5^b$	$w = 6^b$	$w = 7^b$
	Steady growth to equilibrium		Damped oscillations to equilibrium		
N	5.44	7.07	6.04	5.16	4.48
P_c	1589.4	1134.8	870.6	709.2	600.5
P_e	3600.0	2770.8	2597.6	2491.9	2420.5
R	666.7	500.0	500.0	333.3	285.7
db	1	2	2	2	2
	$w = 8^b$	$w = 9^a$	$w = 10^a$	$w = 11^a$	$w = 12^c$
	Damped oscillations to equilibrium				
N	3.95	3.52	3.18	2.89	2.65
P_c	522.8	463.0	417.2	379.3	349.8
P_e	2370.1	2330.4	2300.6	2277.0	2256.5
R	250.3	222.2	200.2	181.5	166.9
db	2	2	2	2	2

^a Values at $j = 800$.

^b Values at $j = 400$.

^c Values at $j = 1200$.

FIG. 6. Dynamics of a two-prey system, $d_c = 8/\text{km}^2$, $d_e = 12/\text{km}^2$, $r_c = 0.7$, $r_e = 1.2$, and $w = 4$ hr (see Table 12).

and handling NAR of 605.5 kcal/hr, enters the optimal diet. However, immediately thereafter (year 84), the diet breadth returns to 1; only Cprey is now pursued when encountered. There follows a period of vacillating prey selection, in which years of $db = 2$ slowly supplant years of $db = 1$, until, at year 155, diet breadth becomes fixed permanently at 2. By about year 280 the system has reached a stable equilibrium, with 7.07 foragers pursuing both prey types (Table 12; $P_c = 1134.8$, $P_e = 2770.8$, and $R = 500$ kcal/hr).

The period of vacillating diet breadth observed here arises because of the tightly coupled interaction between prey selection and prey density. In years 81 and 82, the harvest of Cprey is 422.8 and 423.1 organisms, respectively. At the end of year 82, 1446.4 Cprey are available for the subsequent interval of foraging. When the diet breadth changes so to include both prey types in year 83, only 290.4 of these Cprey are harvested. Forager requirements in year 83 are met by a mixed diet that includes 722.7 Eprey, which are abundant and thus frequently encountered, pursued, and consumed. Because of the suddenly reduced exploitation, Cprey recovers (at the end of interval 83) to 1564.1 individuals, at which density the NAR of foraging for it alone (656.0 kcal/hr) is high

enough to exclude Eprey from the optimal diet. Subsequently, Cprey again bears the full brunt of the exploitation, and after 4 years it has declined again to numbers at which its marginal NAR is below the pursuit and handling NAR of Eprey. The pattern repeats. As the human group continues to grow (whether one or two prey are in the diet, the inclusive NAR still is above maintenance levels throughout the period of oscillation), so the overall trends persist. Eventually Cprey does not recover sufficient numbers to cause Eprey to be excluded from the diet.

Vacillation of diet breadth is the consequence of encounter-contingent foraging rules with logistic renewal of prey. When a diminishing marginal NAR dictates that a new type be added to the diet, the suddenly reduced exploitation of prey of higher rank causes them to rebound in numbers. This raises the marginal NAR so to exclude the type newly added. In this example, the period of oscillation is transitory although of fairly long duration.

Table 12 elicits further observations. Addition of a second prey type sustains a larger equilibrium population of foragers (compare Tables 9 and 12, for $w \geq 4$), but as before the increase in the equilibrium density of foragers is not proportional to the increase in biomass of prey. Measured in kilocalories at carrying capacity, Eprey adds 30.4% to the resource "biomass," but when it enters the diet it causes the foraging group to grow by closer to 40%. This presumably is due to the relatively high intrinsic rate of increase of Eprey. As before, increasing effort beyond $w = 4$ hr causes the equilibrium population of foragers to shrink.

The system is persistent over a broad range of efforts. However, overshoot and damped cycles become apparent at about $w = 5$, growing in relative magnitude and duration as effort intensifies. At $w = 13$ the system crashes in year 12. A detailed examination of these simulations shows that the initiation of diet breadth vacillation is earlier and its duration briefer as effort (w) grows. By $w = 9$ hr, the diet breadth changes permanently from one to two types in year 6, without vacillating.

We now can formulate the dynamic equivalents of the predictions of the diet breadth model: (1) a prey type is included in the optimal diet whenever the marginal NAR of foraging drops below the pursuit and handling NAR of the type; (2) a growing forager population eventually will incorporate all prey types with a pursuit and handling NAR higher than its maintenance NAR; (3) any prey type with a pursuit and handling NAR lower than the forager's maintenance NAR will be outside of the equilibrium diet; and (4) oscillatory behavior may occur at points of diet change. Of these (1), (3), and (4) were demonstrated above; (2) is a logical consequence of (1) and the fact that the foraging population changes in size until the marginal equals the maintenance NAR. Rule (3) must be qualified because of the possibility of cycles which periodically "pick up" a

prey type ranked below maintenance NAR, whenever R_j dips below maintenance levels.

A Generalized Analysis of the One-Prey System

To this point we have presented results which show how the foraging population responds to input parameters taken one at a time. Insights can be gained from this procedure, but it also is useful to represent these interactions more generally. For instance, we might depict the simultaneous effects of more than one input parameter, or lump parameters into classes which have similar effects. Here we present an instance of the former approach, by analyzing the joint outcome of two parameters likely to be of special interest to economic and ecological anthropologists: w , or foraging effort, and θ , or maintenance energy requirements (see Appendix).

The equilibrium values of N_j for an array of w - θ combinations are shown in Fig. 7. The maintenance energy requirements (θ) range from 250 to 5000 kcal/day and foraging effort (w) ranges from 2 to 12 hr/day. The area bounded by the three-dimensional surface contains the feasible and dynamically persisting solutions. To the left of this region (dashed line margin), σ typically is small relative to the initial foraging efficiency. Overshoot and fluctuations lead to extinction of the foraging group, particularly as the equilibrium density drops toward 2 with increasing effort (w) and lower requirements (θ). To the right (solid line margin) certain combinations are excluded by a more direct constraint—even in the best of circumstances (with C_{prey} at its most abundant, its carrying capacity) the forager cannot harvest energy at a rate greater than 965.3 kcal/hr. Thus, for instance, it cannot meet a maintenance requirement of 3000 kcal in 3 hr of foraging.

Within these boundaries we can view the equilibrium density of the foraging population for any combination of foraging effort and maintenance requirements. This adds considerable realism to the analysis because of the likelihood that w and θ co-vary. Note that the effect of w (with θ held constant) is parabolic and skew toward the higher values of w (except for the lowest values of θ). In fact, the values given in Table 9 lie along the $\theta = 2000$ isocline of this surface. Thus the forager population size at equilibrium has a peak in the lower end of the work effort range. The effect of demand (θ , w held constant) is asymptotic, with the equilibrium density of the foraging group decreasing at an accelerating rate as its requirement for energy grows. The joint result of these parameters is sloping surface, with a gently curved ridge of high equilibrium densities extending from the lowest values of w and θ , roughly to the point at which w equals 7 hr and θ equals 5000 kcal. The consequences of changes in w

FIG. 7. The equilibrium solutions for a one-prey system as a function of foraging effort (w) and maintenance requirements (θ). The three-dimensional surface encompasses the region of values which are both feasible and dynamically persistent (based on C_{prey} ; forager parameters as in Table 7; S was set at 0.5 (θ) when testing the dynamic persistence of the equilibria).

or θ are most dramatic for low values of w . Note also that foragers which increase effort may risk extinction (from fluctuations) unless they also increase maintenance requirements. For instance, if individuals with a maintenance requirement of 1000 kcal increase their foraging effort from 5 to 9 hr they might also have to increase θ in order to remain within the dynamically persistent set of equilibrium outcomes.

Figure 7 reinforces several points made earlier. The highest sustainable densities of foragers generally are associated with intermediate levels of foraging effort and low levels of maintenance demand. The equilibrium density of the foragers responds in a regular but curvilinear manner to changes of the input parameters. The figure emphasizes that the consequence of varying w depends on θ , and vice versa. It is a clear implication of this figure that population ecology relationships cannot be understood by anthropological uses of carrying capacity, if these ignore the economic dimensions of the interaction.

DISCUSSION

Notes before Proceeding

In our descriptions of the model we have tried to state clearly how the mathematical logic can be envisioned in real-world terms and how it simplifies actual processes. Before proceeding with the discussion we will address some additional assumptions. As with some of the limitations discussed earlier, it might be possible in these instances to complicate the model with greater fidelity to reality and its variety. But it also might not be productive to do so, an argument powerfully developed by Starfield and Bleloch (1986). The temptation to complicate a model must be balanced against the heuristic utility of keeping it relatively simple.

(a) To this point we have counted productive, unisex adults exclusively; the model and results have been described in terms of foragers but not a realistic foraging group, which would differentiate the sexes and include dependents, young and old. This nonforaging component of a real hunter-gatherer population can be incorporated in the analysis as currently designed by elevating θ to cover their needs (if we remember to add these dependents to N_j). This would assume that these are dependent, nonreproductive individuals who gain their resources from the net product of the those who do forage and reproduce.

(b) Also, strictly speaking, the model assumes that all nonmaintenance energy production goes into (or if there is a shortfall, comes out of) population growth. This is equivalent to defining maintenance so that it includes all energy consumption except that which correlates with reproduction above or below replacement.

(c) For convenience, we have chosen parameters so that N falls in the range of 2 to 12 individuals, treating small numbers as if they obeyed the laws of large numbers. In the actual world, lone foraging groups of this size would be severely buffeted by stochastic incidents, perhaps overwhelming the envisioned trends. We can circumvent this problem by ignoring it (we are not here concerned with stochasticity) or by increasing the scale of the input parameters by one more more orders of magnitude. For instance, if the foraging area is increased from 300 to 3000 km², the equilibrium number of foragers and prey also is increased by a factor of 10. Again, though, if we keep our focus on the structural consequences of the model (the qualitative aspects of the results and their relative magnitudes) such rescaling has no advantages.

(d) Finally, our "resources" have a decidedly vertebrate cast to them, in their size, density, intrinsic rate of increase (e.g., Table 5), and other features. It will take additional work to determine if invertebrate

and plant foods have unique population properties that must be modeled differently. It is worth noting that plant growth seems to correspond to the logistic model which we have utilized for our "prey" (see Starfield and Bleloch 1986: 124-129).

Analytical Summary

In this model the population growth and food choice of a hunter-gatherer population responds dynamically to prey exploitation and depletion. Analyses based on this system show the population ecology relationship to have a variety of interesting properties:

(1) The dynamic relationship between predator and prey numbers is curvilinear. At equilibrium, multiplying the carrying capacity or intrinsic rate of increase of prey by some factor does not have a commensurate or (if w is varied) a constant effect on the equilibrium size of the foraging group. Neither the dynamic properties nor the equilibrium density of the foraging population can be predicted from knowing only the biomass of prey and the requirements of the foragers.

(2) The dynamic properties of the system include steady growth to stable equilibrium, damped cycles, stable limit cycles, and extinction of either the predator or its prey. Shifts among these possibilities can result from small quantitative changes in factors such as foraging effort and prey density at carrying capacity.

(3) The ecological properties of the interaction between forager and resources are highly sensitive to economic considerations: the magnitude of the nonforaging energy needs (θ) and the duration of the foraging effort (w). This is a consequence of the feedback term in the forager population equations, which makes growth dependent on the relationship between marginal and maintenance NAR. In general it appears that the largest equilibrium foraging group will be generated by low values of θ and intermediate values of w .

(4) If hunter-gatherer population densities are determined by the marginal NAR of foraging, it will be rare for the foragers to harvest prey at the equilibrium density which produces the MSY.

(5) The initial sizes of the forager or prey populations have some effect on the dynamic trajectory of the system, but do not influence the equilibrium outcome, in cases in which there is one.

(6) Analysis of a two-prey system allows us to formulate the dynamic equivalent of the optimal diet model. At equilibrium, the foraging population takes all prey types with a pursuit and handling NAR equal to or greater than their maintenance NAR. Oscillatory behavior often may oc-

cur at points of diet expansion and contraction. Two-prey systems appear to exhibit the same range of dynamic properties as one-prey systems.²

Implications

Two aspects of this model are central to its dynamic behavior: First, prey resource exhibit a logistic population response, and, second, the forager population expands and contracts according to the marginal net productivity of its hunting and gathering. These two features substantiate the claim that the model is more realistic than standard accounts of carrying capacity, which incorporate neither of them. The relationship between forager and prey biomass is time dependent; it is consistent (that is to say, predictably determined by a few key variables) but it is not proportional, linear, or direct. As a consequence, approaches which phrase the forager–resource interaction in terms of stable equilibrium and fixed relationships between forager and prey biomass (reviewed in Glassow 1978:34–36) almost certainly will mislead about the nature of their interaction. This point is emphasized in the subsequent discussion.

Ethnography, archaeology, and modeling. Hunter–gatherer analyses using foraging theory have stressed its heuristic value (e.g., Winterhalder 1987). The present study highlights an additional benefit: the combination of foraging theory and population biology models gives access to problem realms otherwise hidden both to ethnography and archaeology. The time scale of this model and that of population ecology processes generally, that is tens to hundreds of years, rests in a rather large analytical gap between the long year of hunter–gatherer ethnography and the short millennia of prehistoric archaeology. The model, its properties, and its dynamic behavior have implications important to both kinds of study which are for the most part empirically invisible to both.

The invisibility has consequences. For instance, depending on the draw, a randomly sampled year from a hunter–gatherer population like that of Fig. 5 could compel the analyst to any one of several dissimilar conclusions, all of them quite likely wrong. One or even several isolated sample points from these population curves simply will not add up to valid generalizations about their properties or causes. The problem is exacerbated if we recall that density-independent factors also are affecting actual study populations. Anthropologists must reevaluate the common practice of using ethnographic samples from one point in time as the basis for elaborate inferences about forager population ecology.

From the longer end of the time scale, because the temporal resolution

² A future publication will extend the analysis to the full set of prey and to additional issues, such as extinction of prey by a foraging population.

of the data is low, the "archaeological filter" (Thomas 1986:256) will tend to smooth out the dynamic qualities of human population ecology. Causation may be elusive or misconstrued just as surely as in the ethnographic example. Are periodically abandoned camps to be explained by migrations or by population fluctuations? Are changes in subsistence remains to be explained by seasonal availability or by diet breadth oscillation? Archaeological data itself may not provide the answer, but it may be misinterpreted if the analyst is unaware of the range of possibilities predicted by evolutionary ecology.

Evolutionary ecology models give us access to questions which ethnography and archaeology alone cannot address.

Beyond carrying capacity. The concepts of carrying capacity and population pressure dominate discussions of human sociocultural and technological development, from hunter-gatherers through the origins of agriculture and the state. Advocates of this approach (and occasionally its critics) generally have accepted several simple propositions: (i) the relevant variables are those of quantity (biomass of resources, size of the human population); (ii) the basic relationship between them is direct and linear (the supportable human population is a constant function of the biomass of exploitable resources); and (iii) there is no feedback between the human population and their resources, unless "carrying capacity" is exceeded and the resource base is damaged or destroyed. All of these seemingly are reasonable premises, but none of them can be sustained if one adopts a dynamic perspective on the interaction between humans and their resources.

In a dynamic view the definition of carrying capacity that has been used in anthropology becomes ambiguous. Anthropologists generally have adopted the K of Fig. 1, interpreting it not as the point at which growth stops but as a constant quantity of available resources. This assigns logistic growth to the forager but denies it to the prey. Once a dynamic interaction is admitted, it no longer is clear how we would define or measure such a quantity, nor what would be the purpose in doing so. Is it the prey carrying capacity in the absence of exploitation? Is it the equilibrium density of the prey? And, if so, how will we allow for factors such as foraging effort in determining the equilibrium? If the system is a damped or stable cycle what are we to measure? Even if we could make a context-specific resolution of these measurement problems, what would we learn? The interesting properties of the dynamic relationship arise from other factors. Extant anthropological concepts of carrying capacity give causal priority to biomass variables that at best are secondary to the dynamic interactions between hunter-gatherers and their resources.

Or, consider a definition which leaves out explicit reference to prey biomass: Carrying-capacity "refers to the upper limit of human popula-

tion growth that can be achieved in a given habitat without eventual degradation of the resource base" (Hayden 1981: 412). This appears to avoid the problems mentioned in the previous paragraph. But it entangles us in a new one: the definition of "degradation." At what point in the depletion of the prey resource does it become degraded? The problem with this definition is like that of the previous paragraph, it is nondynamic. Definitions which refer to a "homeostatic equilibrium point" or which require that resources not be "depleted" (reviewed in Glassow 1978: 33) have similar problems.

Hunter-gatherer population ecology. The revisions implied by these statements touch on several views fundamental to recent characterizations of hunting and gathering economies. We offer several brief examples; all will require elaboration as the behavior and implications of the system are better understood.

Anthropological studies offer few generalities more often repeated and analytically suggestive than the observation that hunter-gatherers "live below the carrying capacity of their environment." But to phrase the point this way surely is to misconstrue it. Forager and prey biomass are interdependent. There is a variety of dynamic possibilities inherent in this relationship. These possibilities are inseparable from economic factors such as foraging effort and maintenance energy demand. Carrying capacity as required by the cited observation—incomplete exploitation by a stable biomass of humans of a fixed and independent biomass of resources—does not exist for predator and prey. Whatever analytical insights may be lurking behind this generality and the ethnographic experience it is meant to summarize, they are not captured nor will they be understood by means of standard anthropological uses of the carrying capacity concept.

The conceptual problem is matched by an empirical one. This is a case in which a few sample points of short duration have been used to make inferences about long-term processes that they alone cannot illuminate. Some healthy skepticism about the empirical basis of the generality is in order.

Similarly influential in recent analyses of hunter-gatherers is the related observation that foragers live a life of "original affluence," working short hours at a productive rate to achieve a comfortable subsistence intake. As formulated by Sahlins (1972), this observation implied that hunter-gatherer economies escape constraints of environmental scarcity and ecological causation; moreover, they fall beyond the reach of the rationality and optimizing postulates that guide formal(ist) economic or ecological modes. Foragers, it is said, live in a "Zen" economy. But we can accept the observation and still reject the methodological and other conclusions associated with it.

The observation—low demand and limited hours of subsistence effort at a productive rate—can more economically be explained by evolutionary ecology models which incorporate all of the assumption Sahlins would have us reject. It seems that central to the foraging mode of production is this ecological reality: acting separately or together, long hours and greater than modest consumption deplete and destabilize a foraging population. The effect is abrupt, as relatively small changes in effort or demand can make the difference between a system that is replete and one that is depauperate (Fig. 7). The “Zen” economy has an ecological master.

This leads to a comment on intensification and socioeconomic development. Boserup (1965) has argued that population growth drives agricultural development. As the density of early agriculturalists increased, so did effort. While per capita production declined, aggregate production increased, fueling further population growth and more agricultural “intensification.” In contrast, similar intensification of hunting and gathering (by increasing effort, w) is impeded by the logistic yield response of the forager’s resources. For the forager, increasing effort lowers individual NAR, as is postulated by Boserup’s model. But unlike the case of food production, longer foraging also quickly diminishes total yield, reducing the sustainable human population of a region. This may mark a fundamental difference between foraging and agricultural production systems, one with significance for their quite dissimilar developmental rates and histories.

Finally, we note that this model encompasses variables expressed at both the individual (e.g., foraging effort, NAR) and population level (e.g., forager population density, stability). This combination raises difficult evolutionary issues: What variables in this system are most directly subject to natural or cultural selection? How will these evolutionary pressures express themselves at the level of the system? It is not self-evident, for instance, just which of the equilibria represented in Fig. 7 will result in particular circumstances. A brief example will evince one possibility, which we might call the route to original poverty. We leave further discussion to the future.

Envision a forager that migrates with a small group into a new range. The individual initially gets a high rate of return and can do well even with a limited effort of 4 hr. Time passes. Prey are depleted. NAR falls. Diet breadth expands. Some years later, while reminiscing, the forager may observe that the group expanded rapidly in size in the past, but recently has ceased to grow. Note that so far our scenario just traces the individual’s experience of a dynamic like that shown in Fig. 6.

Now, imagine a change in this scenario which links the individual’s behavior and experience to population-level consequences. Noticing the

decline in NAR, our new immigrant compensates by increasing his or her initially modest foraging effort ($w = 4$ hr) to 5 or more hours. This changes the equilibrium conditions for the *populations* of foragers and prey (shifting our attention from Fig. 6 to Table 12), with the long-term result that the system will sustain fewer of each. The individual forager experiences the population consequences of this action only indirectly. But he or she may directly feel the new decline in NAR (as prey are now depleted to yet lower levels) and may again increase foraging effort. The effect is reinforcing, so that without some countervailing pressure, very soon we have the lonely, impoverished, and hard-working Calvinist mentioned earlier.

In his review article, Glassow notes that "the concept of carrying capacity has come to be one of the foundation stones of modern cultural ecology. . . ." (1978: 31). But, as the foundation has here shifted (at least for studies of foragers), it is time to look to a remodeling of the walls and roof. Enough has been said to suggest the direction of that effort and to raise fair optimism about its promise. Analysis of ecological causation by means of biomass-to-biomass relationships strayed rather too far from the structural context of population-resource processes. The pertinent issues simultaneously are ecological *and* economic (as suggested by Glassow), requiring that we match more detailed structural analyses of ecological components (e.g., logistic prey responses, diet selection) to economically laden concepts such as marginal and maintenance NAR. The latter linkage may be especially revealing, as it puts resource consumption, with all of its socioeconomic implications, into the causal center of the population-ecology relationship.

CONCLUSIONS

Evolutionary ecology models fulfill their potential when they help us to discover and understand in detail the consequences of our assumptions, and when they suggest new avenues of inquiry. Although the present model departs from the same logistic equation that has inspired the carrying capacity literature, it has shown the population-ecology relationship to have properties quite beyond and different from those developed in that literature. These novel properties arise from features of the model which enhance its realism relative to extant interpretations. The foraging population grows or declines as a function of the net marginal product of hunting and gathering, diet selection is sensitive to the changing densities of the resources being harvested, and the prey respond logistically to their exploitation. By giving attention to the structural context of the hunter-gatherer food quest, the model begins to chart the interaction of processes that are simultaneously microecological and microeconomic.

APPENDIX: EQUILIBRIUM CONDITIONS FOR THE ONE-PREY CASE

At equilibrium, the foraging efficiency or net acquisition rate (R) equals the maintenance foraging efficiency (σ):

$$R = \sigma = \frac{\theta}{w}. \quad (1)$$

In general, R_j , the foraging efficiency at time j , equals

$$R_j = \frac{\sum f_{ij} e_i - S_c T_s}{\sum f_{ij} t_i + T_s}, \quad (2)$$

where f_{ij} = proportion on prey i in diet at time j ; e_i = net energy value of prey i (kcal); t_i = time to pursue and handle prey i (hr), S_c = energy cost of searching for prey (kcal/hr); and T_s = average search time between prey encounters (hr).

$$T_s = \frac{1}{\sum d_i s_v 2s_r}, \quad (3)$$

where d_i = density per square kilometer of prey i ; s_v = forager search speed (km/hr); and s_r = forager search radius (km).

At equilibrium, Eq. (2) reduces to

$$R_j = \sigma = \frac{e_i - s_c T_s}{t_i + T_s}. \quad (4)$$

Substituting Eq. (3) for T_s into Eq. (4) and solving for d_i gives the equilibrium prey density (d):

$$d_i = \frac{\sigma + S_c}{s_v 2s_r [e_i - \sigma(t_i)]}. \quad (5)$$

The equilibrium prey population (P) is simply the product of the equilibrium prey density and the forager's range (A_c):

$$P = A_c d. \quad (6)$$

Determining the equilibrium harvest rate (h) is a matter of recognizing that at equilibrium prey population size does not change, i.e., $P = P_{t+1} = P_t$, and also that, mechanistically, the model harvests from population P_t and then increments growth to population P_{t+1} . Substituting P for P_t and P_{t+1} gives

$$P = (P - h) \frac{Ke^r}{K - [(P - h)(1 - e^r)]}, \quad (7)$$

where K = prey carrying capacity and r = prey intrinsic rate of increase. Solving for h gives

$$h = \frac{P \times [(Ke^r + P - Pe^r) - K]}{(Ke^r + P - Pe^r)}. \quad (8)$$

Since harvest rate is governed by the function

$$h = \frac{N \times w \times 365}{T_s + t_i}, \quad (9)$$

it is a simple matter to solve for the equilibrium forager population size (N),

$$N = \frac{h \times (T_s + t_i)}{365w}, \quad (10)$$

where

$$T_s = \frac{1}{ds_v 2s_r}.$$

Note that these equations determine the feasible equilibrium values, without establishing which are also dynamically persistent. Experiments with the dynamic model can be used to establish the boundaries around the latter. The three-dimensional graph was prepared using Surfer software.

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