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Journal

Conservation Biology, 11(6)

ISSN

0888-8892

Authors

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Publication Date

1997-12-01

DOI

10.1046/j.1523-1739.1997.95184.x

Peer reviewed

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Conservation Biology, Vol. 11, No. 6 (Dec., 1997), 1354-1364.

Stable URL:

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A Forager-Resource Population Ecology Model and Implications for Indigenous Conservation

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Abstract: *Population ecology and foraging theory can be combined to simulate the population dynamics of hunter-gatherers and their prey resources. Such simulation study is important to issues of conservation because many of the population processes that link human foragers and their prey occur over time scales that elude both ethnographic and archaeological fieldwork. To demonstrate, we used the model to examine hunter-gatherer population dynamics. We focused on a prey characteristic that affects its susceptibility to over-exploitation: the intrinsic rate of increase, r . We found that forager-prey systems can stabilize without intentional conservation behavior and that prey "switching," fall-back foods, and in certain circumstances, a higher r contribute to resource species persistence. Furthermore, a prey's vulnerability to local depletion or extinction may depend on the demographic characteristics of the suite of resources harvested along with it. The model can serve as a "null hypothesis" for examining intentional resource conservation and presents points in concordance with, as well as divergent from, tenets in conservation biology. In particular, we discuss the implications of these findings for indigenous resource conservation in Amazonia (e.g., the overhunting of large primates and avifauna and the adoption of new procurement technologies) as well as the "Pleistocene Overkill Hypothesis."*

Modelo de Ecología Poblacional Forraje-Recurso y sus Implicaciones en la Conservación Local

Resumen: *La ecología de poblaciones y la teoría de forraje se puede combinar para investigar la dinámica poblacional entre cazadores-recolectores y sus especies de presa. Este tipo de investigación basada en el uso de simulaciones por computadora es importante para el tema de la conservación del medio, puesto que muchos de los procesos poblacionales entre cazadores-recolectores y sus presas ocurren a una escala temporal que elude tanto a la etnografía como a la arqueología. Como demostración, usamos este modelo para examinar la dinámica poblacional de cazadores-recolectores. Nos concentramos en una característica de las presas que afecta su susceptibilidad de sobre-explotación: el ritmo intrínseco de crecimiento, r . Comprobamos que el sistema de cazador-recolector puede estabilizarse sin una conducta deliberada de conservación y que cambios de presa, comida de emergencia y algunas veces, un valor de r mayor, contribuyen a la persistencia de especies. La vulnerabilidad de una presa al decremento local o extinción puede depender de las características demográficas de las especies que están siendo recolectadas junto con la presa. Este modelo se puede usar como una "hipótesis nula" para una investigación sobre la conservación intensional de recursos y presenta puntos tanto en concordancia como de divergencia con principios de la biología de la conservación. En particular discutimos las consecuencias de este modelo para la conservación de recursos locales en la Amazonía (i.e., la sobre-explotación de primates grandes y avifauna y la adopción de nuevas tecnologías) así como la "Hipótesis de la Mortandad Masiva del Pleistoceno."*

Paper submitted March 2, 1995; revised manuscript accepted January 31, 1997.

Introduction

Recent debates about the extent to which indigenous peoples are conservationists have focused on the people's knowledge of local ecology and their beliefs about the management of resources (Usher 1987; Callicott 1989; Redford 1990; Cox & Elmqvist 1991; Bennett 1992; Alcorn 1993; Gadgil et al. 1993; Holdgate & Munro 1993; Redford & Stearman 1993a, 1993b; Robinson 1993; Peres 1994). We shift the perspective to questions of behavior. We ask how individual-level foraging tactics and success affect population dynamics and, especially, the long-term stability and survival of hunter-gatherers, and the resource populations on which they depend. Although some of our specific results will be familiar to population ecologists, some are novel and all have the advantage that they arise from an encompassing analytical framework that can be applied to important practical problems in conservation biology.

Our objectives are several. We describe a simulation model based in optimal foraging theory and population ecology. We use that model to ask how characteristics of individual foraging tactics and resource populations might make particular species susceptible to over-exploitation and local depletion or extinction (as defined by Redford 1992). We end with the contention that evolutionary ecology models—informed with case-specific data—offer important insights on past and present foraging behavior. They serve as a necessary complement to analyses of ecological knowledge and beliefs. We hope to demonstrate that because foraging models lie at the juncture of economic and ecological analysis, they will be an essential component of any prescriptive scenario that envisions resource management for sustained harvest by a future analog of hunter-gatherers.

Computer Modeling of Foraging Behavior

Regrettably, there is virtually no long-term empirical record of the population dynamics of human foragers and their prey, *prey* being defined for our purposes as any animal, plant, or insect resource utilized for human subsistence. Multi-year, quantitative data on human demographic variables have seldom been recorded by anthropologists; similar information on the harvest of prey species and their population properties is virtually absent from ethnographic monographs. Further, it is not clear that standard anthropological or archaeological methods could have provided such information. Ethnography seldom is quantitative on the issues of our concern and it embraces a time period too short for the interpretation of population dynamics. By contrast, due to its low quantitative resolution, the archaeological record cannot provide sufficient detail.

Simulation modeling that incorporates foraging theory and population biology offers an alternative approach to this problem. Simplified models as a research strategy for the investigation of admittedly complex problems have much to recommend them (Foley 1985; Richerson & Boyd 1987). They are an important basis of resource management (e.g., Starfield & Bleloch 1986; Sutherland 1996; Belovsky et al. 1994; but see Hall 1988). To our knowledge only two other papers (Fryxell & Lundberg 1994; Gleeson & Wilson 1986) have explored the population dynamics of adaptive diet selection by a predator faced with more than one type of resource.

What then is the minimal set of elements that will meet our objective: examination of hunter-gatherer resource use from the perspective of population ecology and conservation? First, we must characterize the population dynamics of each of the prey species. Functionally, this component of the simulation must tell us how well each of these species can recover from exploitation of varying intensities. To do this, we adopt the logistic equation of population growth (Emlen 1973).

Second, we must supply our human population with a tactic for selecting which of these resources they will choose to harvest. It also must describe the resulting parameters of the food quest (e.g., foraging efficiency among others). We use the encounter-contingent foraging model (Schoener 1974; Stephens & Krebs 1986), which analyzes the choice of a forager that has just discovered evidence of a particular prey and must decide to harvest (pursue and handle) this resource item or continue searching in hopes of locating and securing something more profitable. The forager includes ranked resource types in its optimal diet in descending order until the next ranked item returns less net energy during pursuit and handling than would be gained by ignoring it. More complicated predictions arise if prey distributions in time and space preclude the simultaneous search (Belovsky et al. 1989). An important feature of this model is that the ranking or profitability of an encountered resource type is independent of its encounter rate (usually approximated as its density). This diet breadth model has been successful in characterizing hunter-gatherer choices in most of the cases in which it has been applied (Winterhalder 1983b; Smith 1991; Kaplan & Hill 1992; Alvard 1994).

Third, we must characterize the population dynamics of the human foraging group. This component depicts how we expect the hunter-gatherer population to grow or decline in size as a function of the effectiveness with which it harvests food. We adopt a variant of the logistic equation: the human population experiences positive or negative growth rates in proportion to the degree that its foraging efficiency exceeds or falls short of a "maintenance" rate (set by a daily maintenance requirement, divided by the number of hours available for daily hunting and gathering).

Functionally, then, prey densities are determined by their population response to exploitation in the previous foraging interval; diet choice is determined by the ranking and densities of the resource species; human population growth is determined by the efficiency of foraging; and, to complete one iteration of the simulation cycle, the size of the human population determines how intensively it exploits the resources it has chosen to harvest, and subsequently its initial density in the next round of the simulation (details in Winterhalder et al. 1988).

Simulation Results

We assign values to the prey species (Table 1) and to the forager population (Table 2) which are scaled to be realistic for human foragers and an array of four prey types representing an uncommon, medium-sized ungulate (APREY) to a smaller but high density fruit, tuber, or vertebrate (GPREY). There are two intermediate-sized prey types (CPREY, EPREY), also differentiated by caloric value and other properties (Table 1; labels are consistent with Winterhalder et al. 1988). A simple diet choice analysis (without any consideration of resource depletion or forager population dynamics) is depicted in Table 3. At the assigned resource densities, the foragers' diet will include CPREY and APREY and generate a net acquisition rate (NAR) of 1098.2 kcal/hour. Because it returns only 605.5 kcal/hour for pursuit and handling, EPREY will be ignored. Were EPREY to be pursued and harvested on encounter, overall foraging efficiency would decline to 982.5 kcal/hour.

One Prey Type

The basic properties of the dynamic simulation can be seen in Fig. 1. We populate a pristine home range of 300 km² with two foragers (0.67/100 km²), as if a migrant pair were encountering for the first time an unexploited

Table 2. Forager population parameters.

Characteristic	Value	Units
Speed	0.5	km/hour
Search radius	0.0175	km
Search cost	4.0	kcal/min
Home range	300.0	km ²
Intrinsic rate of increase	0.02	—
Maintenance requirement	2000.0	kcal/day
Critical threshold	1000.0	kcal/day
Time spent foraging	5.0	hours/day

habitat. The single resource species, CPREY, begins at its carrying capacity of 8/km².

With an abundant prey species, the foragers' initial NAR (965.3 kcal/hour) is well above their maintenance rate and the human population grows. As it grows, exploitation pressures increase and CPREY population densities decline as harvests exceed their logistic recovery potential. Foraging efficiency also drops as search costs to locate CPREY individuals increase. The system comes to a stable equilibrium as the NAR approaches the maintenance rate of 400 kcal/hour. The foragers have depleted CPREY to a point that the efficiency of the food quest only allows for individual replacement. The forager population stabilizes at 4.27 (1.42/100 km²); CPREY equilibrates at 1014 (3.38/km²; Table 4, no. 1).

Even this very simple system affords us observations of interest to questions of hunter-gatherers and conservation. First, under conditions of encounter-contingent foraging, the equilibrium harvest will rarely fall at the maximum sustained yield (MSY) for a resource species. In this case, for instance, the resource has been exploited to a level at which the foragers obtain 89% of the MSY (Winterhalder et al. 1988). Simultaneous MSY for all prey would be rarer yet should the harvest include multiple species. Secondly, this simulation shows how forager-prey systems can stabilize without intentional conservation behavior, given density-dependent feedback between foraging efficiencies and population growth. Stability itself cannot be taken as evidence either for conservation or against self-interested (optimizing) hunting and gathering.

Table 1. Value assigned to resource population parameters.

Resource type ^a	Value ^b	Time ^c	Cost ^d	Carrying capacity ^e	Rate of increase ^f
APREY	60000	1864	6	0.8	0.5
CPREY	13800	235	6	8.0	0.7
EPREY	2800	174	6	12.0	1.2
GPREY	240	26	6	300.0	2.0

^aAPREY, uncommon, medium-sized ungulate; CPREY and EPREY, two intermediate-sized prey types differentiated by caloric value and other properties; GPREY, high-density fruit, tuber, or vertebrate.

^bValue of resource type *i* (kcal).

^cTime required to pursue and capture *i* (minutes).

^dCost in energy of pursuit and capture of resource type *i* (kcal/minute).

^eCarrying capacity density of *i* (no./km²) in absence of exploitation.

^fIntrinsic rate of increase of resource *i*.

Table 3. Deterministic diet breadth analysis without resource depletion.

Resource type ^a	Resource ranking (pursuit & handling) (kcal/hour)	Foraging NAR (kcal/hour) ^b
CPREY	3163.4	965.3
APREY	1571.3	1098.2
boundary of optimal diet		
EPREY	605.5	982.5
GPREY	193.8	613.9

^aSee Table 1 for definitions of resource types.

^bNAR is net acquisition rate.

Figure 1. Human foragers' net acquisition rate of energy (NAR) in one-species simulation (A) and population sizes for human foragers and prey in the one-species (CPREY) simulation, showing smooth growth to equilibrium (B). Symbols are placed every 50th iteration and CPREY's population size was converted to place both populations on a similar scale. See Table 1 for explanation of prey types.

Addition of Second Prey Type

The addition of a second prey species, EPREY, increases the system's realism and complexity and produces a novel result (Fig. 2). The EPREY has a pursuit and handling efficiency (605 kcal/hour) which is below the initial efficiency with which the forager can harvest CPREY (965.3 kcal/hour) but above the maintenance rate (set in this simulation at 500 kcal/hour). Thus EPREY initially is outside of the optimal diet. However, as the forager population grows in size and the population of CPREY diminishes, the marginal foraging efficiency eventually drops to the point that it becomes profitable to begin harvesting EPREY whenever it is encountered. The subsequent behavior of the system is novel: within a few iterations of being added, EPREY is dropped from the diet only to return after several more iterations. This pattern of switching between a diet breadth of one and two items begins at iteration 38 and repeats nine times before EPREY enters the diet permanently and the system again approaches a stable equilibrium (at 7.07 foragers, or 2.36/100 km²; Table 4, no. 2).

Diet breadth switching has a simple explanation. Immediately prior to the addition of EPREY, CPREY is providing virtually all of the foragers' food and is absorbing the full impact of their exploitation. As a consequence it is depleted to the low population densities which give it only a modest logistic recovery potential. The small increase in the hunter-gatherer population and the mar-

Figure 2. Human foragers' net acquisition rate of energy (NAR) in two-species simulation (A) and two-species (CPREY & EPREY) simulation, demonstrating smooth growth with switching (B). See Table 1 for explanation of prey type.

ginal decline in NAR that bring EPREY into the diet cause an abrupt shift in the composition of the harvest. Exploitation suddenly is apportioned among the two species (in a ratio proportional to their relative encounter rates). Released from heavy cropping, CPREY quickly recovers in density, soon raising the NAR of foraging for it alone sufficiently so that EPREY is dropped from the diet. Diet breadth switching lasts for 24 simulation iterations against the continuing trend of declining NAR and resource densities.

Under conditions of encounter-contingent foraging, each resource added to the diet may induce diet breadth switching. Switching will at least temporarily buffer higher ranked resources from excessive depletion. If such switching is a general phenomenon and is prolonged in real foraging systems, it may constitute an important source of protection for high ranking resource species.

Generally, this result suggests a means of studying how and to what degree adding species to the optimal set might affect the impact of foraging on those resources already being sought. In a conservation setting such a result might be accomplished by artificially elevating the rank of marginally unprofitable prey types, for example, by subsidizing their harvest.

Resource Vulnerability

Using this model, we can investigate how forager tactics and prey population characteristics affect the probability of resource over-exploitation, localized depletion, and ecological extinction. We focus on r , the intrinsic

Table 4. Summary of simulation results at equilibrium or end of simulation iterations.^a

Identification	Forager population	Net acquisition rate (NAR)	Resource population ^b
1. One-resource ^c	4.27	400	CPREY = 1014
2. Two-resource ^d	7.07	500	CPREY = 1135 EPREY = 2771
3. Four-resource ^e	6.04	400	CPREY = 870 APREY = 0 (extinct) EPREY = 2598 GPRESY = 90000
4. 2x APREY r^f	7.26	398	CPREY = 457 APREY = 127 EPREY = 2343 GPRESY = 90000
5. 2x CPREY r^g	7.48	357	CPREY = 968 APREY = 0 EPREY = 536 GPRESY = 90000
6. Delete GPRESY ^h	0.0	0.0	CPREY = 2400 APREY = 240 EPREY = 3600

^aDescription, by experimental run (parameters as in Tables 1 and 2, unless specifically noted otherwise).

^bSee Table 1 for definitions of resource (type) population.

^cSee Fig. 1.

^dSee Fig. 2.

^eSee Fig. 3.

^fWill the increase of APREY's r from 0.5 to 1.0 buffer it from extinction, all other conditions as in simulation 3? Answer: Yes, elevating the intrinsic rate of increase allows APREY to persist. System undergoes damped oscillations.

^gSee Fig. 4.

^hIs the intermittent harvest of GPRESY in simulation 5 buffering the system from greater instability? Answer: Yes. Removal of GPRESY causes forager population extinction at iteration 73; all resource species survive. GPRESY served in simulation 5 as a below-maintenance efficiency, "fall-back" food.

rate of increase, because it is an important and much analyzed variable in the conservation biology literature (e.g., Pimm et al. 1988; Laurance 1991; Pimm 1991; but see Belovsky et al. 1994). Robinson (1993) draws attention to "density compensation," the degree to which a species responds to a decline in density by increasing its achieved rate of increase (recruitment or recovery potential). Higher r entails greater degrees of density compensation.

A Multi-Species Simulation

In the third simulation we add all four resource species (Fig. 3). The CPREY and APREY comprise the initial diet; EPREY enters at iteration 39, producing a short bout of diet breadth switching. The APREY declines quickly to about 10 individuals by iteration 86, and then persists at very low levels (in effect, ecological extinction) before going locally extinct at iteration 273. After damped oscillations, the system stabilizes with 6.04 foragers (2.01/100 km²; Table 4, no. 3). The extirpation of APREY indicates that multi-species simulations can result in at least one resource being over-exploited. Our experience with this model suggests that this is not uncommon.

Persistence as a Function of a Species's r

The fourth simulation shows the effects of a resource's intrinsic rate of increase on its persistence under foraging pressure. All parameters are the same as in the previous simulation, except that we double APREY's r (from 0.5 to 1.0) to see if we can induce its persistence (Table 4, no. 4). Following damped oscillations, the system equilibrates at 7.26 foragers (2.42/100 km²). No resource species goes extinct. Other factors being equal, a high r confers protection on a prey species. From a conservation perspective, we should worry most about high profitability resources (those most likely to be harvested) with a low r .

Persistence as a Function of Co-Harvested Species's r

The comparative baseline for this analysis is the fourth simulation, in which APREY has an r equal to 1.0 and all resource species survive forager exploitation. In this case we look for effects among prey species by doubling the r of the top ranked resource, CPREY (from 0.7 to 1.4). Although increasing the r of a species may confer protection on it (that is, a high r species may be less vul-

Figure 3. Human foragers' net acquisition rate of energy (NAR) in four-species simulation (A) and four species run (B); (EPREY enters the diet at iteration 39, as the foraging NAR has dropped to 590.2 kcal/hour below GPREY's pursuit and handling rate of 605.5 kcal/hour; APREY goes extinct at iteration 273 [indicated by the arrow] after a long period of very slow decline in equilibrium density [it has the lowest r of all resources]). System demonstrates damped oscillations. See Table 1 for explanation of prey types.

nerable to extinction), a high r resource may put co-harvested species at risk by encouraging rapid forager population growth and higher forager densities.

The outcome is shown in Fig. 4 (Table 4, no. 5). It is a complex pattern of switching and cycles. The human population grows rapidly and EPREY enters the diet at iteration 53. Foraging efficiency drops below the maintenance requirement of 400 kcal/hour at iteration 70 and the human population begins to decline. Because of overshoot, NAR declines to 170.7 kcal/hour at iteration 72 and GPREY enters the diet. GPREY buffers the declining fortunes of the foragers, but it cannot help APREY, which goes extinct at iteration 78. We find this kind of system may be prone to damped or stable limit cycles in combination with diet breadth switching and that a high r species within the harvested set may put other resources at risk, especially those with relatively low r .

A Fall-Back Resource

Figure 4 suggests that GPREY may be buffering forager-resource instabilities. Because it is ranked below the maintenance foraging efficiency, GPREY is ignored in most circumstances, despite its abundance (high K) and high r . It enters the diet only when an overshoot of the human population produces rapid depletion of higher ranked resource types, causing foraging efficiency to

Figure 4. Human foragers' net acquisition rate of energy (NAR) in a four-species simulation, where CPREY (the top-ranked resource, see Table 3) has its intrinsic rate of increase doubled from 0.7 to 1.5 (A). Doubling CPREY's r causes APREY to go extinct at iteration 78 (indicated by the arrow), showing that a high r in a harvested species will support a larger human population and may put other harvested prey species at risk of extinction (B). System shows complex switching and oscillations. See Table 1 for explanation of prey types.

plunge. The GPREY appears to reverse the precipitous descent of the NAR, prompting us to wonder: What would happen if GPREY were not available? In this instance we replicate the parameter conditions of the previous simulation but eliminate GPREY from the environment.

EPREY enters the diet at iteration 53, and briefly buffers a rapidly declining NAR. Human population growth and resource depletion continue until iteration 70, when the NAR drops below 400 kcal/hour. The forager population begins to shrink, but not so quickly as to reverse its over-harvesting of the resource species. By iteration 73, the NAR has dropped below 0 kcal/hour and the human population has died out (Table 4, no. 6). All three resource species recover to their carrying capacity levels.

A high density, high r species that normally is marginally outside of the equilibrium diet (because it has a pursuit and handling efficiency somewhat less than the forager's maintenance rate) may modulate system fluctuations and thus act to stabilize relationships between foragers and resources. This is the simulated equivalent of "fall-back" foods. Parallel to this observation, Gleeson and Wilson (1986) and Fryxell and Lundberg (1994) both found that prey types with profitabilities below the "break even" point for the predator conferred local stability on predator-prey systems with optimal diet choice.

Discussion

Although we write in terms of human foragers and their prey resources, the model we have illustrated is general with respect to species. Consequently, the results should be applicable to any forager-resource system characterized by encounter-contingent food selection and logistic population growth. Our simulation improves on the realism of the standard Lotka-Volterra equations by allowing for a predator with multiple prey and for diet choice which changes dynamically as a function of prey densities. Thus, we can observe indirect interactions among prey that happen to share a common predator.

Constraints that may limit the model's general applicability are equally important. The results presented focus on direct human predation and on the effect of varying the intrinsic rate of increase for the resource species. We thus deal with depletion rather than interference competition or habitat depression (Charnov et al. 1976), noting with Sutherland (1996:176) that "it [depletion] is theoretically less elegant than interference but may well be of much greater importance" to density dependent population processes. The dynamic model also does not encompass indirect human effects such as habitat modification (although these could be approximated by experimentally repeating simulations with differing prey densities). Perhaps more importantly, encounter-contingent prey selection ignores habitat patchiness, including the possibility of refuge areas from which prey can escape predation and restock the harvested range (Joshi & Gadgil 1991; for a comprehensive review see Sutherland 1996). Other evolutionary ecology models (e.g., the patch-choice model and marginal value theorem) make predictions different from those examined here (Smith 1983; Winterhalder 1983b) and should be part of a more comprehensive analysis of foraging and conservation.

Resource Use in Amazonia

Examples of the model's applicability to elucidating patterns of human forager-prey dynamics are found in the literature about Amazonia, the home of a wide diversity of animal species as well as indigenous groups.

Pimm et al. (1988) (see also Pimm 1991; Terborgh & Winter 1980; Frankel & Soule 1981; Shaffer 1981; Soule 1986; Robinson 1993) give theoretical and empirical reasons to believe that low r , small population size, and high coefficients of variation in population size are important factors contributing to the likelihood of species extinction. Our results confirm that a prey species' chance of extinction increases by its having a low r . They also suggest that an effective human forager can greatly reduce prey population density and induce population fluctuations.

Redford (1992, citing Yost & Kelley 1983) draws attention to the local defaunation of tropical forests at the

hands of subsistence hunters. In less than a year, the 230 inhabitants of three Waorani villages in the Ecuadorian Amazon killed 3165 mammals, birds, and reptiles. He adds that the "most commonly taken game animals are almost always the largest members of their group and usually the largest species in the forest" (Redford 1992: 417). Given that many of these animals play important roles in seed dispersal, herbivory, pollination, and predation, the cascading effects of their local depletion or extinction may have much larger indirect effects on community structure and composition.

The relationship between low rates of reproduction and large body sizes indicates that the high-ranking species, often the most attractive to human hunters, may also be the ones least able to rebound from exploitation (e.g., Vickers 1991). In other examples from the Neotropics, Mittermeier (1987:134) writes

... there is no doubt that a preference exists for the larger species in the Neotropics, especially *Lagothrix*, *Ateles*, *Alouatta*, *Cebus apella*, and *C. albifrons* ... *Lagothrix* and *Ateles* have slow reproductive rates and consequently have suffered the most from heavy hunting pressure. Indeed, they have been exterminated from large areas of Amazonia with otherwise suitable forest habitat.

Large primates are especially vulnerable to hunting because of their low reproductive rates, their relatively long inter-birth intervals, and the fact that not all mature females are reproductively active at any one time because of complex patterns of group structure (Peres 1990).

Not only are large primates at risk, but large avifauna are also susceptible to overharvesting. The family Cracidae consists of 49 species of large, Neotropical forest-dwelling birds. They range from smaller chachalacas and medium-sized guans to larger curassows. As strict frugivores, these birds probably play an important role as seed dispersers for plants, but their large size also renders them desirable as prey. The Cracidae family contributes the most avian biomass extracted by hunters in the Neotropics, yet they are not well-equipped to sustain such high hunting pressure. These species have a slow recovery rate due to an average clutch size of two, the attainment of sexual maturity at age 3, and a liberal estimate of only 75% of pairs annually nesting successfully (Silva & Strahl 1991).

Ojasti (1984:178) writes "by and large, subsistence hunting is the most important kind of exploitation of native animals in Latin America." He found that the most important sources of meat in the Amazon basin were large mammals: white-lipped peccary (*Tayassu pecari*) ranked first followed by the tapir (*Tapirus terrestris*) and collared peccary (*Tayassu tajacu*). Similarly, in Ayres et al.'s (1991) study of the community of Dardanelos in Brazil, 8850 kg of game was killed by hunters in the first 4 months of 1978. White-lipped peccaries represented nearly 70% of the total weight of game killed, and

other important game species were the tapir, collared peccary, and brocket deer (*Mazama* sp.). *T. pecari* lives in large groups, occurs in relatively low group density, and is severely affected by hunting because single encounters between one or more hunters and a group can destroy a large proportion of a local population.

By linking foraging models to population ecology, our simulation approach shows how we can predict such relationships between subsistence economics and conservation biology. For instance, enhanced income opportunities in the non-foraging sector might elevate the maintenance NAR which will induce people to hunt and gather. We can predict which species will continue to be exploited and at what intensity. In his work with the Sumu Indians of Nicaragua, Godoy (1994; Godoy et al. 1995) proposed that schooling and increased income could foster conservation in the long run by encouraging agricultural innovation, fertility reduction, wage labor, and out-migration. In the short run, however, as residents experience a moderate increase in income, foraging may intensify due to the adoption of newer, more efficient procurement technologies. Also, despite the decrease in reliance on wild game and plants in a richer economy, a few forest goods will still be in high demand and thus are likely to be harvested unsustainably. Ayres et al. (1991:91) found that before road construction in Mato Grosso, Brazil, inhabitants of a small village harvested a wide range of game, including a number of small-bodied species. After the road linked them to a larger economy in 1980, "fewer species were taken overall, and large-bodied species comprised a higher proportion . . . hunting had become a commercial activity." Our approach might supplement the work of Godoy and Ayres et al. by making specific predictions of the resources that would be harvested or ignored as a result of external economic and social changes.

Vickers's (1991:53) 10-year study with the Siona-Secoya Indians of Ecuador led him to conclude that "when given traditional native conditions of low human population density, dispersed settlements, and a subsistence economy, most of the game species utilized by native Amazonian communities can be hunted on a sustainable basis." But he recognized that "traditional native conditions" are becoming the exception in light of widespread technological changes in procurement technologies. "The most obvious deviation from aboriginal conditions is the fact that the shotgun has replaced the blowgun and spear in most hunting" (Vickers 1991:77).

The effects of technological innovation can be incorporated into simulation models through changes in pursuit time or cost, giving us predictions about which species will face increased hunting pressure. As Redford and Robinson (1987:662) point out, use of modern technology has not only allowed native Amazonian hunters to increase the scope of their hunting (e.g., by harvesting nocturnal species with headlamps), but also to in-

crease the intensity of hunting, "particularly of the larger species." In their comparison of the shotgun versus the blowgun and spear in Waorani hunting, Yost and Kelley (1983) found that as the size of the animal increases, so does the benefit and cost-effectiveness of the shotgun. Shotguns were found to be 57% more productive on a per-hour basis than the blowgun, mostly due to the more generalized effectiveness of the modern technology. Whereas a blowgun can provide a steady supply of meat shot in the canopy and a spear enables a hunter to make periodic kills of large terrestrial animals, the shotgun is effective at both. Similarly, Hill and Hawkes' (1983) study of Aché bow hunters found that the knock-down and kill rate at any distance is higher with a shotgun than a bow. The shotgun's average return rate is 1.6 kg/hour as compared to the bow's 0.53 kg/hour. Large game makes up 87% of the take with a shotgun but only 24% of the take with a bow. Similar to the previous case, the shotgun is less efficient and cost effective for smaller game.

Community-level effects are also important. Pimm (1991) notes that the resilience of a species depends in part on the community to which it belongs. This simulation shows how one set of community relationships—the linkages of a predator and its prey, and indirectly among its prey—might operate. Especially important is the vulnerability of a low r resource species that shares a predator with an abundant, high r species. For instance, Godoy (1994) found that cash earned from increased wage labor by the Sumu Indians was spent by purchasing chicken, ducks, and cattle. Ayres et al. (1991) examined the effects of road construction on the economy of a small Brazilian Amazon village and found that the number of backyard domestic animals (chickens, ducks, pigs, turkeys, and sheep) more than doubled after road construction. We might predict that the adoption of domestic animals with high reproductive rates by indigenous households will lead to the overexploitation of those wild game species with higher profitability but low r .

Indigenous Conservation

From the perspective of conservation behavior, it is appropriate to think of this simulation as the null hypothesis. What is likely to happen in the absence of current restraint which looks to future benefits? The diet choice model assumes foragers act to secure the greatest possible short-term gain from their foraging, without attention to the long-term consequences for resource populations. By extension it helps to isolate the circumstances in which we might expect conservation to occur. By separating sustainable exploitation from genuine conservation, the model provides a baseline for reliably determining when conservation actually is present (Alvard 1994).

Pinkerton (paper presented at the Canadian Anthropology Society Conference, Vancouver, B.C., May, 1994)

proposes that three conditions enhance the likelihood of game management by indigenous peoples: the prey species 1) must have a fairly regular and an observable life cycle, and thus offer the possibility of knowledgeable intervention; 2) must be important to the well-being of the foragers, and thus worth the effort of management; and 3) must be vulnerable to over-exploitation, that is the foragers must be effective enough in their techniques to require self-restraint. The model described here provides an independent means of predicting the species for which conditions 2 and 3 are likely to pertain. Alvard (1993, 1994, 1995) uses the diet breadth model to test whether "rate maximization" or "conservation" hypotheses better predict foraging behaviors. He finds that the Piro in the Peruvian Amazon select prey by species and sex-age class as predicted by short-term optimization models, not by indices of vulnerability to over-exploitation. Apparently sustainable harvests by the Piro are not the result of their having adopted intentional conservation behaviors.

Foraging theory may offer other insights into issues of conservation. In at least one instance, our approach offers a prediction that is opposite to one extant in the conservation biology literature. Frankel and Soulé (1981: 14) cite "predator switching" as a reason that a predator is unlikely to extinguish a resource on which it depends. As a prey species becomes relatively rare the predator drops it from the diet in order to focus on more abundant fare. The underlying mechanism is presumed to be the efficiency of having a limited number of search images. In the encounter-contingent model, a prey type worth pursuing on encounter is always worth pursuing, however rare it might become. Conversely, one not worth pursuing on encounter does not become so simply because its density increases. This is known as the *zero-one rule* (Stephens & Krebs 1986). Foraging theory suggests that predators do not substitute abundant for rare prey types; rather, they add and drop prey species only at the diet breadth margin. Thus, a dwindling resource species is not released from exploitation simply because it has declined in numbers. This prediction may help to explain Alvard's (1995:800) finding among the Piro that

hunters tended to avoid depleted areas and preferred to hunt in the areas where returns were highest; they did not, however, ignore pursuit opportunities in areas that were significantly depleted of prey . . . Such pursuits often occurred as hunters moved through depleted areas near the village to hunt in the more productive areas.

This finding serves as another piece of evidence to support Alvard's assertion that the Piro are engaging in rate-maximizing, rather than conservationist, behaviors. In their study of shotgun hunting, Hames and Vickers (1982:374) found that their "data indicate that hunters are essentially opportunistic and will tend to take high-ranking animals regardless of their levels of depletion or the possibility of their becoming extinct."

Pleistocene Extinctions

Biologists apparently accept that predators rarely extirpate species on which they prey (Frankel & Soulé 1981). The same is not believed true of human foragers. Burney (1993) and Owen-Smith (1987) summarize extensive albeit circumstantial evidence that human hunting was a contributing factor in a majority of Pleistocene extinction episodes. "[T]he first animals to go extinct are often the very large, slow-breeding herbivores" (Burney 1993: 540), presumably high-ranking species attractive to human hunters but with low reproductive rates. Owen-Smith (1987) proposes a "keystone herbivore" hypothesis in which megaherbivore populations, under stress due to climate change, are exploited to extinction by human hunters. Extensive habitat changes consequent on their demise, abetted by human harvesting, then led to the extinction of smaller herbivores and associated species. The combination of climate and habitat change with shifting human predation explains extinction patterns that resist accounts based in these causes taken separately. As for the initial step in this scenario, "Megaherbivores are indisputably more vulnerable to sustained human predation than smaller species [largely because] their maximum rate of population recruitment is under 10 percent per annum . . ." (Owen-Smith 1987: 358). Our model suggests the plausibility of these accounts, and it could be used to examine some of the structural as well as the more quantitative details of the proposed mechanisms.

Belief Versus Behavior

Gadgil et al. (1993:155; see also Cox & Elmqvist 1991; Posey 1989; Usher 1987; Carothers 1990; Callicott 1989) make the argument that conservation of biological diversity will be enhanced through "empowering communities of indigenous people to manage their own resource base," perhaps through an institution of extractive reserves (Salafsky et al. 1993; Peres 1994). Much of the indigenous conservation literature that underwrites this view has focused on systems of meaning rather than foraging practices and their outcomes for resource population ecology. Nonetheless, this literature implies the hope that the actual practices of indigenous peoples provide guidance to the sustained management of the ecosystems in which they reside; it urges a practical and applied message about the material lives and well-being of foragers and the species on which they depend. This prescriptive message neglects foraging economics and makes population ecology worrisome. People do not always act consistent with their beliefs, and even if they do act in such a way, they are not always successful in realizing their intentions (Hames 1991). To devise policies that lead to resource conservation through indigenous management, we believe it will be necessary to un-

derstand the distinctive features of the foraging *economy*, as a matter of behavior with practical consequences (Winterhalder 1983a; Hames 1991; Joshi & Gadgil 1991; Alvard 1993, 1994, 1995).

Conclusion

In this analysis we simulate linkages between optimal diet selection at the level of individual behavior and the population dynamics of the predator and multiple species of prey. Our model allows both for depletion and productivity (density-dependent replacement) of the exploited resource species. It attempts to harness the strengths of neo-Darwinian theory (behavioral ecology) to the prediction of ecological relationships at the level of populations, thus to join analytical problems that traditionally have been studied separately (Sutherland 1996).

We found that encounter-contingent foraging rarely will yield a MSY harvest, although the forager-resource (predator-prey) system can stabilize at sustainable levels without conservation efforts. Adding a resource species to the diet may induce diet breadth switching which at least temporarily buffers higher-ranked resource types from intensive exploitation. In multi-species simulations, low r species are vulnerable to extinction through over-exploitation, particularly if the forager population is inflated by the presence of profitable, high r species. Further, high r resources appear to be associated with system instability in the form of complex cycles. Encounter-contingent foraging demonstrates the linked fates of the species within a forager's diet: a resource species' vulnerability to a predator sometimes will depend on the suite of resources that are harvested along with it.

Given the theoretical source of the relationships incorporated into this model, our firmest claim is that it may highlight structural properties of these relationships. It perhaps can give a rough approximation of their quantitative magnitudes. Empirical data specific to individual cases would be needed to make the more precise predictions that would be subject to testing. Sutherland's (1996) work with the ideal free distribution provides an example of how this might be done. Through an emphasis on behavior, an ability to incorporate local environmental and technological diversity, and the capability to examine forager-prey dynamics over a long temporal scale with high resolution, simulation modeling that incorporates foraging theory and population biology can provide valuable insights on human resource use and conservation. "The important question now is not which traditional practices, as practiced in the past, are sustainable, but rather which conditions cause people to conserve their resources, and which conditions favor destruction, or overexploitation, of local resources" (Schmink et al. 1992:8).

Acknowledgments

We thank S. Gerety, E. Alden Smith, B. Tucker, and the intrepid foragers of the Spring 1994 Course, Anthropology 260 (J. Doerfer, T. Hargrove, M. Riley, and K. Taulbee), who consumed bagels with enthusiasm as they made creative and challenging use of this simulation in laboratory exercises.

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