

# The Primitive Hunter Culture, Pleistocene Extinction, and the Rise of Agriculture

Replaces California Institute of  
Technology Social Science Working

Paper # 37

---

Vernon L. Smith

*University of Southern California and California Institute of Technology*

The hypothesis that megafauna extinction some 10,000 years ago was due to “overkill” by Paleolithic hunters is examined using an economic model of a replenishable resource. The large herding animals that became extinct, such as mammoth, bison, camel, and mastodon, presented low hunting cost and high kill value. The absence of appropriation provided incentives for the wastage killing evident in some kill sites, while the slow growth, long lives, and long maturation of large animals increased their vulnerability to extinction. Free-access hunting is compared with socially optimal hunting and used to interpret the development of conservationist ethics, and controls, in more recent primitive cultures.

## 1. Introduction

Many archaeologists and other scientists believe that the available evidence supports the hypothesis—startling to nonspecialists—that the unusual incidence of large-animal extinctions throughout the world during the late Pleistocene period was caused, to an important extent, by Paleolithic hunters. Even if true, the extinction of large animals is but one of the more dramatic examples of the very substantial impact that primitive as well as modern man has had on his “natural” environment (Heizer 1955). The purpose of this essay is threefold: (1) to acquaint

Support from the National Science Foundation, the Center for Advanced Study in the Behavioral Sciences, and the Fairchild Distinguished Scholar program at Caltech is gratefully acknowledged. I wish also to express my debt to Robert F. Heizer for a great deal of help and encouragement in the course of many discussions on the topic of this paper and for providing me with a guide to the relevant archaeological literature. If I have been a poor student, he bears no responsibility for the final product.

[*Journal of Political Economy*, 1975, vol. 83, no. 4]  
© 1975 by The University of Chicago. All rights reserved.

economists with some of the evidence and hypotheses from other sciences concerning the role of primitive man as hunter par excellence, (2) to parameterize some important features of these observations and hypotheses in the context of a model of the primitive hunter culture which, in the face of animal extinctions, turns increasingly to agriculture, and (3) to attempt to demonstrate to archaeologists and other scientists the potential that economic analysis may have in unifying and integrating this body of evidence and conjecture. In what follows, the reader should bear in mind that much of the "evidence" to which reference will be made is subject to dispute; certainly the interpretation of that evidence is controversial.

It is my belief, in reading the archaeological literature in this area, that there is a natural economic rationale for "overkill" as a possible explanation for the large-animal extinctions which has not been adequately or fully articulated. Briefly stated, the large extinct herbivores hunted by primitive men, such as the mammoth and bison, were gregarious herd animals, easily located, and apparently easily approached and struck with crude missile weapons or stampeded into "jumps." Multiple kills were therefore likely, but because of their large size, even a single kill represented high value. The combination of low hunting cost and high value would make large animals the most economical prey. Furthermore, in the absence of appropriation or other incentives for the individual hunter to attach value to the live animal stock, wastage killing was possibly commonplace. Biologically, the larger genera of animals are characterized by slow growth, long lives, and long periods of maturation, and are therefore the most vulnerable to hunting pressure. That is, the hunter harvest is more likely to exceed net biological growth, causing a decline in biomass.

In Section 2, some of the facts, conjectures, and interpretations of late Pleistocene extinctions are summarized. In Section 3, a particularly simple form of existing models of production from common-property replenishable resources is used to stylize the hunter-agrarian economy. This permits a comparative-statics treatment of the effect of prey size, vulnerability, and value, and of predator technology and population, on prey biomass and extinction potential (Section 4). Socially optimal hunting is modeled in Sections 5 and 6 and the Appendix, on the assumption that institutional mechanisms of control (property-right systems or cultural or legal constraints that internalize the social costs of individual hunter actions) are adequate to support the optimal sustained-yield harvesting of prey. These optimal patterns are compared with free-access hunting. This analysis is used to develop the conditions under which it may be optimal to "conserve" or, alternatively, to destroy a hunted species and to compare such cases with the corresponding free-access solutions.

## 2. The Hypotheses of Pleistocene Extinction

One of the great scientific puzzles studied extensively by archaeologists, paleontologists, and geologists is the cause and process of the unprecedented wave of large-animal extinction in the late Pleistocene period. Martin (1967, pp. 75, 82–86) suggests the loss of over 200 genera worldwide and lists 80 late Pleistocene extinct animals in continental North America of which 49 had an average adult body weight in excess of 110 pounds (the "megafauna"). These megafauna included camels, horses, bison, mastodons, llamas, ground sloths (including a giant the size of an elephant), mammoths (the largest, *Mammuthus imperator*, was 13 feet tall and considerably larger than the African elephant), beavers, short-faced bears, armadillos, several saber-tooth cats (including *Smilodon*, the tiger), shrub oxen, moose, tapirs, antelope, and many more. Of the 49 genera in the late Pleistocene, 33 became extinct at a time which could have roughly coincided with the arrival of the Paleo-Indians in North America. Of the 31 smaller extinct mammals listed by Martin, only one could have been associated with man. Those terminal Pleistocene megafauna apparently found in "direct association" with man include ground sloths, camels, mastodons, horses, mammoths, shrub oxen, tapirs, and the extinct bison. Evidence of human predation is clearest in the case of mammoth and extinct bison. That Clovis fluted-point hunters killed mammoth around 11,000 years ago is hardly open to question, and sometime later, perhaps after the sudden disappearance of the mammoth, the Folsom point was developed and used to kill now-extinct bison (Haynes 1964). The Clovis, Folsom, and subsequent Scottsbluff point projectile technologies seem specifically designed for big-game hunting.

Although accelerated extinctions had occurred in periods earlier than the late Pleistocene, they had affected marine organisms, plants, and the smaller mammals as well as the larger mammals. Furthermore, the pattern of worldwide extinction of the larger mammals seems suspiciously to correlate with the migration chronology of man. This has led Martin (also see Sauer 1944) to the hypothesis that Pleistocene extinction was due to overkill by Paleolithic hunters armed with the stone-tipped spear, fire, and the communal hunting party. Martin (1967, p. 75) states:

Except on islands where smaller animals disappeared, extinction struck only the large terrestrial herbivores, their ecologically dependent carnivores, and their scavengers. Although it may have occurred during times of climatic change, the event is not clearly related to climatic change. One must seek another cause. Extinction closely follows the chronology of prehistoric man's spread and his development as a big-game hunter. No continents or islands are known in which accelerated extinction

definitely predates man's arrival. The phenomenon of overkill alone explains the global extinction pattern.

A scenario built around this hypothesis goes as follows: For 200,000 years prior to the arrival of man, the large herbivores of North America were increasing in diversity and experienced no shrinkage of range. They evolved and survived over tens of millions of years in the presence of numerous environmental changes and predators. Several genera had emigrated over the Bering land bridge to the hospitable environment of North America. Consequently, the North America of 15,000 years ago was comparable to nineteenth-century Africa in terms of the huge, strange, "unlikely" beasts that grazed the plains and browsed the forests and brush. Then, approximately 12,000 years ago, the first Paleolithic men, ancestors of many of the present-day Indians, arrived across the exposed Bering land bridge. They were hunters, perhaps driven to wider migration by the dwindling herds of prey in Eurasia. They brought with them the culture, skill, and technology of big-game hunting—the spear, perhaps the atlatl (spear thrower), fire, and stone projectile points. At some time in this migration, they developed the Clovis fluted point—a work of craftsmanship in stone carefully adapted to the demands of killing large animals. These hunters preyed on gregarious herds of mammoth, bison, and perhaps mastodon, camels, tapirs, horses, and other animals which were easy to locate and probably showed little fear of the new predators. By 11,000 years ago, this efficient new predator had wiped out the mammoth and was concentrating on now-extinct species of bison. The bison may have been killed by jumps (as was common within historic times by Indians) and perhaps fire drives, and by this time the Clovis point was giving way to the Folsom projectile point. The population of Paleo-Indians expanded rapidly across North and South America, appearing at the southern tip of South America by 10,000 years ago, and, one may conjecture, lived affluently for as long as the game was plentiful. As the herds disappeared, their predators, the saber-toothed tiger, dire wolf, and hyena, became extinct. Hunting effort was directed at smaller, less vulnerable game which produced a relatively meager existence and was eventually replaced by an agricultural technology in which subsistence depended on crops of corn (and later beans and squash) supplemented with small game.

The scenario is plausible but is by no means an established fact. That man arrived about 12,000 years ago is probable, as there is no firm radiocarbon dating of any earlier evidence of man (Haynes 1967). That man hunted mammoth and, later, two species of now-extinct bison is surely a certainty based on documented kill sites (Haury, Antevs, and Lance 1953; Gross 1951; Agogino and Frankforter 1960; Leonhardy 1966).<sup>1</sup> Hester

<sup>1</sup> This is conjecture on my part, but it seems plausible that the Bering land bridge might have acted as a filter through which only the most able hunting tribes could have

and Wendorf (1962, pp. 166–67) report that the most common hunting pattern for both mammoth and bison was to stalk and kill animals while they were drinking in a pond or stream. Killing occurred by means of spears aimed at the thoracic region, although in one site, the presence of boulders suggests they were used to kill wounded mammoth. A second pattern was the stampede, probably present in three kill sites of early man. The animals (extinct bison) were driven into a stream or over a cliff, sometimes in numbers as high as several hundred. At the Olsen-Chubbuck site in Colorado, well-preserved and carefully excavated remains of bones and artifacts prove that about 8,500 years ago some 200 *Bison occidentalis* were stampeded into an arroyo only 5–7 feet deep. The injured animals were killed by projectile points generally of the Scottsbluff type. About 75 percent of the animals were then systematically butchered (Wheat 1967). The killing of bison in the sixteenth to eighteenth centuries by stampeding them over carefully selected "jumps" is quite well established (Kehoe 1967; Butler 1971).

Whether the early Americans stampeded animals by fire drives is not known, nor is it critical to the overkill hypothesis. The first account of the southwestern Indians, by Cabeza de Vaca, records that the inhabitants of what is now southwest Texas burned favorable animal ranges in order to deprive the animals of forage and force them to frequent areas where they could be more easily hunted (Covey 1961, p. 81; cited by Jelinek 1967, p. 197). Burning of this type (and there is abundant evidence for the occurrence of fires in association with man) could have been a more effective means by which man contributed to Pleistocene extinction than by the occasional fire drive. In the case of herd animals such as *Bison* that are easily stampeded, it is not clear that fire drives were even functional unless it was to ensure that the confused animals would not stampede in the wrong direction!

That the mammoth was gone by 10,000–11,000 years ago is also likely, based on radiocarbon dating. That there existed a big-game hunting tradition is also clearly established by the widespread occurrence of the Clovis projectile point type. It is found from Florida to Nova Scotia, in the high plains, the Southwest, across the Midwest, and in the South. It was a large projectile, 7–15 centimeters long and 3–4 centimeters wide. Bases were concave, and a fluting or channeling extended from the base up to one-half the length of the point. They were flaked by percussion and the base edges ground down to prevent cutting of the thongs that

passed. The bridge would not have been a suitable viaduct for a gatherer culture, "because no likely food sources but game existed for most of the year in the tundra areas they traversed" (Jelinek 1967, p. 195). Hence, the early North Americans may have been the product of a selection process that favored only the most mobile, skilled, and dedicated hunters. This could help explain why megafauna extinction in North America was more rapid than in Europe, Asia, and Africa.

secured them to the spear shaft.<sup>2</sup> Early American points were probably too heavy, large, and ill-designed for arrow tips. Spears, thrust or thrown as a javelin, or darts—perhaps propelled by the atlatl—were the main tool of the hunt. Clovis points date back to 12,000 years ago and apparently evolved into the Folsom. The Folsom point dates from about 10,000–11,000 years ago and is much less widely dispersed than the Clovis. The Folsom point is more delicately made, with fine-edge flaking, and is associated with the hunting of the extinct *Bison antiquus*. The Scottsbluff and several similar points date from about 9,000 years ago and are associated with the killing of the slightly smaller extinct *Bison occidentalis*. By 7,000–10,000 years ago, projectile points had been adapted to the killing of modern smaller game such as sheep, the so-called American bison, deer, and antelope. A primitive maize, perhaps in the early stages of domestication, has been dated by radiocarbon to around 5,000–6,000 years ago (Mangelsdorf and Smith 1949).

Until recently, the commonly accepted cause of late Pleistocene extinctions was climatic change and a reduction in grassland areas. This view probably still predominates. Thus, according to Guilday (1967, p. 121), “the fact that the late Pleistocene extinctions were so widespread and geographically almost simultaneous does call for a major overlying cause, however. I suggest that the prime mover was post-Pleistocene desiccation. Evidence for such an episode is present on all continents, and its effects would have been both swift and lethal. It may have been the spur to turn man from hunting to a life centered around animal husbandry and agriculture.” This states the climatic as against the “overkill” extinction hypothesis. The desiccation referred to is associated with a drier climate following recession of the last great ice sheet.<sup>3</sup> A variant of the climate hypothesis attributes extinction to the effect of more severe seasonal fluctuations (colder winters, warmer summers) on those mammals with longer gestation periods (Slaughter 1967). But here we have an identification problem, for it is the mammals with longer gestation periods, longer periods of maternal care, and longer lives that are most vulnerable to hunting pressure.

<sup>2</sup> Jelinek (1967, p. 196) notes the significance of this design technology for the hypothesis of a vulnerable fauna (mammoth): “Grinding would prevent the edges of the point from cutting the lashing that bound it to a shaft if the point was subjected to repeated lateral stress” as would occur “in a point on a thrusting spear or lance whose shaft remained in the hand of the hunter after it penetrated the animal—a technique that would be most effective against a relatively easy quarry and of little use against a skittish and fearful prey.”

<sup>3</sup> However, desiccation followed the three previous glaciation periods and in one instance was probably more severe. “Recent pollen evidence from western America seems to indicate that in at least some areas occupied by the extinct fauna the conditions following the retreat of an earlier glaciation (Illinoian) were probably more arid and as warm or warmer than at present. Thus conditions of temperature and aridity do not appear likely as direct causes of extinction” (Jelinek 1967, p. 194).

Finally, of course, there is the multiple-cause, or combination, hypothesis, here defined by Hester (1967, p. 170): “I take the view that Pleistocene man could not have caused the extinction of the North American megafauna until after natural causes had greatly reduced the population of each species.” However, Hester’s study of historical extinction (extinction or near extinction of species since European settlement) in North America lists (1) hunting by primitive man and (2) hunting by civilized man with firearms as the first and second major factors in order of frequency.

Much of the earlier skepticism surrounding the “overkill” hypothesis stems from a disbelief (to some extent perhaps a romantic disbelief) in the ability of primitive men to accomplish, with primitive instruments, the destruction of such huge creatures, already the prey of the formidable saber-toothed tiger and dire wolf. Yet these men were not genetically, in terms of intelligence and skill capacity, that different from modern man. Also, modern studies of predation by the timber wolf on Isle Royale indicate that moose stock may be strengthened by the killing of old, weak, and diseased animals (Mech 1970). The large kill sites of mammoth and bison suggest wastage—killing beyond immediate butchering requirements—so that there is some reason to believe that man was orders of magnitude more effective in predation than his animal competitors. Overfishing in historic times is well known. The demise of great whales (and recently the Alaskan king crab) is well known, and the capacity of man for wholesale rivalrous killing, even with the most primitive of weapons, is dramatically documented in the following *Palo Alto Times* (March 13, 1973) account:

In the course of a few hours early Sunday a shoal of 637 pilot whales were driven into a narrow fjord on the island of Vaga (Faeroe Islands, Denmark) by stone-throwing islanders in an armada of small boats. Then they were slaughtered with long spears and knives in a gruesome spectacle that has been part of Faeroese life for centuries. The whales churned their tails furiously in shallow water . . . The shoal of whales was one of the biggest since more than 2000 pilot whales were killed in one day east of here 20 years ago.

Some time between 12,000 and 3,000 years ago the early Americans turned from an exclusively hunting and gathering culture to one based more and more on agriculture. I assume that men found it to their economic advantage to make this change. It is perhaps significant to the overkill hypothesis that man did not turn from big game to smaller game except as a supplement to agriculture, as a result of the large-animal extinctions. Even the plentiful American bison apparently was hunted only incidentally until after the introduction of riding horses by the

Spanish in historic times.<sup>4</sup> It may have been the case that only the largest herding animals were economical to hunt with the tools of Paleolithic man.

Perhaps the weakest element in the overkill hypothesis is the scant direct evidence that early North Americans hunted extensively any of the extinct animals other than mammoth and bison.<sup>5</sup> Extinct horse, camel, tapir, mastodon, and antelope have been found in mammoth and bison kill sites but not so as to clearly demonstrate death by the spear<sup>6</sup> (or other means attributable to paleohunters). At the Lehner Ranch site in Arizona (Haury, Sayles, and Wasley 1959) nine mammoths and at least one each of horse, bison, and tapir occur in a single bone bed. Directly associated with these bones was evidence of man's destruction of at least some of the animals. Thus, Clovis spear points were found in situ among ribs of a mammoth and a bison. However, Irwin-Williams (1967, p. 346) reports that at a kill site near Puebla, Mexico, "the character of the assemblage (bones and projectile points) indicates hunting and butchering activities involving mastodon, mammoth, horse, camel, four-horned antelope, etc." But the fact that such evidence is not firm or more widespread is puzzling in view of the fact that there is much evidence for the hunting of the horse as well as mammoth at an earlier date in Europe. Sites such as Solutré in France contain the remains of an estimated 100,000 horses (MacCurdy 1933, p. 173; cited by Jelinek 1967, p. 195). But for the purposes of this paper, it is enough to assume that the earliest Americans subsisted primarily on mammoth and bison, turning to gathering, agriculture, and supplemental game as these animals became extinct.

The abandonment of agriculture and the return to the hunting of

<sup>4</sup> When the horse was reintroduced to the New World by the Spanish in the sixteenth century, *Equus* had been extinct throughout the Americas for only about 8,000 years. In North America horse bones are among the most common Pleistocene fossils (Martin and Guilday 1967, pp. 41-42). Upon reintroduction, the horse reproduced and spread rapidly and thrives today in the wild, as does the burro, under extremely arid conditions in Nevada, Arizona, and Utah. This development makes it the more puzzling that late Pleistocene extinction of the horse would have been due to desiccation.

<sup>5</sup> The survival of African megafauna is often cited as negative evidence for the overkill hypothesis. But this view has been challenged by several writers. Martin (1967, pp. 110-11) notes that some 50 genera (about 30 percent) disappeared in Africa during the Pleistocene. Most of this extinction occurred before 40,000-50,000 years ago and "seems to coincide with the maximum development of the most advanced early Stone Age hunting cultures. . . . The case of Africa neither refutes the hypothesis of overkill nor supports the hypothesis of worldwide climatic change as a cause of extinction." Jelinek (1967, p. 194) also suggests that Africa is not comparable to those areas of the northern hemisphere where extinction occurred, because the African flora was more favorable for gathering. Thus, gathering may have been sufficiently economical to have reduced the hunting stress to which the African megafauna was exposed.

<sup>6</sup> Martin (1973, pp. 969-74) explained the absence of kill sites for horse, camel, and ground sloths by the hypothesis that they were killed too quickly and easily to leave extensive fossil traces. The idea is that vulnerability to overkill and archaeological visibility are inversely related.

bison by some American Indian groups in historic times (seventeenth and eighteenth centuries) is well established. According to Wedel (1936), "the introduction of the horse deeply affected the Pawnee, as it did most of the plains tribes. . . [leading to] the tendency toward a nomadic, bison-hunting mode of life made possible by the horse. . . . From a sedentary tribe the Pawnee became one in which the chase and maize culture shared almost equally."

The more revolutionary effect of the horse on the "fighting Cheyenne" of the northern plains is reported by Strong (1940, pp. 359, 370, 375-76). Wedel (1940, p. 327) reports that the Cheyenne and Arapahoe abandoned their villages, pottery arts, and horticulture to become bison hunters, while the Plains Apache (already subsisting on bison herds in 1541 as reported by the Spanish explorer Coronado) merely adapted the horse to a preexisting bison culture. Apparently, the vast encampments with large tepees of bison hide familiar to later European settlers depended on a substantial increase in the bison harvest made possible by the riding horse.

### 3. A Model of the Primitive Hunter-Agrarian Economy

I have characterized the Paleo-Indian as a big-game hunter who turned to agriculture as his chief prey became extinct but whose descendants returned to a more nomadic hunting economy after the introduction of the riding horse. This stark representation will be stylized in an economic model of subsistence based on free-access hunting and/or agriculture in which the biomass of game is determined by biological growth considerations that are autonomous but are affected by the harvest product of the hunt.

Consider an economy of population  $n$ , each member of which is free to engage in hunting or agriculture<sup>7</sup> as a productive activity. Hunting activity is applied to a single homogeneous species of biomass,  $M$ , such as mastodon, mammoth, or bison, and yields a per capita output of  $m$  per unit of time. Agricultural activity is applied to the production of a single homogeneous crop, such as corn or beans, and yields a per capita output of  $c$  per unit of time. Then  $H$  units of hunting labor per capita, and  $A$  units of agricultural labor per capita, are employed, with  $L = H + A$ , the total per capita labor available. The production function for corn is  $c = g(\gamma A)$  and for meat  $m = f(\beta H, M/n)$ ; in which it is assumed that increasing the stock of game and of hunters by the same proportion has no effect on the per capita output of meat. The parameters  $\beta$  and  $\gamma$  are efficiency parameters for labor in hunting and farming, respectively.

<sup>7</sup> I shall refer to the alternative to hunting as "agriculture," but it could just as well be gathering. To the early North Americans, the only viable alternative to hunting prior to 5,000-6,000 years ago would seem to have been gathering.

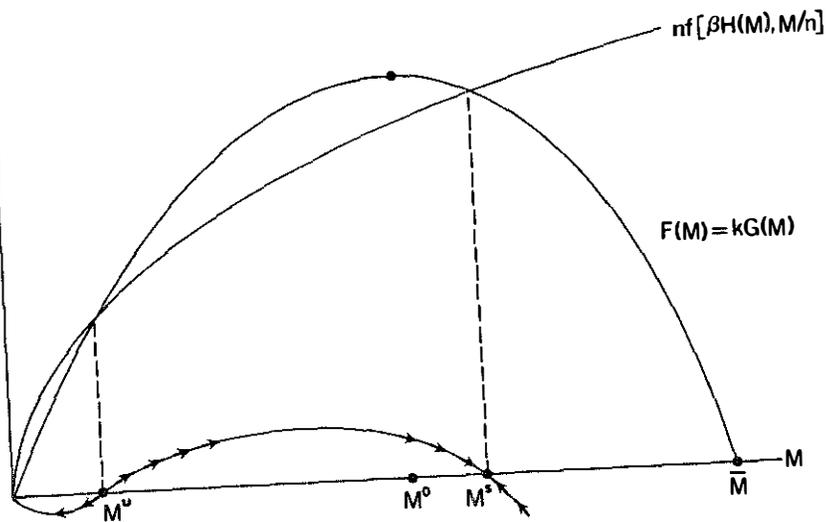


FIG. 1

Thus, an increase in  $\beta$  increases the hunting efficiency of labor. The effect of a technological change in weapons, or the introduction of the horse into the Plains Indian culture, is assumed to be captured by an appropriate increase in  $\beta$ .

It will be understood, without always making it explicit, that all of the variables are dated, that is,  $M = M(t)$ ,  $H = H(t)$ , and so on with  $n$ ,  $L$ ,  $\beta$ , and  $\gamma$  given constants.

The hunted resource is assumed to be subject to a biological growth law (see, e.g., Lotka 1956; Smith 1968; Plourde 1971), which, in the absence of predation by man, is given by  $M'(t) = F[M(t)]$ . It will be assumed that  $F(M)$  can be written in the form  $F(M) = kG(M)$ ,  $k > 0$ ,  $G''(M) < 0$ ,  $M \geq 0$ ;  $G'(M^0) = 0$ ,  $G(M) \geq 0$ ,  $0 \leq M \leq \bar{M}$ , where  $\bar{M}$  is the maximum naturally sustainable stock of the hunted biomass (see fig. 1). The parameter  $k$  expresses the biotic growth potential and therefore the predator vulnerability of the species in the sense that an increase in  $k$  increases the growth rate of the stock for  $0 < M < \bar{M}$  but does not increase the natural equilibrium stock,  $\bar{M}$ . It may be supposed that a great many factors influence  $k$ . A change in climate affecting reproduction, infection by disease, or a change in food availability would alter  $k$  for a given genus. Among different genera,  $k$  would vary with growth characteristics such as feeding habits, energy requirements, gestation period, age of maturation, life span, and efficiency of food

conversion. Generally, the larger genera of mammals are slower growing, have longer gestation periods, require longer periods of maternal care, and live longer. These factors spell greater vulnerability to hunting pressure in that a given tonnage reduction in biomass will require longer to regenerate. In this regard, the modern forms of those extinct species hunted by or found in association with primitive man have relatively long lives (and gestation periods): llama, 20 years (10–11 months gestation); camel, 45 years (10–14 months); horse, 25–30 years (11–12 months); elephant, 60–80 years (22 months); and bison, 18–22 years (9 months). It is perhaps significant that the American bison (*Bison bison*) familiar to nineteenth-century European settlers dates no further back than Paleo-Indian times and is believed to represent a dwarfed form of the extinct *Bison occidentalis* (Edwards 1967). Also, mammoth kill sites commonly contain the remains of the giants of the species (*Mammuthus imperator*, 4.0 m high; *Mammuthus columbi*, 3.6 m high), both larger than the largest African elephant (3.52 m high) (Martin and Guilday 1967).

On the matter of size, age of maturity, and speed of growth, Hammond (1961, p. 321) observes that a considerable reduction in size has occurred over the last 50 years in the major beef breeds of cattle due to deliberate selection for early maturation in body proportions. Hence, under common-property conditions we have Paleolithic hunters selectively harvesting the larger, slower-growing mammals due to emphasis on consuming the stock. But under appropriation with domesticated animals and emphasis on sustained-yield harvesting, investment favors the smaller, earlier-maturing animals which provide a higher biomass growth rate.

When each member of a population of size  $n$  applies  $H$  units of labor to hunting, this yields a harvest of  $nm = nf(\beta H, M/n)$  units of the replenishable resource, and the net growth rate of the resource is given by

$$M'(t) = F(M) - nf(\beta H, M/n). \quad (1)$$

Each of  $n$  individuals is assumed to choose  $(H, A)$  so as to maximize a utility function  $u(c, m)$  subject to  $L = H + A$  and the above production constraints. By substituting  $c = g[\gamma(L - H)]$  and  $m = f(\beta H, M/n)$ , the problem can be expressed

$$\max_H u\{g[\gamma(L - H)], f(\beta H, M/n)\}.$$

If  $u(g, f)$  is concave in  $H$  for given  $M$ , an interior maximum is defined by the condition

$$-u_1 \gamma g' + u_2 \beta f_1 = 0, \quad 0 < H < L. \quad (2)$$

Equation (2), requiring the marginal rate of transformation between corn and meat to be equal to their marginal rate of substitution, can be regarded as determining an economic equilibrium between  $H$  and  $M$ .

That is, for each resource stock,  $M$ , there is a corresponding economical expenditure of hunting labor so that (1) and (2) together determine a differential equation in  $M'(t)$  and  $M(t)$  only. An illustrative solution to (1) and (2) is shown graphically in figure 1. The curve at the bottom of figure 1 represents growth in the biomass of the hunted resource net of harvested units. The equilibrium harvest function,  $nf(\beta H, M/n)$ , is shown intersecting the growth function,  $F(M)$ , at two points  $M^u$  and  $M^s$ , both of which satisfy (1) and (2) when  $M'(t) = 0$ . Stability in the neighborhood of a point  $M^s$  where  $M'(t) = 0$  requires  $dM'/dM < 0$ . Differentiating (1) and (2), one can easily verify that the sign of  $dM'/dM$  is ambiguous, even where  $F'(M) < 0$ , given only the concavity of  $u$ ,  $f$ , and  $g$ . In the illustration of figure 1, point  $M^s$  is shown as locally stable while  $M^u$  is not.

More specific results will be derived and illustrated graphically, while those parameters essential to the subsequent applications of the model are retained, by introducing the following simplifying assumptions:

1.  $u(c, m) = c + vm$ ,  $u_1 = 1$ ,  $u_2 = v$ . Corn and meat are perfect substitutes, and value is measured in subjective corn-equivalent units. The parameter  $v$  is the society's subjective value of meat relative to corn. Thus,  $u$  is the per capita income (welfare) of the society.

2.  $f(\beta H, M/n)$  and  $g[\gamma(L - H)]$  are increasing, concave, and homogeneous of degree 1, with  $f(0, M) = f(\beta H, 0) = g(0) = 0$ . Hence, letting  $x = \beta Hn/M$  be hunting intensity, that is, total hunting labor per unit biomass, we can write

$$f(\beta H, M/n) = (M/n)\phi(x), \quad \phi' > 0, \quad \phi'' < 0, \quad \phi(0) = 0,$$

$$f_1 = \phi'(x) > 0, \quad f_2 = \phi - x\phi' > 0,$$

$$g[\gamma(L - H)] = \gamma(L - H), \quad g' = 1.$$

Applying these assumptions, (2) becomes  $\beta v\phi'(x) = \gamma$ , or

$$\frac{\beta Hn}{M} = \phi'^{(-1)}\left(\frac{\gamma/\beta}{v}\right) = \phi'^{(-1)}(\tau/v), \quad (3)$$

where  $\tau$  is a relative efficiency parameter, that is, the efficiency of labor in agriculture relative to hunting, and  $\tau/v$  is the real wage or the opportunity cost of hunting (the value of the corn forgone). Under these assumptions, (1) becomes

$$M'(t) = F(M) - M\phi[\phi'^{(-1)}(\tau/v)]. \quad (4)$$

At an equilibrium point,  $M^*$ ,

$$M'(t) = F(M^*) - M^*\phi[\phi'^{(-1)}(\tau/v)] = 0, \quad (5)$$

and the stability condition, near  $M^*$ , is

$$\frac{dM'}{dM} = F'(M^*) - \phi[\phi'^{(-1)}(\tau/v)] < 0. \quad (6)$$

Equilibrium can also be expressed as occurring at  $M^*$  where the average biological growth rate,  $a(M^*; k)$ , is equal to the harvest intensity (output per unit biomass),  $\phi$ . That is, rewriting (5) and substituting  $F(M) = kG(M)$ ,

$$\frac{kG(M^*)}{M^*} \equiv a(M^*; k) = \phi[\phi'^{(-1)}(\tau/v)]. \quad (7)$$

#### 4. Comparative Statics of Hunting

The marginal effect of any of the parameters  $k$ ,  $v$ ,  $n$ , and  $\beta$  on equilibrium hunting effort,  $H^*$ , and equilibrium biomass,  $M^*$ , can be deduced by differentiating (3) and (7). By differentiating  $u^* = \gamma(L - H^*) + (vM^*/n)\phi(x^*)$ , the effect of such parameters on equilibrium per capita income can also be ascertained. In determining such effects, any factor which reduces the equilibrium stock of the resource may also, in the limiting case, produce extinction (see Gould [1972] and Clarke [1973] for analyses of extinction). From (7), it is clear that extinction of a species due to hunting pressure will occur if  $a(0; k) < \phi[\phi'^{(-1)}(\tau/v)]$ , that is, if  $\tau/v < \phi'\{\phi^{-1}[a(0; k)]\}$ . It follows that unless  $\phi(x)$  has an upper bound below  $a(0; k)$  there is always a real wage rate small enough (i.e., a return on agricultural labor that is small enough) to produce extinction.

The effect of changes in the indicated parameters on  $(M^*, H^*, u^*)$  is summarized below:

$$1. \quad \frac{dM^*}{dk} = -\frac{a}{ka'} > 0, \quad \frac{dH^*}{dk} = \frac{H^*}{M^*} \frac{dM^*}{dk} > 0,$$

$$\frac{du^*}{dk} = (v/n)(\phi - x\phi') \frac{dM^*}{dk} > 0,$$

where  $a' = [\partial a(M^*; k)]/\partial M^* < 0$ . Consequently, if larger animal species have a lower biotic growth potential (i.e., smaller  $k$ ), this will tend to (i) reduce the equilibrium stock (and increase the possibility of extinction), (ii) encourage agricultural effort at the expense of hunting, and (iii) decrease per capita income.

$$2. \quad \frac{dM^*}{d\beta} = -\frac{(\phi')^2}{a'\phi''\beta} < 0, \quad \frac{dH^*}{d\beta} = \frac{H^*}{M^*} \frac{dM^*}{d\beta} - \frac{M^*\phi'}{n\beta^2\phi''} - \frac{H^*}{\beta} \cong 0,$$

$$\frac{du^*}{d\beta} = vH^*\phi' + \frac{v}{n}(\phi - x\phi') \frac{dM^*}{d\beta} \cong 0.$$

The greater the efficiency of hunting labor, the smaller the equilibrium stock of animals. One implication is that larger animals and/or gregarious animals that tend to congregate in herds, such as mammoth, bison, antelope, camels, and llamas (among the extinct genera), would have comparatively high visibility and low search cost, making them easier prey and increasing  $\beta$ . Thus, Edwards (1967, p. 149) argues that "human technology, including use of missile weapons, greatly reduces the counter-attacking defensive advantages of large size and emphasizes concealment and speed of flight. At this point . . . the genetically selected optimum body size of many forms declines sharply." Also, the introduction of the riding horse into the Plains Indians culture by the Spanish would have had the effect of increasing bison hunting efficiency and reducing the stock of bison. Armed with the horse and the bow, the Plains Indians in another 200 years could possibly have depleted the stock of bison as effectively as did Buffalo Bill and the U.S. cavalry.

However, changes in hunting efficiency could either increase or decrease hunting effort and per capita income ( $dH^*/d\beta \geq 0$ ,  $du^*/d\beta \geq 0$ ). Greater hunting efficiency could release labor for agricultural employment or so reduce the animal stock that the society is made poorer. It would appear that this was not the effect of the horse on the Plains Indians, many of whom were uprooted from their agrarian activities but who achieved greater affluence as bison hunters. This affluence could have been a temporary phenomenon; that is, in the short run, given the animal stock, we have  $dM^*/d\beta = 0$  and  $du^*/d\beta = vH^*\phi' > 0$ . The short-run effect of an increase in hunting efficiency is always to increase per capita income.

$$3. \quad \frac{dM^*}{dv} = -\frac{(\phi')^2}{va'\phi''} < 0, \quad \frac{dH^*}{dv} = -\frac{M^*\phi'}{\beta vn\phi''} + \frac{H^*}{M^*} \frac{dM^*}{dv} \geq 0,$$

$$\frac{du^*}{dv} = \frac{M^*\phi}{n} + \frac{v}{n}(\phi - x\phi') \frac{dM^*}{dv} \geq 0.$$

The greater the consumption value of the hunted resource, the smaller will be the equilibrium biomass. Hunting labor and per capita income could also be smaller depending on how much the biomass of animals is depleted (if the species becomes extinct, then, obviously, hunting will cease):

$$4. \quad \frac{dM^*}{dn} = 0, \quad \frac{dH^*}{dn} = -\frac{H^*}{n} < 0,$$

$$\frac{du^*}{dn} = -(vM^*/n^2)(\phi - x\phi') < 0.$$

In a mixed economy, increasing the human population causes no change in the stock of animals but reduces hunting effort and per capita income. With constant returns in agriculture, equilibrium requires total hunting intensity to be constant. Consequently, any increase in population will be offset by a corresponding decrease in each individual's hunting labor. This is a very strong empirical implication of the model, for it asserts that (under our technological assumptions) once a hunting society diversifies into agriculture (or gathering), the pressure of increasing population on animal stocks disappears. Of course, the moment decreasing returns occur in agriculture, this result no longer holds.

It should be noted that the assumption of a mixed economy is presumed not to apply to the Paleo-Indians. For a pure hunter culture we have  $H = L$ , and the equilibrium animal stock is defined by  $F(\hat{M}) - \hat{M}\phi(\beta Ln/\hat{M}) = 0$ . Hence,

$$\frac{d\hat{M}}{dn} = \frac{(\beta Ln/M)\phi'}{D} < 0$$

if  $D = a' + (\beta Ln/M^2)\phi' < 0$ , which is required for stability.

### 5. Institutional and Analytical Aspects of Optimal versus Free-Access Hunting

Economists have long been familiar with the proposition that unconstrained nonpriced access to any common-property resource such as a fishing or hunting ground (Gordon 1954; Scott 1955; Smith 1968; Plourde 1971) leads to the inefficient use of such resources. This inefficiency takes the form of a reduction of the natural biological stock of the resource below the optimal stock required for sustained-yield harvesting. The phenomenon can be described as an instance of market (or price mechanism) failure after Bator (1958) or of property-right failure after Demsetz (1967). It is perhaps more accurately described as an instance of incentive failure caused by cultural or institutional inadequacies. What fails is the private incentive of the individual to harvest (and "conserve" the stock) at socially optimal levels over time. In principle, optimality can be achieved by (1) simulating the market that has failed, for example, by instituting a user charge—somewhat erroneously called a "tax"—for the resource, thereby inducing the individual to economize user payments by conserving his use of the resource; (2) instituting a property-right system which induces the individual to conserve his use of the resource as a means of maximizing the return on his property; (3) constraining individual hunting activity by social or legal restrictions such as quotas, sharing rules, licensing, or prohibitions; and (4) limiting the hunting harvest by enculturating voluntary conservationist values or behaviour.

Property rights, social or legal restrictions on individual harvesting, and the enculturation of conservationist behaviour have all been used extensively and ingeniously by primitive peoples at one time or another. However, the evidence is recent, for there appears to be no evidence to suppose that Paleolithic practices exhibited such sophistication. It is the hypothesis of this section that sometime after the extinction of the megafauna, human culture developed a sensitivity to the need to prevent overharvesting. Whether man as a superpredator was in fact the principal agent in the extinction of the large herbivores and their dependent carnivores and scavengers, it is plausible to assume that men saw parallels between hunting and the loss of the valued prey, from which arose oral and religious traditions, myths, and superstitions which had the effect and perhaps the intention of conserving common-property resources. At some point the ancestral message became a directive to "take sparingly of the bounty of nature."

Heizer (1955) provides pages of documented examples of primitive strictures on the harvesting of replenishable resources. One of the most common techniques was the private ownership of land—fishing holes, hunting grounds, nut-bearing trees, and grass seed areas (see Heizer [1955, p. 4] for numerous reference summaries on land ownership). Constraints on harvesting from common-property lands took many forms. Great Lakes Indians stripped only a portion of the fiber off basswood trees in order that the wound would heal and the tree live. Vancouver Island Indians "never fully strip the bark from a cedar tree lest the tree die and its spirit curse the man who peeled the bark and he die also" (Heizer 1955, p. 4). The Choctaw had laws regulating the game that could be killed by one family, with strict accounting by the captain of each band. The Kaska trap marten in a given area only every 2 or 3 years. The Iroquois spared the females of hunted species during the breeding season; the sparing of pregnant females was widespread. The Yurok had "game laws" the violation of which would cause loss of "hunting luck" (Heizer 1955, pp. 4–5). The Naskapi of Labrador are cited as typical of numerous tribes that believe animals and plants were created to help man (Heizer 1955, p. 6). In return for killing an animal, the hunter must protect it from profane treatment, such as wasting the animal or letting dogs gnaw its bones, lest the animal take offense and spoil the success of the hunter. Certain species may be hunted by some tribes but avoided by others in the belief that the tribe's ancestry traces to such species. Many tribes believe that game is watched over by supernatural authorities who become angry with men if too many deer are killed or if they merely wound the animals (Heizer 1955, p. 7).

Many more such examples could be cited, but evidence for conservationist ethics and institutions (defined as any set of strictures, laws,

or practices which limit the harvesting of common-property resources) is widespread among primitive peoples in historic or near historic times. Such primitive practices may appear to be exceedingly crude rationing devices. But every efficient price system has its dual equivalent quota system, and modern legislators no less than primitive peoples find it more natural to think in terms of quota restrictions on external effects than in terms of prices.

Among primitive peoples who have invented property-right systems, there are instances of sophistication that would rival the modern property deed. Thus, among the Karok private ownership of a particular fishing ground did not mean owning the land along the river but owning the right to fish a given stretch of the river regardless of who owned the land (Kroeber and Barrett 1960, pp. 3–4). A fishing right might entitle the owner to use the spot every third night and day, with the right transferable by sale or inheritance. Similarly, the right to hunt or share in the hunting of sea lions on a particular rock was owned, and each person on a particular stretch of coast had rights to some cut of a beached whale, with residents of other areas denied such rights except by inheritance or purchase (Kroeber and Barrett 1960, p. 115).

The possibility of the existence of property rights or quota regulations governing hunted resources raises the issue of optimal versus free-access harvesting of species. In the following analysis, the assumptions of the previous simple model of production from a common-property hunted resource and an appropriated agricultural resource will be used to state an optimal control model. Primarily, the model will be used to study the conditions for optimal versus free-access species extinction.

If  $\delta$  is the time preference discount rate for an individual and we assume that instantaneous utility,  $u = c(t) + vm(t)$ , is additive over time, then total welfare for the economy is

$$\lim_{T \rightarrow \infty} \int_0^T u e^{-\delta t} dt,$$

to be maximized subject to the production function and resource constraints and the resource growth equation (1). Making the substitutions  $c = \gamma(L - H)$  and  $m = (M/n)\phi(x)$ , the current-value Hamilton-Lagrange criterion is (Arrow 1968)

$$\Psi = \gamma(L - H) + \left(\frac{vM}{n}\right) \phi\left(\frac{\beta H n}{M}\right) + \mu M \left[ a(M; k) - \phi\left(\frac{\beta H n}{M}\right) \right]$$

to be maximized with respect to the control variable  $H$ , where  $0 \leq H \leq L$ . Necessary conditions, according to the maximum principle, are

that

$$\text{if } \frac{\partial \psi}{\partial H} \begin{cases} < 0, \text{ then } H = 0, \\ = 0, \text{ then } 0 \leq H \leq L, \\ > 0, \text{ then } H = L, \end{cases} \quad (8)$$

$$\mu'(t) = \delta\mu - \frac{\partial \psi}{\partial M}, \quad (9)$$

$$M'(t) = M[a(M; k) - \phi(x)], \quad (10)$$

and the transversality conditions

$$\lim_{t \rightarrow \infty} e^{-\delta t} \mu(t) M(t) = 0, \quad \lim_{t \rightarrow \infty} e^{-\delta t} \mu(t) \geq 0.$$

Letting  $\xi = n\mu$ , condition (8) implies the following:

$$\text{if } \frac{r}{v - \xi} \begin{cases} > \phi' \left( \frac{\beta H n}{M} \right), \text{ then } H = 0, \\ = \phi' \left( \frac{\beta H n}{M} \right), \text{ then } 0 \leq H \leq L, \\ < \phi' \left( \frac{\beta H n}{M} \right), \text{ then } H = L. \end{cases} \quad (11)$$

Consequently, if we define  $\phi'_0 = \phi'(0)$ ,  $\xi_0 = (v - r/\phi'_0)$  if  $\phi'_0 > r/v$ , with  $\xi_0 = 0$  otherwise, and let the separating boundary between a pure hunter economy and a hunter agrarian economy be  $\xi(M) \equiv v - r/\phi'(\beta L n/M)$ , then (9) and (10) can be written<sup>8</sup>

$$\xi'(t) = \begin{cases} \xi[\delta - F'(M)], \text{ if } \phi'_0 < \frac{r}{v - \xi}, \text{ or } \xi > \xi_0; & (12a) \\ \xi[\delta - F'(M)] - (v - \xi) \\ \times \left\{ \phi \left[ \phi'^{(-1)} \left( \frac{r}{v - \xi} \right) \right] - \left( \frac{r}{v - \xi} \right) \phi'^{(-1)} \left( \frac{r}{v - \xi} \right) \right\}, & \text{if } \xi(M) \leq \xi \leq \xi_0; & (12b) \\ \xi[\delta - F'(M)] - (v - \xi) \left[ \phi \left( \frac{\beta L n}{M} \right) - \left( \frac{\beta L n}{M} \right) \phi' \left( \frac{\beta L n}{M} \right) \right], & \text{if } \phi' \left( \frac{\beta L n}{M} \right) > \frac{r}{v - \xi}, \text{ or } \xi < \xi(M); & (12c) \end{cases}$$

<sup>8</sup> These conditions are sufficient as well as necessary if  $\Psi$  is concave in  $M$  for given  $\xi$  and  $t$  and for  $H$  set at its maximizing level. Under the assumptions in the text,  $\Psi$  is concave in  $M$  for  $v \geq \xi \geq 0$ .

$$M'(t) = \begin{cases} Ma(M; k), \text{ if } \xi > \xi_0; & (13a) \\ M \left\{ a(M; k) - \phi \left[ \phi'^{(-1)} \left( \frac{r}{v - \xi} \right) \right] \right\}, & \text{if } \xi(M) \leq \xi \leq \xi_0; & (13b) \\ M \left[ a(M; k) - \phi \left( \frac{\beta L n}{M} \right) \right], \text{ if } \xi < \xi(M). & (13c) \end{cases}$$

Note that the equality condition in (11) reduces to (3) for free-access harvesting when  $\xi = 0$ . The  $\xi$  is interpreted as the market value of a live unit of the animal stock. Ordinarily we would think of  $\xi$  as being nonnegative. A negative value would correspond to animals that are a public nuisance requiring a bounty for optimal social control. This value is zero to the individual in the absence either of adequate property rights in live animals or of harvesting restrictions which impute value to live animals. Thus, enculturated limitations on free-access harvesting, such as lead hunters to believe they will receive supernatural punishment if they harvest too much game, impute a positive value,  $\xi$ , to live animals. One does not need to pass judgment on the merits of such devices for social control over the chase to appreciate their behavioral (and imputed price) effects.

Since  $\xi$  is the social marginal value of a live animal, the quantity  $v - \xi$  in (11)–(13) is the net marginal value of a harvested animal. Since  $\phi - (\beta H n/M)\phi'$  for  $H \leq L$  is the marginal physical product of the biomass of game (biological capital), equations (12b) and (12c) require the net marginal value productivity of the game stock,  $(v - \xi)[\phi - (\beta H n/M)\phi']$  for  $H \leq L$ , to equal net interest on investment in a live animal less capital gains,  $\xi[\delta - F'(M)] - \xi'$ , where the interest rate,  $\delta - F'(M)$ , is reckoned net of the biological "own" rate,  $F'(M)$ . The biological rate,  $F'(M)$ , is analogous to a capital depreciation rate when  $F'(M) < 0$  and a capital appreciation rate when  $F'(M) > 0$ .

Equations (12) and (13) provide two first-order autonomous differential equations in  $[\xi(t), M(t)]$  which, together with the transversality conditions and initial conditions, must be satisfied along an optimal bionomic development path. Paths satisfying (12) and (13) will be characterized by the usual phase diagram representation in  $(\xi, M)$  space.

In figures 2–4 the set of points  $E(\xi)$  is defined by the condition  $\xi'(t) = 0$  in (12) and represents the stationary state asset demand for the animal stock. The set of points  $B(\xi)$  is defined by the condition  $M'(t) = 0$  in (13) and represents the stationary state asset supply of animals. Properties of these functions and the phase diagrams in figures 2–4 are derived in the Appendix.

Along  $E(\xi)$  the value of the marginal product of the game stock is

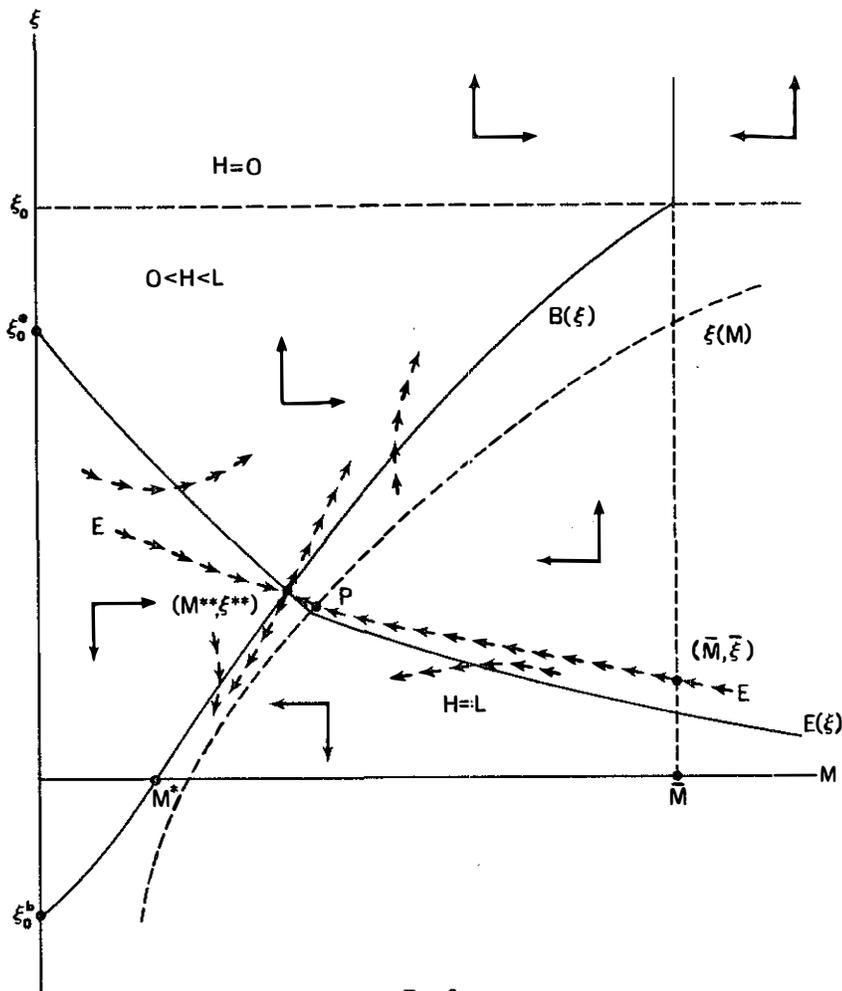


FIG. 2

equal to interest net of biological growth. Hence, an increase in the animal stock reduces biological growth, increases net interest, and reduces the price of live animals. Along  $B(\xi)$ , the harvest intensity is equal to average biological growth. For a mixed economy, increases in the live animal price reduce the harvest per unit of biomass and increase the game stock.

An optimal equilibrium path yielding a mixed economy in the stationary state is shown in figure 2. Starting with initial conditions  $(\bar{M}, \bar{\xi})$ , it is socially desirable for the culture to specialize in hunting. As the game stock is depleted and its value rises, optimality requires the economy eventually (beginning at  $P$ ) to begin agricultural production. In long-run

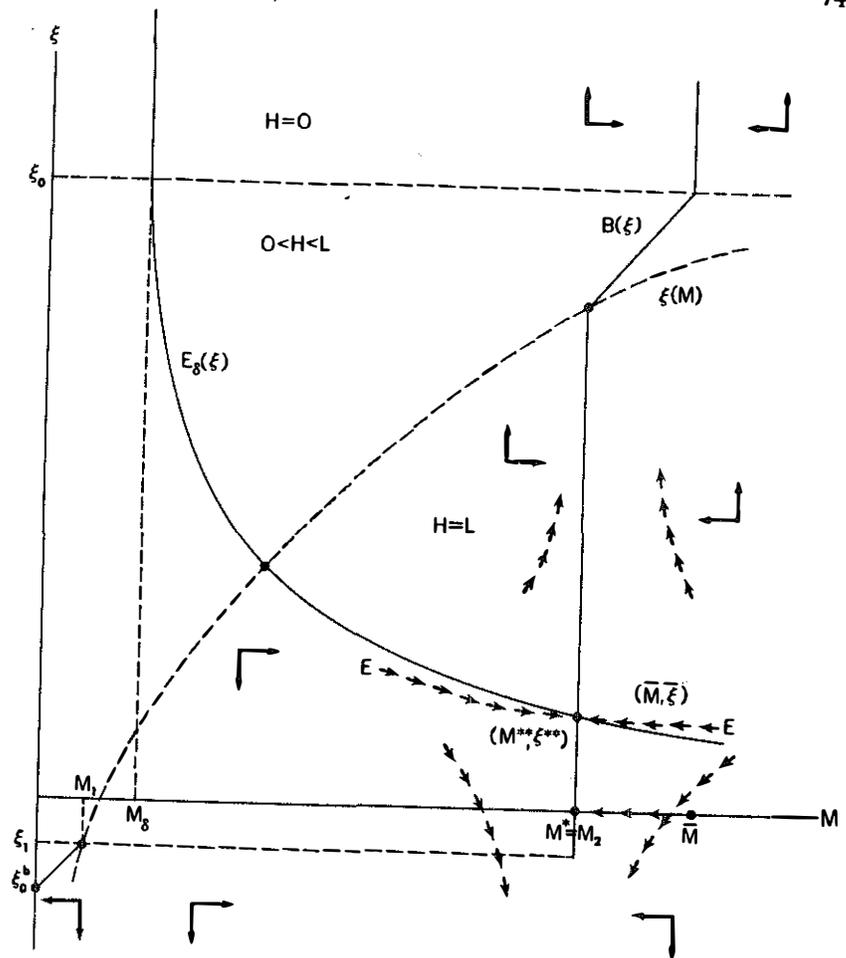


FIG. 3

equilibrium at  $(M^{**}, \xi^{**})$ , both hunting and agriculture reach stable levels of production. Figure 3 illustrates an optimal path for an economy that begins as, and remains to the end, a culture of specialized hunters. In this case, the free-access economy produces a socially optimal equilibrium.

Agricultural specialization may occur following a period of hunting that causes extinction. This is illustrated in figure 4 in which  $\xi_0^b > \xi_0^e$ , where  $B(\xi_0^b) = E(\xi_0^e) = 0$ . At all prices  $\xi \leq \xi_0^b$ , the harvest rate exceeds the growth rate for every live animal stock, causing extinction. At all prices  $\xi \geq \xi_0^e$ , interest on investment in animals exceeds the net value of the marginal product of live animals for every animal stock. Hence,  $\xi_0^b \geq \xi_0^e$  implies that, along an optimal development path, the

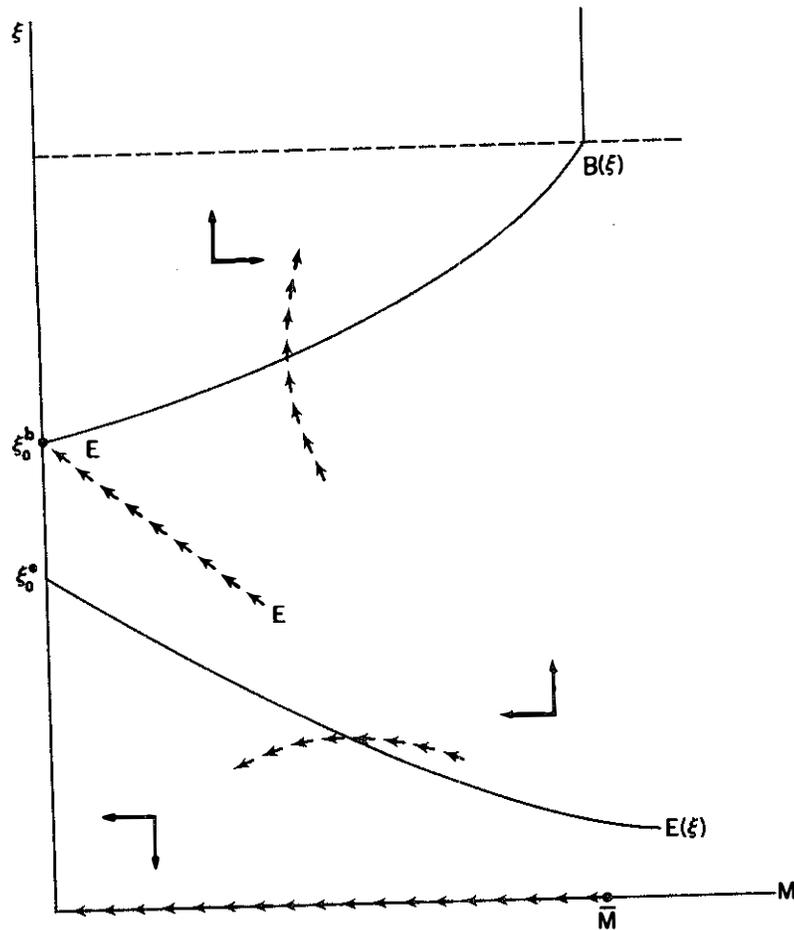


FIG. 4

economy perpetually consumes capital and must eventually wipe out the stock of live animals and specialize thereafter in agriculture. Along an optimal path beginning at  $(\bar{M}, \bar{\xi})$  one would at first observe a pure hunter culture, then a mixed economy, and ultimately an agrarian economy.

The effect of free-access harvesting and its contrast with an optimal development path are obtained by setting  $\xi = 0$  for all  $t$ . This condition replaces those stated in (12) and corresponds to the nonexistence of a market in live animals or of any equivalent valuation system for expressing the opportunity costs of the current harvest. In effect, the "demand" for biological capital is perfectly elastic at  $\xi = 0$ . If  $\xi_0^b > 0$ , the free-access economy eventually harvests to extinction as in figure 4. If  $\xi_0^b < 0$ , such an economy harvests short of extinction and conserves an animal stock  $M^* = B(0) > 0$  as in figures 2 and 3.

Figures 2 and 4 apply to "high-impatience" economies,  $\delta \geq F'_0$ . For low-impatience economies,  $\delta < F'_0$ , extinction of an animal species will never be optimal since the net cost of biological capital  $\delta - F'(M) \rightarrow 0$  as  $M \rightarrow M_\delta$ , making it optimal to stop biological capital consumption at  $M = M_\delta$  for all capital prices  $\xi \geq \xi_0$ . This means that the static asset demand for biological capital becomes completely inelastic at  $M = M_\delta$ ,  $\xi \geq \xi_0$ , as illustrated by  $M = E_\delta(\xi)$  in figure 3. However, the concept of "high" or "low" impatience must be measured relative to the biotic growth potential of the hunted species. Using the simple parameterization  $F(M) = kG(M)$ , a relatively high (low) impatience economy is defined by  $\delta/k \geq G'_0(\delta/k < G'_0)$ . If  $F'_0 = kG'_0$  is finite for any given species, it is clear that there always exists a cultural impatience rate,  $\delta$ , high enough that it may be optimal to harvest the species to extinction.

## 6. Comparative Stationary States of Hunting

For interior solutions  $0 < H < L$ , the effect of the parameters  $(\delta, r, v, k)$  on the optimal stationary-state level  $M^{**}$  is obtained by implicit differentiation of the following equations:

$$\xi[\delta - F'(M^{**})] - (v - \xi)(\phi - x\phi') = 0, \quad (14)$$

$$a(M^{**}; k) - \phi(x^*) = 0, \text{ where } x^* = \phi'^{-1}\left(\frac{r}{v - \xi^{**}}\right). \quad (15)$$

Since

$$D = \begin{vmatrix} \delta - F' + \phi & -\xi F'' \\ -\frac{(\phi')^2}{\phi''(v - \xi)} & a' \end{vmatrix} < 0,$$

we deduce

$$\frac{dM^{**}}{dk} = -\frac{(\delta - F' + \phi)a}{kD} > 0,$$

$$\frac{dM^{**}}{dr} = \frac{\phi'(\delta - F') + \phi'(\phi - x\phi')}{\phi''(v - n\xi)D} > 0,$$

$$\frac{dM^{**}}{dv} = \frac{(\phi')^2(\delta - F')}{\phi''(v - \xi)D} < 0,$$

$$\frac{dM^{**}}{d\delta} = -\frac{(\phi')^2\xi}{\phi''(v - \xi)D} < 0.$$

The optimal stationary-state animal stock is smaller (and the prospect of extinction greater) the lower the biotic potential of the species, the lower the efficiency of labor in agriculture relative to hunting, the higher the cultural value placed on meat, and the higher the culture's preference for present over future consumption. Certain features of the prey stock

may affect both  $r$  and  $k$ . Thus, if larger animals have a lower biotic potential and are easier to hunt, this implies lower  $r$  and lower  $k$ , yielding a magnified decrease in  $M^{**}$ .

These results and the similar conclusions of Section 4 for free-access hunting do not provide any new evidence on the causes of Pleistocene extinction. They are offered in an attempt to demonstrate the use of a coherent economic framework for the study and evaluation of extinction or other hypotheses concerning the primitive hunter culture.<sup>9</sup> It is hoped that the framework of this paper will enhance the possibility of a more comprehensive evaluation of the limited qualitative cross-cultural, chronological, and regional data on hunting-gathering-agricultural activities in primitive societies.

**Appendix**

In this Appendix, properties of the differential equations (12) (13) and their phase diagram representation will be developed in greater detail. First consider (12):

1. From (12a) we have  $\xi'(t) \cong 0$  according as  $\delta - F'(M) \cong 0$  for  $\xi > \xi_0$ . Let  $\delta - F'(M) \leq 0$  for  $0 \leq M \leq M_\delta$  and  $\delta - F'(M) > 0$  for  $M > M_\delta$ . Then  $\xi'(t) \leq 0$  in the region ( $\xi > \xi_0$ ,  $0 \leq M \leq M_\delta$ ), and  $\xi'(t) > 0$  in ( $\xi > \xi_0$ ,  $M > M_\delta$ ). This is illustrated by the vertical arrow above  $\xi_0$  in figure 2 for the case in which  $M_\delta = 0$ , that is,  $\delta - F'(0) \geq 0$ . It should be noted that  $\xi_0 = 0$  in the event that  $\phi_0 \leq r/v$ , that is, hunting is uneconomical relative to agriculture at all hunting intensities even when live animals have zero value. This degenerate case leads to agricultural specialization from time zero, which must be distinguished from agricultural specialization following the hunting of prey to extinction.

2. From (12b)-(12c), let  $M = E(\xi)$  be defined by the set of points  $[(\xi, M) | \xi'(t) = 0, 0 \leq \xi \leq \xi_0, M \geq 0]$ . The condition  $\xi'(t) = 0$  requires

$$\delta - F'(M) = \left( \frac{v - \xi}{\xi} \right) \left\{ \phi \left[ \phi^{(-1)} \left( \frac{r}{v - \xi} \right) \right] - \left( \frac{r}{v - \xi} \right) \phi^{(-1)} \left( \frac{r}{v - \xi} \right) \right\}, \quad \xi(M) \leq \xi \leq \xi_0, \quad (16a)$$

$$\left( \frac{v - \xi}{\xi} \right) \left[ \phi \left( \frac{\beta Ln}{M} \right) - \left( \frac{\beta Ln}{M} \right) \phi' \left( \frac{\beta Ln}{M} \right) \right], \quad \xi < \xi(M), \quad (16b)$$

that is, the net rate of interest must equal the relative value marginal productivity of the biomass of prey. The function  $E(\xi)$  implied by the interior solution (16a) is derived graphically in figure 5 for two distinguishing cases: (1) if  $F'_0 \leq \delta$ , the curve labeled  $E(\xi)$  is obtained; (2) if  $F'_0 > \delta$ , the curve labeled  $E_\delta(\xi)$  is the result. The curve in quadrant I of figure 5 is the relative value marginal productivity of the biomass. Quadrant II shows net interest as a function of the biomass of game. For each price of live game  $\xi$  such that net interest equals

<sup>9</sup> For example, if the environment was economically more favorable for gathering in Africa than it was in North America, then the overkill hypothesis is not inconsistent with the greater survival of megafauna in Africa.

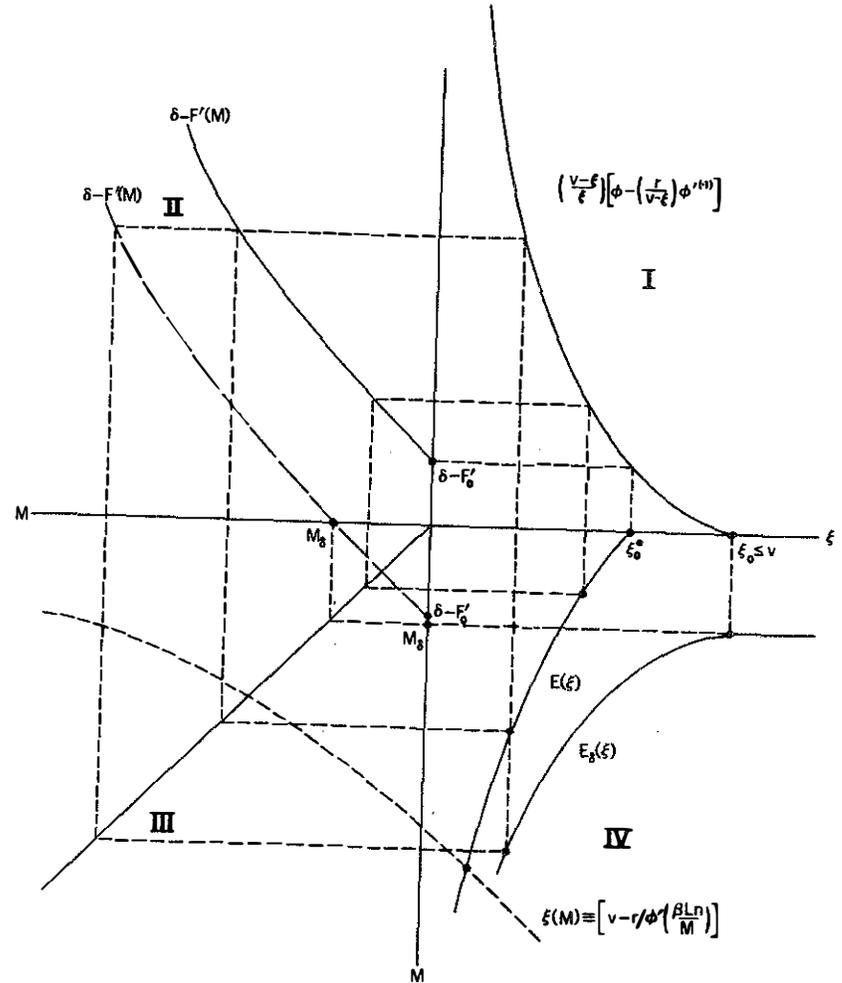


FIG. 5

relative value marginal productivity, we associate a biomass  $M \geq 0$  in quadrant IV. Curve  $E(\xi)$  or  $E_\delta(\xi)$  represents economic equilibrium in the capital market where capital gains (losses) vanish. Quadrant IV also illustrates the boundary  $\xi(M) \equiv [v - r/\phi'(\beta Ln/M)]$  separating the interior region  $\xi(M) \leq \xi \leq \xi_0$ , representing a mixed hunter-agrarian economy, from the region  $\xi < \xi(M)$ , representing the specialized hunter economy. This boundary is monotone increasing,  $\xi'(M) = -(r\phi''\beta Ln)/[(\phi')^2 M^2] > 0$ ,

$$\text{with } \lim_{M \rightarrow 0} \xi(M) = -\infty \text{ if } \lim_{x \rightarrow \infty} \phi'(x) = 0, \text{ and } \lim_{M \rightarrow \infty} \xi(M) = \xi_0.$$

Some key properties of  $E(\xi)$  are summarized below.

a) At  $M = 0$ , if  $\delta - F'_0 \geq 0$ , then  $\xi = \xi_0^* \leq \xi_0 \leq v$  satisfies (16a). At  $M = M_b$ , if  $\delta - F'_0 < 0$  and  $\delta = F'(M_b)$ , then  $\xi = \xi_0$ .

b) 
$$\lim_{M \rightarrow \infty} E^{-1}(M) = 0,$$

since  $\phi - (\beta Ln/M)\phi' \rightarrow 0$  in (16b) while  $\delta - F' > 0$ .

c) The function  $E(\xi)$  is monotone decreasing; that is, differentiating (16a) and (16b), it can be verified that  $dM/d\xi < 0$  and from (12b) and (12c) that  $\partial \xi'(t)/\partial \xi > 0$ ,  $\xi \leq \xi_0$ , as illustrated by the vertical arrows in figure 2.

Now consider (13):

1. From (13a),  $M'(t) \geq 0$  according as  $0 < M \leq \bar{M}$ , if  $\xi > \xi_0$  as indicated by the horizontal arrows above  $\xi_0$  in figure 2.

2. From (13b) and (13c), let  $M = B(\xi)$  be defined by the set of points  $[(\xi, M) | M'(t) = 0, \xi \leq \xi_0, M \geq 0]$ . This implies

$$a(M; k) = \begin{cases} \phi \left( \frac{\beta H n}{M} \right), & \text{if } \frac{\beta H n}{M} = \phi^{(-1)} \left( \frac{r}{v - \xi} \right), \\ \phi \left( \frac{\beta L n}{M} \right), & \text{if } \frac{\beta L n}{M} \leq \phi^{(-1)} \left( \frac{r}{v - \xi} \right). \end{cases} \quad (17)$$

For each  $\xi \leq \xi_0$ , this equation provides a corresponding  $M \geq 0$ . Points on  $M = B(\xi)$  represent biological equilibrium in the prey stock. In figure 6, let  $k = k_1$ , giving the monotone decreasing percentage average rate of biomass growth  $a(M; k_1)$ . Since this function is everywhere below the harvest per unit of biomass when the economy specializes in hunting, it follows that we have an interior maximum  $0 < H < L$  for every  $\xi$  and a corresponding  $M$  determined by the intersection  $a(M; k_1) = \phi \{ \phi^{(-1)} [r/(v - \xi)] \}$ . At  $\xi = \xi^*$  equilibrium is at  $Q^*$ , while at  $\xi = \xi'' < \xi^*$  equilibrium is at  $Q''$ . For this case the function  $B(\xi)$  will be in the region  $\xi(M) \leq \xi \leq \xi_0$  as shown in figure 2. But if  $k = k_2$  the constraining boundary set defined by  $\phi(\beta Ln/M)$  intersects  $a(M; k_2)$  at two points corresponding to a biomass  $M_1$  and  $M_2$  as shown in figure 6. Consequently, for any  $\xi$  such that  $\xi_1 < \xi < \xi_2$ , where  $M_1 = B(\xi_1)$ ,  $M_2 = B(\xi_2)$  (e.g.,  $\xi = \xi''$  in fig. 6), hunting intensity is constrained at the level  $\beta Ln/M$  and the harvest intensity is  $\phi(\beta Ln/M) < a(M; k_2)$ , with  $M'(t) > 0$  for all  $M_1 < M < M_2$ . Thus, at  $\xi_1$  an increase in the stock above  $M_1$  reduces harvest intensity by more than growth intensity because hunting effort cannot be increased. The stock rises until  $M_2$  is reached, where the growth rate is depressed to the level of the harvest. Hence, equilibrium on  $M = B(\xi)$ , just above  $\xi_1$ , is reached because of naturally occurring diminishing returns to biomass growth and cannot be influenced by the control  $H$ . In figure 3 this means that the function  $B(\xi)$  intersects the boundary  $\xi(M)$  and is discontinuous at  $M_1 = B(\xi_1)$ . This phenomenon is a property of labor-scarce economies, since for  $L$  large enough  $B(\xi)$  will be entirely in the interior set for a mixed economy.

Some key properties of  $B(\xi)$  in the interior  $[\xi(M) < \xi < \xi_0, M \geq 0]$  are:

a) At  $M = 0$ ,  $\xi = \xi_0^* \geq 0$  satisfies (17).

b) At  $M = \bar{M}$   $a(\bar{M}; k) = 0$  and  $\xi = \xi_0$ .

c) The function  $B(\xi)$  is monotone increasing, that is, from (17),  $dM/d\xi > 0$ . From (13b) and (13c), referring to figures 3 and 6, if:

i)  $\xi < \xi_1$ , then (a)  $M'(t) > 0$  if  $M < B(\xi)$ ; (b)  $M'(t) < 0$  if  $B(\xi) < M < M_1$ ; (c)  $M'(t) > 0$  if  $M_1 < M < M_2$ ; and (d)  $M'(t) < 0$  if  $M > M_2$ .

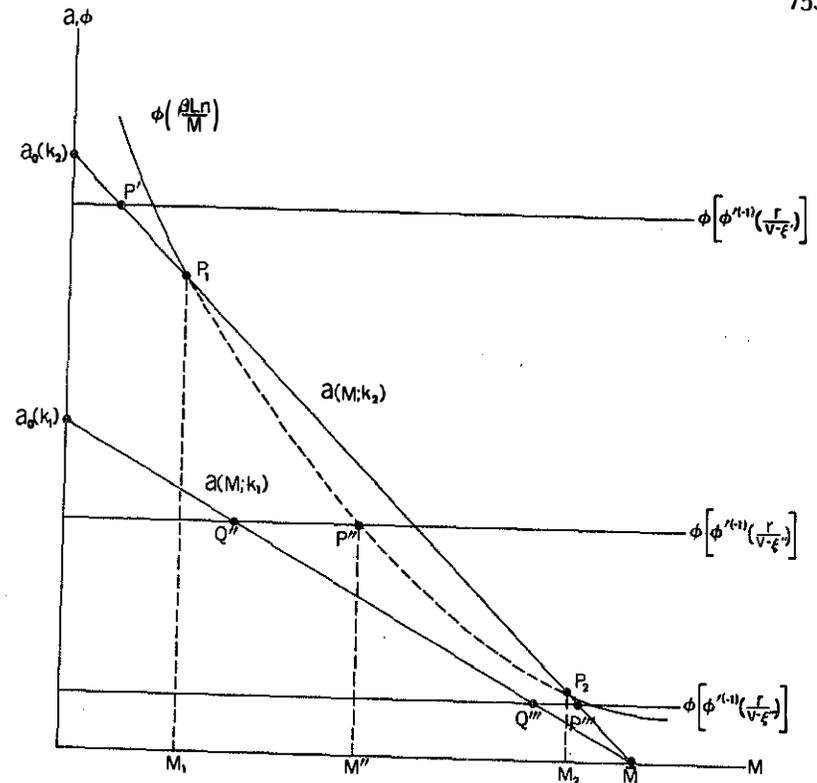


FIG. 6

ii)  $\xi_1 < \xi \leq \xi_2$ , then (a)  $M'(t) > 0$  if  $M < M_2$  and (b)  $M'(t) < 0$  if  $M > M_2$ .

iii)  $\xi_2 < \xi < \xi_0$ , then (a)  $M'(t) > 0$  if  $M < B(\xi)$  and (b)  $M'(t) < 0$  if  $M > B(\xi)$ . Each of these directions of motion is illustrated by the horizontal arrows in figure 3.

References

Agogino, G. A., and Frankforter, W. D. "A Paleo-Indian Bison-Kill in Northwestern Iowa." *American Antiquity* 25, no. 3 (January 1960): 414-15.  
 Arrow, K. J. "Applications of Control Theory to Economic Growth." In *Mathematics of the Decision Sciences*, pt. 2, edited by G. B. Dantzig and A. F. Veinott, Jr. Providence, R.I.: American Math. Soc., 1968.  
 Bator, F. "The Anatomy of Market Failure." *Q.J.E.* 72 (August 1958): 351-79.  
 Butler, B. R. "A Bison Jump in the Upper Salmon River Valley of Eastern Idaho." *Tebiwa*, vol. 14, no. 1 (1971).  
 Clarke, C. W. "Profit Maximization and the Extinction of Animal Species." *J.P.E.* 81, no. 4 (July/August 1973): 950-61.  
 Covey, C., ed. *Cabeza de Vaca's Adventures in the Unknown Interior of America*. New York: Collier, 1961.

- Demsetz, H. "Toward a Theory of Property Rights." *A.E.R.* 57 (May 1967): 347-73.
- Edwards, W. E. "The Late-Pleistocene Extinction and Diminution in Size of Many Mammalian Species." In *Pleistocene Extinctions*, edited by P. S. Martin and H. E. Wright, Jr. New Haven, Conn.: Yale Univ. Press, 1967.
- Gordon, H. S. "The Economic Theory of a Common Property Resource: The Fishery." *J.P.E.* 62, no. 2 (April 1954): 439-51.
- Gould, J. R. "Extinction of a Fishery by Commercial Exploitation: A Note." *J.P.E.* 80, no. 5 (September/October 1972): 1031-39.
- Gross, Hugo. "Mastodon, Mammoth, and Man in America." *Bull. Texas Archeological and Paleontological Soc.*, no. 23 (October 1951): pp. 101-31.
- Guilday, J. E. "Differential Extinction during Late-Pleistocene and Recent Times." In *Pleistocene Extinctions*, edited by P. S. Martin and H. E. Wright, Jr. New Haven, Conn.: Yale Univ. Press, 1967.
- Hammond, J. "Growth in Size and Body Proportions in Farm Animals." In *Growth in Living Systems*, edited by M. X. Zarrow. New York: Basic Books, 1961.
- Haury, E. W.; Antevs, E.; and Lance, J. F. "Artifacts with Mammoth Remains, Naco, Arizona." *American Antiquity* 19, no. 1 (July 1953): 1-24.
- Haury, E. W.; Sayles, E. B.; and Wasley, W. W. "The Lehner Mammoth Site, Southeastern Arizona." *American Antiquity* 25, no. 1 (July 1959): 1-30.
- Haynes, C. V. "Fluted Projectile Points: Their Age and Dispersion." *Science*, June 19, 1964, pp. 1408-13.
- . "Carbon-14 Dates and Early Man in the New World." In *Pleistocene Extinctions*, edited by P. S. Martin and H. E. Wright, Jr. New Haven, Conn.: Yale Univ. Press, 1967.
- Heizer, R. F. *Primitive Man as an Ecologic Factor*. Kroeber Anthropological Society Papers no. 13. Berkeley: Univ. California Press, 1955.
- Hester, J. J. "The Agency of Man in Animal Extinctions." In *Pleistocene Extinctions*, edited by P. S. Martin and H. E. Wright, Jr. New Haven, Conn.: Yale Univ. Press, 1967.
- Hester, J. J., and Wendorf, F. "Early Man's Utilization of the Great Plains Environment." *American Antiquity* 28, no. 2 (October 1962): 159-71.
- Irwin-Williams, C. "Associations of Early Man with Horse, Camel, and Mastodon at Hueyatlaco, Valsequillo (Puebla, Mexico)." In *Pleistocene Extinctions*, edited by P. S. Martin and H. E. Wright, Jr. New Haven, Conn.: Yale Univ. Press, 1967.
- Jelinek, A. J. "Man's Role in Extinction of Pleistocene Faunas." In *Pleistocene Extinctions*, edited by P. S. Martin and H. E. Wright, Jr. New Haven, Conn.: Yale Univ. Press, 1967.
- Kehoe, T. F. "The Boarding School Bison Drive Site." *Plains Anthropologist*, vol. 12, no. 35 (February 1967).
- Kroeber, A. L., and Barrett, S. A. *Fishing among the Indians of Northwestern California*. Anthropological Records, vol. 21, no. 1. Berkeley: Univ. California Press, 1960.
- Leonhardy, F. C., ed. *Domebo: A Paleo-Indian Mammoth Kill in the Prairie-Plains*. Lawton, Okla.: Great Plains Hist. Assoc., 1966.
- Lotka, A. *Elements of Mathematical Biology*. New York: Dover, 1956.
- MacCurdy, G. G. *Human Origins*. Vol. 1. New York: Appleton-Century, 1933.
- Mangelsdorf, P. C., and Smith, C. E., Jr. "New Archaeological Evidence on Evolution in Maize." *Botanical Museum Leaflets*, vol. 13, no. 8 (1949).
- Martin, P. S., and Guilday, J. E. "A Bestiary for Pleistocene Biologists." In *Pleistocene Extinctions*, edited by P. S. Martin and H. E. Wright, Jr. New Haven, Conn.: Yale Univ. Press, 1967.

- Martin, Paul S. "Prehistoric Overkill." In *Pleistocene Extinctions*, edited by P. S. Martin and H. E. Wright, Jr. New Haven, Conn.: Yale Univ. Press, 1967.
- . "Discovery of America: Pleistocene Extinctions Following Migration to the Western Hemisphere." *Science*, March 9, 1973, pp. 969-74.
- Mech, David L. *The Wolf*. Garden City, N.Y.: Nat. Hist. Press, 1970.
- Plourde, C. "Exploitation of Common-Property Replenishable Natural Resources." *Western Econ. J.* 9 (September 1971): 256-66.
- Sauer, Carl O. "A Geographical Sketch of Early Man in America." *Geographical Rev.* 34, no. 4 (1944): 529-73.
- Scott, A. "The Fishery: The Objectives of Sole Ownership." *J.P.E.* 63, no. 2 (April 1955): 116-24.
- Slaughter, B. H. "Animal Ranges as a Clue to Late-Pleistocene Extinction." In *Pleistocene Extinctions*, edited by P. S. Martin and H. E. Wright, Jr. New Haven, Conn.: Yale Univ. Press, 1967.
- Smith, V. L. "Economics of Production from Natural Resources." *A.E.R.* 58 (June 1968): 409-31.
- Strong, W. D. "From History to Prehistory in the Northern Great Plains." In *Essays in Historical Anthropology of North America*. Washington: Smithsonian Inst., 1940.
- Wedel, W. R. *An Introduction to Pawnee Archeology*. Bureau of American Ethnology, bull. 112. Washington: Smithsonian Inst., 1936.
- . *Culture Sequences in the Central Great Plains*. Washington: Smithsonian Inst., 1940.
- Wheat, J. B. "A Paleo-Indian Bison Kill." *Scientific American* 216 (January 1967): 44-51.