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Deferred Harvests: The Transition from Hunting to Animal Husbandry

We define *animal husbandry* as prey conservation. Conservation is rare among extant hunters and only likely to occur when prey are highly valued, private goods. The long-term discounted deferred returns from husbandry must also be greater than the short-term returns from hunting. We compare the returns from hunting and husbanding strategies as a function of prey body size. Returns from husbanding are estimated using a maximum sustainable yield (MSY) model. Following Charnov (1993), allometric analyses show that the MSY is nearly independent of prey body size. The opportunity costs of husbanding are measured as prey standing biomass times the discount rate. Since standing biomass scales positively with body size, the opportunity costs of husbanding are greater for larger animals. An evolutionary discount rate is estimated following Rogers (1994) to be between 2.4% and 6%. Using these values, the prey body size for which hunting and meat-only husbanding provide the same return is approximately 40kg. Animals greater than 40kg are predicted to be hunted. *[animal husbandry, evolutionary ecology, allometry, hunting, Neolithic transition]*

The subsistence transition that occurred at the end of the Pleistocene has been of continuing interest to anthropologists (Binford 1968; Byrd 1994a; Childe 1952; Flannery 1965; Harris 1977, 1998; Henry 1995; Price and Brown 1985; Winterhalder and Goland 1997; Zeder 1994; and others). During this transition, humans moved from a full-time hunting and gathering way of life to one based on food production. This Neolithic transition was a watershed shift in the subsistence strategy for our species. Associated with the transition were a number of well-documented components including sedentism (Bar-Yosef and Belfer-Cohen 1989; Brown 1985; Harris 1977; Liebermann 1993), increased population density (Cohen 1977; Harris 1977), as well as the development of political, social, and economic complexity (Brown 1985; Byrd 1994b; Harris 1977; Price and Brown 1985; Wright 1978).

A major feature of the transition was the change in our relationship to other organisms. Humans shifted from being hunters and gatherers to resource husbanders. We went from exploiting the somatic potential of other organisms to co-opting and increasing their reproductive potential. An important aspect of this change involved the timing of resource use. Most hunter-gatherers focus on short-term returns, while food producers have a more farsighted perspective (Woodburn 1982). This difference has major implications for how individuals make subsistence decisions. In this article, we focus on the shift from hunting to animal husbandry by applying an evolutionary ecology approach. From the perspective of evolutionary theory and rational choice theory in economics (see Smith and Winterhalder 1992), animal husbandry presents a number of interesting theoretical problems. Models to explain why the transition occurred, as well as when and where it did, have tended to focus around climate change, resource stress, and population pressures as the key causal variables (e.g., Binford 1968; Childe 1952; Cohen 1977; Flannery 1973; Harris 1977, 1998; Hole 1996; McCorriston and Hole 1991; Price and Brown 1985; Rosenberg 1990). This is interesting because, as we will argue below, animal husbandry involves deferring benefits at a time when, according to many arguments, resources were becoming scarce (Cohen 1977:40; Hecker 1984; Kent 1988). While in hindsight animal husbandry seems like a logical long-term solution, husbandry in the short term was a costly proposition to its early practitioners.

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Foraging Theory, Game Conservation, and Traditional Hunters

To understand the economics of husbandry from a hunter's point of view, it is useful to review work on resource conservation. Recent empirical work has produced a growing consensus that resource conservation in traditional hunting economies is not as common as previously thought (Alvard 1993, 1994, 1995, 1998; Hames 1987, 1991; Low 1996; Low and Heinen 1993; Ruttan and Borgerhoff Mulder 1999; Smith 1983). Original confusion resulted because many subsistence behaviors are *apparently* conservative when they are associated with sustainable harvests or the harvests are biased in ways that are consistent with genuine conservation. Such outcomes are termed *epiphenomenal conservation* (Hunn 1982).

To avoid this sort of confusion, Alvard (1995, 1998) developed an operational definition of *conservation* to allow empirical testing using foraging theory. Foraging theory predicts subsistence decisions by assuming that hunters maximize foraging return rates independent of long-term depletion effects (for a review see Kaplan and Hill 1992). *Conservation* is defined as subsistence behavior where the conserver checks his or her level of resource use to some point below what would be fitness maximizing in the short term. The costs of this restraint are exchanged for future long-term, sustainable benefit. Using the short-term cost criterion alone, behavior that has unintended conservation-like consequences but no short-term costs can be rejected as conservation.

While the basic foraging models describe foragers as short-term maximizers, the resource conservation models describe foragers as long-term maximizers (Alvard 1993, 1998). Slobodkin (1961, 1968; see also Errington 1946) argued that a "prudent predator" would harvest those members of the prey population with the lowest reproductive value. *Reproductive value*, defined by Fisher (1958), is a function of age and is the relative number of offspring that remain to be born to an individual of age *x*, taking into account the probability that the individual will live to age *x*. Reproductive value is low among young animals because mortality for most mammals is very high in the young and many do not attain reproductive age. Critical to the argument developed below, resource conservation predicts intraspecific selectivity similar to a husbanding or management strategy. To maximize long-term return rates, harvests are biased toward males and low reproductive value individuals. In fact, one way that archaeologists show that prehistoric people were husbanding animals is by examining the sex and age distribution of faunal remains. Animal husbandry is revealed with a characteristic mortality signature consisting of a disproportionate number of young males (Redding 1981).

Alvard tested the foraging and conservation hypotheses among the Piro of the Peruvian Amazon. This work indicates that hunters killed prey types predicted by foraging theory regardless of the prey species' vulnerability, reproductive value, or state of local depletion (Alvard 1993, 1994, 1995). Indeed, hunters harvested a number of species at rates greater than the maximum sustainable yield (MSY) (Alvard et al. 1997). Work with Wana blowgun hunters and trappers of Indonesia indicates similar results (Alvard 2000). In short, the data indicate that Piro and Wana hunters maximize their short-term return rates in spite of potential negative long-term consequences. Numerous other studies agree (Hames 1987:96; Hames and Vickers 1982: 374; Kaplan and Hill 1985:236; Smith 1991:256; Winterhalder 1981:97). In contrast, pastoralists practice a conserving strategy by slaughtering young male animals who neither have high reproductive value nor are necessary for the reproduction of a herd, leaving individuals with higher reproductive value behind to reproduce more prey (see Barth 1961:8; Cribb 1991:29; Dahl and Hjort 1976; Kuznar 1991, 1995; Redding 1984). The lack of prey conservation among hunters and its arguable presence among husbanders (see below) indicates that the differences between these strategies can shed light on significant shifts in human decision making that accompanied the Neolithic transition.

Why Resource Conservation by Subsistence Hunters Is Rare

While truly altruistic conservation is unexpected, evolutionary theory does not rule out conservation per se. Rogers (1991) points out that conservation may or may not evolve depending on both its short-term and long-term costs and benefits. Three factors are hypothesized to pattern the costs and benefits of conservation (Alvard 1998). The first relates to issues of ownership, private property, and territoriality. A number of researchers have suggested that conservation is unlikely in traditional horticultural and hunter-gatherer societies because the resources they use are often open access (Hames 1987, 1991; Smith 1983). No one owns an open-access resource, and everyone has the right to consume it (see Schlager and Ostrom 1992). Individuals are unlikely to provide a public good by altruistically limiting their own harvest of such resources if others who have not necessarily sacrificed anything are free to share the benefits (Olson 1965; see also Boone 1992; Hawkes 1992). These sorts of problems have been termed *collective action problems*, or *Tragedy of the Commons problems*, (Acheson 1989; Hardin 1968, 1993; Olson 1965) and have long been a topic of study by resource economists (Tietenberg 1996).

Ownership helps prevent competitors from free-riding and can help to solve the collective action problem. Resource owners are more motivated to conserve because ownership increases the probability that they can realize the benefits of their short-term sacrifice. Ownership, however, implies resource defense and territoriality. If territorial defense costs are high and private ownership difficult, resources remain open access and conservation is less likely because of collective action problems (Alvard 1998). Ingold (1980:5; see also Harris 1996:448; Reed 1984:2) has addressed the issue of common versus restricted access in his analysis of the development and character of reindeer exploitation. He noted that the relationship between hunter and prey is essentially that of predation whereas the relationship between a pastoralist and livestock is essentially that of protection and defense (Ingold 1980:27). Dyson-Hudson and Smith (1978), in their analysis of territoriality, note that resources that are both predictable and *locally* abundant are likely to be defended; a closely managed animal herd fits their definition of a defendable resource perfectly.

Second, for a resource to be economically defendable and for conservation to provide benefits, the resource must have sufficient value. Relative scarcity adds to the marginal value of a resource, assuming there is demand (Tietenberg 1996). If a resource is abundant and not limiting, an additional unit of resource has less value to a consumer than if the resource is scarce. If resources have less value, the returns from the defense required to make them a private good decline, and conservation is less likely (Beckerman and Valentine 1996; Tietenberg 1996). The corollary is that the *less* abundant a resource, the greater its value, the greater the return for defense and ownership, and the *more* likely conservation will pay off.

Lastly, if the resource's opportunity costs are high, then conservation is also unlikely. In the case of conservation, the opportunity costs accrue from not exploiting the resource immediately. To understand opportunity costs, it is useful to introduce the economic concept of discounting. Much evidence shows that people tend to prefer present consumption to future consumption (e.g., Loewenstein and Elster 1992). The discount rate is the economic measure of the rate at which current income is valued over future income (Fisher 1930). Time preference refers to the tendency to favor certain schedules of resource consumption over others. The rate that future benefits are discounted and measured in terms of present value is the discount rate.

The concept of discounting is important for understanding both resource conservation and animal husbandry. Time preferences are thought to exist for two reasons (Fisher 1930). The first is because of some probability that future benefits will not be realized. The second is because compounding gain is lost with delayed consumption. For example, a hunter may discount a future goat and prefer to kill it today because its future benefits may not be realized; the goat may be killed and eaten by someone else, or perhaps the hunter may die. Even if the future goat is 100% assured, however, the hunter may still discount it because present use of the goat could result in higher long-term benefits. This can occur if the current benefits compound over time. In modern market economies, cash resources can be put into a bank with compounding gains equal to the interest rate. In nonmarket, biological systems, the resource can be invested in a growing population of descendants. A hunter could use a goat to feed his offspring or use it to obtain additional mating opportunities.

Animal Husbandry Is Prey Conservation

We argue that animal husbandry is an example of resource conservation as we defined above. Animal husbandry can be considered conservation because the criterion of restraint is met. Husbanded animals are prey that are not pursued upon encounter. According to the strict prey choice model, foragers are predicted to always pursue prey that are in the optimal diet and ignore those that are not (Stephens and Krebs 1986). The optimal diet is the suite of prey that when pursued upon encounter will maximize the rate of return. A short-term cost is paid for husbandry (the animals are not immediately pursued, killed, and eaten), and the benefits (the animal and its descendants) are deferred to some future point. Others have also noted the conceptual similarities between conservation and animal husbandry (Russell 1988:15).

Defined theoretically as conservation, animal husbandry is predicted to arise and persist in competition with a hunting strategy under conditions that favor conservation. First, the prey resources would have to be private rather than open-access goods. Next, for the costs of defense to be justified, the prey resources would have to have increased value. Finally, the discounted deferred returns from husbandry must be higher than the short-term returns from hunting.

The first two conditions were discussed in the classic economic treatment of property rights by Demsetz (1967). From that discussion one can see how increased competition for valuable game resources can lead to the development of private property and the territoriality required to avoid the free-rider problem of conservation. Demsetz cites the work of Leacock (1954) and Speck (1915) on native North American hunting territories and the fur trade. Leacock argued that territoriality was minimal before the development of the fur trade of the 1700s. The value of game, especially beaver, increased dramatically with the trade, as did the scale of hunting. As Demsetz (1967:352) notes, the geographic evidence collected by Leacock indicated an unmistakable correlation between early centers of fur trade and the oldest and most complete development of private hunting territories.

While increased resource value and territoriality are required, they are not sufficient conditions for successful conservation or husbandry to develop, as the near extinction of the beaver during the fur trade demonstrates (see Krech 1999: chap. 7 and references). Even if resources are valued to the point that territorial defense pays, it may not be in the best interest of the hunter to husband if the opportunity costs of conserving are too high (see also Acheson 1989:364). The discounted deferred returns from husbandry must be higher than the short-term returns from hunting. In the last section of this paper, we will discuss this last prediction in more detail.

Discounting and the Opportunity Costs of Animal Husbandry

Rogers (1991) developed a model to examine how conservation might evolve if resource inheritance (in this case territories) was uncertain. He imagined two strategies. The Conserve strategy pays a short-term cost in reduced fertility but increases the fertility of those who inherit the territory. The Prodigal strategy does not conserve and hence does not pay the cost of conservation but bequeaths poor territories to descendants. In Rogers's model, individuals need territories in order to breed, and fertility is greater in better territories. Rogers obtains the counterintuitive result that conservation is *not* favored as inheritance approaches certainty. The problem is that the conserver's population is growing, but the resources (in this case a territory) do not. This is a classic Malthusian conundrum (see Wood 1998 for a recent review). Rogers concludes that this is a difficult hurdle to surmount.

One way to mitigate (but not completely avoid) this problem is to imagine that the territories in Rogers's model are biological resources—perhaps a herd of ungulates. If the reproductive rate of the herd is greater than the discount rate, it may pay to conserve the herd. If tended properly, a parent can manage a growing herd of ungulates so that each child receives as much as was originally held by the parent. As long as the reproductive rate of the "territory" keeps pace with that of the conservers, there are always animals for subsequent generations to inherit.

One might ask, however, where will all the animals graze? Eventually the pasture will deplete, the growth rate of the herds will drop below the discount rate, and conservation will no longer be the best strategy. How long a system of conservation like this can maintain before collapsing into exploitation remains a theoretical and empirical question. The dilemma of feeding growing herds in the interest of one's progeny potentially explains the predatory expansionism typical of pastoral societies (Bailey 1980; Barfield 1989; Khazanov 1994).

How fast would a herd have to grow for its conservation to pay off? This question can be answered by examining Clark's (1990) work with MSY models (see Table 1 for a description of the parameters used in this paper). These models calculate the maximum number of animals that can be removed from a population on a regular, sustainable basis without driving the population extinct (Caughley 1977). Standard mammalian MSY models assume density-dependent logistic population growth with the highest rate of growth occurring at intermediate density levels (Figure 1). In such a context, to obtain the largest sustainable harvest from an animal population, harvesters should maintain the population at a density *(N)* near

(1) $N = 1/2 * K$

and harvest at the rate of

(2) $H = 1/2 * r_{max}$

This yields a maximum annual harvest in animals per year of

(3) $\text{MSY} = r_{max}K/4$

where K = carrying capacity and r_{max} = the maximum intrinsic rate of increase (Caughley 1977).

Table 1. Symbols used in text.

Symbol	Parameter
N	Density (#/km^2)
K	Carrying capacity (#/km^2)
r_{max}	Maximum intrinsic rate of increase
r	Intrinsic rate of increase
H	Harvest rate
W	Body mass (kg)
$W*$	Maximum body size to be husbanded
s	Standing biomass ($N * W$)
i	Discount rate
b_1	Coefficient for the r_{max}-body mass allometric equation
b_2	Coefficient for the density-body mass allometric equation
b_3	Coefficient for the biomass-body mass allometric equation
A_1	Constant for the r_{max}-body mass allometric equation
A_2	Constant for the density-body mass allometric equation

Clark (1990) criticized these models because they assume a zero discount rate. That is, the resources harvested

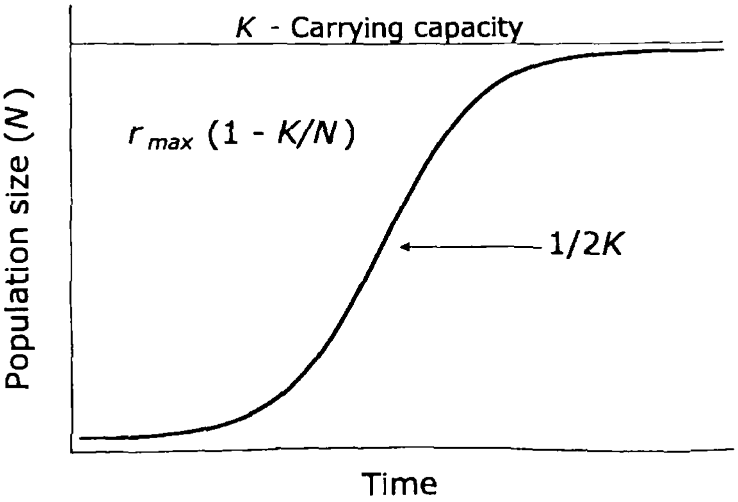

Figure 1. Model of logistic population growth. At low population densities, growth is rapid, exponential, and reaches a maximum at 1/2*K*. Since population growth is the greatest, 1/2*K* is the population size that provides the MSY. After this point, density-related factors take hold, and growth begins to slow until density equals the carrying capacity *(K)*, births equal deaths. and growth is zero.

at some distant point in the future are implicitly assumed to be worth as much as resources harvested today. In other words, MSY models assume that resources harvested 10, 20, or 30 years from now have the same value as resources harvested today. Clark argues that MSY models do not take into account the opportunity costs of *not* harvesting above the maximum sustainable yield. These costs accrue from not consuming the resource in the short term. At a more basic level, the issue is one concerning the proper criterion of optimality (Bulmer 1994). MSY models assume *a priori* that sustainability is the goal on which harvesters base their decisions. From an evolutionary as well as rational economic view, sustainability is only a viable tactic if it leads to greater fitness in the former case or greater profits in the latter. Clark concluded that for a maximum sustainable yield strategy to be favored, the reproductive rate of the resource population must be greater than the discount rate—the rate of return from the best current alternative investment. If the discount rate is higher than the reproductive rate of the prey species, the optimal choice is to harvest the resource as rapidly as possible and invest the capital in the current investment with the higher payoff. Clark's often cited example explains why economically rational whalers often overharvest whales rather than hunt them sustainably. Because whale reproductive rates are often lower than the interest rate, economically rational whalers can receive a higher return by harvesting whales to the point of extinction than they can get from harvesting whales at the MSY indefinitely.

Should the Piro Conserve Collared Peccaries or Spider Monkeys?

Using Clark's reasoning we can pose the same theoretical question of Piro hunters (see also Alvard 1998). The Piro, whom we mentioned earlier, hunt a variety of game including collared peccaries *(Tayassu tajacu)* and spider monkeys *(Ateles paniscus)*. Collared peccaries are piglike ungulates that weigh around 20 to 25kg. This species provides the greatest amount of hunted meat in the Piro diet. Black spider monkeys are medium-sized primates of the family Cebidae with adult body weights of between 6 and 10kg (Alvard 1993). These species vary in reproductive rate and body size—both factors that determine the payoff to husbanding. If meat is valued sufficiently and territoriality provides sufficient assurance that future benefits can be realized, which species would be more profitable to husband, collared peccaries or spider monkeys?

Alvard (1998) calculated the maximum sustainable yield per year for both species (Table 2). The carrying capacity is calculated for an arbitrarily chosen area of 314km^2, an area with a radius of 10km—the maximum distance a Piro hunter can travel away from the village and return before dark. The population at MSY is $1/2K$, or 1,857 for peccaries and 2,095 for monkeys, but the MSY are significantly different—780 peccaries and 84 spider monkeys. In a common currency, the MSY strategy returns 17,160kg a year for peccaries and only 756kg a year for spider monkeys.

For husbanding to be favored, future productivity from husbanding must be greater than what could be had from investing the animal resources into reproduction today at interest rate (i). An extreme exploit strategy: kill all in one year, returns a lump sum of 81,708kg of peccaries and 37,710kg for spider monkeys. For the exploit strategy to be favored over a husband strategy for peccaries, the lump sum must be invested in a current investment that has an annual return greater than the MSY:

(4) $Ki > rK/4$

or to simplify,

(5) $i > r/4$

For peccaries this obtains if $i = 21\%$. For spider monkeys, exploit pays if the current alternative returns only 2% or more. Other things being equal, this comparison shows that peccaries are much more likely to be conserved than spider monkeys. This is because the opportunity cost of conserving peccaries is lower than it is for spider monkeys. It would take 50 years at the MSY rate to recoup the lump sum for spider monkeys but only 4.7 years for peccaries.

In spite of the peccaries' high reproductive rate, the Piro do not conserve them. Why? Unlike modern whalers, Piro hunters do not have credit markets in which to invest their peccary profits. They do invest, however, in their own reproduction in the evolutionary sense. One can imagine two options for Piro hunters. The first is for hunters to harvest as much peccary in the present as would maximize their short-term fertility and survivorship. They can do this by investing the meat directly into offspring or into mating opportunities (Hawkes et al. 1995; Trivers 1972). The second option is for hunters to harvest peccaries at a lower but perhaps more sustainable level and pay a short-term fertility

Table 2. The data to calculate the maximum sustainable yield. The lump sum column is the return if the entire population was killed. The last column presents rate of return that must be found for the lump sum to be invested and yield a return as high as the MSY.

Species	K (per 314km^2)	r_{max}	MSY ($rK/4$)	Body Wt. (kg)	MSY (kg)	Lump sum (kg)	Rate
Collared peccary	3,714	0.84	780	22	17,160	81.708	21%
Spider monkey	4,191	0.08	84	9	756	6,804	2%

and survivorship cost in exchange for the long-term benefits associated with sustainable resources.

Apparently, the returns from peccary conservation would be lower than what hunters obtain from unrestrained peccary harvesting. Why? First, peccaries are a costly-to-defend, open-access resource. Restraint on the part of any one hunter provides a public good enjoyed by all hunters. Second, data show that the Piro peccary harvest is currently less than the MSY. That is, the current harvest *is* already sustainable (Alvard et al. 1997). Peccaries are abundant relative to demand, and the Piro enjoy a diet flush with meat (Alvard 1993). Finally, the Piro may have a short-term time preference (a high discount rate) with respect to peccaries and other prey resources (Alvard 1998).

Animal Husbandry

With this background, we can now address the transition that occurred in human history at the Pleistocene/Holocene boundary. In the Old World, the transition defines the boundary between the Paleolithic and the Neolithic (~12,000 yr. ago). This is the period when the first plants and animals were being husbanded for food production. In the New World, the transition occurred independently a few thousand years later (Wing 1983). Indeed, independent transitions from foraging to food production occurred at different locations around the globe. Sheep and goats were the first animals domesticated, possibly as early as 11,000 years ago, and certainly by 9,000 years ago at sites such as Zawi Chami, Shanidar, Jarmo, Tepe Sarab, Ganj Dareh, and Tepe Ali Kosh in the foothills of the Zagros mountains near the present-day border of Iran and Iraq (Flannery 1969:86; Hole 1989:97, 1996:273; Mason 1984; Meadow 1989; Redding 1984:239; Ryder 1984). Subsequently, they were introduced to the Levant and Anatolia around 9000 B.P. during the Prepottery Neolithic B phase (Harris 1998:8; Levy 1992; Uerpmann 1989). Larger animals, such as cattle, pigs, horses, and camels, were domesticated later. Horses and camels were domesticated relatively late in prehistory (post-5500 B.P. and 5000 B.P. respectively), after profound economic, social, and ecological changes had altered people's lives in southern Asia (Ben-Shun 1989; Bokonyi 1984; Levine 1999; Mason 1984; Zarins 1992). Our model, in its present form, cannot include all of the essential complexities of such late domestication events. Our model explains the initial domestication of small stock such as sheep and goats. Later, we will consider the conditions that would have altered the parameters of our model to make larger animals attractive as conservable resources.

A number of researchers have offered explanations of why and how the transition to animal husbandry occurred (Flannery 1969, 1973; Hole 1989, 1996; Reed 1984; Uerpmann 1989). A recent attempt to understand animal husbandry from a behavioral ecology perspective is the work of Russell (1988). Russell used an approach incorporating optimal foraging theory's prey choice model to predict the order in which prey species were first husbanded. Like other models, Russell envisions population pressures driving the system. In his scenario, greater human population density led to prey depletion and depressed hunting returns. When hunting return rates dropped to lower than what could have been obtained from husbandry, the transition occurred. In this sense, husbanded prey and hunted prey represent two distinct prey types.

Russell collected quantitative data on productivity and labor costs for the husbanding of camels, cattle, sheep, and goats and calculated the respective return rates for each species, averaged over one year (Russell ignores pigs). With herds of 100 animals, camels have the highest return (665 kilocalories per hr.), followed by cattle (615 kcal/hr.), sheep (203 kcal/hr.), and goats (109 kcal/hr.). Based on these results, Russell predicted that as human population density increased and hunting returns declined, prey species would be husbanded in the order of their profitability: first cattle and camels, then sheep and goats. As mentioned earlier, however, the archeological record indicates domestication occurred in just the opposite order. The smaller species and less profitable (at least in the short term) types were husbanded before the larger ones. Why was this the case?

Russell claims that the archeological record is misleading (1986:341). A more satisfying answer is that Russell's approach exposes some ambiguity in his prey choice model. The critical issue is the length of time over which the models assume foraging return rates are expected to be maximized. The time scale over which Russell's model assumes individuals will optimize is too myopic. He assumes a 0% discount rate (Kagel et al. 1986). Husbanding, however, is not a strategy where payoffs are measured in the short term. The conservative nature of husbanding requires an approach that examines the long-term payoffs of alternative strategies. It is true, as Russell demonstrated, that the short-term return rates for husbanding are higher for larger-bodied animals compared to smaller-bodied animals if herds are of equal size (say 100 head). It takes time for herds to grow, however, and the payoffs occur at some point in the future. Herds are biological populations that can grow, and different species have different rates of increase. These differences affect the value of different species as potentially husbanded resources. Table 3 presents estimates of the maximum intrinsic rate of increase (r_{max}) for cattle, sheep, goats, and camels, based on data from modern species presented in Dahl and Hjort (1976). Herds of sheep and goats with r_{max} values between 0.6 and 0.7 can grow significantly faster than herds of cattle or camels that have r_{max} values less than half as large (0.22–0.25).

Figure 2 shows the effect of herd growth rates on relative return rates. Because herds of sheep and goats grow much faster than herds of cattle or camels, after 70 years return rates are higher for sheep and goats. Also important

Table 3. Data from Dahl and Hjort (1976) used to iteratively calculate r_{max} from Cole's (1954) equation.

Species	Annual birthrate	Age at first reproduction	Age at last reproduction	r_{max}
Camel	0.5	3	23	0.225
Goat	2.0	1	9	0.700
Sheep	1.5	1	9	0.600
Cattle	0.5	2	13	0.255

is that absolute herd yield (kg per year) also increases much faster for sheep and goats. Starting with a population of two individuals, goats reach a herd size of 100 in 24 years—for sheep in 40 years. A herder would have to wait 55 years to achieve a herd of 100 camels and 72 years for a herd of 100 cattle. Return rates, as calculated by Russell, and the absolute herd yield are higher for goats after only one human generation and for sheep after only 2.5 human generations, compared to cattle and camels. This result suggests that their higher rates of population growth were one reason why sheep and goats were husbanded before camels and cattle.

These results beg a number of questions, however. How does a strategy of husbanding these animals compare to a hunting strategy? Herds of smaller animals grow more quickly, and most of them can be kept at higher densities than larger-bodied animals. Is this important? To answer these questions, below we develop a model of animal husbandry that predicts the range of body sizes that should be husbanded.

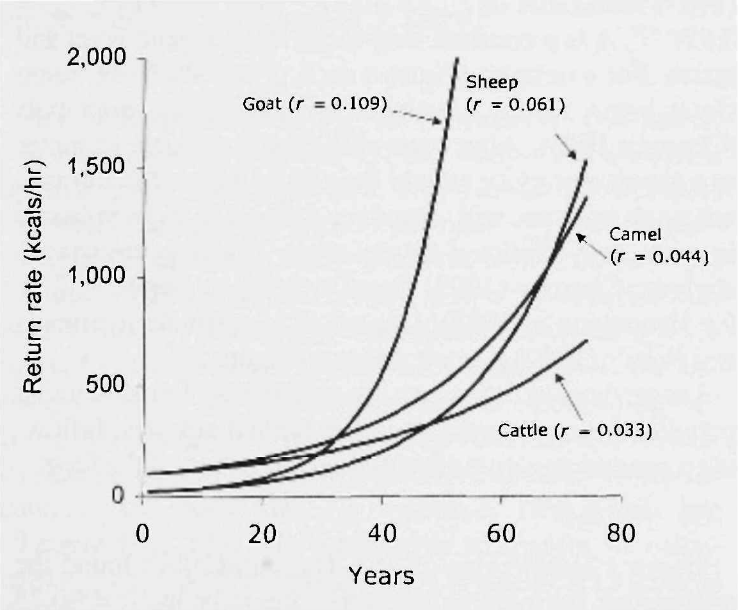

Figure 2. Effect of herd growth on return rates to husbanding. Herd size increases with time according to the reproductive rate of each species. Because of economies of scale, return rates increase accordingly. Since sheep and goats reproduce much faster than cattle or camels, over time return rates for these animals rapidly match, then surpass, return rates for the larger-bodied species. Herd growth is estimated here using the intrinsic rate of increase. Herds begin with a size of two individuals. Original return rate data for husbanding from Russell (1986).

The Model

The model contains a number of assumptions. Foremost, we assume that the transition to husbandry occurred under conditions of increasing population density. We also assume that populations became more sedentized and less mobile. And finally, we assume that the benefits to husbanding depend on the value of animal resources to individual fitness. Evidence in support of these assumptions will be provided in the discussion section. At low human density or high prey abundance, hunters can more easily obtain optimal quantities, and resources have diminishing returns on fitness. In this context, there is no incentive for hunters to pay the short-term costs of conserving if time and effort can be better spent on other fitness-enhancing activities and long-term benefits are small (Alvard 1998; Kaplan and Hill 1992; Smith 1987). Recall that this is one of the reasons offered above to explain why Piro hunters do not husband peccaries. During the transition period, we expect competition for resources to have increased with human density (and/or depleting resources) and prey to have become more valuable. Fitness returns no longer diminish because prey become increasingly rare. Full-time hunters would find that return rates for hunting begin to drop as competition increases and animals become scarce. The point at which a hunter might consider husbanding and not hunting a scarce prey item would depend on the resource's value and its discount rate.

Allometry

There are two major reasons for discounting—uncertainty over future benefits and the opportunity costs associated with lost compounding gain. We will reserve the question of uncertainty and its impact on husbanding for later and will focus now on the issue of compounding gain. The future discounted value of husbanded animal resources varies according to the type of animal. As noted by Clark (1990), the prey's reproductive rate is especially critical for determining whether it is more economical for hunters to maintain the population at the MSY or exploit it as rapidly as possible.

Reproductive rate varies with a number of parameters, but body size explains much interspecific variance. In fact, body size correlates with many of the characteristics that determine the cost and benefits of husbanding (Peters 1983; Schmidt-Nielson 1984). As we will show, larger animals are bigger packages and, all other things being equal, will be preferred in the short term simply because they represent more resource. They reproduce more slowly, however, than smaller-bodied animals. In addition, larger animals live at lower densities but at higher biomass (kg per unit area) than small-bodied types (Figure 3). These allometric relationships between body size, density, and reproductive rate provide a powerful analytic tool for examining the costs and benefits of animal husbandry. The first step to determine the benefits from husbanding, and the best animals to husband, will be to calculate the maximum sustainable yield for a range of prey body sizes. The MSY represents the benefits to husbanding. This will be compared to what could be obtained from hunting the same animals.

Many morphological, physiological, and life history traits vary between species with body size according to the following relationship (Peters 1983):

(6) $X = AW^{b}$

W is body mass, A is the intercept, b is the slope of the line for the linear relationship of the log-transformed variables:

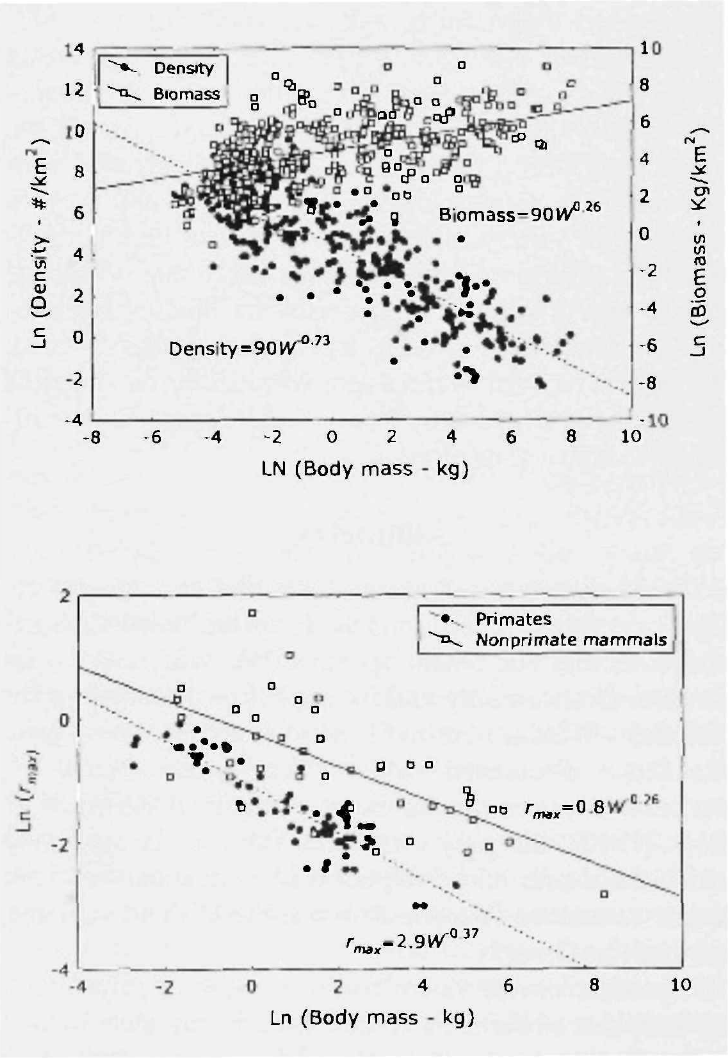

Figure 3. Allometric relationships of body mass for mammals. The top figure plots both density (number of individuals per km^2) and biomass (density times body weight per km^2) as a function of body mass for a sample of 368 mammalian herbivore species (data from Damuth 1987). The bottom figure plots r_{max} as a function of body weight for a sample of 72 primate species (Ross 1992) and 40 nonprimate mammal species (Henneman 1983).

(7) $\log(X) = \log(A) + b[\log(W)]$

The most well-known allometric relationship is described by Kleiber's rule, which states that metabolic rate is a function of body mass where $b \cong 0.75$ power (Kleiber 1961).

To estimate the MSY (kilograms of biomass harvested per year per square kilometer) for potentially husbanded species of different sizes, we use three variables and two well-documented allometric life history relationships. The variables are the maximum intrinsic rate of increase (r_{max}), density (N), and body mass (W). r_{max} is a measure of a species' maximum rate of population growth in an environment where resources are not limiting. Density is the number of individuals per unit area. Body mass is weight in kilograms for adults.

Across a variety of taxa, the data indicate that larger-bodied species reproduce slower. There is a general negative allometric relationship between body size and reproductive rate with the general form

(8) $r_{max} = A_1 W^{b_1}$

As discussed below, r_{max} is one of a number of life history variables that are predicted to scale allometrically to the approximate power of -0.25 of body weight (Charnov 1993). A variety of data sets show slopes between $b_1 = -0.25$ and $b_1 = -0.37$ (Charnov 1993; Henneman 1983; Robinson and Redford 1986; Ross 1992). For example, for a sample of 40 nonprimate mammal species, Henneman (1983) found that $\ln(r_{max}) = -0.27 * \ln(W) - 0.11$ or, $r_{max} = 0.9W^{-0.27}$. A is a constant that varies with trophic level and taxon. For example, primates as a group show the same slope but a lower A value than nonprimate mammals (Charnov 1993). After controlling for body size, primates as a group reproduce slower than other types of mammals, but small primates still reproduce faster than large primates in a manner predicted by equation 7. Using covariance analysis, Charnov (1993) found a common slope of -0.31 for Henneman's (1983) data set of nonprimate mammals and Ross's (1992) primate data set (Figure 3).

Larger-bodied organisms are also usually found at lower population densities than smaller-bodied animals, following a general negative allometric relationship of the form:

(9) $N = A_2 W^{b_2}$

Using a sample size of 368, Damuth (1987) found the relationship for mammalian herbivores to be $\ln(N) = -0.73 * \ln(W) + 4.5$ or $N = 90W^{-0.73}$ Inversely, standing biomass (density times body mass divided by unit area) *increases* with body size. In this case, $b_3 = 0.26$. Figure 3 demonstrates these two allometric relationships.

These are useful relationships because they can be used to calculate MSY as an allometric function of body size. Recall that MSY theory shows that yield is maximized at approximately MSY = $(Kr_{max})/4$. If it is assumed that the densities (N) reported by Damuth (1987) are at carrying capacity, maximum sustainable yields in kilograms can be calculated as

(10) $\mathrm{MSY} = (NWr_{max})/4$

Because density (N) and reproductive rate (r_{max}) are related allometrically to body mass (W), equations 8 and 9 can replace them in equation 11, to get

(11) $\mathrm{MSY} = (A_2W^{b2}) * (A_1W^{b1}) * W/4$

or,

(12) $\mathrm{MSY} = (90W^{-0.73}) * (0.9W^{-0.31}) * W/4$

Assuming $A_2 = 90$, $b_2 = -0.73$ (Damuth 1987), and $A_1 = 0.9$ (Henneman 1983), $b_1 = -0.31$ (from Charnov [1993] for primates and nonprimate mammals), the MSY is between 22.7kg per km^2 per year for an animal that weighs 50kg and 14.6kg per km^2 per year for an animal that weighs 3,000kg. Note the large difference in body size but that the MSY does not differ proportionally. Charnov (1993), in fact, argues that MSY should theoretically be *independent* of body mass. This result obtains because of the nature of the allometric relationships between r_{max}, density, and body size. Smaller species reproduce faster and live at higher density but are small bodied; these effects nearly cancel one another out using the exponents from Henneman and Damuth. The exponents suggested by Charnov (1993) for the density and r_{max} allometric equations ($b_1 = -0.25$ and $b_2 = -0.75$) sum to equal W^{-1} or $1/W$. This cancels exactly when multiplied by the W term in equation 11. Consequently, MSY is independent of body mass and dependent primarily on the constants A_1 and A_2:

(13) $\mathrm{MSY} = A_1A_2/4$

Using these exponents and the constants $A_2 = 90$ and $A_1 = 0.9$ from above, the MSY for any body-sized species is approximately 20.2kg per km^2. This estimate, however, is too high. The estimate used to calculate r_{max} from Henneman (1983) and Ross (1992) is derived from Cole's (1954) formula. Cole's equation uses age at first reproduction, annual fecundity, and age at last reproduction, but ignores mortality. Charnov (1993) provides a correction for this overestimation. He notes the invariant relationship between the product of age at first reproduction and mortality, the product of age at first reproduction and yearly fecundity, and body size for mammals (for details see Charnov 1993:124). For nonprimate mammals, he calculates $r_{max} = 0.4W^{-0.25}$. Using $A_1 = 0.4$ in equation 13 reduces the MSY for any body-sized species to approximately 9kg per km^2. This is a more realistic estimate of the yield.

While MSY is the same across body sizes, standing biomass, s (density multiplied by body mass), scales positively with body size. The larger the species, the greater the standing biomass to the approximate power of positive 0.25. This means that husbanding larger-bodied animals requires much more "capital" in terms of standing biomass to achieve the same MSY than does husbanding smaller-bodied animals. The relationship indicated in Figure 3 shows that for a mammal the size of a camel (~500kg), 450kg of biomass are standing per km^2, while for a mammal the size of a sheep (~30kg) only 217kg are standing per km^2.

This has important implications for a husbanding strategy. Recall that the delayed benefits of husbanding are discounted by the opportunity costs—the costs of not using the resource immediately. The standing biomass represents the resources that husbanders do not consume. The lower the discount rate compared to the returns expected from husbanding, the more likely husbanding will pay off. Since the amount of biomass *not* being used is greater for larger animals, the opportunity costs of husbanding are greater for larger animals. The opportunity costs are measured by multiplying the standing biomass (s—this represents what could be obtained from a hunting strategy) times the discount rate (i).

(14) $si > Kr_{max}/4$

Density cancels, to leave

(15) $i > r_{max}/4$

This is exactly the same result obtained with equation 5. In this case, the carrying capacity is equal to the standing biomass ($K = s$). If the opportunity costs (standing biomass multiplied times the discount rate) are greater than the productivity that could be obtained from husbanding (the MSY), hunters are predicted to exploit that body-sized species rather than husband it.

It might be argued that we have overestimated the opportunity cost of husbanding because there are diminishing returns to hunted resources; that is, the cost of forgoing the 100th ungulate is less than forgoing the first. It should be noted that we assume increasing population density, resource shortages, and competition at the time of the transition. Competition pushes the system down to the linear end of the diminishing returns curve. In other words, there is no 100th ungulate. Game is rare, each animal is valuable, and the cost of forgoing a large-bodied animal is high.

Setting the Discount Rate

Knowing the evolutionary discount rate is important for understanding the time depth that humans should take into account when the costs and benefits of subsistence and reproductive decisions occur at some point in the future. An evolutionary-based discount rate was formulated deductively by Rogers (1994), who hypothesized an evolved time preference by natural selection. He concluded that the evolved human time preference, or discount rate (i), should depend critically on three factors: (p), the rate of population growth, (R), the average relatedness between the individual and his offspring, and the generation length, (T):

(16) $i = (-\ln R)/T + p$

Delayed benefits that accrue to descendants are discounted because the longer benefits are deferred, the less related descendants become. At some point in the future, direct descendants become as related to ego as ego is related to the average person in the present population. For example, after 240 years, or 9 generations (generation time in this case is 30 years), the coefficient of relatedness between the descendant receiving the husbanded animals and their ancestor is $R = 0.002$. For comparison, the average degree of relatedness between individuals in the Piro village of Diamante is $R = 0.027$ (Alvard 1998). The average degree of relatedness for 12 Yanomamo villages is $R = 0.086$ (Chagnon 1988). Assuming $R = 0.5$ between parent and offspring, after 156 years the direct descendants of an individual Piro in Diamante today would be as related to ego, on average, as any two individuals chosen randomly from the village in the present.

If the average coefficient of relatedness between parent and offspring is 0.5, and one generation is about 30 years, the discount rate is 2.4% plus the rate of population growth according to Rogers. Future reproduction is additionally discounted by the rate of population growth because delayed reproduction contributes a smaller proportion of the larger future population than does current reproduction if the population is growing. Rogers assumes that the rate of population growth must have been zero on average prehistorically and thus did not contribute to the evolved time preference. He concludes with an average discount rate of 2.4%.

Recent demographic work with the Ache, a hunting and gathering group in Paraguay, suggests that perhaps a higher rate is justified. Using the best demographic data to date from a precontact foraging period, Hill and Hurtado (1996) found that the Ache have had an annual growth rate of over 2.5% for at least the last 100 years. They argue that hunters and gatherers in general may be characterized by periods of rapid growth interspersed with population crashes. In this scenario, long-term, average population growth remains near zero, but individuals are exposed to a selective environment where most years are characterized by nonzero growth. If that were the case prehistorically, selection would favor a time preference greater than 2.4%—in the case of the Ache, as high as 5% (Alvard 1998). Indeed, it is now apparent that humans experienced much environmental variability in their evolutionary past that could have affected population growth rates (Potts 1996). This predicts the possibility of adaptive plasticity with respect to how schedules of reward are preferred (Hansson and Stuart 1990).

Calculation of the Maximum Body Size to Husband

As mentioned above, for husbanding to be favored, its future benefits must be discounted and still be greater than the returns expected from hunting. Recall equation 15, where $i > r_{max}/4$ for hunting to pay off. For husbanding to pay, the inverse must be true, $i < r_{max}/4$. To calculate the body size below which husbanding pays *(W^*)*, we replace r_{max} with its body mass function (equation 8) and simplify to get

$$(17) \quad W^* = e^{[\ln(4i) - A]/b}$$

Note that prey density is not a factor here. This is because a change in density affects both the MSY and the opportunity costs as measured by standing biomass. Standing biomass increases as density increases, but so does MSY and the effects cancel. W^* is, however, sensitive to the r_{max} function and the discount rate. If we follow Charnov (1993) and assume that $b_1 \approx -0.25$, $A_1 = 0.4$, and the discount rate is 2.4%, which corresponds to zero population growth on the part of the humans, the maximum body size to husband is 309kg. If a discount rate of 4% is used, the maximum body size to husband falls to around 40kg. A 4% discount rate corresponds to a 1.6% population growth rate. The results for a variety of ranges of reasonable discount rates are presented graphically in Figure 4.

The predicted body size falls within the range of probable body sizes for the species first domesticated. Data on modern domesticated sheep show much variability but bracket the predicted size. As examples of the extremes, adult male Nilotic sheep weigh between 11 and 25 kg, while male Lohi sheep from India weigh up to 68kg (Dahl and Hjort 1976). Goat sizes vary as well, but again within the predicted range. Indian Jumnapai male goats can weigh up to 79kg, while East African Mubende male goats weigh 20 kg (Dahl and Hjort 1976). We discuss the subsequent domestication of larger animals below.

Discussion

We have applied principles derived from evolutionary ecology, conservation biology, economics, and archaeology in a cross-disciplinary approach to address a classic question within the field of anthropology—the transition from hunting to animal husbandry. By operationally defining animal husbandry as conservation, we could predict that husbandry likely arose during conditions that favored resource conservation. Conservation is more likely when goods are privately owned/territorially defended rather than open access, when resources are sufficiently valued/scarce to justify the costs of defense, and when the opportunity costs of restraint are low. Even if resources are highly valued and well defended, however, husbanding may not be the best strategy if the opportunity costs are too

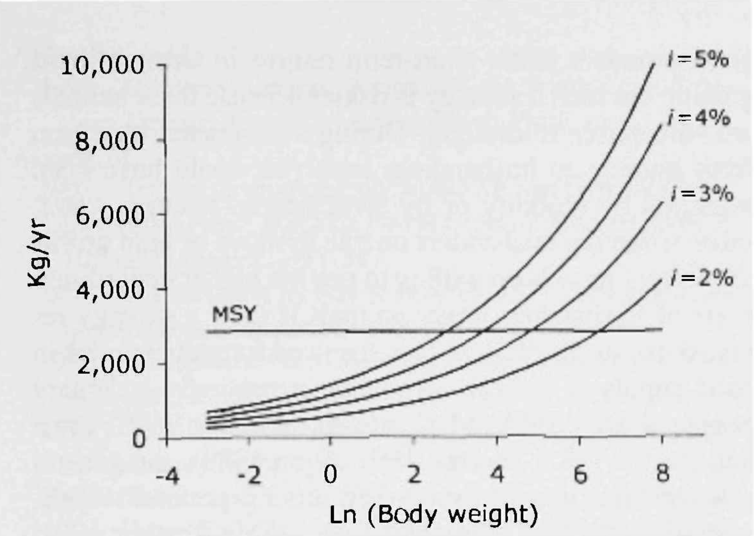

Figure 4. Annual harvest in kilograms per 314 km^2 as a function of body size for both the husbanding strategy (MSY) and the hunting strategy. MSY is 2,844 kg/yr and is independent of species' body size. The returns from the hunting strategy assume an extreme exploit strategy where total biomass is harvested and invested at the discount rate. Hunting returns increase with prey body weight because larger animals are found at greater biomass. The MSY line and hunting line cross at W^* This is where the benefits from husbanding and its opportunity costs are equal. Above W^*, the opportunity costs of husbanding are too high, and the prey type should be pursued and consumed upon encounter. W^* depends on the discount rate. Returns from hunting and the corresponding W^* values are plotted for four values of i. For 2%, W* = 640kg; for 3%, W* = 126kg; for 4%, W* = 40kg; and for 5%, W* = 16kg. As mentioned above, 314 km^2 is an area with a radius of 10km—the approximate distance a hunter can travel from a central place and return before dark.

high. As we have shown, prey body size predicts much of the variance in the parameters of interest (reproductive rate, density, and biomass) for measuring the benefits and opportunity costs of husbanding alternative prey types.

The first two conditions that favor conservation were not discussed to any great extent in this article, but current archaeological research on the period of the Neolithic transition in the Middle East indicates that the circumstances were conducive to resource conservation. Human populations were growing and becoming more sedentary, perhaps as a result of resource stress provoked by global cooling during the Younger Dryas period (ca. 11,000 to 10,000 B.P.—Bar-Yosef 1998; Byrd 1994a; McCorriston and Hole 1991; Sherratt 1997). In a number of complex but generally confirmed models of domestication, archaeologists and ethnographers have established that population growth of forager bands leads to the packing of people into a finite environment (Aldenderfer 1998; Binford 1987; Haaland 1995; Harris 1977; Hitchcock 1982; Kuznar 1989; Price and Brown 1985). Packing necessarily leads to reduced mobility and the territorial defense of resources as suggested by Dyson-Hudson and Smith (1978). Reduced mobility reduces constraints on women's fertility, which in turn increases population growth (Binford and Chasko 1976; Haaland 1995; Harpending and Wandsnider 1982; Kuznar 1989; Reed 1984). The net result creates the conditions of increased population density, increased pressure upon resources, and the consequent increase in resource value essential to our model. The packing/sedentism model has been useful for explaining the origins of sedentism, cultural complexity, and food production in the Middle East (Bar-Yosef and Belfer-Cohen 1992; Flannery 1973; Harris 1969, 1977, 1998), East Africa (Close and Wendorf 1992; Haaland 1995), Andean South America (Aldenderfer 1998; Kuznar 1989, 1995; MacNeish 1983), and in Eastern North America (Brown 1985; Watson 1989).

As one expects from work that resides on the margins of many fields, more questions were raised than answered, and there are many opportunities for fruitful future investigation. For example, why did hunting continue to coexist alongside husbandry? In the manner of most models, this article takes a relatively complex phenomenon and simplifies it. The transition from hunting and gathering to food production was not a simple one, however. For example, strong evidence shows that both wild and domesticated animal resources were used concurrently long after the initial incorporation of husbanded resources in the economies of the ancient Middle East (Stein 1989; Zeder 1994) and the Andes (Olivera 1998). Ethnographers commonly observe that pastoralists, reluctant to slaughter and eat their valuable livestock, actively hunt wild herbivores as sources of meat. Examples are found in pastoral settings and among people as diverse as those of the South American Andes (Custred 1977; Flannery et al. 1989; García 2001; Kuznar 1995), Tibet (Ekvall 1968; Goldstein and Beall 1990), East Africa (Evans-Pritchard 1940; Klima 1970; Robertshaw and Collett 1983), Siberia (Ingold 1980), Europe (Creighton and Segui 1998), the Middle East (Barth 1961; Cribb 1991), and the Navajo (Downs 1972; Luckert 1975). The persistence of hunting might be expected for two reasons. First, our model predicts that hunting remains the optimal choice for larger prey because the opportunity costs of husbanding them were too high. Cattle, pigs, and camels were not husbanded until at least a millennium after sheep and goats. Below we discuss a number of possibilities that may have dropped the opportunity costs of husbanding these animals to the point that hunting them was no longer as profitable (Russell 1988). Second, the analysis above uses predicted values of r_{msy}, density, and biomass. There is much scatter around the regression lines in Figure 3. One would expect variation within species as well. For foragers exploiting local prey populations whose reproductive rates were lower than the predicted values, the benefits to husbanding would also have been lower, and hunting would have been the optimal strategy. Zeder (1994:119) reports what she terms a remarkable dichotomy between sites where domesticates and wild animal resources dominated. Sites with a predominance of wild fauna are located in marginal arid environments where husbanding may not have provided sufficient returns.

Why were gazelles or other animals of the appropriate size not husbanded? While goats and sheep fall in the range of predicted body size, so do a number of other prey present in the Middle East at the time of the transition. One hypothesis is that other medium-sized ungulates were not husbanded because of behavioral characters that made these species more difficult to manage (Baskin 1974). These extra costs could decrease the return rates from husbanding these species significantly, independent of their body size. Gazelles *(Gazella gazella)* were the favored prey of the Natufians and other groups who lived in the Levant region of the Middle East between 10,000 and 8,000 B.C. (Byrd 1989). Gazelle behavioral characters make them difficult animals to defend in large numbers and, hence, more costly to conserve. They cannot be herded in large groups or driven long distances as can sheep and goats (Clutton-Brock 1981). This may have been the reason that a number of other prey were also never husbanded, including roe deer (*Capreolus capreolus*—22kg), ibex *(Cabra ibex)*, and various equids (*Equus* spp.).

Larger types, such as cattle and camels, were eventually incorporated into the suite of domesticates (in terms of our model, W^* increased). What may have caused larger-bodied prey to be husbanded? There are a number of possibilities. According to our model, one way that W^* would increase is if people's time preference became less myopic, i.e., the discount rate lowered. Recall that there are two important parameters that Rogers (1994) uses to estimate the discount rate: population growth and the average coefficient of relatedness *[R]* between parents and offspring. Holding the coefficient of relatedness constant at $R = 0.50$, if human population growth slowed, the opportunity costs of husbanding large game would decline. Such population crashes have been hypothesized for foragers as mentioned above. At zero population growth (a discount rate of 2.4%), W^* increases to 309kg. Inbreeding would also increase W^*. Rogers assumes $R = 0.5$, which gives the 2.4% in the absence of population growth. The average coefficient of relatedness between parents and offspring will increase if endogamy becomes more common (cousin marriages for example), perhaps because of increased sedentism. In fact, sedentism is cross-culturally correlated with increased group cohesiveness and territorial defense of resources (Charles and Buikstra 1983; Kuznar in press). If R increases to 0.6 in the absence of population growth, the discount rate drops to 1.8%, and W^* increases to 976kg.

Another idea to explain the move to larger game is the risk reduction hypothesis suggested by Mace (1993). Larger animals like camels and cattle reproduce more slowly but are better able to cope with drought. Mace shows that keeping herds of smaller animals like sheep and goats promises better short-term returns in terms of herd growth, but such a strategy is riskier because these animals are susceptible to drought. During a protracted transition from hunting to husbanding, such risk could have been managed by mobility or by switching to hunting. Later, more sedentary husbanders unable to move or hunt profitably might have been willing to pay the higher opportunity costs of husbanding larger animals if such a strategy reduced risk of shortfall. In fact, the need for reducing risk in food supply is hypothesized for increasingly sedentary people (Harris 1998; McCorriston and Hole 1991; Price and Brown 1985; Sherratt 1997; Stein 1989), and general risk aversion is well established among pastoralists ethnographically (De Boer and Prins 1989; Fratkin 1991; Kuznar 1991, 2000; Mace 1993).

Finally, a strategy of milk and blood extraction, part of a secondary products revolution (Sherratt 1981), may have eventually dropped the opportunity costs of husbanding large animals to the point that hunting them was no longer as profitable (Russell 1988). It is unclear when this may have occurred during the process of animal husbandry, although such intensification is common among many extant husbanders (Dyson-Hudson and Dyson-Hudson 1980).

In conclusion, we have provided an analytical model that provides baseline predictions of the timing of initial animal husbandry and the optimal size of animal to be domesticated. The model, in which we suggest that animal husbandry is a special case of resource conservation, is based on optimal foraging assumptions rooted in evolutionary theory. Because of the model's groundedness in well-established theory and its focus on a few key variables, its parameters can be altered to provide explanations and testable predictions of the domestication of various animals. Using this model, we were able to explain the initial domestication of sheep and goats approximately 10,000 years ago, and by considering factors extraneous to the model, such as human demography, risk reduction considerations, and human protection of ungulates from predation, we were able to suggest subsequent domestication events. We do not claim that this model explains all domestication, nor do we consider all potentially important factors in domestication. However, the model does provide an analysis of several key factors and allows for both explanation of archaeological data as well as suggests future lines of inquiry. These analytical tools not only allow for a better understanding of past domestication events but also bring into focus the nature of conservation and broaden our perspective on common property phenomena.

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