

**IS RESOURCE DEPRESSION THE SAME AS POPULATION DEPRESSION?
MODELING ARTIODACTYL POPULATION DEMOGRAPHICS UNDER HUMAN PREDATION**

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This paper will attempt to identify the critical variables of population dynamics for deer (Odocoileus sp.) through the modeling of deer populations both under and free from hunting pressure. The dynamics of these models, combined with modern ecological studies, will demonstrate the robust nature of deer populations and the overall ability of deer to withstand fairly substantial losses from human hunting. The paper will conclude with a discussion of the implications of the findings for arguments regarding resource conservation by prehistoric Californians.

Over the past 20 years zooarchaeologists have increasingly used the Diet Breadth Model to track the effects of human predation on highly ranked prey items (e.g., Broughton 1999; Hildebrandt and Jones 1992; Holdaway and Jacob 2000; Kay 1994; Nagaoka 2002). In the majority of these studies, the abundances of high- and low-ranked prey taxa are compared through time using body mass as a proxy for prey rank in the standard diet breadth model (Broughton 1999 and references therein). A decline in the abundance of highly ranked items is assumed to indicate a reduction in overall foraging efficiency, requiring a broadening of the diet and a switch to lower ranked taxa. When such a reduction is evident in the archaeological record it is attributed to “resource depression.”

The (often tacit) assumption in these studies is that resource depression is the result of prey population declines or a reduction in the actual number of prey animals available to hunters. Because resource depression is measured in terms of ratios of large to small animals, it is possible that decreases in the ratio are the result of an increase in small taxa in the record, while large taxa are hunted at constant rates. To parse out the most likely effects of human predation on high-ranked taxa, it is important to closely examine the population dynamics of specific high-ranked prey. An understanding of the potential for a species to be over-hunted to the point of local population decline or even extirpation is critical to the interpretation of the archaeological record regarding conservation issues.

THE IMPORTANCE OF RECRUITMENT RATES

In a study of predator-prey relationships, Winterhalder and Lu (1997) determined that the most important variable in the ability for a key prey resource to maintain a healthy population was its recruitment rate (defined below). In general this does not bode well for large-bodied mammals whose recruitment rates tend to be inversely proportional to their body size. This generally lower recruitment leads to population densities which are also inversely related to body size (Figure 1). Exceptions to these rules, however, would be ideal prey animals, since their large body size, coupled with high recruitment rates and densities, would provide humans with large-package, fairly renewable resources. These resources are also the most prone to being misidentified by archaeologists as vulnerable to over-predation.

Recruitment rates are dependent on birth rates and newborn mortality. Birth rates are dependent on the rate of development, longevity, and average litter size. Animals which develop slowly require greater maternal investment, which takes away from further reproduction by their mothers. The age at which animals reach sexual maturity also drives recruitment, because younger-breeding individuals are less likely to die before giving birth to offspring and will give birth to more offspring over their lifespan. Because most mammals reproduce throughout their lives, average longevity is also an important factor in reproduction. In general, species with large litters tend to have more robust populations.

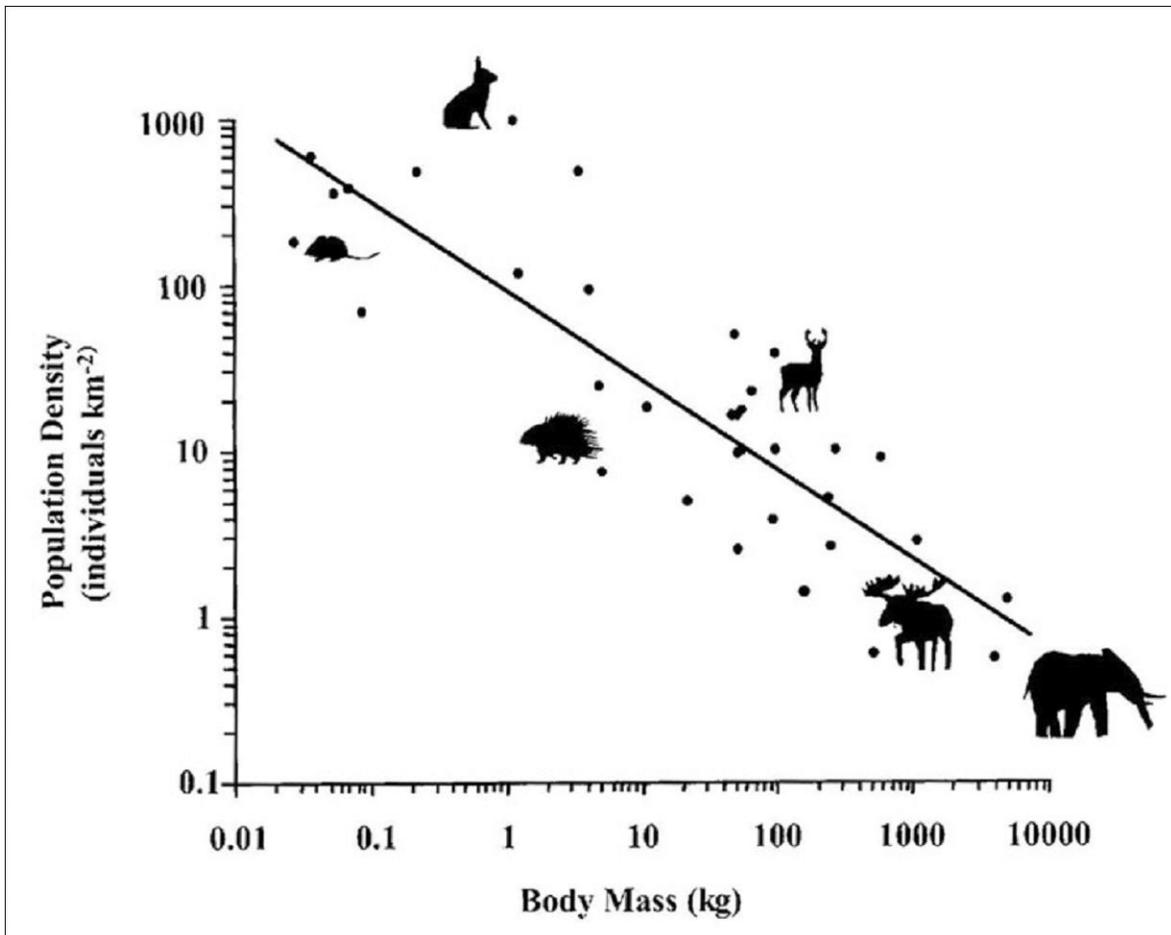


Figure 1. Population density vs. body mass for mammals. Both axes are log scaled. Regression line: $\log_{10}(\text{population density}) = 1.962 \pm 536 \times \log_{10}(\text{body mass})$. Data from Nowak 1999; figure from Waguespack and Surovell 2003.

Mortality rates for animals in their first year often drive recruitment, as more individuals are born each year than can possibly survive. Once individuals reach maturity, their survival rates are often many times greater than in the first years of life.

DEER LIFE HISTORY

Deer (*Odocoileus* sp.) meet all criteria for healthy birth rates. They are reproductively receptive at 1.5 years old and give birth to their first offspring a little after two years of age. They remain fertile throughout their adult lives, recorded to be as long as 22 years but averaging 10 to 12 years (Kie and Czech 2000). Average birth rates are between 0.66 and 1.96. On average a two-year-old doe calves a single offspring, while all older does calve twins. These high birth rates are often mediated by high mortality during the first year of life.

Regardless of high mortality rates for fawns, high birth rates lead to extremely high population densities for deer. While some population density estimates for herds of white-tailed deer range up to 100/mi.² more conservative modern estimates place population densities at around 10/mi.² (Table 1). Assuming that modern densities are close to prehistoric densities, a 10-km foraging radius would have

Table 1. Modern Deer Population Densities in California (compiled from Loft et. al 1998).

UNIT	AREA (KM ²)	LOW/HIGH ESTIMATE	POPULATION	DENSITY DEER/KM ²	10 KM RADIUS
North Coast	42735	Low	170,000	3.98	1250
		High	250,000	5.85	1838
Cascade Area	18130	Low	35,000	1.93	606
		High	70,000	3.86	1213
South Coast	20202	Low	16,000	0.79	249
		High	79,000	3.91	1229
Northeast California	26418	Low	25,000	0.95	297
		High	100,000	3.79	1189
NE Sierra Nevada	9324	Low	10,000	1.07	337
		High	40,000	4.29	1348
E. Sierra Nevada	19425	Low	10,000	0.51	162
		High	65,000	3.35	1051
Cen. Sierra Nevada	27195	Low	90,000	3.31	1040
		High	130,000	4.78	1502
S Sierra Nevada	22792	Low	30,000	1.32	414
		High	95,000	4.17	1309
N Central Coast	16317	Low	90,000	5.52	1733
		High	140,000	8.58	2696
S Central Coast	40404	Low	70,000	1.73	544
		High	202,000	5.00	1571
Total (average)	242964		858,588	3.53	1110

contained 1,110 deer. At an average meat weight of 50 lbs per animal, that would produce over 55,000 lbs. of meat. (Note that these densities are based on modern studies and therefore represent populations in areas heavily disturbed by humans.)

Deer are an ideal species for testing notions of susceptibility to population depression, because their remains are ubiquitous in archaeological assemblages; they are one of the largest, if not the largest, terrestrial mammal available to most aboriginal hunters; and, because of their importance in modern wildlife management programs, they are extremely well studied in a variety of contexts. Modern studies and model fitting have provided fairly accurate input variables with which to model population dynamics both under and free from human predation.

DEER POPULATION MODEL

Model Summary

A deer population model was built based on modern management parameters. Natural deer populations are regulated by density-dependent reproduction and density-dependent mortality of fawns. The model tracks four age classes: fawns, yearlings, two-year-olds, and adults older than two. These are meaningful categories because the mortality of fawns is up to three times that of all others in the population, yearlings do not reproduce, two-year-olds reproduce but at a lower rate and adults reproduce at a normal rate. It can be assumed that this model tracks only females. Natural sex ratios appear to be close to 2:1 in favor of females and, because deer are polygynous, male population size has very little effect on overall population size. Population dynamics were modeled for a population free from human predation and populations under varying levels of both density-dependent and density-independent human predation.

Table 2. Input Parameters for Deer Population Ecology Model.

AGE CLASS	NATURAL SURVIVAL RATE	UNAVOIDABLE LOSS	INITIAL BIRTH RATE	INITIAL POPULATION
Fawn	--	--	--	
Yearling	0.5	0.1	--	
2-year old	0.85	0.05	1.5	
Adult >2	0.85	0.05	2.3	1210

Model Construction

Model parameters are given in Table 2. The initial size of the deer population has little effect on the outcome of the model, provided there is a sufficient number of individuals to reproduce. Similarly, the ratio of age classes is not important, as it balances quickly based on density-dependence and standard mortality rates. Survival rates for all non-fawn age classes are drawn from wildlife management literature (White 2000). Fawn mortality is density-dependent and is based on a best-fit logarithmic model of mule deer in Colorado (Bartmann et al. 1992) represented by the equation:

$$(1) S_F = \frac{e^{(1.1906-0.0195xDensity)}}{1 + e^{(1.1906-0.0195xDensity)}}$$

Density-dependent reproduction was calculated using a simple subtractive formula:

$$(2) \text{Adults: } 2.3 - (.001 \times \text{population})$$

$$(3) \text{2-year-olds: } 1.5 - (.001 \times \text{population})$$

Density-dependent hunting rates were determined using this equation from Van Deelan and Etter (2003):

$$(4) y = \frac{k * density}{x + density}$$

where

k = maximum rate of harvest

x = density of prey at $k/2$

The maximum allowable yield k was calculated using goal-seeking software in Microsoft Excel which calculated yields of density-independent (or constant) hunting.

The model calculates population each year starting just after the birth pulse. Human kills are subtracted from each age group. Natural mortality is then subtracted. For fawns this mortality follows density-dependent rates; for all other individuals the mortality is the larger of the parameter value or the hunting loss plus the “unavoidable loss” input parameter. Following mortality, a new birth pulse is predicted using density-dependent reproductive values. The model runs through 1,000 permutations (“years”).

Model Results: No Hunting Pressure

Results of the simple model of population dynamics free from predation demonstrates the natural stable-limit cycle (Figure 2). This cycle of “boom-and-bust” is common for all mammals but especially for large herbivores. The major declines in population are generally the result of over-grazing of fodder. Die-offs associated with starvation allow the vegetation to re-grow, creating pristine habitat on which the remaining individuals can graze. The increases in nutrition lead to increased survival and reproduction, creating population booms which once again lead to over-grazing and crashes. These cycles continue indefinitely.

Model Results: Density-Independent Human Predation

Goal-seeking software in Microsoft Excel was used to calculate the maximum sustainable and maximum allowable yields for density-independent hunting. Deer were hunted at the same rate throughout

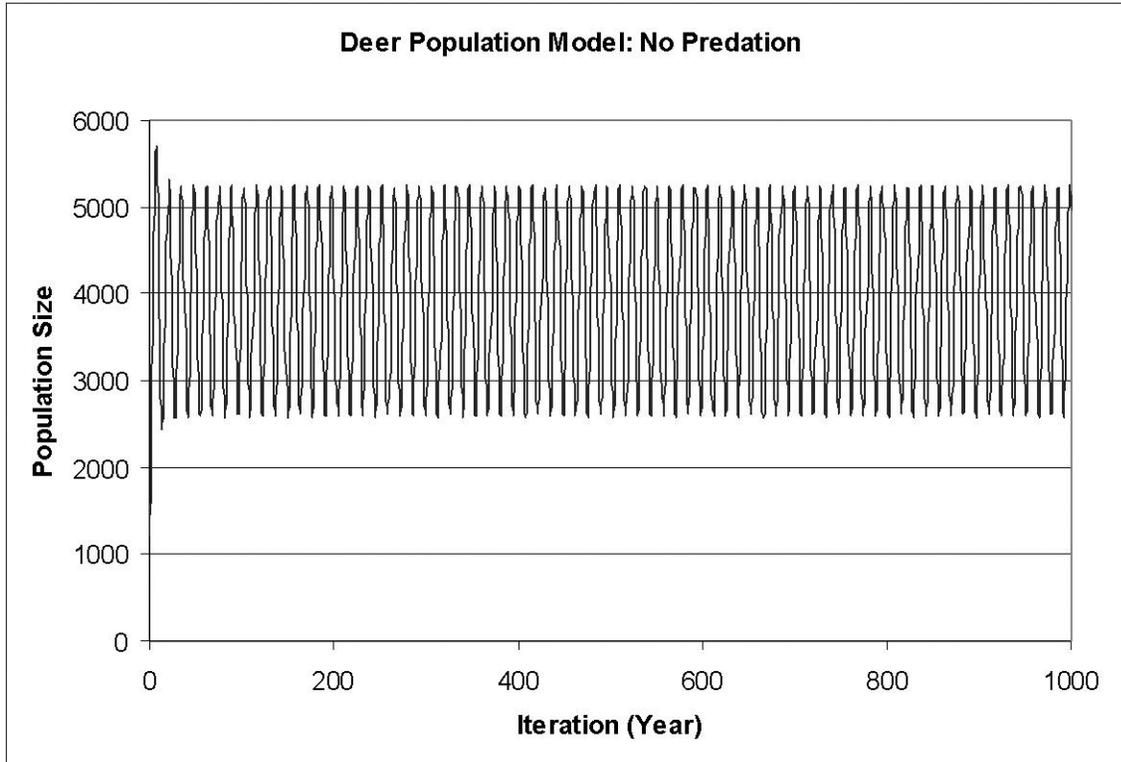


Figure 2. Deer population model without predation exhibiting a stable limit cycle.

the model run regardless of population densities. The maximum sustainable yield (MSY) is the maximum percentage of the population which can be hunted year-in and year-out while maintaining population equilibrium. In this case the MSY is capable of sustaining yields over 1,000 years of hunting. The maximum allowable yield (MAY) is the largest percentage of the prey population that can be harvested without causing the population to collapse.

Given the input parameters and a 10-km foraging radius, the MSY is 24.7 percent and the MAY is 37 percent (Figures 3 and 4). At MSY hunters are able to take 1,140 deer per year. Furthermore, it could be argued that by mediating the effects of the stable limit cycle, the deer population is actually healthier under human predation, reaching a stable equilibrium much more quickly. At MSY the population is at 38.91 deer/mi.², while at MAY the population is stable but below the level at which deer would remain economically feasible for humans (>.01 deer/mi.²).

Model Results: Density-Dependent Human Predation

The density-dependent human predation model was set up in similar fashion to the density-independent model. In this model the intensity of human hunting for deer varied depending on the density of deer within the foraging radius (e.g. the encounter rate). It can be assumed under the diet breadth model that reduced levels of deer hunting are mediated by an expansion of the diet breadth or more intensive procurement of lower-ranked items already in the diet. Goal-seeking software was again used to calculate the MSY. The MAY remains the same, because the density-dependence of foraging at MAY is essentially a non-factor. As k approaches MAY the value of x is close to zero, and therefore the equation for density dependence approaches k , regardless of density, and predation remains constant (see Equation 4, above).

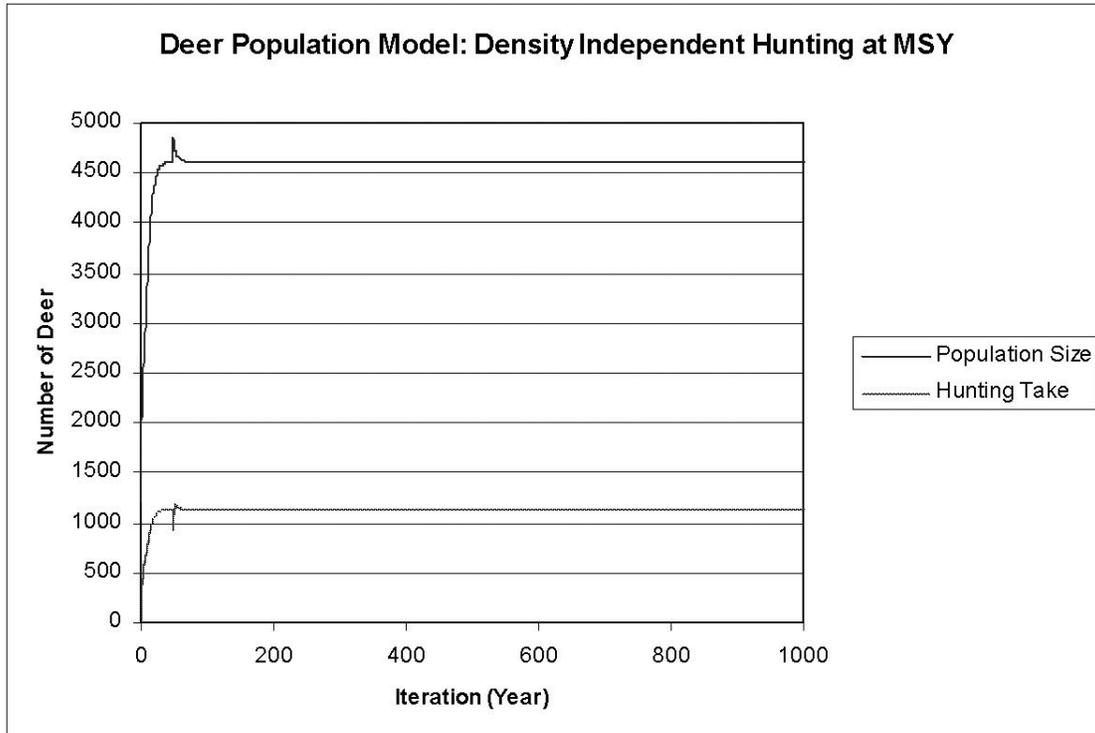


Figure 3. Deer population in 10-km radius foraging area under density-independent hunting. Hunting rate of 24.7 percent (maximum sustainable yield). Population at equilibrium = 4,614. Hunting take = 1,140.

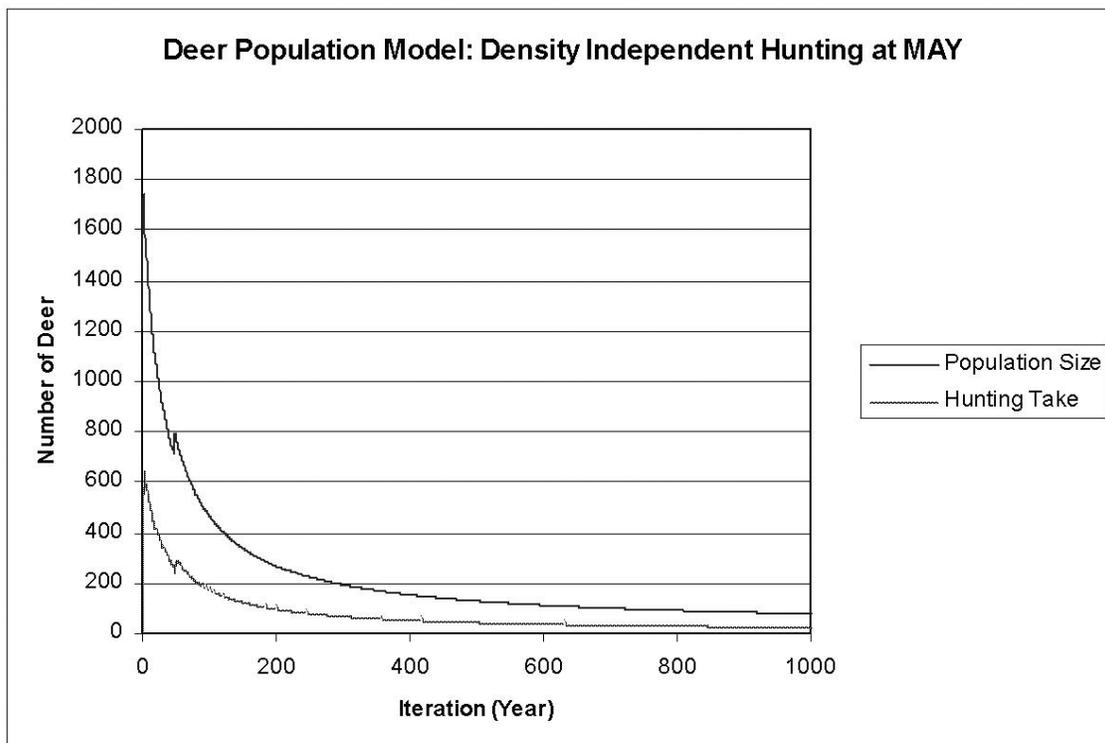


Figure 4. Deer Population in 10-km radius foraging area under density independent hunting. Hunting rate of 24.7 percent (maximum allowable yield). Population at equilibrium = 79. Hunting take = 29.

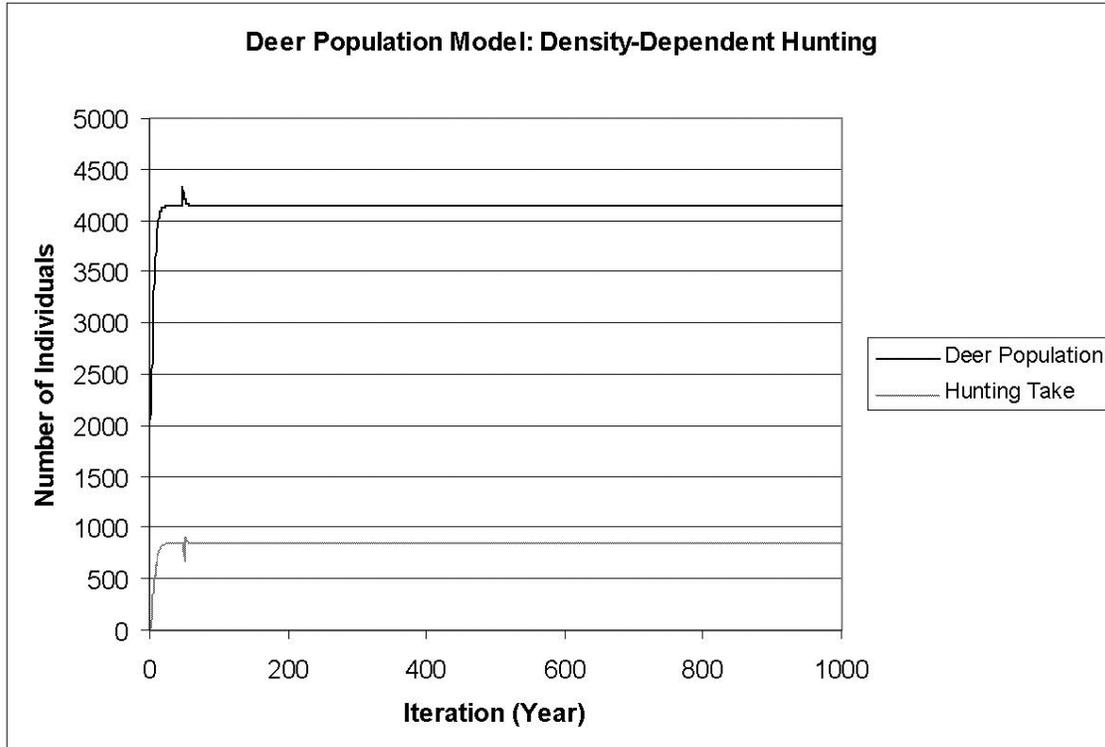


Figure 5. Deer Population in 10-km radius foraging area under density-dependent hunting. $k=0.356$ (maximum sustainable yield), hunting rates vary between 13 and 21 percent. Population at equilibrium = 4,143. Hunting take = 851.

At MSY ($k=0.356$), hunting is curtailed by density-dependence, thereby maintaining the deer population at a higher level than in the density-independent model (Figure 5). In this run hunters are hunting at rates between 13 and 21 percent, with hunting takes of 250-903 animals per year.

Harvesting Rate and Population Growth

These models, rather than providing actualistic data testable with the archaeological record, demonstrate a number of interesting aspects of deer population dynamics. The single most important aspect of this model is the effect of population growth as it relates to density. Figure 6 represents the rate of growth of the population at given densities from zero to a theoretical carrying capacity (assuming logistical growth). By keeping the population densities at, or near, MSY, hunters would optimize population growth, allow for more kills, and assure that deer populations grow at the maximum rate. Furthermore, this culling of the herd by human hunters will mediate the boom-and-bust cycles typical of unhunted populations.

This would indicate that some hunting would maintain growth in deer populations while increasing hunting yields. The question that concerns archaeologists, however, is whether human hunting could have led to a decline in the overall population of deer in a specific area. The models presented above, along with other supporting evidence, would suggest that it would be very difficult to hunt-out a deer population.

ROBUSTICITY OF DEER POPULATIONS

Beyond the model, wildlife management and ecology literature on deer agree that predation is not generally a limiting factor on deer populations. For instance, Taber (1956) finds that “in the shrub land, for every buck shot, 10 other deer die, mostly of starvation. In the chaparral the equivalent ratio is 1:21.”

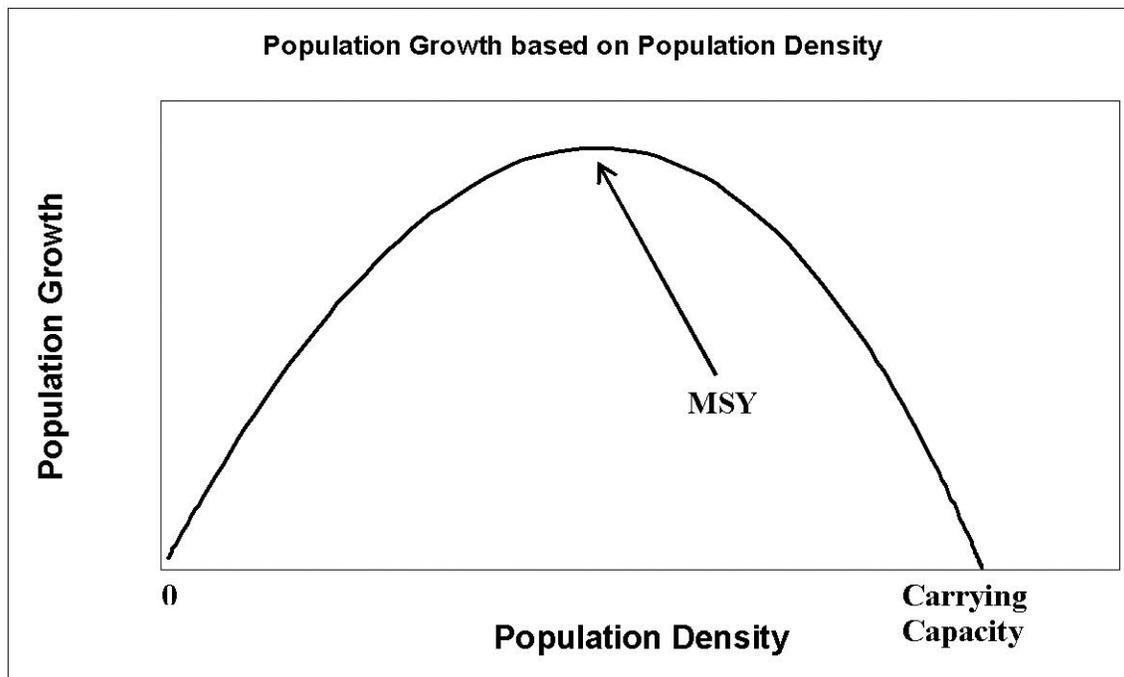


Figure 6. Logistical rate of growth as population density increases. MSY maximizes the growth function. Note that MSY is at much lower population densities than carrying capacity.

Essentially, hunting at 10-20 times the rate in the study would have no effect on deer populations. More recently, Kie and Czech (2000) have concluded that “predation [of any sort] should not be considered as a regulating factor without simultaneously considering habitat conditions.” In a study in western Washington, Brown (1961) found that “winter losses probably have a greater effect on the management of our deer populations than all other forms of mortality combined.”

However, predation by wolves has been shown to effectively reduce deer populations in some specific scenarios. In a recent review of wildlife literature, Ballard and colleagues (2001) reviewed studies of the effects of wolf (*Canis lupus*) predation on four populations of black-tailed deer (*Odocoileus hemionus columbianus*), 17 populations of mule deer (*O. hemionus*), and 19 populations of white-tailed deer (*O. virginianus*). They found that, in instances in which deer populations were well below carrying capacity, wolves effectively limited those populations. It is possible that a combination of wolves and humans could have reduced deer populations to the point of reduced foraging returns.

However, numerous instances of modern population booms have attested to the ability for deer populations to rebound quickly, reaching populations well above carrying capacity (i.e. Brown 1961; Kie and Czech 2000). Even a short reprieve from hunting by either species would allow populations to rapidly reach high densities.

PREHISTORIC HUMAN IMPACTS

Several aspects of human land-use and behavior would likely have led to increased rather than decreased deer populations. Prehistoric anthropogenic burning, as well as human perception of game abundances, would have epiphenomenally protected and fostered growth in deer populations.

Aboriginal burning is well documented throughout prehistoric California (Anderson 2005; Lewis 1993; Stewart 2002). Burning was used to drive game (including deer), to keep forests clear of debris, to encourage the growth of forbs and grasses and possibly to increase the health and productivity of oak groves.

Epiphenomenally, burning would have halted vegetation succession at its early stages. Deer populations thrive in early successional environments where biomass is easily accessible and not locked up in large, woody plants. Furthermore, in many parts of northern California, the burning of chaparral to provide a mosaic of climax vegetation and more open grasslands would provide deer with ideal habitat into which they could expand. So, while some burning may have been done with the express purpose of hunting deer, the effects of this burning may have increased the available habitat into which deer could expand. Modern data support this claim as deer populations boomed following clear-cut logging in California, Oregon and Washington during the early parts of the twentieth century (Gilbert and Raedeke 2004).

In the paper from which the hunting rates for the model above are drawn (Van Deelan and Etter 2003), the authors find that as density decreases, hunter perception of the scarcity of game increases disproportionately such that hunters perceive there to be fewer deer than there actually are. This “perception gap” would lead foragers to expand diet breadth earlier than necessary. Once this expansion to likely-more-abundant prey animals occurred, the reduced pressure on the deer population would allow it to rebound, if it had fallen at all.

PREHISTORIC CONSERVATION?

There are many value judgments associated with the word “conservation,” as well as many definitions of the term. Because this paper is based on theory derived from behavioral ecology, I define conservation as the act of taking a short-term loss in favor of long-term or sustained future gains. Given this definition (and an utter lack of archaeological data in this paper) what are the prospects for conservation of deer by prehistoric Californians? This paper has demonstrated that short-term and long-term gains are not mutually exclusive in regards to the hunting of deer in California. Hunting, it appears, provides short-term gains without detriment to the deer population. In fact, hunting may mediate boom-and-bust cycles for deer populations, and other human hunting techniques (such as burning) may have the effect of increasing habitat suitability for deer, thereby increasing local population densities. Under a strict behavioral ecology definition, then, it seems unlikely that prehistoric Californians were practicing “conservation.” In fact, it seems unlikely that it was necessary to do so with this particular prey species.

WOLVES IN CALIFORNIA

It appears that humans would have been unable to adversely effect deer populations. It is possible that the combination of wolves and humans could have done so. Evidence for wolves in California, especially in the Bay Area, Central Valley, and along the coast, is spotty, owing to problems in identifying canid remains to species. A better understanding of wolf paleo-biogeography is necessary to answer this question.

SUMMARY AND CONCLUSIONS

This paper sought to demonstrate that prey-specific population dynamics must be taken into account when analyzing the effects of human predation. Deer, a fast-reproducing, large-bodied mammal, was used to demonstrate that while body mass and prey rank are likely correlated, the density and recruitment rates of prey species may not be. Furthermore, human behaviors in prehistoric California may have in fact encouraged growth in deer populations through such practices as burning.

On a broader scale the example of deer population resiliency demonstrates that resource depression is not all-or-nothing. Some resources are more prone than others to over-exploitation, and it is likely that single human groups depressed populations of some prey species while effectively hunting others at sustainable levels.

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