HUMAN ECOLOGICAL IMPLICATIONS OF MIGRATORY DEER BEHAVIOR
IN SIERRAN PREHISTORY

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ABSTRACT

The expanding archaeological data base on the Stanislaus National Forest revealed a correspondance between prehistoric site distribution and the behavior of migratory deer. Spatial analysis of this correspondance has been proceeding along with mapping migration routes, ranges, and delay areas of four contiguous deer herds. Empirical correlation between cultural geography and deer migration patterns does not demonstrate an inherent connection between the two systems but provides a model that imparts a dynamic relationship to the static distribution of sites within the context of the Sierran environment and incorporates the testable hypothesis that populations of human hunter-gatherers and deer have similar response functions to mountain geography and variations in climate and phenology. Such a model may be applied toward explaining, in part, subsistence/settlement patterns of prehistoric montane populations, and as an element in more comprehensive predictive cultural resource models.

INTRODUCTION

Shortly after a program of broadscale archaeological surveys was established on the Stanislaus National Forest several years ago, a correspondance between the distribution of prehistoric sites and the behavior of migratory deer began to be revealed. The State fish and game officer and local deer expert, Jim Maddox, was especially impressed by the alignment of sites along or near migration corridors, which he was mapping at that time. Archaeological survey crews also routinely observed deer trails in close proximity to sites and could often follow them from one site to another.

This association has been noted elsewhere and, like all such observations, seems obvious in retrospect. Mountain topography imposes constraints on and provides opportunities for travel for large mammals, including people and deer. Since "deer appear to prefer the shortest and easiest route of travel to get to their respective summer and winter ranges" (Maddox 1984), and since it can be assumed that efficiency of travel to resource areas was also important to prehistoric hunters and gatherers (Bettinger 1980), it is not surprising that the optimal routes for deer and humans would coincide. It is further evident that since large herbivores are an important dietary constituent for many hunter-gatherers, they are obliged to maintain proximity to populations and so a study of herbivore movements will help in understanding prehistoric human economic behavior and in modelling site locations (Grady 1977; Tainter 1984).

Beginning with these reasons, further analysis of the correlation of site distribution and deer migratory patterns was conducted to see whether the behavior of deer could explain, in part, the spatial archaeology by conferring a dynamic relationship to what is primarily a static array of prehistoric sites. This paper presents preliminary
results of that analysis. The analytical context is first established with a brief overview of the geography and spatial archaeology of the Stanislaus National Forest, followed by a description of the migratory behavior of the Forest's mule deer. At this stage the analysis is general and lacks mathematical rigor and temporal control, but is suggestive of further work.

ENVIRONMENTAL CONTEXT

Geography

The Stanislaus National Forest encloses a portion of the long, gentle west slope of the Sierra Nevada, from the upper foothills to the crest, including the front country of Yosemite National Park. The uplifted Sierran granitic block with its roots beneath the Paleozoic marine sediments and capped with remnant volcanic mud and lava flows from the Paleozoic and Mesozoic Eras provides a magnificent geological setting for its vast mantle of conifer and hardwood forests.

Nearly the full width of its broad, sloping benchland is cut by deep, steep canyons of the Mokelumne, Stanislaus, Tuolumne, and Marced Rivers that drain west into the Central Valley. The elevation differences in these canyons can range from 305 to 610 meters in a half-mile or less. The shallower slopes of the parallel ridges between these canyons are dissected by numerous tributary drainages. The polished granitic rock of the high country was shaped by the Pleistocene mountain icecap which fed valley glaciers extending downcanyon to altitudes of 900 to 1220 meters.

The mosaic of vegetation types is distributed and controlled primarily by climate and soils. They occur as broad bands oriented northwest and southeast and occupy general elevation zones although there is much mixing in response to elevation, aspect, and soils.

The hot, dry foothills below 1070 meters is dominated by oak woodland and chaparral. These communities of live oak (Quercus chrysolepis and Q. wislezenii), digger pine (Pinus sabiniiana), California Buckeye (Aesculus californica), manzanita (Arctostaphylos sp.), and often pure stands of chamise (Adenostoma fasciculatum) grow on steep south facing slopes, mostly occupying the major river canyons. Stands of blue oak (Q. douglasii), more common to the lower foothills, occur as inclusions within oak woodland and on xeric sites in the yellow pine forest at higher elevations.

Between 610 and 2000 meters is the main timber area of the lower montane forests. The fire adapted ponderosa pine forest dominates sites of low summer soil moisture. Its important tree associates are black oak (Q. kelloggii), and incense cedar (Calocedrus decurrens), with an understory of bear clover (Chamaebatia foliolosa) and manzanita. Black oak woodland, intolerant of dense forest cover and wet soils with poor aeration, grows in forest openings on xeric sites with shallow soils or around margins of dry meadows.

On wetter sites white fir (Abies concolor), and its large sugar pine (P. lambertiana) associate, become dominant, forming the mixed conifer forest. Understory trees and shrubs are quite diverse. Big maple (Acer macrophyllum), oak, dogwood (Cornus nuttallii), manzanita, bear clover and ceanothus (Ceanothus sp.) are common while alder (Alnus rhombifolia), maple, dogwood, black cottonwood (Populus trichocarpa), azalea (Rhododendron occidentalis), and other shrubs form a characteristic riparian community.
In snow country at higher elevations, ponderosa pine and mixed conifer communities interfinger with the Jeffrey pine and red fir upper montane forests. Red fir (Abies magnifica) overwhelmingly dominates the forest named after it but is mixed with white fir at lower elevations and lodgepole pine (P. Murrayana) on moist soils above 2000 meters. The dense canopy of red fir forest creates only a light understory of ceanothus, manzanita, and huckleberry oak (Q. vaccinifolia). Jeffrey pine (P. Jeffreyi) replaces ponderosa pine at higher elevations or cold drainage bottoms, associated with incense cedar, white fir, black oak and black cottonwood.

The red fir forest gives way to the open stands of relatively short lodgepole pine with little shrub or herbaceous understory. Lodgepole pine does well around meadows, in glacially scoured basins, in joint planes on granitic ridges and other wet areas. It has been colonizing many meadows in recent years.

Above 2400 meters, with a growing season of only 7-9 weeks and the possibility of a killing frost during any month of the year, is the highest zone in which trees are found. Open, scattered stands and individuals of mountain hemlock (Tsuga Mertensiana), western white pine (P. monticola), whitebark pine (P. albicaulis), western juniper (Juniperus occidentalis) and occasionally lodgepole pine comprise the subalpine forest.

The only deciduous forest on the Stanislaus is the pure groves of aspen (Populus tremuloides) at high elevations, providing fall color around wet meadows and in rock piles at the base of cliffs where there is an adequate supply of groundwater.

A very important nonconiferous vegetation community is the meadow. Ranging in size from a few square meters to several hundred acres meadows are found included in every montane and subalpine forest type and in the alpine zone above timber line. Although the 4,500 acres of meadows on the Forest only comprise 0.5% of the total land area, they are a highly productive habitat which is a center of foraging activity for wildlife. Surrounding forest also provides convenient escape and nesting cover.

Finally, there are rock outcrops barren of vegetation except for bryophytes, lichen, and woody species which are able to put down roots in pockets of soil along cracks and crevices.

Spatial Archaeology

The spatial distribution of archaeological sites is riparian oriented: most sites are located on terraces along drainages and around meadows and springs. In the lower foothills, outside Forest boundaries, large occupation sites are found along the broad valleys of the major rivers. As elevation is gained and the river valleys become steep and narrow canyons, sites are few and small, mostly bedrock mills occasionally associated with a light deposit of lithic debitage and artifacts on available flats. In this upper foothill and mountain front country the occupation sites with any substantial cultural deposit are located within the tributary drainage basins on the uplands above the canyons. Within the montane forest the larger sites are situated in forest openings or around meadows. Elsewhere, small sites are often found on benches of side slopes along volcanic ridges where contact between the lahar and underlying granitic rock generates springs and seeps. Sites away from water sources are characterized by deposits of cultural lithics on ridge saddles between drainage basins.
Archaeological deposits are found in all biotic zones up into the alpine habitat of the crest zone. Meadows and lakes are the common sites for prehistoric occupation in the high country above 2130 meters.

On some ridge tops Pliocene and Miocene volcanic deposits provided aphanitic rhyolite, andesite, basalt, and welded tuff for stone tools and are often the site of quarries and lithic workshops. Local chalcedony, chert, and metasedimentary rock from Paleozoic and Mesozoic marine sediments along the foothills were also used, as were quartz and opalized wood, among other rock types. Most of the stone artifacts and debitage found in archaeological deposits, however, are of obsidian, predominantly from the Bodie Hills and Casa Diablo sources, which was traded or procured directly over the Sierran crest.

All archaeological deposits excavated on the Forest so far have shown a depth of at least 50 cm and often more than a meter, even for very low artifact and flake densities. Obsidian hydration analysis has indicated that the deposits have been vertically mixed and for the most part lack stratigraphic integrity. The essentially surface sites are found in the shallow soils of the crest zone or in shallow pockets of sediments among granitic outcrops.

Recent data recovery projects have established a cultural chronology for the Stanislaus River basin and indicate human occupation of the Forest during the entire Holocene (Moratto 1984:299, Peak, et al. 1986, Peak 1986).

Figure 1 compares the percentage of total Forest acreage for each vegetation type with the percentage of those types associated with prehistoric sites. This was generated by querying the Forest data base, which does not contain the microhabitats often associated with sites. It is adequate, however, for the scale of the present analysis. The habitat types associated with sites more or less coincide with the amount of acres represented by each. Ponderosa pine forest includes Jeffrey pine in Fig. 1. As expected, meadows, black oak woodland, and riparian forest associated with sites are proportionally greater than their total acreage because of the favorable site habitats and higher productivity of food plants. Ponderosa pine forest also contains a high proportion of black oak woodland and meadows (having individual areas too small to factor out for the data base) which gives it an overwhelming representation. In fact, the black oak woodland has been substantially reduced during the past century by logging and fire suppression.

Deer Migration Patterns

The antiquity of deer migration patterns in the central Sierra Nevada is unknown; it is assumed that they were last established when the possibility existed— with the melting of the Sierran ice cap toward the end of the Tioga glaciation. Mule deer have existed in western North America as part of the Blancan Mammal Age fauna since the late Pliocene, according to fossil remains which have characteristics similar to the modern species (Opdyke, et al. 1977). Their behavior has evolved with the landscape, as an integral part of the ecosystem. Populations of the California mule deer (Odocoileus hemionus californicus) from the valley and lower foothills would have spread into the mountain front and adapted to the seasonal changes along the elevation gradient. From contemporary observation of deer behavior it is known that they are conservative pioneers of lateral areas but quick to pioneer upslope. This conservativeness plus optimal foraging
strategy and the geographic barriers of river canyons and divides, have established distinct herds with their separate ranges.

It is useful to mention here the occupation of the lower foothills bordering the Central Valley by non-migratory herds. These resident deer are now greatly reduced in numbers and absent from heavily settled areas, but according to the journals of early nineteenth century explorers and trappers the population was higher and the habitat much more favorable than in the mountains.

The Stanislaus National Forest contains four herds of mule deer each occupying ranges that are coextensive with the drainage basins of the major rivers (Fig. 2). These are the Railroad Flat, Stanislaus, Tuolumne and Yosemite Herds. In order to simplify this presentation, only the Stanislaus Herd will be considered.

The Stanislaus deer herd occupies a 650 square mile range within the Stanislaus River drainage basin. Although there is considerable overlap with neighboring herds, including the Walker River herd, composed of Rocky Mountain mule deer from the east side, the range is fairly well defined by the North fork of the Stanislaus River and Highland Creek on the north, the Sierran crest on the east, a ridge on the south and the limits of the upper foothills on the west. As with the other migratory deer the range of the Stanislaus herd is divided into winter, intermediate and summer seasonal ranges (Fig. 3).

The winter range extends to approximately 1380 meters. It encompasses the foothill woodland/chaparral and ponderosa pine forest. Early winter forage is browse such as buckbrush, western mountain mahogany and California redberry. By mid-winter new grasses dominate the diet until March when migration begins. Deer on the traditional home winter range are organized in matriarchal family groups composed of an older doe, her current year's fawns and her previous year's female offspring. Older males are solitary. Migration parallels new spring plant growth. It begins about mid-March to April, depending on weather, snow melt and availability of forage, and ends six to ten weeks later at the start of fawning. Deer become organized in temporary migratory bands for the leisurely trek through the intermediate to the summer range.

The intermediate range extends from the upper edge of the winter range to the lower edge of the summer range at about 2000 meters. It comprises the lower montane forest, including ponderosa pine and mixed conifer communities. Traditional routes, termed migration corridors, are used for travel. They are composed of several trails and may be as narrow as 100 meters or as wide as 3 kilometers, depending on topography (Fig. 4). At one or more places along a migration corridor is an expanded area where deer will delay their migration from a few days to three or four weeks. Since spring migration tends to follow meadow alignments, the spring delay or holding areas are frequently associated with meadows. At this time grasses, rushes, sedges and forbs are the preferred food plants. On the other hand the fall delay areas usually occur along ridgetops and southwest facing sideslopes, among stands of mountain whitethorn, deerbrush or bear clover, with mixtures of manzanita and black oak. Browse, especially oak foliage, and acorns are the primary forage at that time.

Many deer summer in the intermediate range but most of the herd continues to their summer range, above 2000 meters, which they reach about mid to late May. This is the area of upper montane and subalpine forest where expanses of exposed granitic bedrock and large meadows are
characteristic. Deer now break up into small matriarchal family groups and male groups. In early June, as fawning approaches, the pregnant does establish fawning territories and the young deer disperse, yearling males joining the male groups.

The propagation units for fawning are meadows or shrub and herb vegetation communities which can supply the food, water and cover needed for birthing and rearing a fawn, an area ranging from 4 to 7 acres. After a few days up to two weeks in what can also be considered the upper holding area some deer move into higher range, even into alpine habitat. They then begin to filter back down to the upper holding and propagation areas between mid-September and early October. By this time the deer are once again organised in small matriarchal groups of yearlings and new fawns.

Family groups begin the fall migration to the lower holding areas about mid-October, using traditional routes. Usually it is deep snow and not cold temperatures that causes this movement. It has been pointed out that deer could safely reside in winter at high elevations in the mountains so far as the food value of upper montane plants is concerned. But deep snow can make a deer easily caught by predators besides covering many food plants and making effective travel difficult. In contrast to the slower spring migration deer tend to make rapid descents to the fall delay sites. Deer will delay in the lower holding areas between 1400 to 1650 meters until late October to mid-November. Bucks then join the matriarchal families in preparation for rut. Autumn storms finally drive the deer to the winter range. (Russell 1932; Dixon 1934; Maddox 1984; Salwasser, et al. 1982)

THE ANALYSIS

The cultural resource inventory record showed that prehistoric sites are distributed along the entire elevation gradient of the Forest and well correlated with deer migration corridors. Further analysis of the record was made in conjunction with newer, more detailed information about deer behavior to possibly reveal other common geographic characteristics and suggest a hypothesis of prehistoric economic behavior.

Analysis began with the 657 sites located within the Stanislaus Deer Herd range. Figure 5 shows how most of the sites are clustered between the upper winter range and the lower summer range and enclose or overlap most of the deer holding areas and population centers. The habitat types associated with the sites within the Stanislaus Deer Herd Range are similar in proportion to those of the entire Forest (Fig. 6, cf. Fig. 1), but mixed conifer forest and meadows have a higher percentage of associated sites. Again, meadows seem to be an important habitat to prehistoric people as much as to modern wildlife, because of their high productivity.

When site density is plotted according to seasonal ranges a slight bimodal distribution is revealed (Fig. 7). This can be partly explained if the intermediate range has been primarily a zone of travel for human populations as with deer. In this case intermediate range sites would tend to be more dispersed than those for winter and summer ranges. The nature of the cold season with its limited resource availability, colder temperatures, and snow at higher elevations would have made the winter range a focus of intensive settlement. Reasons for higher site density in the summer range, however, are not so obvious since the movement of the warm season along the elevation
gradient is constantly affording fresh plant foods (but with a decreasing growing season, from 6 to 10 months in the foothill woodlands to only 7 to 9 weeks in the subalpine forest). The summer range must be especially attractive since the maximum site density there greatly exceeds the maximum density for the other seasonal ranges. This pattern differs from that expected in the southwest where, according to Tainter, "site density will in general decrease with increasing elevation", because of a decrease in zonal productivity (1984:27). A similar expectation could have been applied to the Stanislaus National Forest prior to compiling the archaeological data base.

The explanation, already hinted at, must be the presence of the large subalpine meadows in the summer range between 2130 and 2440 meters. This is indicated by Figure 8, which gives the percentage of the 58 meadows in the Stanislaus Deer Herd range associated with sites and the percentage of the 657 sites associated with meadows, for each seasonal range.

Figure 9 shows the percentages of sites associated with deer range elements--that is, migration routes, population centers, and holding areas--for each seasonal range. The sites were classified simply according to the presence of single or multiple features: lithic scatters, bedrock mills, and compound sites with a more substantial cultural deposit and associated bedrock mills. Two things should be noticed.

First, there is no proportional difference in site types between the seasonal ranges. This implies the use of the intermediate and summer ranges for a latitude of human activities comparable to that of the winter range, probably by family groups rather than by male hunters, as would be the case if high elevation sites were the result only of deer hunting activity.

Second, plots of total associated sites maintain the bimodal distribution. But compared to the site density bar chart (Fig. 7) the winter range shows more sites associated with deer range elements than the summer range. Further, according to Figure 5, the major site distributions in the winter range are totally encompassed by deer population centers whereas there is more overlapping and isolation in the intermediate and summer ranges. This could indicate a greater proximity between human and deer groups during the winter, less so in the summer, and least during the spring and fall migrations. Also, it may have been a more productive foraging strategy for people to reduce competition with deer for similar food plants during the spring and fall by locating temporary residences apart from herd concentrations, to increase hunting efficiency by reducing disturbance to migrating deer, and to decrease interference with fawning in the summer range.

Figure 5 also shows the central location of primary sites in each seasonal range (good survey data is missing for the southwestern part of the winter range, outside Forest boundaries, although large village sites are known there; the winter range should be split into upper and lower ranges, the lower range possibly being inhabited during periods of lowered snowline). When distances are divided between primary sites in the intermediate range and those in the winter and summer ranges, respectively, the equidistant points fall on or near the seasonal range boundaries. This intensive occupation midway between winter and summer ranges implies the existence of spring and fall villages used as "holding areas" for people or occupied during the entire warm season.
In partly accounting for site distribution patterns it was proposed that the prehistoric human population may have been in competition with deer for food plants. To help substantiate this, each food plant species used by the ethnographic Miwok Indians (as recorded in Barrett and Gifford 1933) was plotted according to habitat, available season, and elevational distribution and compared to the food habits of mule deer in the Sierra Nevada. The results are summarized in Figure 10 as the percentage of food plants, grouped into bulbs & corms, greens, and seeds, available in each seasonal range. Except for greens, each group is available in decreasing numbers of species from summer to winter range. The decrease in diversity may have little relationship to habitat productivity when site density in relation to meadows is taken into consideration.

Some food plants were commonly used by people and deer. The principle food plants of the spring and fall recorded for the Miwok are also principle forage for deer: clover in the spring and acorns in the fall. Mushrooms are used by both to a lesser extent in the winter. It has been determined that black oak acorns contribute as much as 27% of rumen volume in deer in the autumn months and from 6% to 20% during the spring. Apparently, deer will eat acorns whenever they are available and "fluctuations in the volume of acorns produced from year to year have significant effects on the deer population" (Bertram and Ashcraft 1983:1-2). This data is significant for the ecology of prehistoric human populations after the acorn became a major dietary component. There was then a strong possibility of competition for acorns during the spring and fall during the late prehistoric period, and possibly for forbs during spring and early summer throughout the Holocene.

There is another line of evidence for the coincidence of human and deer behavior. The ethnographic record for Miwok subsistence patterns lacks detail about the seasonal use of the mountains. Existing information, however, indicates a difference between the mountain Miwok who inhabited the range of migratory deer and Miwok who inhabited the lower foothill range of the non-migratory resident deer. The latter apparently did not travel into higher elevations but, rather, made excursions into the valley to hunt and trade with the Yokuts (Barrett and Gifford 1933). Their economic base was probably the seasonal round, with use of a small range of summer camps for seed harvest and occupation of winter villages beginning with the acorn harvest, similar to that of the foothill Yokut to the south (Gayton 1948). The resident foothill deer herds provided a reliable meat source and springs were the primary fresh water source during the summer when streams and rivers were dry.

Miwok social organization seems to reflect this in their Land (Tuwuka) and Water (Kikua) Moieties in which the Water Moiety predominated in villages above 760 meters (Gifford 1916). Further, according to Powers (1976:350), the nickname "Wa-li", meaning "down" or "earth world", "appears to have been originated by the Yosemite Indians and others living high up in the mountains, and applied to the lower tribes with a slight feeling of contempt".

In conclusion, this preliminary analysis demonstrates that the resource patterns of each deer range and the timing, direction, routes, and features of seasonal migration (subject to environmental variation) may be used to help model archaeological site function and the movements of prehistoric human groups. It also provides a few hypotheses which can guide further research.
1. Human and deer populations have had similar responses to the constraints and opportunities of the mountain ecosystem. Topography provides both barriers and routes of upland access, and seasonal variation along the elevation gradient provides a time transgression of optimal productivity of plant resources, extending their availability.

2. If deer can be considered both a resource competitor and prey, the seasonality of food plant production and migration of deer herds conditioned the prehistoric transhumance subsistence strategy in maintaining proximity to deer groups without interfering with their behavior and minimizing mutual use of productive resource patches.

3. The archaeological sites within a deer range are a systemic unit, the result of an evolving subsistence system that is generally coextensive with and partially isolated from the equivalent of each range. That is, the dynamic relationships between sites are elevational, between seasonal ranges, rather than lateral, and may be contained, for the most part by the natural range boundaries.
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PERCENT OF HABITAT TYPES BY ACREAGE AND SITE ASSOCIATION

Stanislaus National Forest

![Bar chart showing the percent acreage and percent site association of various habitat types.]

**KEY TO HABITAT TYPES**
- MC = Mixed Conifer Forest
- PP = Ponderosa Pine Forest
- JP = Jeffrey Pine Forest
- LP = Lodgepole Pine Forest
- RF = Red Fir Forest
- DP = Digger Pine/Oak Woodland
- CHAP = Chaparral
- BRD = Black Oak Woodland
- GRS = Grassland
- MTM = Montane Meadow
- RIP = Riparian Woodland
- BA = Barren Rock
- WA = Water Bodies

Percent Acreage

Percent Site Assoc.
FIGURE 2. Deer Herd Ranges of the Stanislaus National Forest.
FIGURE 3. Seasonal ranges of the Stanislaus Deer Herd.

AREAS SHARED BY ADJACENT HERDS
STANISLAUS DEER HERD
TUOLUMNE AND ALPINE COUNTIES

AREAS SHARED BY ADJACENT HERDS

HOLDING AREAS BELOW 6,500 FT.

HOLDING AREAS ABOVE 6,500 FT.

MIGRATION ROUTES
STANISLAUS
DEER HERD
TUOLUMNE AND
ALPINE COUNTIES

AREAS SHARED BY ADJACENT HERDS

MAJOR DISTRIBUTIONS OF PREHISTORIC SITES

-- BOUNDARIES OF WINTER AND SUMMER RANGES

DEER POPULATION CENTERS AND HOLDING AREAS

• PRIMARY SITES
PERCENT HABITAT TYPES BY ASSOCIATION WITH PREHISTORIC SITES
Stanislaus Deer Herd Range

FIGURE 6. Percent habitat types by association with prehistoric sites.
PREHISTORIC SITE DENSITIES
Stanislaus Deer Herd Range

Sites per Acre

- Winter: 0.0048
- Intermediate: 0.0037
- Summer: 0.0043

Seasonal Ranges

Sites per Acre
- Average
- Maximum
Percent of Sites by Deer Range Elements
Stanislaus Deer Herd Range

Seasonal Ranges

Winter
Intermediate
Summer

Site Types
- Compound Site
- Bedrock Mill
- Lithic Scatter
- Total Associated

Percent of Sites by Deer Range Elements
DISTRIBUTION OF FOOD PLANTS BY DEER RANGES

Stanislaus Deer Herd

Seasonal Ranges

- Bulbs & Corms
- Greens
- Seeds
- Total

Seasonal Ranges

Winter
Intermediate
Summer