

# Consequences of a Mammalian Predator-Prey Disequilibrium in the Great Basin Desert

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Many of the world's large natural areas are held in high esteem because they harbor abundant wildlife and serve as ecological reference points for change in community structure (Sinclair 1977; Western & Pearl 1989). Nevertheless, the restoration of some natural areas to pristine conditions has been controversial because it is unclear what "pristine" means (Chase 1986) and because communities are dynamic, even in the absence of human perturbations (Connell & Sousa 1983; Martin & Klein 1984). A goal of conservation biologists has been to maintain assemblages of native (e.g., nonintroduced or nonalien) species, but this cannot be accomplished without knowing not only how communities change but why. Here, using four types of data — historical, archaeological, anthropological, and ecological — we demonstrate recent community-level changes in the Great Basin Desert of North America and argue that such changes were an unforeseen consequence of human livestock-grazing practices. Specifically, we show that (1) mule deer populations irrupted, following by mountain lions, a predator-prey system that was largely absent 100 years ago; (2) deer populations increased because of habitat changes promoted by livestock and wild horses; and (3) lions, now the largest carnivores in this desert system, affect community dynamics. Our findings illustrate the complexities inherent in the emerging fields of restoration ecology and conservation biology, especially in cases where the goal of national parks is to remove species that occur in an area as a result of human activity. Taken literally, this might require removal

of deer and lions from many refuges and natural areas, including Great Basin National Park.

The Great Basin Desert is a sagebrush-steppe biome situated between the Sierra-Cascade and Rocky Mountain cordilleras in parts of eight states in the western United States (Fig. 1). Because of its remoteness, it was the last unexplored area of the contiguous United States (Berger 1986). To evaluate changes in the lion-mule deer system during the past 100 years, we relied on four types of evidence. First, journals of early explorers from 1776 to 1875 (Fletcher 1980; Fremont 1844; Papez 1976; Russell 1955; Simpson 1875; Smith 1953) were examined. They revealed few observations of deer and much difficulty in acquiring meat, "a country so completely barren and destitute of game" (Smith 1827, from Fletcher 1980). Since early visitors to the Great Basin usually followed the easier routes, which included rivers, plains, bajadas, and low mountain passes to California (Fig. 1), it is possible that primary deer habitats were not encountered. Historical records may not be the best indicators of wildlife numbers. However, since (1) explorers reported abundant wildlife including deer from other regions (Fremont 1844; Lewis & Clark 1893; Mattes 1962), and (2) difficult-to-see mountain sheep were reported regularly, as were pronghorn in the Great Basin, it seems probable that the meager descriptions of Great Basin deer reflect their relative lack of abundance.

Second, we examined reports of the clothing worn by North American Indians in the central Great Basin, and at the Basin's northwestern edge where deer were abun-

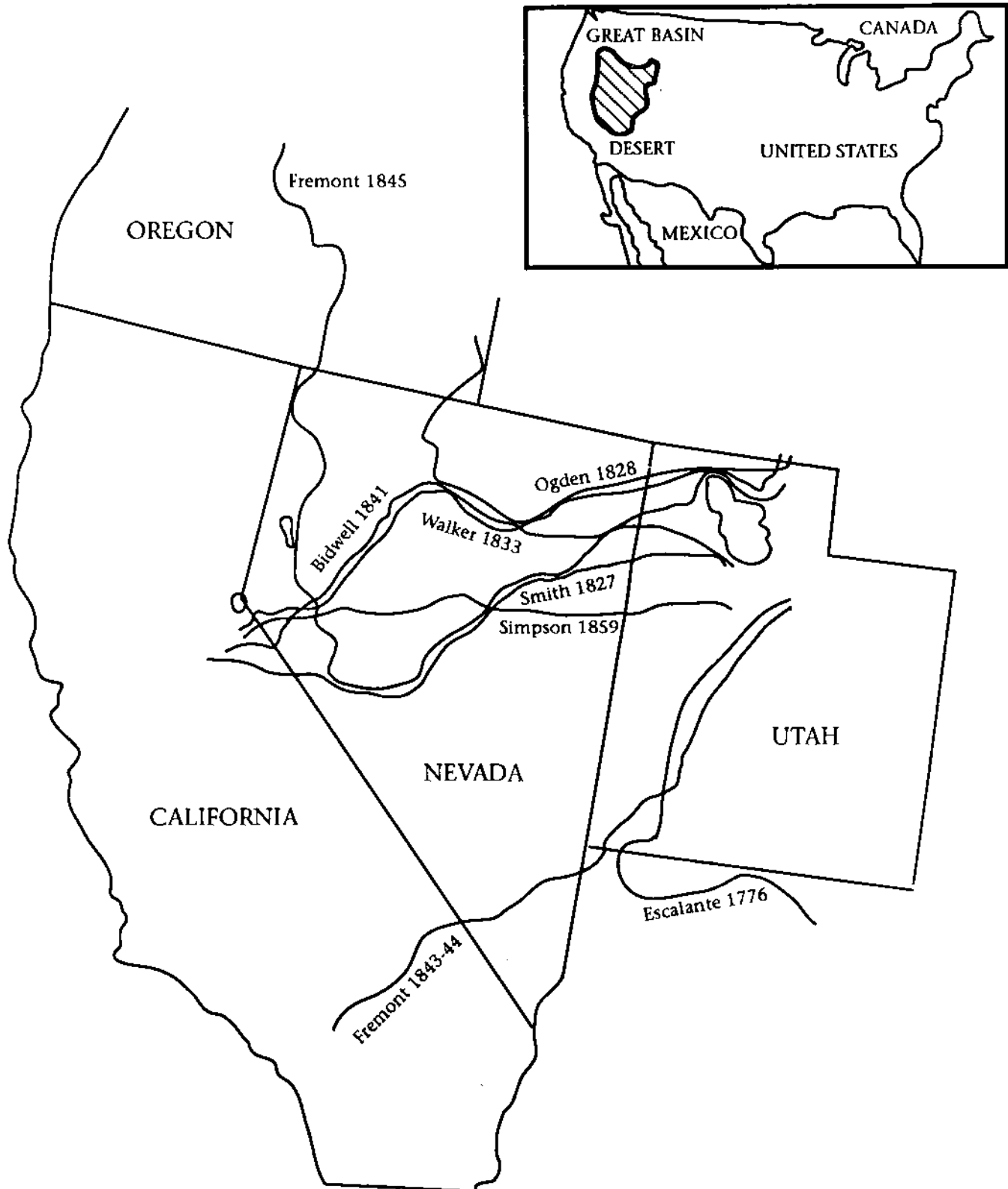


Figure 1. Overview of explorer travel routes through the Great Basin Desert (modified from Fletcher 1980). Inset shows relative location of the Great Basin with reference to Canada, Mexico, and the United States.

dant. Because these groups are closely related geographically and in customs (Powers 1875), cultural differences in food harvest and dress should be minimal. Most native people were referred to by early settlers as "diggers" and were characterized as eating "rats, lizards, grass-seeds," pine nuts, and rabbits (Simpson 1875). Large mammals were hunted where available, but these were primarily bighorn, with secondary reliance on pronghorn (Brook 1980). The only skins the native Americans in central Nevada were described as wearing were rabbit (Fletcher 1980; Simpson 1875). Where deer occurred, such as in the western Sierra Nevada Range and in California's segment of the northwestern Great Basin, deer were used in the diet and dress of the native people (Fletcher 1980; Powers 1875). A third indication of the deer paucity in the Great Basin is the abundance of petroglyphs and pictographs depicting pronghorn and bighorn but not deer (Heizer & Baumbach 1962; Pippin 1977) although the purposes of such artworks remain uncertain.

Finally, archaeological data support the supposition that there were few deer prior to European colonization (Grayson 1983). If deer were abundant it makes sense to expect that they would have been regularly harvested and their bones would have subsequently been discovered. However, holocene large mammal osteological remains from caves of inferred nonhuman origin indicate few deer (McGuire 1980), and bighorn and pronghorn bones may be more than 50 times as common at paleo sites intensively occupied by humans (Grayson 1988; James 1983; Thomas 1983). Collectively, the evidence from four disparate lines — historical descriptions, native American clothing, paleolithic art, and archaeological cave sites — suggests deer were uncommon.

Given the paucity of post-Pleistocene deer, why has colonization of the Great Basin been so rapid during the twentieth century? Numerous studies (Wagner 1978; Workman & Low 1976; Young & Sparks 1985) point to widespread habitat changes resulting from massive numbers of unregulated livestock in the western United States, including the Great Basin. Wild horses also have been an exotic large-bodied grazing herbivore of the Great Basin since at least 1911 (Berger 1986). By removing large quantities of graminoids, these exotic species favored the spread of forbs and shrubs, items important to deer. While the historic numbers of exotic species, which also included domestic sheep, remain unknown (see Wagner 1978), estimated population sizes in 1980 were 270,000 sheep and goats, 32,000 wild horses, and 310,000 cattle (Berger 1986). As a result of the disproportionate biomass of exotic ungulates during the last 100 years, habitats were radically altered, followed by an increase in deer (Berger 1986; Gruell 1986) and subsequently in lion populations.

Evidence on the past distribution of large carnivores

is meager, but based on the pre-1900 distribution of Great Basin's ungulates, pronghorn and bighorn, lions would not have been expected. Indeed, lion remains are virtually lacking, whereas bobcat and canid bones are relatively more common at mid- and late Holocene cave sites (Grayson 1988; James 1983). Even today, accounts of lion predation on pronghorn do not exist, presumably because pronghorns are fleet and rely on open habitats to detect predators, whereas lions, being ambush predators, rely on cover. The expansion of lions, at least in Nevada (Stiver 1988), presumably resulted from vegetation changes that favored mule deer, but lions may now exert effects on other species. Although the range of lions extensively overlaps that of deer, and lions may prey on sheep, bighorns do not appear to support lion populations in the absence of deer. In the eastern Mojave Desert, where pockets of Great Basin habitat containing recently introduced mule deer extend into the desert, lions occur; however, lions are lacking in nearby mountain ranges that contain bighorns but no deer (Wehausen 1990).

Community changes often result from important environmental perturbations, including man's influence (e.g., Pleistocene overkill or the introduction of rabbits into Australia). However, recent examples of human-induced predator-prey disequilibrium are lacking, although the introduction of dingos into Australia exerts considerable pressure on marsupials (Caughley et al. 1980) while relative stability is found in unperturbed predator-prey systems (Powell 1980). In our case, two species irrupted; deer, as a consequence of man's dissemination of livestock, followed by mountain lions. In addition to deer, Great Basin lions prey upon porcupines, elk, bighorn sheep, several species of lagomorphs (Robinette et al. 1959), and even coyotes and bobcats. While impacts on these species remain unknown, lions are now keystone predators that have striking effects on adult bighorn sheep, which in the pre-1900s Great Basin probably experienced little effective predation except for early man (James 1983; Grayson 1988; Pippin 1977; Thomas 1983). Currently, however, lion predation on sheep has had significant localized impacts. In the Wasuk and Snake ranges of Nevada, where bighorn sheep reintroductions have failed due to lions, deer were originally rare, as presumably were lions. And in the Owens Valley region of the western Great Basin, 72 lion-killed bighorns were found between 1975–1990 (Wehausen, unpublished data). One reintroduction in the Sierra Nevada Range persists only because lions are controlled. These data illustrate recent, and unforeseen, demographic and community-level effects of lions.

Our findings have political and biological relevance for those involved in the restitution of natural communities. Although the word "natural" remains controversial because it lacks a temporal dimension (Chase 1986;

Patton 1987), it is clear that the distribution and abundance of Great Basin deer and lions have changed over the last one hundred years, modifications that would not have been possible in the absence of human-induced habitat changes promoted by livestock and wild horses. If natural areas, including national parks or monuments, are to represent the communities present before European man, then it may be appropriate to alter lion and deer densities in the Great Basin. Species such as horses and cattle are obvious aliens, but those "native species" that increased greatly as a result of human activities are often ignored when the question of pristine community structure is considered.

Interestingly, the issue of pristine communities has assumed a more prominent role in the management of some North American ecosystems than it has elsewhere. For example, in Asia and Africa, local people have directly influenced assemblages of native species for hundreds if not thousands of years, both directly and through indirect effects of livestock. In such cases it is virtually impossible to distinguish between human and natural effects (Western 1989), let alone to define what is "natural". The point of our paper is not to suggest policy about the removal of deer or lions in reserves of the Great Basin. Rather, we wish to illustrate that in this system, as well as the Greater Yellowstone area and presumably in many others, it will become increasingly difficult to discern constituents of pristine communities.

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