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Trophic cascades involving cougar, mule deer, and black oaks in Yosemite National Park

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A B S T R A C T

Using a historical reconstruction, we discovered a potential trophic cascade involving cougar (*Puma concolor*), mule deer (*Odocoileus hemionus*), and California black oak (*Quercus kelloggii*) in the Yosemite Valley of Yosemite National Park in California. Our objective was to determine whether large deer populations in the absence of a top-level carnivore were suppressing tree regeneration. As human visitation increased in the early 1900s and cougar became increasingly scarce, the mule deer population irrupted in the 1920s. In August 2006, we undertook a retrospective study of black oak recruitment (i.e., growth of seedling/sprouts into tall saplings and trees) by inventorying all black oaks in stands accessible to deer and greater than 0.5 ha in size (18 stands, 2921 trees). We similarly inventoried oaks within sites representing refugia from deer browsing (4 stands, 481 trees). While significantly diminished oak recruitment has occurred since the 1920s in stands accessible to deer ($p < 0.01$), continuous recruitment of oaks was found in refugia sites. We also found less oak recruitment in areas of high human activity near the park's visitor center ($p < 0.01$), possibly due to behaviorally-mediated effects of lower cougar and higher deer densities. Overall our results are consistent with trophic cascade theory involving large predators, herbivores, and plants. The long-term lack of oak recruitment is also an indicator of a probable loss of biodiversity.

1. Introduction

Historically, ecologists generally viewed food-webs as regulated by bottom-up forces (Ray et al., 2005). This view started to change when Hairston et al. (1960) initiated a continuing debate when they suggested that predators maintain plant biomass at high levels by limiting herbivore populations. Later termed trophic cascades, this "top-down" view of food-web interactions contradicted the prevailing bottom-up view that food-webs were nutrient-driven, as reflected in the classic food pyramid. More recently, ecologists have recognized that both top-down and bottom-up forces affect the abundance and diversity of flora and fauna within a food-web (Polis and Strong, 1996). Because interactions within a food-web can be complex and the relative strength of top-down vs. bottom-up forces can vary, the importance of trophic cascades in ecosystem processes and functions has remained controversial (Schmitz et al., 2000; Halaj and Wise, 2001; Shurin et al., 2002; Borer et al., 2005).

One source of controversy may be associated with the unraveling of ecosystems that often occurs whenever humans significantly affect trophic levels (Terborgh et al., 2001). Thus, the paucity of documented cases of terrestrial trophic cascades involving large predators may be an artifact

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of viewing seriously altered systems after carnivore extirpation, a situation which characterizes many current ecological investigations (Steneck and Sala, 2005).

Historical reconstructions of plant community dynamics may be particularly useful for understanding trophic cascades since they can provide direct evidence about the previous ecosystem states (Jackson et al., 2001). Furthermore, such assessments may be valuable for guiding interpretations of long-term trophic interactions following the removal or reduction of carnivores. Using tree rings as a basis for determining when trees became established, herein we report on a historical reconstruction of a potential trophic cascade involving cougar (*Puma concolor*), mule deer (*Odocoileus hemionus*), and California black oak (*Quercus kelloggii*) in the Yosemite Valley of California. Other than recent studies conducted by Binkley et al. (2005) and Ripple and Beschta (2006) on the Colorado Plateau, we are not aware of additional reports on the presence or absence of cougars triggering a trophic cascade.

Based on theoretical models of predator/prey dynamics, the overshooting of carrying capacity by ungulates would be rare or infrequent with an intact predator/prey system (Boutin, 1992; Ballard et al., 2001). Leopold (1943) in summarizing his research on this topic wrote,

> "We have found no record of a deer irruption in North America antedating the removal of deer predators. Those parts of the continent which still retain the native predators have reported no irruptions. This circumstantial evidence supports the surmise that removal of predators predisposes a deer herd to irruptive behavior".

More recently, Flueck (2000) reviewed literature from northern latitudes around the world and similarly found no reports of "deer [cervid] irruptions in unmodified continental environments containing complete large predator and prey communities". Furthermore, when predation is either eliminated or reduced, the subsequent decline in carrying capacity following an ungulate population irruption likely occurs because herbivores over-utilize their forage base (Leopold, 1943; McCullough, 1979; Ripple and Beschta, 2005). Our hypothesis (below) linking black oak recruitment (i.e., growth of seedling/sprouts into tall saplings and trees) in Yosemite Valley to the presence of predators is consistent with the above theory on the overshooting of carrying capacity as well as with Leopolds's (1943) and Flueck's (2000) findings.

Cougar were displaced from Yosemite Valley early in the 20th century and a deer population irruption followed in the 1920s (Wright et al., 1933; Dixon, 1934a). Thus, we undertook this study to evaluate any effects on the current age structure of black oak as mediated through potentially high levels of deer browsing. We hypothesized that any long-term gap in black oak recruitment is mainly associated with low density of predators and high browsing pressure by mule deer (see Fig. 1). We also considered alternative hypotheses for any reductions in black oak recruitment including: (1) fluctuations in climate, (2) lack of fires, (3) conifer invasion, (4) land use, and (5) loss of aboriginal influences.

Fig. 1 – Mature black oaks and a lack of young oaks near the visitor center in Yosemite Valley. The mule deer in the foreground is foraging for acorns and oak seedlings (W.J. Ripple, September 2006).

2. Yosemite Valley history

Humans occupied Yosemite Valley for at least the last 3000 years and paleoecological evidence suggests that aboriginals began burning in the valley about 650 years ago (Anderson and Carpenter, 1991). Coincident with this new burning practice, pollen from pond sediments showed a rapid shift from a conifer dominated forest to a more open oak system in the valley (Anderson and Carpenter, 1991). Prior to the 1850s, Yosemite Valley was occupied by a tribe of Miwok Indians that harvested black oak acorns and habitually used fire and hand-eradication methods to control brush and tree growth (Earnst, 1943; Reynolds, 1959). When Euro-Americans entered the valley in the 1850s, they found little undergrowth and a "park-like" setting, with clear open views throughout the valley (Earnst, 1943).

By the early 1860s, settlers in Yosemite Valley began plowing portions of the floodplain, planting crops, and grazing livestock. During the 1880s, settlers attempted to clear young trees and brush which, in the absence of fire, had proliferated throughout the Valley (Earnst, 1943). Mule deer were very scarce around the turn of the century since, in defiance of existing game laws, hunting of them was common (Dixon, 1934a). By the second decade of the 20th century, Yosemite National Park had an active predator removal program. Grinnell and Storer (1924) described professional cougar hunter Jay Bruce's success at killing cougar in the Yosemite area, "... a total of 31[cougar] being taken in the three winter seasons, 1915–1918". During this period of predator reduction, Yosemite ranger Forest S. Townsley wrote to Joseph Grinnell, "Coyotes, Lions, bob-cats seem to be very much on the decrease..." (Runte, 1990).

By the 1920s, the National Park Service began to note an increase in Yosemite Valley's mule deer population. Wildlife biologist Dixon (1934a) reported, "Through protection from predatory natural enemies and human hunters, the deer in Yosemite [Valley] increased so rapidly that they were numerous there by 1925". In addition to intense browsing on oak seedlings, Dixon (1934b) suggested that the deer were the cause of a decline of the evening primrose (*Oenothera hookeri*) in the valley. Other National Park Service wildlife biologists (Wright et al., 1933; Cahalane, 1941) similarly noted the absence of cougar, abundant deer, and browsing impacts to the vegetation. They suggested that vegetation was being threatened due to increases in the deer population following displacement of cougar from Yosemite Valley. In an attempt to preserve native flora, in 1930 and 1931 the Park Service trapped and removed 137 deer from Yosemite Valley (Dixon, 1934a). Although deer removals in the early 1930s provided temporary relief from overbrowsing, within a few years their numbers again increased and additional deer were removed in the 1940s.

To monitor deer impacts to vegetation, the park service constructed several deer-proof fenced exclosures in 1934. At the Bridal Veil meadow exclosure, Allen et al. (circa 1970) observed that a variety of plant species comprising the dense tall growth inside the fence were entirely absent in the immediate vicinity outside because of deer foraging impacts. At the El Capitan exclosure, they found oak seedlings to be much more numerous inside than outside the fence.

In a study of vegetation of Yosemite Valley, Heady and Zinke (1978), observed abundant black oaks in the seedling and mature size classes, but fewer oaks than would be expected in the intermediate size classes. They also noted relatively heavy browsing impacts by deer on woody browse species. Recently, Fritzke (1997) suggested a linkage between the lack of long-term black oak recruitment and deer browsing in the valley.

3. Study area

Yosemite Valley was originally shaped by glaciation, resulting in jagged peaks, rounded domes, waterfalls, and a U-shaped canyon. Following glaciation, the valley floor (comprising an area of ~18 km^2) became largely covered with alluvial sediments.

The Mediterranean type climate of the central Sierras is characterized by hot, dry summers and cool, moist winters. Most precipitation occurs during the winter as either rain or snow. Yosemite Valley lies in the lower montane forest zone, with a prevalence of trees such as California black oak, interior live oak (*Quercus wislizeni*), ponderosa pine (*Pinus ponderosa*), incense-cedar (*Calocedrus decurrens*), and white fir (*Abies concolor*). Major predator species within the park include cougar, black bear (*Ursus americanus*), and coyote (*Canis latrans*), with ungulates represented only by California mule deer that are found in the valley year round. Among others, small mammal species include California ground squirrel (*Spermophilus beecheyi*) and western gray squirrel (*Sciurus griseus*).

California black oak reproduces by sexual and asexual mechanisms. Sexual reproduction consists of acorn crops after oaks are at least 30 years old. Asexual reproduction involves basal sprouting after disturbance, such as fire. Black oak is somewhat shade tolerant as a seedling, but less so as a sapling or small pole (McDonald, 1969). Initial seedling development is typically not limited by low light levels because acorns are relatively large and provide the bulk of carbohydrates for initial growth. Since the majority of a seedling's biomass lies in the roots, they are able to persist in low light for years until disturbance reduces overstory shade, thus allowing an oak seedling to continue its vertical growth. As black oaks grow they become increasingly shade intolerant, with the crown requiring full sunlight (McDonald, 1969).

Deer, small mammals, and insects consume black oak acorns, sprouts, and foliage. Gray squirrels disseminate acorns by burying them singly in the ground, a process that often results in the establishment of seedlings away from the parent trees. Black oak lives to 500 years, but in the absence of disturbance can be crowded out by conifer invasion or die because of shade intolerance. The spatial extent of black oak stands in Yosemite Valley has declined during the 20th century, and observers typically attribute this decline to lack of fire and conifer invasion (Earnst, 1943; Reynolds, 1959). Since 1970 the park service has implemented a prescribed burning program in Yosemite Valley. The visitor's center and nearly all other building and campground development (mostly <4 km from the visitor's center) occur near the east end of the valley. In contrast, the west side of Yosemite Valley and the Mirror Lake area on the far northeast end are relatively undeveloped except for some roads and/or trails.

4. Methods

We selected all black oak stands greater than 0.5 ha in size from a park service vegetation type map of Yosemite Valley. We only selected stands dominated by black oak, thus avoiding stands heavily invaded by conifers. A total inventory of tree diameters was conducted within the selected stands of all black oaks $\geqslant$1 cm diameter at breast height (DBH). Tree diameter measurements were made using a Biltmore stick. We inventoried oaks in all selected open-grown (accessible to deer) stands as well as those in refugia sites where there were physical barriers to deer access. These refugia included strips of land occurring between the main highway and river comprising terraces and other surfaces generally above the floodplain, often with high cutbanks. Our examination of the oak seedlings and saplings indicated very low levels of browsing in the refugia stands. Beschta (2005) described similar refugia along the Yellowstone River where he found low browsing levels on strips of land between the river and a highway. We compared oak age structure for the deer-accessible sites to that of the refugia sites (spatial control).

We obtained increment cores at breast height (~1.4 m above the ground) from 3 to 4 oaks in each inventoried stand and used these data to establish age–diameter relationships for estimating the breast height age of each inventoried tree. We mounted, dried, and sanded the cores before counting tree rings with the aid of a dissecting microscope. Cross dating of cores to identify ring anomalies was not accomplished due to low variability in ring widths. Based on sectioning young oak trees adjacent to the park, we added 11 years to this estimated age at breast height to account for tree height growth from ground level to 1.4 m above the ground. Measured tree diameters, in conjunction with the age–diameter relationship, were used for determining historical trends in black oak tree recruitment in Yosemite Valley (e.g., Beschta, 2005). An exponential function was fitted to measured tree frequencies and establishment dates before the deer irruption (pre-1920) for deer-accessible stands and to all tree frequency and establishment data for refugia stands.

We established a 4 m wide belt transect through the centroid of each surveyed oak stand, along its long axis, within which the number and height of all oak seedlings were recorded. The total length of each transect was also recorded. Basal area measurements (using a 5 m^2/tree basal area factor gage) were obtained at up to 4 equally spaced points along the transect, with a minimum of 40 m separation between measurement locations. We searched for cougar fecal droppings in each oak stand while walking between measured trees. We surveyed evening primrose plants in order to obtain an estimate of deer browsing intensity that was independent of black oaks. Since evening primrose only grow in wet areas, a search and enumeration of this species was made at all oak stands growing in wet sites. Each evening primrose plant was classified as unbrowsed (buds intact) or browsed (buds browsed off).

Other covariates recorded for each stand included (1) distance from visitor center and (2) fire history. Since cougar generally avoid humans (Van Dyke et al., 1986), distance from the visitor center data were used to investigate whether more browsing and less oak recruitment occurred near the center of greatest human activity. In other national parks, researchers have found evidence of lower predation risk, higher ungulate densities, and more browsing on plants in areas of high human activities (Hebblewhite et al., 2005; Ripple and Beschta, 2006; Beschta and Ripple, 2007). Information on the number of times each stand burned since 1930 was obtained from a Park Service fire history map of Yosemite Valley.

We used *t*-tests (unequal variances) to determine any significant differences between covariates associated with deer-accessible oak stands vs. refugia oak stands, as well as for stands near the visitor center compared to stands farther away from the visitor center. The nonparametric Wilcoxon rank-sum test was used when data were not normally distributed. Since we were performing multiple comparisons, we applied the False Discovery Rate (FDR) procedure and adjusted the results as described by Benjamini and Hochberg (1995). We used the Palmer Drought Index (Cook et al., 2004) to examine general climatic patterns for the periods 1800–1919 vs. 1920–1999. We considered $p \leqslant 0.05$ from any test to represent a statistically significant outcome.

5. Results

We found and measured the diameters of 2921 black oak trees (DBH range 1–190 cm, $\bar{x} = 38$ cm) in 18 deer-accessible stands and 481 oak trees (DBH range 1–135 cm, $\bar{x} = 10$ cm) in 4 refugia stands. Deer-accessible stands ranged from 0.65 to 2.50 ha in size, while available refugia stands were smaller, ranging from 0.14 to 0.68 ha.

We obtained a total of 27 readable increment cores from black oaks occurring along Yosemite's valley bottom. Regression analysis indicated that the number of tree rings (*y*) was highly correlated with DBH (*x*) ($y = 5.35x^{0.795}$, $r^2 = 0.77$, $p < 0.01$). A statistically significant, but somewhat different relationship, was obtained for 13 readable cores from black oaks occupying hillslopes adjacent to canyon walls ($y = 14.94x^{0.592}$, $r^2 = 0.61$, $p < 0.01$).

The age structure of deer-accessible oak stands in Yosemite Valley was considerably different from that associated with refugia stands. The deer-accessible stands (Fig. 2a) show few young trees and lack of recruitment since the early 1900s. In contrast, oaks within the refugia stands (Fig. 2b) show continuous recruitment over time with more young trees than old ones, a normal feature of uneven-aged forest dynamics when recruitment is on-going. There were no significant differences in the number of fires since 1930 and oak seedling densities between the deer-accessible and refugia oak stands ($p \geqslant 0.14$, Table 1). We found a marginal difference in oak basal area between deer-accessible and refugia stands, but

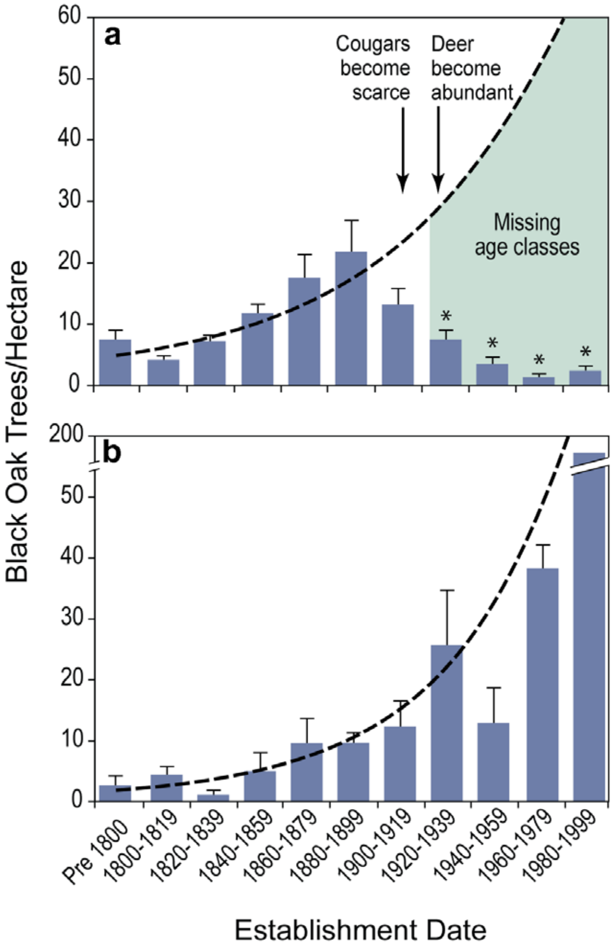

Fig. 2 – California black oak age structure (with standard error bars) for (a) deer-accessible oak sites and (b) refugia sites with low deer browsing; all sites are within Yosemite Valley. The exponential functions (dashed lines) are based on (a) tree frequencies and establishment dates before the deer irruption (pre-1920) and (b) tree frequency and establishment data between 1800 and 1999. The age structure in (a) illustrates a general cessation of oak recruitment (i.e., missing age classes) since the early 1900s, which is in contrast to generally continuous recruitment in (b). Age classes outside the lower 95% confidence interval of the exponential equation are represented by *.

Table 1 – Summary statistics of covariates for deer-accessible oak stands (generally those experiencing intensive oak browsing by deer) and refugia oak stands (with little or no oak browsing by deer)

Covariate description	Deer-accessible stands ($n = 18$)			Refugia stands ($n = 4$)			p-value	Statistical test
	mean	min	max	mean	min	max		
Number of fires since 1930	1.8	0	5	1.8	0	4	0.98	t-test
Conifer basal area (m^2/ha)	10.5	0	22.4	22.7	17.6	33.9	0.05[a]	Rank-sum
Oak basal area (m^2/ha)	12.9	4.9	21.5	6	0.6	12.9	0.07	t-test
Oak seedlings (#/ha)	716	167	2567	897	639	1173	0.14	Rank-sum
Oak seedling height (cm)	17.2	9.7	38	57.6	47.6	65	<0.01	Rank-sum
Oak recruitment since 1920 (#/ha)	13.1	0	45.1	86.8	74	106.7	<0.01	t-test

[a] Not considered significant due to false discovery rate from multiple comparisons.

this was not statistically significant ($p = 0.07$). We also found marginally higher ($p = 0.05$) conifer basal area in the refugia stands when compared to the deer-accessible stands but this was not significant after conducting the FDR procedure. Mean oak seedling height and the mean number of oaks originating since 1920 was significantly lower in deer-accessible stands than for refugia stands ($p < 0.01$).

Since deer-accessible oak stands occurred up to 8 km from the visitor center, we classified all stands as either 0–4 km from the visitor center ($n = 11$) or 4–8 km from the visitor center ($n = 7$). There were no significant differences in number of fires since 1930, conifer and oak basal area, seedling density, and seedling height between oak stands 0–4 km vs. 4–8 km from the visitor center ($p \geqslant 0.18$, Table 2). However, significantly more oaks originated since 1920 in stands 4–8 km from the visitor center when compared to those 0–4 km from the visitor center ($p < 0.01$) where we found on average 20.1 vs. 2.1 oaks/ha, respectively. We found cougar scat in 3 of the 18 deer-accessible stands, all at distances 4.1–6.5 km from the visitor center. Mean recruitment of black oaks since 1920 in stands with observed cougar scat was higher than in stands without observed scat (35.6 vs. 8.4 trees/ha, $p = 0.02$).

A total of 91 evening primrose plants were found in 4 out of 7 wet-site oak stands of which approximately 98% had been browsed, as indicated by the absence of flower buds. The 4 wet-site stands with primrose were all located away (4.3–5.5 km) from the visitor center whereas the three wet-site stands with no observed primrose were all located near (0.8–2.1 km) the visitor center. For the 18 deer-accessible stands, we found significantly more oak recruitment since 1920 in dry-site ($\bar{x} = 18.8$ oaks/ha, $n = 11$) than wet-site ($\bar{x} = 4.2$ oaks/ha, $n = 7$) stands ($p = 0.03$).

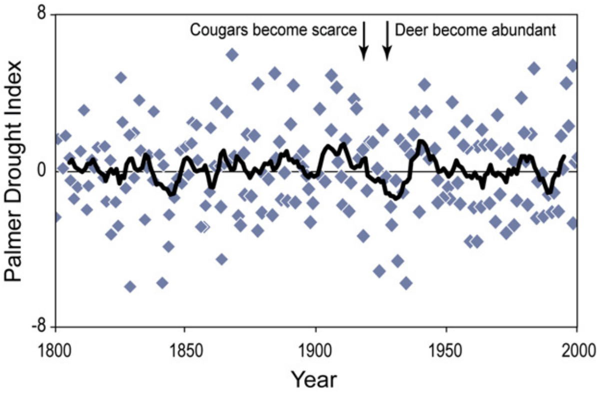

Fig. 3 – Annual values (closed diamonds) of Palmer Drought Index for Yosemite Valley and a 10-year moving average (continuous line) over a 200-year period of record ("point 47" data from Cook et al., 2004). Positive values of the index indicate wet periods and negative values dry periods.

There were no apparent differences in drought/wet period fluctuations in the Palmer Drought Index (PDI) data when comparing the periods before 1920 to those since 1920 (Fig. 3). We calculated the mean PDI for the periods 1800–1919 and for 1920–1999 and found that they were not significantly different ($p = 0.62$).

6. Discussion

Our age structure data for deer-accessible oak stands (Fig. 2a) illustrate a major recruitment gap in Yosemite Valley occurring after 1920 where we found, on average, only 13 oaks/km^2. This compares to 87 post-1920 oaks/km^2 in the browsing refugia

Table 2 – Summary statistics of covariates for oak stands near (0–4 km) the visitor center and those away (4–8 km) from the visitor center

Covariate description	0–4 km stands ($n = 7$)			4–8 km stands ($n = 11$)			p-value	Statistical test
	mean	min	max	mean	min	max		
Number of fires since 1930	1.1	0	3	2.2	0	5	0.18	t-test
Conifer basal area (m^2/ha)	7.3	0	18.7	12.5	0.3	22.4	0.15	t-test
Oak basal area (m^2/ha)	13.1	5.7	21.5	12.8	4.9	20.7	0.89	t-test
Oak seedlings (#/ha)	795	188	2567	665	167	1646	0.79	t-test
Oak seedling height (cm)	15.8	9.7	32.5	18	9.8	38	0.48	Rank-sum
Oak recruitment since 1920 (#/ha)	2.1	0	6.6	20.1	0	45.1	<0.01	t-test

stands, representing nearly a 7-fold difference between these two groups of stands. Furthermore, oak recruitment rates for the deer-accessible stands decreased with time as the 20th century progressed, with very low recruitment occurring by the end of the century (Fig. 2a). The oak age structure data show the recruitment decline starting between 1900 and 1920, which is during the predator eradication period and just before the deer irruption of the 1920s. This downturn in oaks may have been due to browsing by an increasing deer population or, since oak grow slowly, the irrupting deer of the 1920s may have killed oak regeneration from the previous decade.

Overall, our results indicate a continuation of the high deer browsing intensities witnessed by early wildlife biologists and park managers after cougar, and perhaps other predators became scarce, and the deer population irrupted in Yosemite Valley (Wright et al., 1933; Dixon, 1934a,b; Cahalane, 1941; Allen et al., circa 1970). Such results are consistent with trophic cascades theory whereby a reduction in large carnivore predation can produce important ecosystem changes, including greater herbivore densities and relatively few young palatable trees.

Due to a lack of case studies, there have been questions in the literature about whether terrestrial trophic cascades driven by large carnivores generally occur (Borer et al., 2005). The results reported here support previous studies regarding the role of wolves (*Canis lupus*) in trophic cascades in Isle Royale (McLaren and Peterson, 1994), Yellowstone (Ripple and Larsen, 2000; Ripple and Beschta, 2004; Beschta, 2005), Banff (Hebblewhite et al., 2005), Wind Cave (Ripple and Beschta, 2007), and Jasper National Parks (Beschta and Ripple, 2007). Our findings in Yosemite Valley are consistent with other studies describing trophic cascades in cougar/mule deer systems on the Kaibab Plateau (Leopold, 1943; Binkley et al., 2005) and in Zion National Park (Ripple and Beschta, 2006). Aspen recruitment on the Kaibab largely terminated following predator reductions, similar to the patterns of reduced cottonwood recruitment and reduced biodiversity in Zion Canyon after cougar became scarce. Our findings also support Leopold's (1943) hypothesis of ungulate irruption and ecosystem degradation after the removal of large carnivores. Thus, this study and other recently published studies involving wolves as well as cougars indicate that terrestrial trophic cascades involving large carnivores may be relatively strong in areas with winter or year-round ungulate use.

In other parts of the United States, deer impacts to oak recruitment in the absence of large carnivores have been documented in a variety of ecosystems. For example, Healy (1997) suggested that high densities of white-tailed deer (*Odocoileus virginianus*) in Massachusetts reduced oak recruitment due to browsing on seedlings. He described these oak stands as having a poorly developed understory and midstory layers similar to what we observed in Yosemite Valley. Russell and Fowler (1999) suggested that browsing by high densities of white-tailed deer caused a lack of Texas live oak (*Quercus fusiformis*) and Texas red oak (*Quercus buckleyi*) recruitment in central Texas. White (1966) found that heavy browsing by mule deer on blue oak (*Quercus douglasii*) seedlings in the California foothills caused a lack of small diameter oak trees. Boyer and Bleich (1979) studied mule deer and California black oak in a state park in southern California where they found, in a system degraded by past domestic livestock grazing, even moderate densities of deer were able to prevent oak recruitment.

Our results of less cougar scat, oak recruitment, and evening primrose in areas near the Yosemite visitor center (low predation risk), compared to more distant locations (high predation risk), are consistent with trophic cascades theory involving behaviorally-mediated effects. This shift in the use of space by the herbivore is typically considered a behavioral effect, since it is a non-lethal mechanism, and occurs when ungulates, under the risk of predation, alter their foraging patterns and movements in a "landscape of fear" (Lima, 1998; Laundré et al., 2001). When predation risk is high, herbivores balance needs for both safety and forage as described by optimal foraging theory (Brown et al., 1999; Berger, 2007) and the effects on plants may be greater than those resulting from changes in predator or prey populations (Schmitz et al., 1997). Furthermore, recent research in carnivore/ungulate systems has found high ungulate densities and/or high levels of browsing near human developments in other national parks in the western North America including Denali (Wolff and Cowling, 1981), Banff (Hebblewhite et al., 2005), Zion (Ripple and Beschta, 2006), Jasper National Parks (Beschta and Ripple, 2007), and Grand Teton National Park (Berger 2007).

While our results are consistent with trophic cascade theory, we nevertheless considered alternative scenarios that might affect oak recruitment including: (1) fluctuations in climate, (2) lack of fires, (3) conifer invasion, (4) land use, and (5) lack of aboriginal influences.

Climate fluctuations do not appear to have caused the lack of oak recruitment as the Palmer Drought Index shows wet and dry periods throughout a 200-year period of record (1800–1999). We found no significant differences when comparing the average PDI before 1920 to that after 1920 and there has been continuous long-term recruitment of oaks in the refugia stands (Fig. 2b). Additionally, Angress (1985) studied Yosemite Valley oaks and soil moisture and suggested that varying levels of soil moisture did not have a significant effect on black oak germination and seedling growth. We found more oak recruitment since 1920 in dry-site than wet-site stands ($p = 0.03$) further indicating that available moisture was not a limiting factor for oak recruitment.

The lack of fire may be hampering black oak recruitment since fire can eliminate competing conifers, open the canopy, and allow asexual reproduction through basal sprouting. However, we do not believe that a lack of fire is the cause for reduced oak recruitment in our deer-accessible stands since we found on-going recruitment in the refugia stands, even though both groups of stands have a similar fire history (Table 1). Additionally, there has been little recruitment of oaks within the valley even with an on-going prescribed fire program implemented by the Park Service since 1970 (Fig. 2a).

Shading and competition from conifer invasion may be a factor in oak decline for large portions of Yosemite Valley, since various studies have documented a general increase in conifers during the 20th century (e.g., Gibbens and Heady, 1964), and oak stands may have been lost to this factor. However, we did not survey stands heavily invaded by conifers, and conifer basal area was greater in the refugia stands than in the deer-accessible stands. It appears that oak recruitment suppression can be nearly complete in the absence of significant conifer invasion as a result of intense deer browsing.

The variable land use history in Yosemite Valley complicates efforts to easily discern potential predator–herbivore effects on plants. Historically, aboriginal inhabitants may have kept carnivore and deer numbers to relatively low levels. Low deer densities in conjunction with frequent low-intensity fires (Reynolds, 1959; Angress, 1985) allowed oaks to recruit over time (our pre-1920 oak age structure data). When Euro-Americans arrived they also hunted deer and predators, thus keeping large mammal numbers down. Until the time deer irrupted, subsequent to the decline in cougar and other predators in the 1910s, black oak recruitment appears to have been on-going (Fig. 2a). While land use practices prior to the 1920s may have affected the overall distribution of black oak stands that are currently left in the valley, oak recruitment prior to the 1920s was occurring in the stands we measured.

Although the study of interactions of herbivory and disturbance events is in its infancy, research is beginning to show the importance of "coupling" press disturbances such as ungulate predation with pulse disturbances such as wildfire on the recruitment of woody browse species (Wisdom et al., 2006; Halofsky, 2007; Beschta and Ripple, 2007). Since the occurrence of fire with moderate-to-high herbivory can be detrimental to tree recruitment, decreased levels of herbivory may be required before some of the potential ecological benefits of fire (i.e., the maintenance of palatable woody species that are adapted to fire) can be attained (Wisdom et al., 2006). We observed essentially no recruitment of basal sprouts on 104 large oaks killed during relatively recent Park Service prescribed burns (authors' observations, 2006). Thus, our results suggest that prescribed burning in the presence of existing levels of ungulate herbivory is likely accelerating the decline of the overstory oaks in Yosemite Valley while providing no improvement in oak recruitment.

The paleoecological data suggest that Yosemite Valley was dominated by conifers before humans began burning the Valley 650 years ago. This perspective has implications for the current management of fire and oaks in understanding the valley's "natural state" before anthropogenic disturbances (Anderson and Carpenter, 1991). The more recent aboriginal peoples in Yosemite Valley probably influenced black oaks in at least two ways: (1) burning the valley which decreased conifers and increased oaks; and (2) killing or displacing large predators and deer. They appear to have modified natural ecosystem structure and processes to create a system that favored oak recruitment, acorn production, and acorn harvest (i.e., frequent burning and low predator/deer densities). Thus, the current park service policy of prescribed burning to remove conifers in conjunction with the current high deer densities is in contrast with both the conifer dominated system prior to 650 years ago as well as the more recent aboriginal system, which likely consisted of fewer conifers, more oaks, and fewer deer.

We did not study the effects of several factors that might influence oak recruitment such as variability in hunting pressure on deer, acorn predation by small mammals and birds, pathogens, periodicity of acorn crops, interaction of available light with browsing pressure, and direct impacts of human trampling on young oaks. However, we propose that they were unlikely to have been major factors affecting the oak recruitment gap documented in this study since our study design included both a temporal control (pre-1920s deer irruption vs. post-1920s deer irruption) and two types of spatial control (deer-accessible vs. refugia oaks as well as near visitor center vs. away from visitor center).

In Yosemite Valley, there are dozens of faunal species that rely on acorns for food and oak trees for nesting and cover. The lack of oak recruitment documented in this study likely indicates a substantial decrease in biodiversity (e.g., shrubs, wildflowers, birds, invertebrates) since early in the 20th century. Thus, in concert with a broader literature (e.g., Rooney and Waller, 2003; Côté et al., 2004), this study supports the concept that, in the absence of large carnivores or control by humans, ungulates can profoundly alter ecosystems.

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REFERENCES

Allen, P., Carter, F., Snell, N., circa 1970. Deer Exclusion Plots. Yosemite National Park Library, Yosemite Valley.

Anderson, R.S., Carpenter, S.L., 1991. Vegetation change in Yosemite Valley, Yosemite National Park, California, during the protohistoric period. Madroño 38, 1–13.

Angress, E.E., 1985. The Decline of *Quercus Kelloggii* in Yosemite Valley: An Evaluation of Fire and Moisture Regimes. M.A. Thesis, San Francisco State University, 54p.

Ballard, W.B., Lutz, D., Keegan, T.W., Carpenter, L.H., deVos, J.C., 2001. Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. Wildlife Society Bulletin 29, 99–115.

Benjamini, Y., Hochberg, Y., 1995. Controlling the false discover rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society, Series B 57, 289–300.

Berger, J., 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3, 620–623.

Beschta, R.L., 2005. Reduced cottonwood recruitment following extirpation of wolves in Yellowstone's northern range. Ecology 86, 391–403.

Beschta, R.L., Ripple, W.J., 2007. Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. Canadian Journal of Forest Research 37, 1873–1885.

Binkley, D., Moore, M.M., Romme, W.H., Brown, P.M., 2005. Was Aldo Leopold right about the Kaibab deer herd? Ecosystems 9, 1–16.

Borer, E.T., Seabloom, J.B., Shurnin, K.E., Anderson, C.A., Blanchetter, B., Halpern, B.S., 2005. What determines the strength of a trophic cascades? Ecology 86, 528–537.

Boutin, S., 1992. Predation and moose population dynamics: a critique. Journal of Wildlife Management 56, 116–127.

Boyer, R.T., Bleich, V.C., 1979. Ecological relationships between southern mule deer and California black oak. General Technical Report PSW-44 Pacific Southwest Forest and Range Experiment Station. US Forest Service, pp. 292–206.

Brown, J.S., Laundré, J.W., Gurung, M., 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80, 385–399.

Cahalane, V.H., 1941. Wildlife surpluses in the national parks. In: Transactions of the Sixth North American Wildlife Conference, pp. 355–361.

Cook, E.R., Woodhouse, C.A., Eakin, C.M., Meko, D.M., Stahle, D.W., 2004. Long-term aridity changes in the western United States. Science 306, 1015–1018.

Côté, S.D., Rooney, T.P., Tremblay, J., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35, 113–147.

Dixon, J.S., 1934a. A study of the life history and food habits of mule deer in California. Part I—life history. California Fish and Game 3, 181–282.

Dixon, J.S., 1934b. A study of the life history and food habits of mule deer in California. Part II—food habits. California Fish and Game 4, 315–354.

Earnst, E.F., 1943. Preliminary Report on the Study of the Meadows of Yosemite Valley. Unpublished document in the Forester's office. Yosemite National Park. File No. 880-01, 68p. plus photographs.

Flueck, W.T., 2000. Population regulation in large northern herbivores: evolution, thermodynamics, and large predators. Zeitschrift fur Jagdwissenschaft 46, 1–28.

Fritzke, S.L., 1997. A California black oak restoration project in Yosemite Valley. Yosemite National Park, California. USDA Forest Service General Technical Report PSW-GTR-160, pp. 281–288.

Gibbens, R.P., Heady, H.F., 1964. The influence of modern man on the vegetation of Yosemite Valley. University of California Press, Division of Agricultural Sciences, Berkeley, 44p.

Grinnell, J., Storer, T.I., 1924. Animal Life in Yosemite. University of California Press, Berkeley, California, 669p.

Hairston, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control, and competition. American Naturalist 94, 421–425.

Halaj, J., Wise, D.H., 2001. Terrestrial trophic cascades: how much do they trickle? American Naturalist 157, 262–281.

Halofsky, J.S., 2007. Evidence of a Trophic Cascade among Wolves, Elk, and Aspen in Yellowstone National Park, USA. Ph.D. Thesis, Oregon State University, 108p.

Heady, J.F., Zinke, P.J., 1978. Vegetation changes in Yosemite Valley. National Park Service O'ccasional Paper No. 5. US Government Printing Office, Washington, DC, 25p.

Healy, W.M., 1997. Influence of deer on the structure and composition of oak forests in central Massachusetts. In: McShea, W.J., Underwood, H.B., Rappole, J.H. (Eds.), The Science of Overabundance: Deer Ecology and Population Management. Smithsonian Books, Washington, DC, pp. 249–266.

Hebblewhite, M., White, C.A., Nietvelt, C.G., McKenzie, J.A., Hurd, T.E., Fryxell, J.M., Bayley, S.E., Paquet, P.C., 2005. Human activity mediates a trophic cascade caused by wolves. Ecology 86, 2135–2144.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., et al., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 294, 629–638.

Laundré, J.W., Hernández, L., Altendorf, K.B., 2001. Wolves, elk, and bison: reestablishing the landscape of fear in Yellowstone National Park USA. Canadian Journal of Zoology 792, 1401–1409.

Leopold, A., 1943. Deer irruptions. Wisconsin Academy of Sciences, Arts, and Letters 35, 351–366.

Lima, S.L., 1998. Nonlethal effects in the ecology and predator-prey interactions. Bioscience 48, 25–34.

McCullough, D.R., 1979. The George Reserve Deer Herd: Population Ecology of a K-Selected Species. University of Michigan Press, Ann Arbor, Michigan, USA, 271p.

McDonald, P.M., 1969. Silvical characteristics of California black oak. USDA. Forest Service Research paper PSW-53, 20p.

McLaren, B.E., Peterson, R.O., 1994. Wolves, moose and tree rings on Isle Royale. Science 266, 1555–1558.

Polis, G.A., Strong, D.R., 1996. Food web complexity and community dynamics. American Naturalist 147, 813–846.

Ray, J.C., Redford, K.H., Steneck, R.S., Berger, J. (Eds.), 2005. Large Carnivores and the Conservation of Biodiversity. Island Press, Washington, DC.

Reynolds, R.D., 1959. Effect of Natural Fires and Aboriginal Burning upon the Forests of the Central Sierra Nevada. MA Thesis, University of California, Los Angeles, 262p.

Ripple, W.J., Beschta, R.L., 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54, 755–766.

Ripple, W.J., Beschta, R.L., 2005. Linking wolves and plants: Aldo Leopold on trophic cascades. Bioscience 55, 613–621.

Ripple, W.J., Beschta, R.L., 2006. Linking a cougar decline, trophic cascade, and a catastophic regime shift in Zion National Park. Biological Conservation 133, 397–408.

Ripple, W.J., Beschta, R.L., 2007. Hardwood tree decline following large carnivore loss on the Great Plains, USA. Frontiers in Ecology and Environment 5, 241–246.

Ripple, W.J., Larsen, E.J., 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. Biological Conservation 95, 361–370.

Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181, 165–176.

Runte, A., 1990. Yosemite: The Embattled Wilderness. University of Nebraska Press, Lincoln, Nebraska, 271p.

Russell, F.L., Fowler, N.L., 1999. Rarity of oak saplings in savannas and woodlands of the eastern Edwards Plateau, Texas. The Southwestern Naturalist 44, 31–41.

Schmitz, O.J., Beckerman, A.P., O'Brien, K.M., 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology 78, 1388–1399.

Schmitz, O.J., Hamback, P.A., Beckerman, A.P., 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removal on plants. American Naturalist 155, 141–153.

Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B., Cooper, S.D., Halpern, B.S., 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5, 785–791.

Steneck, R.S., Sala, E.A., 2005. Large marine carnivores: trophic cascades and top-down controls in coastal ecosystems past and present. In: Ray, J.C., Redford, K.H., Steneck, R.S., Berger, J. (Eds.), Large Carnivores and the Conservation of Biodiversity. Island Press, Washington, DC, pp. 110–137.

Terborgh, J., Lopez, L., Nuñez, V.P., et al., 2001. Ecological meltdown in predator-free forest fragments. Science 294, 1923–1925.

Van Dyke, F.G., Brocke, R.H., Shaw, H.G., Ackerman, B.B., Hemker, T.P., Lindzey, F.G., 1986. Reactions of mountain lions to logging and human activities. Journal of Wildlife Management 50, 95–102.

White, K.L., 1966. Structure and composition of foothill woodland in central Coastal California. Ecology 47, 229–237.

Wisdom, M.J., Vavra, M., Boyd, J.M., Hemstrom, M.A., Ager, A.A., Johnson, B.K., 2006. Understanding ungulate herbivory—episodic disturbance effects on vegetation dynamics: knowledge gaps and management needs. Wildlife Society Bulletin 34, 283–292.

Wolff, J.O., Cowling, J., 1981. Moose browse utilization in Mount McKinley National Park, Alsaka. The Canadian Field-Naturalist 95, 85–88.

Wright, G.M., Dixon, J.S., Thompson, B.H., 1933. Fauna of the National Parks of the United States. Fauna Series No. 1, US Government Printing Office, Washington, DC, 157p.