RESEARCH ARTICLE

SIMULATED EFFECTS OF TWO FIRE REGIMES ON BIGHORN SHEEP: THE SAN GABRIEL MOUNTAINS, CALIFORNIA, USA

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ABSTRACT

An isolated population of bighorn sheep (*Ovis canadensis nelsoni*) occupies fire-adapted chaparral ranges in the San Gabriel Mountains, California, USA. During 1976 to 2006, the amount of high-suitability habitat on bighorn sheep winter-spring ranges resulting from fires (HSF) ranged from 670 ha to 3392 ha, and population estimates for sheep, which were correlated with HSF, ranged from 130 to 740 individuals. During the past 100 years, the majority of changes in the HSF were associated with a fire regime dominated by periodic large, wind-driven, high-intensity crown fires, which resulted in high variability in the HSF. Prior to European settlement, the fire regime likely included smaller, variable intensity fires that burned during summer, but that also would have influenced the HSF. The size of those smaller fires today is effectively constrained by current fire management strategies, including exclusion and suppression. We predicted that smaller summer fires would increase the amount of high-suitability habitat and reduce the variability observed in the HSF during contemporary times, and the outcomes of our comparisons were consistent with those predictions. Small fires can be implemented by prescription, and can help to stabilize and maintain a self-sustaining population of bighorn sheep in the San Gabriel Mountains.

Keywords: bighorn sheep, California, chaparral, fire history, fire regime, *Ovis canadensis*, prescribed fire, San Gabriel Mountains, wilderness

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INTRODUCTION

In the San Gabriel Mountains of southern California, USA, bighorn sheep (*Ovis canadensis*) occupy winter-spring ranges dominated by chaparral vegetation for at least four months each year. Chaparral is a fire-adapted community characterized by moderate-to-long fire return intervals that are separated by intense crown fires; such fires reduce shrub canopy cover and result in an ephemeral (Biswell *et al.* 1952, Hanes 1971, Keeley and Davis 2007) and highly nutritious herbaceous forage crop (Biswell *et al.* 1952, Taber and Dasmann 1958) that enhances habitat quality for bighorn sheep by increasing nutrient availability and visual openness (Holl *et al.* 2004, Bleich *et al.* 2008). Between fires, plant succession leads to increases in shrub height and canopy cover, both of which reduce habitat suitability by restricting access and the ability of those specialized ungulates to detect predators.

During 1976 to 2006, the amount of high-suitability habitat on bighorn sheep winter-spring ranges resulting from fire (HSF) varied from 670 ha to 3392 ha (Holl and Bleich 2010), and influenced the distribution, habitat selection, recruitment of young, and overall abundance of bighorn sheep (Holl *et al.* 2004, Bleich *et al.* 2008, Holl and Bleich 2010). During that period, the population ranged from 130 to a high of 740 ±49 (95% CI) (Holl and Bleich 2009). This isolated population meets criteria for listing as a distinct vertebrate population segment under the Endangered Species Act (Holl 2002). As a result, bighorn sheep inhabiting the San Gabriel Mountains have been categorized as a Sensitive Species by the US Forest Service (USFS), with a management goal to maintain a self-sustaining population (USFS *et al.* 2004).

Habitat quality is recognized as the primary issue affecting persistence of bighorn sheep (Bleich 2009). Prescribed fire is the only practical technique to enhance habitat quality on the steep, chaparral-dominated slopes preferred by those ruminants (Bleich and Holl 1980, USFS *et al.* 2004, Bleich *et al.* 2008, Holl and Bleich 2010), but "managed wildfires" could also be used if addressed in a wilderness fire management plan after appropriate management direction. Implementation of prescribed burning—or managed wildfire—has been constrained, however, as described by Conard and Weise (1998). Some of these constraints revolve around air quality or water quality, risk aversion on the part of fire personnel and agencies, equipment and manpower resource conflicts with fire suppression mandates, budgets, existing legislation, and public opposition. As a result, opportunities to enhance habitat and achieve the management goal for bighorn sheep through the use of fire have been limited to habitat benefits resulting from wildfires. Current management direction is to suppress all ignitions, which, over the long term, increases fuel loading and the losses associated with large wildfires.

Unlike individual wildfires, which are isolated events and are recorded in fire histories, fire regimes summarize the repeated pattern of fire that characterizes an ecosystem (Heinselman 1981), and provide additional insights into ecological processes potentially not affected by singular events. The current fire regime in southern California chaparral is complex. The highest frequency of fires occurs during summer and is positively associated with human activities; however, the largest areas burned occur during fall in response to low fuel moisture and foehn (Santa Ana) winds (Conard and Weise 1998; Keeley and Fotheringham 2001, 2003). Furthermore, the historical fire regime in the San Gabriel Mountains has changed as a result of management direction.

Prior to European settlement, fires ignited by lightning and Native Americans likely were limited by fuel loads or environmental conditions, but not by suppression activities. Fires ignited during summer burned with variable intensities, alternating between smoldering and high-intensity fires (Conard and Weise 1998); fire size would have been affected by weather, fuel moisture (Green 1981), fuel volume or condition (Minnich 1983, Minnich and Chou 1997), or by physical characteristics of the landscape (Pyne *et al*. 1996). Such variable-intensity fires, which may have averaged 3600 ha in size (Lombardo *et al*. 2009), would have affected habitat suitability for bighorn sheep.

Currently, fires ignited during summer are suppressed effectively by modern equipment and tactics, with the result that the major change in the fire regime has been a reduction in the area burned by small fires (Lombardo *et al*. 2009). A decline in area burned by small fires should result overall in lower availability of, but greater variability in, high-suitability habitat for bighorn sheep because habitat changes are associated primarily with large, wind-driven wildfires. Recognizing the management focus on bighorn sheep—and newly available information on the relationships between fire history, bighorn sheep demographics, and changes in the historical fire regime—our objectives were to: (1) describe the current fire regime in bighorn sheep habitat; (2) describe changes in the availability of suitable habitat during the twentieth century; and, (3) evaluate the potential for small, prescribed fires to be effective in increasing the amount of, and reducing variability in, HSF when considered in the context of the current fire regime.

METHODS AND MATERIALS

Study Area

The San Gabriel Mountains, located in Los Angeles and San Bernardino counties (34°19' N; 117°45' W), are part of the Transverse Range that extends eastward from the coast of California toward the Mojave Desert. More than 95% of the mountain range is administered by the Angeles or San Bernardino national forests. Elevations range from 200 m to 3300 m; below 1850 m the climate is Mediterranean, and is characterized by hot, dry summers and cool, moist winters, and 95% of the precipitation occurs between 1 October and 1 May (Bailey 1966). Cooler temperatures and precipitation in the form of snow are common above 1850 m. Santa Ana winds, with speeds exceeding 100 km hr^{-1}, occur frequently during September through December (Conard and Weise 1998, Keeley and Fotheringham 2003).

Bighorn sheep are distributed among four subgroups (Figure 1), of which three (Cattle Canyon, East Fork San Gabriel River, and Twin Peaks [sometimes referred to as the San Gabriel Wilderness subgroup]) each use a single winter-spring range; one subgroup (Cucamonga) makes use of five winter-spring ranges (Middle Fork Lytle Creek, South Fork Lytle Creek, Deer Canyon, Cucamonga Canyon, and Barrett-Cascade Canyon). Individual winter-spring ranges occur at elevations of 1000 m to 2100 m, and range in area from 150 ha to 3235 ha, with a mean of 1190 ha.

An essential component of each winter-spring range is escape terrain, which consists primarily of steep and rocky escarpments where shrub densities are low and rarely exceed 30% canopy cover (Holl and Bleich 1983). Approximately 73% of the total winter-spring range used by bighorn sheep is within congressionally designated wilderness areas established since 1964, and are areas in which management options are severely constrained (Bailey and Woolever 1992; Bleich 1999, 2005).

The dominant vegetation on winter-spring ranges is chaparral composed primarily of chamise (*Adenostoma fasciculatum* Hook & Arn.), California lilac (*Ceanothus* spp.), manzanita (*Arctostaphylos* spp.), scrub oak (*Quercus dumosa* Nutt.), and mountain mahogany (*Cercocarpus betuloides* Nutt.); following a fire, these species sprout from root burls, seeds, or both. Stands of trees dominated by interior live oak (*Q. wislizeni* A. DC.) and bigcone Douglas-fir (*Pseudotsuga macrocarpa* [Vasey] Mayr) occur in drainages on the steep slopes adjacent to winter-spring ranges.

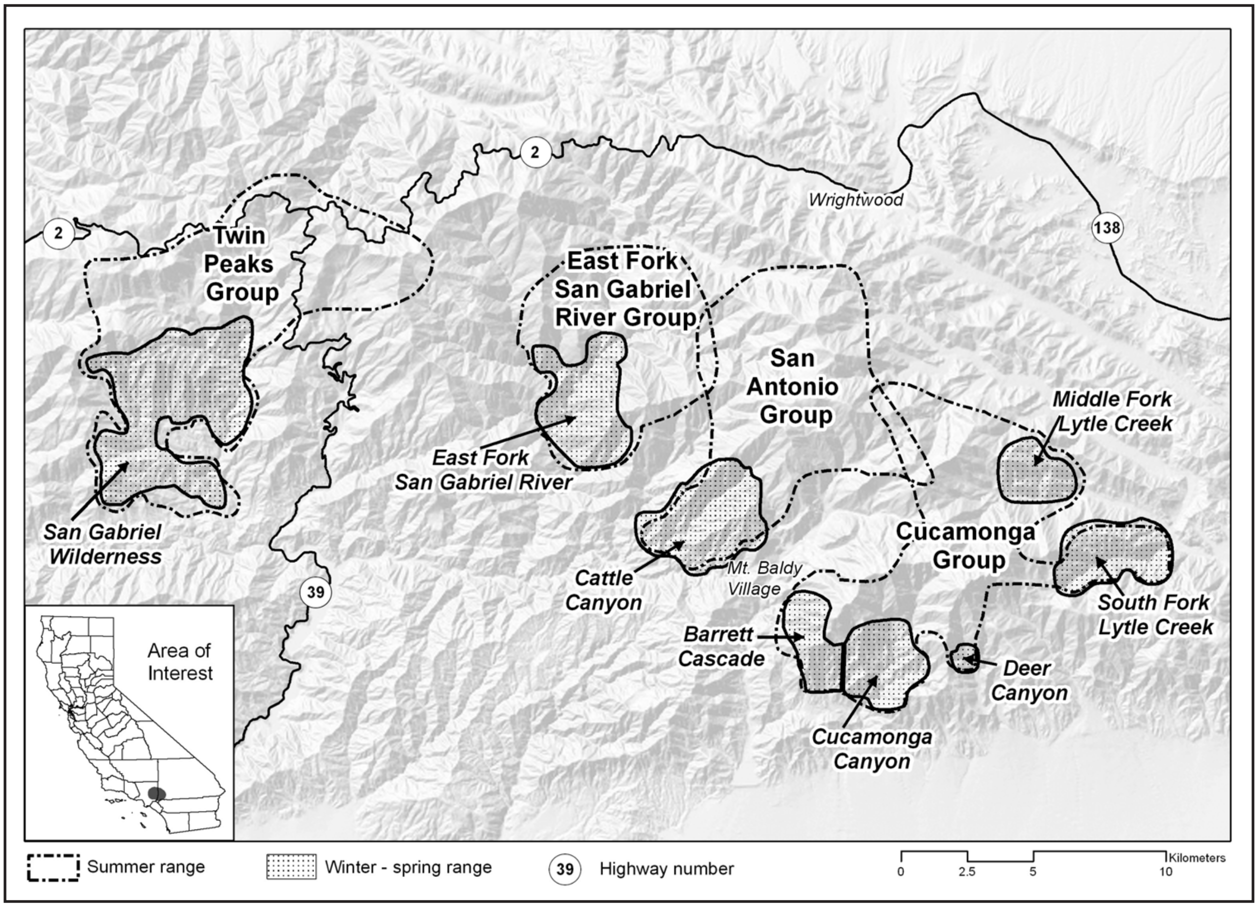


Figure 1. Distribution of seasonal ranges used by bighorn sheep in the San Gabriel Mountains, Los Angeles and San Bernardino counties, California, USA.

Chaparral has adapted to periods of drought by becoming dormant during summer. In Los Angeles County, live fuel moisture in chaparral peaks in early April, and declines through summer, hitting its nadir in late August (Los Angeles County Fire Department 2012). As moisture levels decline in chaparral shrubs, the vegetation becomes more susceptible to fire (Hanes 1971, Keeley and Davis 2007, Dennison *et al.* 2008).

Mammal species diversity in the San Gabriel Mountains is high and, with the exception of grizzly bears (*Ursus arctos*; Storer and Tevis 1955), the range supports a full complement of native carnivores capable of preying on large ungulates, including bobcat (*Lynx rufus*), mountain lion (*Puma concolor*), and coyote (*Canis latrans*; Vaughan 1954). Black bears (*Ursus americanus*), which are potential predators of bighorn sheep, were translocated to the San Gabriel Mountains in 1933 (Burghduff 1935). Mountain lions can be important sources of mortality among bighorn sheep (Wehausen 1996, Festa-Bianchet *et al.* 2006) but black bears, and bobcats and coyotes (Bleich *et al.* 1997), are less apt to prey on those specialized ungulates.

In California, bighorn sheep were first protected in 1883, were accorded the status of a "fully protected species" in 1933 (Bleich 2006), and were not a game animal in our study area. There has been one translocation of 23 bighorn sheep to historically occupied habitat within the range, and two translocations, during 1985 and 1987, during which a total of 48 individuals was moved to the Los

Padres National Forest (Bleich *et al.* 1990). There is no evidence that diseases have affected the population during recent times (Holl and Bleich 2009, 2010). Mitochondrial DNA haplotype frequencies indicate that bighorn sheep occupying the San Gabriel Mountains represent a population distinct from others in California (Bleich *et al.* 1996), a phenomenon likely exacerbated by anthropogenic features such as Interstate Highway 15 (Epps *et al.* 2005), which now separates the San Gabriel Mountains from the San Bernardino Mountains immediately to the east. Additional, detailed descriptions of the population and its habitat have been provided by Weaver *et al.* (1972), DeForge (1980), Holl and Bleich (1983), and Holl *et al.* (2004).

Fire Regime

We obtained historical fire data from the USFS Pacific Southwest Regional GIS database and California Department of Forestry and Fire Protection California Fire History 07. We identified the year, size, and percentage of each winter-spring range burned by a wildfire during 1910 to 2007, and we categorized the seasonal occurrence of each fire as summer or fall based on the date of ignition. We categorized fires that began in June, July, or August as summer fires, and those ignited during September, October, or November as fall fires.

Among those fires for which ignition dates were not available in the historical record, we considered the number of winter-spring ranges burned by individual fires to be a surrogate for ignition date. Using that criterion, we categorized the seasonal occurrence of fires as fall if they burned >1 winter-spring range, based on the assumption that suppression was unsuccessful because of extreme conditions associated with high temperatures, low humidity, and Santa Ana winds. Similarly, we categorized fires as summer if the size was <555 ha—the largest fire recorded to have occurred during summer—and it was restricted to a single winter-spring range.

We used mean fire size, average percentage of winter-spring range burned, and mean fire return interval (MFRI) to describe the seasonal fire regime. The MFRI was the mean number of years between wildfires that occurred anywhere on a particular winter-spring range (Lombardo *et al.* 2009). We used the Mann Whitney U-test to test for differences in fire size and in MFRI, between fall and summer fires.

Habitat Availability and Bighorn Sheep Abundance

In the San Gabriel Mountains, bighorn sheep selected habitat on winter-spring ranges that had burned within the previous 15 years, and avoided areas that were otherwise suitable, but that had not burned within that period of time (Bleich *et al.* 2008). Hence, we calculated HSF for each year as the sum of the area of winter-spring range that had burned each of the previous 15 years (Holl and Bleich 2010).

Evaluating the effects of small fires. We conducted simple comparisons to test our prediction regarding the effects of small prescribed fires on the amount and variability of HSF. Our models included the actual HSF during 1976 to 2010; we used that 25-year period because it included large and small fires that influenced HSF and, ultimately, the response of bighorn sheep (Holl and Bleich 2009, 2010). We simulated the effect of small fires on the HSF with two management strategies. For each strategy, the area of the prescribed burns was 186 ha—the mean size of recent wildfires during summer on these ranges—and the first of those simulated burns occurred in 1986. In Strategy 1, a prescribed fire was implemented every five years somewhere on the total area of winter-spring ranges (i.e., four total burns among the eight winter-spring ranges, with each occurring at five-year intervals). In Strategy 2, smaller prescribed burns were implemented each year for four consecutive years on a single winter-spring range (i.e., one burn per year for four consecutive years on a specific winter-spring range); a total of four series of smaller burns was initiated at five-year intervals, with each series occurring on an individual winter-spring range. Thus, Strategy 1 involved four separate burns, each 186 ha in size, on separate winter-spring ranges at five-year intervals. Each burn in the series of burns implemented in Strategy 2 affected <186 ha but, collectively, totaled 186 ha per individual winter-spring range, and each series was repeated among a total of four different winter-spring ranges at five-year intervals. We evaluated the effects of those simulated fires by comparing the mean and coefficient of variation (CV) of the actual HSFs during 1986 to 2010 with those of the hypothesized HSFs—first as modified by application of Strategy 1, and then by application of Strategy 2—over the same period of time.

Bighorn sheep demography. Population surveys in the San Gabriel Mountains have been conducted annually since 1976 (Holl *et al.* 2004; Holl and Bleich 2009, 2010). We classified bighorn sheep as adult females; young of the year; or Class I, Class II, Class III, or Class IV males (Geist 1968). In 1995, when the population was at its nadir (Holl and Bleich 2009), we calculated the effective population size (N_e; the number of breeding bighorn sheep in the San Gabriel Mountains) according to the method of Franklin (1980). Among sexually dimorphic polygynous mammals, such as bighorn sheep (Shackleton 1985), the number of individuals of each sex that contributes to the next generation generally is not equal (Hogg 1984). We used the ratio of adult males to adult females observed during the 1995 aerial survey (Holl *et al.* 2004), the population size in 1995 as reconstructed by Holl and Bleich (2009), and Franklin's (1980:139) estimator to derive N_e. We defined adult males as those with large horns (Class II, Class III, and Class IV), which are responsible for the majority of the breeding by male bighorn sheep (Hogg 1984).

RESULTS

Fire Regime

During 1910 to 2010, multiple wildfires occurred on ≥1 bighorn sheep winter-spring range; additionally, several large fires including the San Gabriel Fire (1919), Thunder Fire (1980), Narrows Fire (1997), and Grand Prix Fire (2003) burned multiple winter-spring ranges. In combination, a total of 37 wildfires affected the eight winter-spring ranges; 13 of those wildfires were categorized as summer events, and 24 occurred during fall. Summer fires were smaller in size ($U_{13, 24} = 248.5$, $P < 0.002$) than fall fires, and also affected a smaller percentage of winter-spring ranges; there was no difference ($P > 0.05$) in MFRI between summer and fall fires that, between them, averaged 19 years (Table 1).

Habitat Availability and Bighorn Sheep Abundance

There were three substantial increases in the HSF during 1915 to 2010. During 1924 to 1928, there were 3750 ha of HSF; during 1957 to 1962, there were 4886 ha of HSF; and dur-

Table 1. Characteristics of wildfires that occurred in bighorn sheep habitat and affected winter-spring ranges in the San Gabriel Mountains, Los Angeles and San Bernardino counties, California, 1910 to 2007.

Season of wildfire	*n*	Mean size ± SE (ha)	Mean winter-spring range burned (%)	MFRI (yr)
Summer	13	186 ±154	13.7	21.1
Winter	24	563 ±113	51.1	18.4

ing 2003 to 2011, there were 3392 ha of HSF (Figure 2). Those increases resulted from large wildfires that burned a total of 3207 ha during events in 1919 and 1924, a total of 4448 ha during events in 1953 and 1957, and a total of 2570 ha in 2003**.** Each substantial increase in HSF was followed by a precipitous decline in HSF, which was concomitant with an increase in fuel loading during 1938 to 1946, 1971 to 1972, and 1994 to 2002 (Figure 2).

Fires on a winter-spring range did not always translate into an increase in HSF. For instance, combinations of small wildfires in 1930, 1938, 1983, and 1984 burned portions of four winter-spring ranges ranging in size from 7 ha to 107 ha, but did not result in a net increase in HSF because larger quantities of habitat on other winter-spring ranges were at the same time maturing and becoming less suitable for bighorn sheep (Holl and Bleich 2010). Additionally, a high percentage of three winter-spring ranges burned during 1968 to 1975, but the resulting increase in HSF quickly declined because benefits attributable to earlier fires had expired.

Population estimates for bighorn sheep in the San Gabriel Mountains during 1976 to 2006 were positively associated (r_{29} = 0.414, P < 0.05) with HSF (Figure 2; Holl and Bleich 2010). When individual time periods were considered, the highest population estimate (740 ±49) was recorded in 1980 (Holl *et al.* 2004, Holl and Bleich 2009) and that estimate was associated with habitat changes resulting

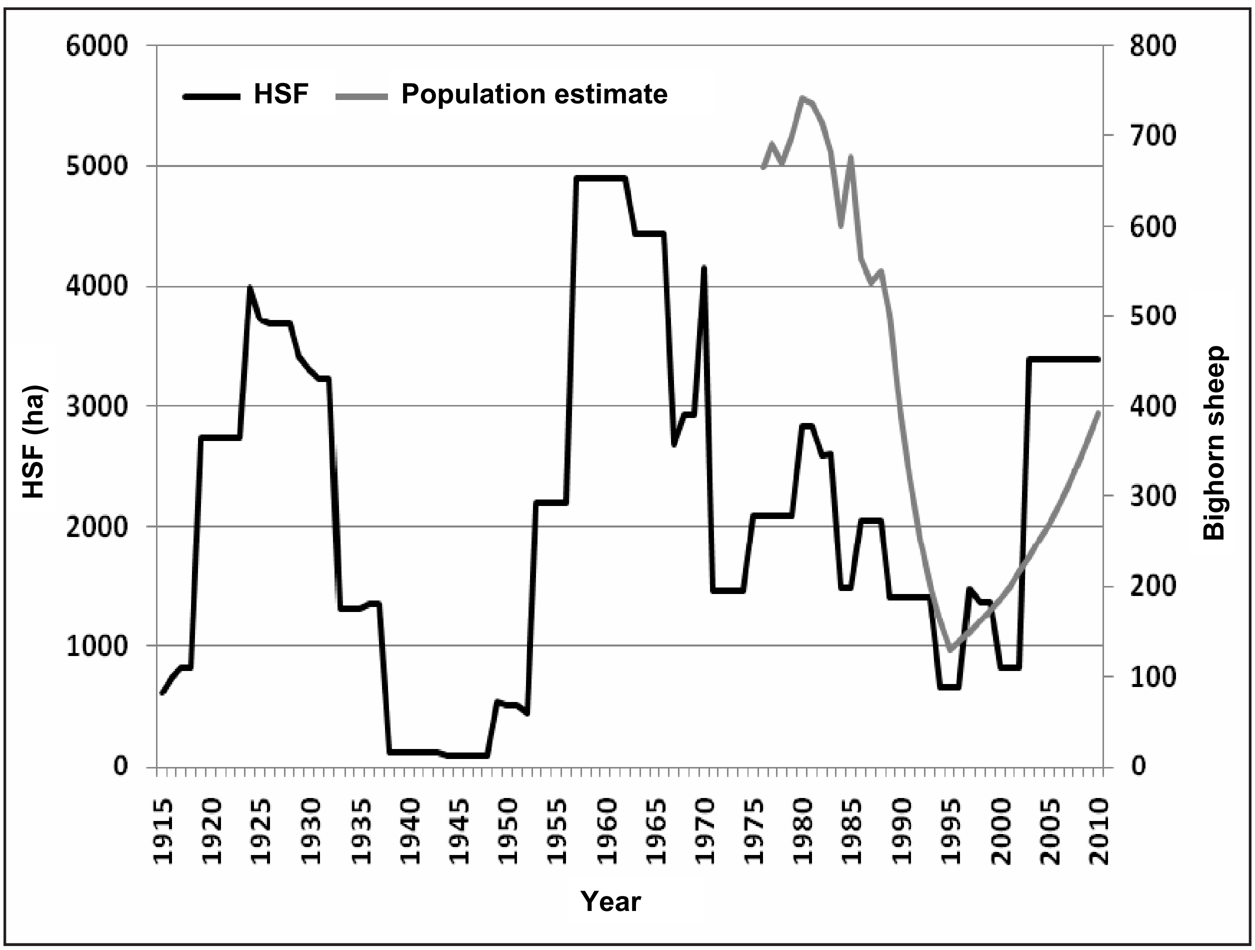


Figure 2. Availability of HSF (high-suitability habitat on bighorn sheep winter-spring ranges resulting from fire) during 1915 to 2010, and bighorn sheep population estimates from 1976 to 2010 in the San Gabriel Mountains, Los Angeles and San Bernardino counties, California, USA.

from large fall wildfires during 1968 to 1975 (Holl *et al.* 2004). The population decline during 1980 to 1995 also was associated with the decline in HSF, and a population increase occurred as a result of an increase in HSF after 1995 (Figure 2; Holl and Bleich 2010). Reconstruction of the population (Holl and Bleich 2009) indicated that 130 bighorn sheep inhabited the range in 1995, among which were 21 adult males and 62 adult males; the effective population size (N_e) in 1995 was 63.

Effects of Small Prescribed Fires

During 1986 to 2010, wildfires burned 3945 ha, and the total additional area treated with simulated prescribed burning was 744 ha under each of the hypothetical management strategies. The mean HSF increased by 528 ha under Strategy 1, but by 700 ha under Strategy 2, and the CV was reduced 11% under Strategy 1 and by 26% under Strategy 2 (Table 2). Management Strategy 2 had a greater influence on availability of HSF during 1986 to 2010 than did Strategy 1 but, after 2001, there was no detectable difference in the HSF between the two strategies (Figure 3). By 2010, each of the hypothetical strategies yielded more HSF than did the current management paradigm, which emphasizes fire exclusion and fire suppression. The HSF is expected to decline after 2012 because the benefits of a wildfire that occurred in 1997 will be expiring soon.

DISCUSSION

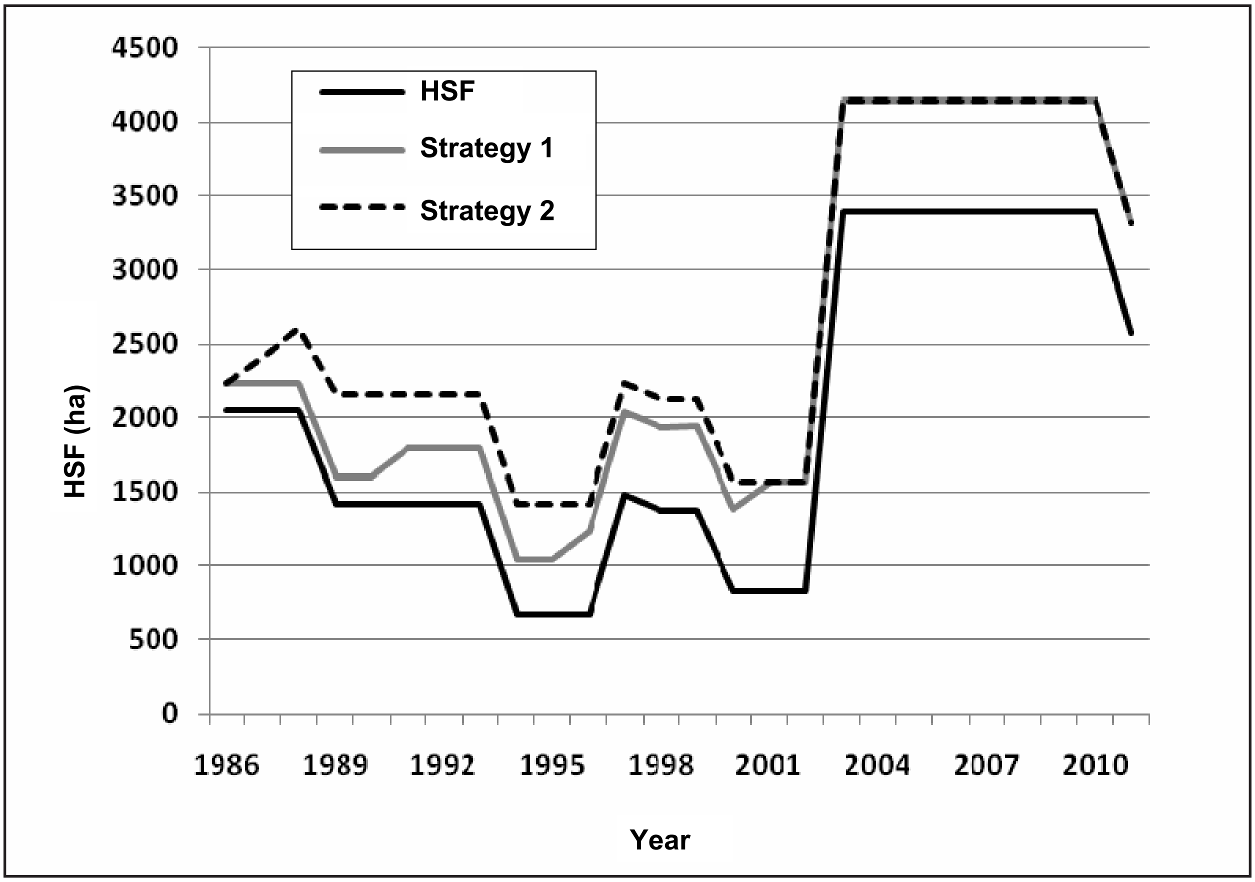
Fire Regime

Twentieth Century. Fire history records for winter-spring ranges occupied by bighorn sheep in the San Gabriel Mountains indicated that fires burned into winter-spring ranges more often during fall when compared with summer (Table 1). This result differs from the frequency of fires recorded in all of Los Angeles County where, overall, the highest frequency of fires occurred in early summer (Keeley and Fotheringham 2001); that difference may be associated with small sample sizes in bighorn sheep habitat or, alternatively, with human activities that are positively associated with the number of ignitions (Conard and Weise 1998, Keeley and Fotheringham 2001). The majority of bighorn sheep winter-spring ranges are in wilderness areas where lightning, and campfires in designated areas, are the primary sources of ignitions when compared overall to Los Angeles County. This county includes the nation's most populous urban-wildland interface and major rail and automobile transportation corridors—both of which increase the probability of ignitions (Syphard *et al.* 2007). Additionally, ignitions during fall resulted in wind-driven wildfires that burned multiple winter-spring ranges; fire on any affected winter-spring range was counted as an event, whereas those categorized as summer fires were limited to a single winter-spring range.

Scenario	Total area burned by wildfire (ha)	Total area burned by prescription (ha)	Mean HSF (ha)	CV
No management	3945	0	1986	53.3
Strategy 1	3945	744	2514	47.1
Strategy 2	3945	744	2686	39.6

Table 2. Differences in the mean availability of HSF (high-suitability habitat on bighorn sheep winter-spring ranges resulting from fire) in the absence of any management strategy compared with availability of HSF following two differing strategies of small prescribed burns in the San Gabriel Mountains, Los Angeles and San Bernardino counties, California, USA.

Figure 3. Amount of high-suitability habitat on bighorn sheep winter-spring ranges resulting from fire (HSF) from 1986 to 2010 compared to amount of HSF following the hypothetical implementation of two different fire management strategies during the same period in the San Gabriel Mountains, Los Angeles and San Bernardino counties, California, USA.



Using our classification criteria, fires that ignited during fall were significantly larger than those categorized as summer fires (Table 1), a pattern similar to that observed throughout Los Angeles County by Keeley and Fotheringham (2001); fall fires also burned three times more winter-spring range than did summer fires (Table 1). This pattern of larger and more intense fires during fall (Keeley and Fotheringham 2001, Keeley and Zedler 2009, Lombardo *et al*. 2009) is not a recent phenomenon associated with increased fuel loads resulting from fire suppression (Minnich 1983) or, in our opinion, from fire exclusion. Rather, the larger and more intense fires during fall are associated with low fuel moisture (Dennison *et al.* 2008) and Santa Ana winds (Moritz 1997; Keeley and Fotheringham 2001, 2003). Smaller fires occur during summer because of higher fuel moistures and lower frequency of Santa Ana winds (Conard and Weise 1998, Keeley and Fotheringham 2001). Additionally, the exposed rocks, low density of shrubs, and overall lower biomass on escape terrain in bighorn sheep habitat reduce flame lengths and rates of spread, thereby facilitating suppression efforts.

There was no difference between summer and fall MFRI, suggesting that a wildfire affected a particular bighorn sheep winter-spring range about every 20 years (Table 1). In contrast, Lombardo *et al.* (2009) reported an MFRI of 28 years within individual stands of bigcone Douglas-fir in the Los Padres National Forest (LPNF) immediately northwest of the San Gabriel Mountains. The lower MFRI on individual winter-spring ranges in the San Gabriel Mountains may be associated with a much higher rate of lightning strikes than on the LPNF (Kay 2007*a*), as well as the proximity of the urban-wildland interface (Syphard *et al*. 2007).

Pre-European settlement. Native Americans used fire to remove vegetation to improve access for travel, provide construction materials, increase the production of edible and medicinal plants, and enhance opportunities for hunting (Keeley 2002, 2004; Anderson 2006); and indigenous peoples were important predators of large mammals (Kay 2007*b*). Fires ignited during summer would have burned with varying intensities, as influenced by fuel moisture, winds, topography, and age-class of vegetation (Conard and Weise 1998, Keeley and Fotheringham 2003); we surmise that ignitions by Native Americans most likely occurred during this season because of difficulties associated with burning during spring when fuel moistures are high, or during fall when Santa Ana winds were likely. Tree ring analysis of bigcone Douglas-fir (Lombardo *et al.* 2009) indicated that fires described in their research occurred approximately every 10 years and the average size was about 3600 ha. Overall, fires described by Lombardo *et al.* (2009) ignited more frequently than the 20 year MFRI we calculated for individual winter-spring ranges, and they were substantially larger than the average sizes of 186 ha and 563 ha during summer and fall, respectively, in bighorn sheep habitat. Cessation of burning by Native Americans and fire management policies during the twentieth century likely have reduced the surface area affected by wildfire and, subsequently, its influence on habitats occupied by bighorn sheep.

Habitat Availability and Bighorn Sheep Abundance

Changes in the HSF during the twentieth century were characterized by distinct peaks during 1924 to 1928 and 1957 to 1962, which were followed by substantial declines in the HSF, and a third peak is suggested during 1997 to 2003 (Figure 2). Each peak during the last 100 years suggests availability of HSF was associated with the occurrence of large wildfires.

Prior to the work of Weaver *et al.* (1972), only qualitative information on the abundance of bighorn sheep in the San Gabriel Mountains was available (Holl and Bleich 1983). Population estimates derived since 1976 indicate, however, that habitat changes resulting from wildfires were associated with density-dependent changes in recruitment rates that affected the abundance of bighorn sheep (Holl and Bleich 2010). Moreover, analyses of long-term data have implicated fire history as an important factor in explaining the distribution of bighorn sheep in the San Gabriel Mountains: those specialized ungulates clearly select habitat on winter-spring ranges that has burned within 15 years (Bleich *et al.* 2008).

During 1980 to 1995, declining habitat suitability, in conjunction with mountain lion predation (Holl and Bleich 2009), reduced the abundance of bighorn sheep and resulted in an effective population size of 63; hence, N_e approached 50, the minimum suggested for large mammals by Franklin (1980). The recurring troughs in HSF and very low N_e associated with the declining HSF suggest that ≥1 population bottleneck has occurred during the last 100 years, and could have reduced genetic diversity in this isolated population. Rather than considering the responses of bighorn sheep to singular fires, our examination of the fire regime indicated a relationship between wildfire history and size, and the abundance of bighorn sheep. Additional factors, including increased rates of predation, likely played a role in the decline of bighorn sheep during 1980 to 1995, but those effects probably occurred secondarily and resulted from changes in vegetation density and forage quality, both of which were concomitant with vegetative succession (Holl *et al*. 2004, Holl and Bleich 2009), and are examples of cascading ecological effects associated with altered fire regimes (Landres *et al*. 1999, Dale *et al*. 2000). Furthermore, Holl and Bleich (2010) described changes in the fire regime and the response of bighorn sheep that had not been noted previously: their examination of the fire regime identified the relevance of small fires to HSF, as well as associated changes in the abundance of bighorn sheep.

Prior to the twentieth century, small fires of variable intensity would have resulted in a mosaic of age classes in chaparral that reduced the variance in HSF on bighorn sheep winter-spring ranges and positively influenced the abundance of bighorn sheep. During the twentieth century, small fires burned <15% of a winter-spring range at intervals of approximately every 20 years (Table 1), thereby reducing their influence on HSF and the response of bighorn sheep to those habitat changes. Our calculations assumed that prescribed burning will not reduce the net area burned by wildfires on an annual basis, because wildfires during fall may not be fuel-limited (Moritz 1997) but, rather, are driven by strong winds.

We considered the total area of prescribed burns used to evaluate each strategy (744 ha) to be reasonable because it approached the area of prescribed burns (810 ha) recently acknowledged by management agencies as necessary to improve bighorn sheep habitat (USFS *et al.* 2004). Moreover, that value was less than the 912 ha average annual accomplishment reported by the Angeles National Forest during 1981 to 1984 (Conard and Weise 1998), further indicating that it was an achievable objective.

In our models, both management strategies initiated prescribed burning the same years and burned the same total areas, and both demonstrated that small prescribed burns will increase the HSF and reduce the annual variability in HSF, consistent with our expectations. Increasing the total availability, and reducing annual variability, of HSF will increase the bighorn sheep population because bighorn sheep are attracted to recently burned areas (Holl *et al.* 2004, Bleich *et al.* 2008) and their abundance is positively associated with HSF (Figure 2; Holl and Bleich 2010). Moreover, bighorn sheep depend on their sense of sight to detect predators (Risenhoover and Bailey 1980, 1985), and low density of vegetation, which enhances visibility, is associated with HSF.

Reducing the variability in HSF will reduce the amplitude of the recently observed (and projected) population declines (Figure 3). Strategy 2 had a greater effect on HSF (Table 2, Figure 3) because each of the fires and resulting improvements in HSF were distributed over a 15-year period, which mitigated the expired benefits of earlier, larger wildfires. In contrast, habitat improvements ascribed to Strategy 1 did not occur frequently enough over 15 years to compensate for the loss of gains associated with previous wildfires; the benefits of some of those fires expired during the extended treatment with fewer, but larger, hypothetical fires.

A single, large prescribed burn, or a series of smaller burns, treating a substantial portion of an individual winter-spring range, will have a positive effect on the HSF of that geographic area, and has the potential to result in a rate of population increase up to five times that on unburned ranges, as demonstrated by Holl and Bleich (2010). Clearly, prescribed burning is a technique that can increase the availability of suitable habitat and, when combined with the indirect effect of enhancing the efficacy of predator evasion, can increase the abundance of bighorn sheep and reduce variability in population size when the temporal component of HSF is considered.

MANAGEMENT IMPLICATIONS

Fire is an ecological component in the San Gabriel Mountains and is requisite to the persistence of this isolated population of bighorn sheep. Large wildfires—which commonly escape initial attack because they are driven by low fuel moisture and Santa Ana winds—can enhance habitat quality and, thereby, contribute to population increases in bighorn sheep; vegetative succession within those burned areas, however, contributes to subsequent declines in habitat quality and, hence, bighorn sheep numbers. Those periods of enhanced HSF and subsequent periods of succession contributed to high variation in availability of HSF during the past 100 years. Recurring population declines can result in population bottlenecks and a concomitant loss of genetic diversity, which has onerous implications for isolated populations of large mammals. Moreover, altered fire regimes can lead to cascading ecological effects.

Properly planned and implemented prescribed burns that presumably mimic burning by indigenous peoples have the potential to reduce variation in bighorn sheep habitat quality and in associated population changes. Unless anthropogenic burns are reinstituted, ecological processes will continue to be compromised and a sensitive species likely will experience additional population bottlenecks, further jeopardizing persistence of this isolated population of bighorn sheep. Habitat quality is recognized by wild sheep biologists across North America as the primary issue affecting persistence of those large herbivores, and constraints associated with implementation of prescribed burns are not insurmountable. Nonetheless, overcoming those constraints will require a critical review of the implementation and monitoring components of the current conservation plan for bighorn sheep inhabiting the San Gabriel Mountains, engaged stakeholders, a renewed commitment to resource management by state and federal agencies and non-governmental organizations, and recognition of the importance of fire to the function of chaparral ecosystems. As emphasized by Agee (2006), it is essential that we make good decisions about the use of fire, not just its control.

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LITERATURE CITED

Agee, J.K. 2006. Foreword. Pages xi-xiii in: N.G. Sugihara, J.W. van Wagtendonk, K.E. Shaffer, J. Fites-Kaufman, and A.E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, USA.

Anderson, M.K. 2006. The use of fire by Native Americans in California. Pages 417-430 in: N. G. Sugihara, J.W. van Wagtendonk, K.E. Shaffer, J. Fites-Kaufman, and A.E. Thode, editors. Fire in California's ecosystems. University of California Press, Berkeley, USA.

Bailey, J.A., and M.M. Woolever. 1992. Determining the future of bighorn herds in wilderness areas. Proceedings of the Northern Wild Sheep and Goat Council 8: 121-135.

Bailey, H.P. 1966. The climate of southern California. University of California Press, Berkeley, USA.

Biswell, H.H., R.D. Taber, D.W. Hedrick, and A.M. Schultz. 1952. Management of chamise brushlands for game in the north coast region of California. California Fish and Game 38: 453-484.

Bleich, V.C. 1999. Wildlife conservation and wilderness management: uncommon objectives and conflicting philosophies. Proceedings of the North American Wild Sheep Conference 2: 195-205.

Bleich, V.C. 2005. Politics, promises, and illogical legislation confound wildlife conservation. Wildlife Society Bulletin 33: 66-73. doi: 10.2193/0091-7648(2005)33[66:IMOPPA]2.0.CO;2

Bleich, V.C. 2006. Mountain sheep in California: perspectives on the past, and prospects for the future. Proceedings of the Northern Wild Sheep and Goat Council 15: 1-13.

Bleich, V.C. 2009. Perceived threats to wild sheep: levels of concordance among states, provinces, and territories. Transactions of the Desert Bighorn Council 50: 32-39.

Bleich, V.C., R.T. Bowyer, and J.D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134: 1-50.

Bleich, V.C., and S.A. Holl. 1980. Management of chaparral habitat for mule deer and mountain sheep in southern California. Pages 247-254 in: C.E. Conrad and W.C. Oechel, technical coordinators. Proceedings of the symposium on the dynamics and management of Mediterranean-type ecosystems. USDA Forest Service General Technical Report PSW-58, Pacific Southwest Research Station, Berkeley, California, USA.

Bleich, V.C., H.E. Johnson, S.A. Holl, L. Konde, S.G. Torres, and P.R. Krausman. 2008. Fire history in a chaparral ecosystem: implications for conservation of a native ungulate. Rangeland Ecology and Management 61: 571-579. doi: 10.2111/07-016.1

Bleich, V.C., J.D. Wehausen, K.R. Jones, and R.A. Weaver. 1990. Status of bighorn sheep in California 1989, and translocations from 1971 through 1989. Transactions of the Desert Bighorn Council 34: 24-26.

Bleich, V.C., J.D. Wehausen, R.R. Ramey II, and J.L. Rechel. 1996. Metapopulation theory and mountain sheep: implications for conservation. Pages 353-373 in: D.R. McCullough, editor. Metapopulations and wildlife conservation. Island Press, Covelo, California, USA.

Burghduff, A.E. 1935. Black bears released in southern California. California Fish and Game 21: 83-84.

Conard, S.G., and D.R. Weise. 1998. Management of fire regime, fuels, and fire effects in southern California chaparral: lessons from the past and thoughts for the future. Proceedings of the Tall Timbers Fire Ecology Conference 20: 342-350.

Dale, V.H., L.A. Joyce, S. McNulty, and R.P. Neilson. 2000. The interplay between climate change, forests and disturbances. Science of the Total Environment 262: 201-204. doi: 10.1016/S0048-9697(00)00522-2

DeForge, J.R. 1980. Population biology of bighorn sheep in the San Gabriel Mountains of California. Transactions of the Desert Bighorn Council 24: 29-32.

Dennison, P.E., M.A. Moritz, and R.S. Taylor. 2008. Evaluating predictive models of critical live moisture in the Santa Monica Mountains, California. International Journal of Wildland Fire 17: 18-27. doi: 10.1071/WF07017

Epps, C.W., P.J. Palsboll, J.D. Wehausen, G.K. Roderick, R.R. Ramey, and D.R. McCullough. 2005. Highways block gene flow and cause a rapid decline in genetic diversity of bighorn sheep. Ecology Letters 8: 1029-1038. doi: 10.1111/j.1461-0248.2005.00804.x

Festa-Bianchet, M., T. Coulson, J.-M. Gaillard, J.T. Hogg, and F. Pelletier. 2006. Stochastic predation events and population persistence in bighorn sheep. Proceedings of the Royal Society B 273: 1537-1543. doi: 10.1098/rspb.2006.3467

Franklin, I.R. 1980. Evolutionary change in small populations. Pages 135-149 in: M.E. Soule and B.A Wilcox, editors. Conservation biology. Sinauer Associates, Sunderland, Massachusetts, USA.

Geist, V. 1968. On the interrelation of external appearance, social behavior and social structure of mountain sheep. Zeitschrift für Tierpsychologie 25: 199-215.

Green, L.R. 1981. Burning by prescription in chaparral. USDA Forest Service General Technical Report PSW-51, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA.

Hanes, T.L. 1971. Succession after fire in the chaparral of southern California. Ecological Monographs 41: 25-52. doi: 10.2307/1942434

Heinselman, M.L. 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. Pages 5-57 in: H.A. Mooney, T.M. Bonnicksen, N.L. Christiansen, J.E. Lotan, and W.A. Reiners, editors. Fire regimes and ecosystem properties. USDA Forest Service General Technical Report WO-26, Washington, D.C., USA.

Hogg, J.T. 1984. Mating in bighorn sheep: multiple creative male strategies. Science 225: 526-529. doi: 10.1126/science.6539948

Holl, S.A. 2002. Conservation strategies for bighorn sheep in the San Gabriel Mountains, California. Los Angeles County Fish and Game Commission, California, USA.

Holl, S.A., and V.C. Bleich. 1983. San Gabriel mountain sheep: biological and management considerations. USDA Forest Service, San Bernardino National Forest, California, USA.

Holl, S.A., and V.C. Bleich. 2009. Reconstructing the San Gabriel Mountain's bighorn sheep population. California Fish and Game 95: 77-87.

Holl, S.A., and V.C. Bleich. 2010. Responses of bighorn sheep and mule deer to fire and rain in the San Gabriel Mountains, California. Proceedings of the Northern Wild Sheep and Goat Council 17: 139-156.

Holl, S.A., V.C. Bleich, and S.G. Torres. 2004. Population dynamics of bighorn sheep in the San Gabriel Mountains, California, 1967-2002. Wildlife Society Bulletin 32: 412-426. doi: 10.2193/0091-7648(2004)32[412:PDOBSI]2.0.CO;2

Kay, C.E. 2007*a*. Are lightning fires unnatural? A comparison of aboriginal and lightning ignition rates in the United States. Proceedings of the Tall Timbers Fire Ecology Conference 23: 16-28.

Kay, C.E. 2007*b*. Were native people keystone predators? A continuous-time analysis of observations made by Lewis and Clark 1804–1806. Canadian Field-Naturalist 121: 1-16.

Keeley, J.E. 2002. American Indian impacts on fire regimes of the California coastal ranges. Journal of Biogeography 28: 303-320. doi: 10.1046/j.1365-2699.2002.00676.x

Keeley, J.E. 2004. American Indian influence on fire regimes in California's coastal ranges. Fire Management Today 64(3): 15-16.

Keeley, J.E., and F.W. Davis. 2007. Chaparral. Pages 339-366 in: M.G. Barbour, T. Keeler-Wolf, and A.A. Schoenherr, editors. Terrestrial vegetation of California. Third edition. University of California Press, Berkeley, USA.

Keeley, J.E., and C.J. Fotheringham. 2001. Historic fire regime in southern California shrublands. Conservation Biology 15: 1536-1538. doi: 10.1046/j.1523-1739.2001.00097.x

Keeley, J.E., and C.J. Fotheringham. 2003. Impact of past, present, and future fire regimes on North American Mediterranean shrublands. Pages 218-262 in: T.T. Veblen, W.L. Baker, G. Montenegro, and T.W. Swetnam, editors. Fire and climatic change in temperate ecosystems of the western Americas. Springer, New York, New York, USA. doi: 10.1007/0-387-21710-X_8

Keeley, J.E., and P.H. Zedler. 2009. Large, high intensity fire events in southern California shrublands: debunking the fine-grain age patch model. Ecological Applications 19: 69-94. doi: 10.1890/08-0281.1

Landres, P.B., P. Morgan, and F.J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9: 1179-1188.

Lombardo, K.J., T.W. Swetnam, C.H. Baisan, and M.I. Borchert. 2009. Using bigcone Douglas-fir fire scars and tree rings to reconstruct interior chaparral fire history. Fire Ecology 5(3): 35-56. doi: 10.4996/fireecology.0503035

Los Angeles County Fire Department. 2012. Live fuel moisture 1981-2012. Vegetation Management Program, Los Angeles County Fire Department, California, USA. <http://fire.lacounty.gov/forestry/FireWeatherDangerLiveFuelMoistureAllAreas.asp>. Accessed 20 February 2012.

Minnich, R.A. 1983. Fire mosaics in southern and Baja California. Science 219: 1287-1294. doi: 10.1126/science.219.4590.1287

Minnich, R.A., and Y.H. Chou. 1997. Wildland fire patch dynamics in chaparral of southern California and northern Baja California. International Journal of Wildland Fire 7: 221-248. doi: 10.1071/WF9970221

Moritz, M.A. 1997. Analyzing extreme disturbance events: fire in the Los Padres National Forest. Ecological Applications 7: 1252-1262. doi: 10.1890/1051-0761(1997)007[1252:AEDEFI]2.0.CO;2

Pyne, S.J., P.L. Andrews, and R.D. Laven. 1996. Introduction to wildland fire. Second edition. John Wiley and Sons, New York, New York, USA.

Risenhoover, K.L., and J.A. Bailey. 1980. Visibility: an important habitat factor for an indigenous, low-elevation, bighorn herd in Colorado. Proceedings of the Northern Wild Sheep and Goat Council 2: 18-28.

Risenhoover, K.L., and J.A. Bailey. 1985. Foraging ecology of mountain sheep: implications for habitat management. Journal of Wildlife Management 49: 292-804. doi: 10.2307/3801714

Shackleton, D.M. 1985. *Ovis canadensis*. Mammalian Species 230: 1-9. doi: 10.2307/3504034

Storer, T.I., and L.P. Tevis, Jr. 1955. California grizzly. University of California Press, Berkeley, USA.

Syphard, A.D., V.C. Radeloff, J.E. Keeley, T.J. Hawbaker, M.K. Clayton, S.I. Stewart, and R.B. Hammer. 2007. Human influence on California fire regimes. Ecological Applications 17: 1388-1402. doi: 10.1890/06-1128.1

Taber, R.D., and R.F. Dasmann. 1958. The black-tailed deer of the chaparral: its life history and management in the north Coast Range of California. Game Bulletin 8: 1-163.

USFS [US Forest Service], California Department of Fish and Game, and Los Angeles County Fish and Game Commission. 2004. Implementation strategy to restore the San Gabriel Mountains bighorn sheep population. USDA Forest Service, Angeles National Forest, Arcadia, California, USA.

Vaughan, T.A. 1954. Mammals of the San Gabriel Mountains of California. University of Kansas Publications, Museum of Natural History 12: 1-153.

Weaver, R.A., J.L. Mensch, W. Timmerman, and J.M. Hall. 1972. Bighorn sheep in the San Gabriel Mountains. Federal Aid in Wildlife Restoration Project Report W-51-8, California Department of Fish and Game, Sacramento, USA.

Wehausen, J.D. 1996. Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. Wildlife Society Bulletin 24: 471-479.