Responses of Bighorn Sheep and Mule Deer to Fire and Rain in the San Gabriel Mountains, California

STEPHEN A. HOLL, Steve Holl Consulting, 7049 Pine View Drive, Folsom, CA 95630 USA
VERNON C. BLEICH, Sierra Nevada Bighorn Sheep Recovery Program, California Department of Fish and Game, 407 West Line Street, Bishop, CA 93514 USA

Abstract: We used retrospective analyses to evaluate relationships between fire history, precipitation, and productivity in bighorn sheep (*Ovis canadensis nelsoni*) and mule deer (*Odocoileus hemionus californicus*) in southern California's San Gabriel Mountains. The number of bighorn sheep increased 5 times faster after fires on chaparral-covered ranges than the number of sheep on unburned chaparral ranges. When individual time periods were considered during 1976-2006, bighorn sheep population estimates were positively associated ($P <0.01$) with the amount to winter-spring range burned during all years except 1989-1995. As vegetation matured and habitat suitability declined, the density of female sheep increased, and recruitment declined. Mule deer recruitment rates were positively associated ($P <0.1$) with the amount of winter-spring range burned during 1976-1989, but not in later years. During 1985-2004, there was a linear relationship ($r^2 = 0.58$, $P = 0.004$) between mule deer recruitment rates and precipitation during pregnancy, whereas bighorn sheep recruitment rates were not associated ($P > 0.05$) with precipitation during pregnancy. During years with less than normal precipitation (1989-1990 and 1999-2004) mule deer recruitment rates were approximately 50% less than recruitment rates during all years with at least normal precipitation, which was also reflected in lower mule deer abundance. We hypothesize that a lack of wildfires combined with drought reduced mule deer availability, and mountain lion (*Felis concolor*) predation was responsible for the population decline in bighorn sheep during 1989-1995.

KEY WORDS: bighorn sheep, California, chaparral, fire, mountain lion, mule deer, *Odocoileus hemionus*, *Ovis canadensis*, precipitation, predation, *Puma concolor*.

INTRODUCTION

Bighorn sheep (*Ovis canadensis nelsoni*) and mule deer (*Odocoileus hemionus californicus*) are sympatric in the eastern half of southern California's San Gabriel Mountains, occupying chaparral for at least 4 months during winter and spring each year (Cronemiller and Bartholomew 1950, Weaver et al. 1972, Holl and Bleich 1983). Chaparral is a fire-adapted community characterized by periodic large and intense crown fires that reduce shrub canopy cover and produce an ephemeral (Biswell et al. 1952, Hanes 1971, Keeley

and Davis 2007) and highly nutritious forage crop (Biswell et al. 1952, Taber and Dasmann 1958). In response to wildfires in chaparral, black-tailed deer (*O. h. columbianus*) move into recently burned areas to consume higher quality forage, which results in improved fawn production and survival (Taber and Dasmann 1957, 1958). High densities of black-tailed deer remain in burned areas for 4-5 years post-fire (Taber and Dasmann 1957, 1958) before declining.

Bighorn sheep in the San Gabriel Mountains are attracted to recently burned

areas (Holl et al. 2004), presumably in search of increased forage quality (Biswell et al. 1952, Hobbs and Spowart 1984). Their distribution is positively associated with those burned areas for ≤15 years after fires and negatively associated with those areas >15 years after fires (Bleich et al. 2008), likely because changes in shrub cover affects their field of vision that is necessary for predator detection (Risenhoover and Bailey 1980). Although the positive effects of wildfire on habitat suitability and resulting influences on demographic parameters of bighorn sheep habitat have been inferred by several authors (Stelfox 1976, Wakelyn 1987, Etchberger et al. 1989, Holl et al. 2004), there are no quantitative descriptions of the relationships between fire history and bighorn sheep demographics (Cain et al. 2005).

The decline in the area burned by wildfires in the San Gabriel Mountains during 1980-1995 (Bleich et al. 2008) appeared to correspond to the decline in population estimates (±SE) for bighorn sheep from 740±49 to 130 individuals (Holl and Bleich 2009) and a similar decline in mule deer during that same period (Holl et al. 2004). During 1997-2003 wildfires burned 70,100 ha in the San Gabriel Mountains and the bighorn sheep population increased to 292±69 by 2006 (Holl and Bleich 2009); however, the abundance of mule deer did not appear to increase immediately, as indicated by the reported buck harvest (California Department of Fish and Game [CDFG] files).

In xeric southwestern mountain ranges precipitation influences nutrient availability (McKinney et al. 2006) and recruitment of young in bighorn sheep (Leslie and Douglas 1979, Wehausen et al. 1987, Douglas 2001, McKinney et al. 2006) and mule deer (Marshall et al. 2002, Lawrence et al. 2004, Bender et al. 2007). Moreover, lower than normal precipitation

was associated with mule deer population declines in the southwest during 1985-1990 (Kucera 1988, Sweitzer et al. 1997, Logan and Sweanor 2001, Kamler 2002). The San Gabriel Mountains are, however, a mesic range with predictably greater annual precipitation (89±6.3 cm, Mt. Wilson, CA) than desert mountain ranges (10.8±0.86 cm, Barstow, CA) occupied by bighorn sheep and mule deer.

Early winter precipitation contributed to variation in lamb recruitment rates during 1976-1984 (Holl and Bleich 1983, Holl et al. 2004, Holl and Bleich 2009) when female bighorn sheep densities were high (Holl et al. 2004). Available data for mule deer indicate precipitation on the central coast of California, a mesic area west of the San Gabriel Mountains, was positively correlated with the reported buck harvest (Longhurst et al. 1976); however, nothing is known about the effects of precipitation on mule deer in this mountain range.

Habitat management for both species in these mountains has been limited to wildfires. Prescribed burning is an effective management technique that mimics the results of a wildfire and will improve mule deer habitat in chaparral (Biswell et al. 1952, Taber and Dasmann 1957, 1958) and it is the only technique available to improve bighorn sheep habitat in this mountain range because excessively steep slopes preclude the use of mechanical equipment. Both species receive additional management consideration by the Forest Service and CDFG because bighorn sheep qualify as a distinct vertebrate population segment (Holl 2002) and they are listed as a regionally sensitive species by the Forest Service and as a fully protected species by the State of California (CDFG Code section 4700), and mule deer are an important game species in this mountain range. Therefore, understanding the relationships between fire, precipitation, and

demographic responses is fundamental to implementing effective management strategies for both species.

Based on our observations in the San Gabriel Mountains during 1976-2006 we conducted this retrospective analysis to evaluate 4 hypotheses:1) wildfires on chaparral ranges increased lamb recruitment in bighorn sheep, similar to that described for black-tailed deer in chaparral (Taber and Dasmann (1957, 1958); 2) as a result of improved recruitment sheep populations on burned ranges increased faster than populations on unburned ranges; and 3) wildfire history was associated with the abundance of bighorn sheep and mule deer. We also hypothesized that (4) precipitation was associated with recruitment in mule deer, which affected their abundance.

STUDY AREA

The San Gabriel Mountains, located in Los Angeles and San Bernardino counties, California (34°19'N; 117°45'W), are part of the Transverse Range. The San Gabriel are essentially isolated from the adjacent Santa Monica and San Bernardino ranges (Epps 2007) by 10 million people along the southern boundary, eight lane freeways along the eastern and western flanks of the range, and the Antelope Valley to the north, which provides little suitable habitat for either species. Over 95% of the mountain range is administered by the Angeles and San Bernardino National forests.

Elevations range from 200-3,300 m; below 1,850 m the climate is Mediterranean, characterized by hot, dry summers and cool, moist winters, where 95% of the precipitation occurs between October 1 and May 1 (Bailey 1966). Cooler temperatures and snow are common above 1,850 m. Springs, which provide surface water, are not uncommon on the steep slopes and permanent streams occur in the bottoms of the larger canyons.

Chaparral, the dominant vegetation below 1,850 m, is adapted to the summer droughts, by becoming dormant during summer. As moisture levels decline in shrubs, the vegetation becomes more susceptible to fire (Hanes 1971, Keeley and Davis 2007). The fire regime is characterized by 30-70 year fire-return intervals and high intensity crown fires (Stephenson and Calcarone 1999, Keeley and Fotheringham 2001, Minnich 2001) that are frequently driven by strong winds during the fall (Keeley and Fotheringham 2001, 2003, Minnich 2001).

Post-fire succession in chaparral has been described in detail elsewhere (Biswell et al. 1952, Hanes 1971, Keeley and Davis 2007). After most fires, fall and winter rains germinate the abundant seeds of annual grasses and herbaceous plants; however, this ephemeral flora is essentially gone by the 3rd year post-fire because of increased crown cover of shrubs, such as chamise (*Adenostoma fasciculatum*), California lilac (*Ceanothus* spp.), manzanita (*Arctostaphylos* spp.), scrub oak (*Quercus dumosa*), and mountain mahogany (*Cercocarpus betuloides*) that sprout from root burls, seeds, or both. Growth is rapid the first season, often exceeding 50 cm in height; as canopy cover increases, it often forms impenetrable stands.

Bighorn sheep are distributed among 4 subgroups (Figure 1), of which 3 each use a single winter-spring range (Cattle Canyon, East Fork San Gabriel River, and San Gabriel Wilderness) and 1 subgroup (Cucamonga) uses 5 winter-spring ranges (Middle and South Forks Lytle Creek, Deer Canyon, Cucamonga Canyon, and Barrett-Cascade Canyons). Additional descriptions of these populations are provided by Weaver et al. (1972), Holl and Bleich (1983), and Holl et al. (2004). Mule deer occur
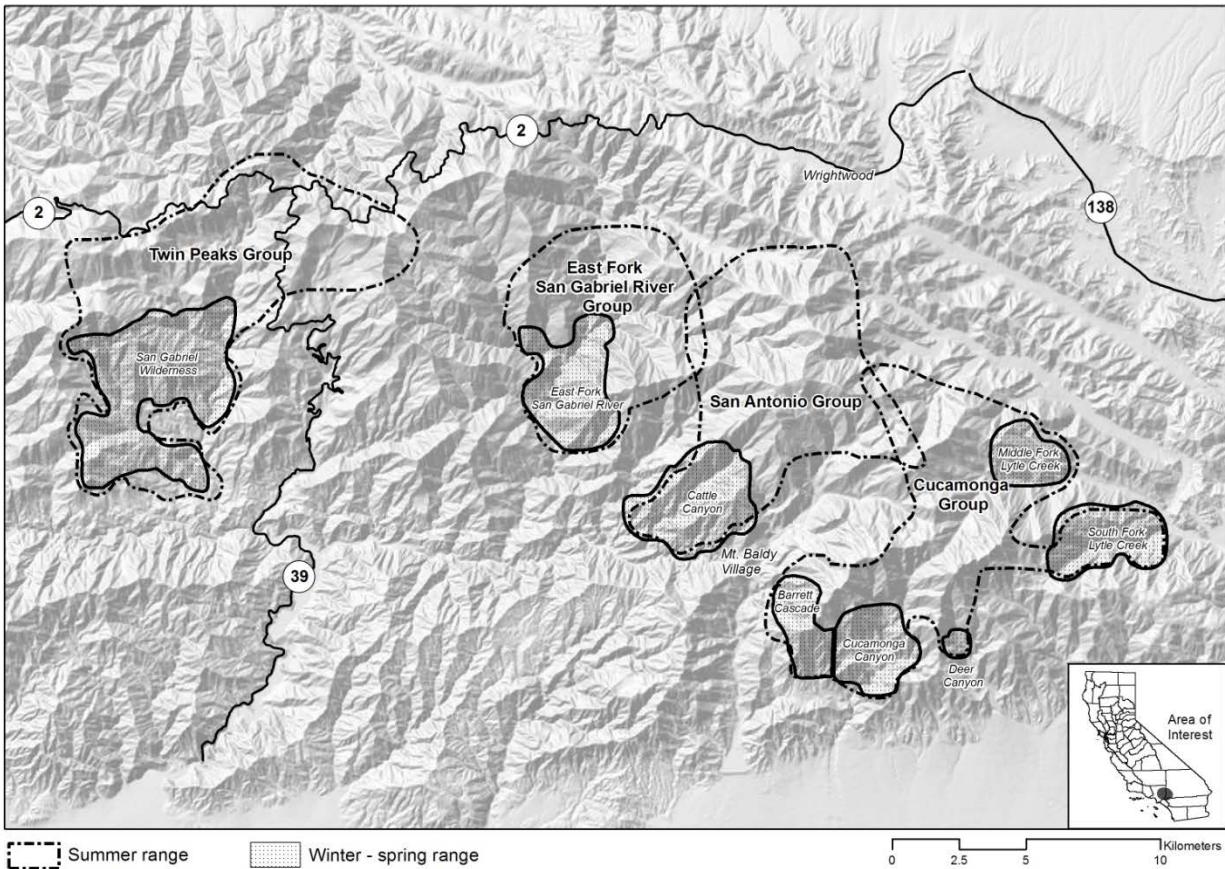
Figure 1. Distribution of bighorn sheep seasonal ranges in the San Gabriel Mountains, California.

throughout the mountain range (Cronemiller and Bartholomew 1950). Both species include resident animals that remain on chaparral ranges year around and migratory animals that migrate above 1,850 m elevation during summer, presumably in search of more nutritious forage (Hebert 1973, Festa-Bianchet 1988). The mountain range also supports a full complement of predators capable of killing bighorn sheep or mule deer, including mountain lions (*Puma concolor*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*) and black bears (*Ursus americanus*); no livestock allotments are permitted on national forest land and no incidents of disease that could have affected population levels of bighorn sheep (Holl et al. 2004) or mule deer (CDFG files) have been reported.

METHODS

We used data from population surveys of bighorn sheep and mule deer, Forest Service fire history reports, and precipitation records from Mt. Wilson, Los Angeles, County, CA collected during 1976-2006. None of these data sets were initially designed to satisfy an experimental design targeted to address our 4 hypotheses; therefore, we used the serendipitous wildfires to compare the response of bighorn sheep between burned and unburned areas and to evaluate chronological responses to fire and precipitation.

Demographic Data for Bighorn Sheep and Mule Deer

We used demographic data from annual March helicopter surveys of bighorn sheep in the San Gabriel Mountains, conducted since 1976 (Holl et al. 2004,

Bleich et al. 2008, Holl and Bleich 2009), to estimate age and sex composition and recruitment rates of bighorn sheep. Similarly, we used data on sex and age ratios obtained during helicopter surveys of mule deer by CDFG personnel during November 1985-2004.

We used the annual reported buck harvest for Los Angeles County, adjusted to include only animals removed from the national forest (79-88% of the total harvest), as an index to estimate changes in mule deer abundance during 1976-2006; hunter tag returns are used by at least 40% of state agencies to track deer population trends (Rupp et al. 2000) and there was a significant correlation between the reported buck harvest and the number of mule deer observed per hour of helicopter survey time in this mountain range during 1985-1998 (Holl et al. 2004), indicating tag returns provided a valid index of abundance. During the surveys all animals that were observed moved in response to the helicopter and no bias in visibility as a result of animal movement or plant succession was detected (Holl et al. 2004, Bleich et al. 2008).

Comparison of Bighorn Sheep Recruitment and Growth Rates between Burned and Unburned Ranges

We calculated 95% confidence limits for recruitment rates following Riney (1956) and compared bighorn sheep recruitment rates from individual winter-spring ranges that burned in 1975, 1997, and 2003 with recruitment rates on unburned ranges during those same periods using Fisher's exact test. We limited these comparisons to 1.5-3.5 years post-fire because the nutritional benefits in chaparral and montane shrublands only lasts 2-3 years (Taber and Dasman 1958, Hobbs and Spowart 1984). All fires occurred during fall, and we did not consider recruitment rates obtained the first March post-fire because those fires would

not have affected nutritional status of young, which were 6-8 months-of-age and weaned when the fires occurred.

We compared the exponential rates of increase for bighorn sheep occupying burned and unburned ranges during 1996-2006, the only period we identified where the abundance of bighorn sheep on multiple burned and unburned ranges could be evaluated simultaneously. The total number of animals counted during the annual surveys was used to calculate the rates of increase (Caughley 1977). Burned ranges were the East Fork of the San Gabriel River, which burned in 1997 and the Cucamonga subunit that burned in 2003. We used 1996 for the initial year in the Cucamonga subunit because some of the winter-spring ranges were not surveyed between 1999 and 2002 and, therefore, could not contribute to the analysis. Unburned ranges were Cattle Canyon and the San Gabriel Wilderness winter-spring ranges which had not burned since at least 1975.

Responses of Bighorn Sheep and Mule deer to Changes in Habitat Suitability Resulting from Wildfires

We used Forest Service fire history data to determine the area burned annually on bighorn sheep winter-spring ranges (Figure 1) and the entire mountain range was used for mule deer. Within those areas the amount of suitable habitat resulting from fire (HSF) was recalculated annually as the area burned ≤15 years ago for bighorn sheep and ≤5 years ago for mule deer. We used 15 years for bighorn sheep because they are positively associated with burned areas for 15 years post-fire (Bleich et al. 2008) and we used 5 years for mule deer because Taber and Dasmann (1957) concluded deer densities in chaparral habitat returned to pre-burn levels approximately 4-5 years post-fire. As a result, the HSF includes a spatial and temporal component.

We used correlation analysis to determine the relationships between bighorn sheep HSF and population estimates (Holl and Bleich 2009) during 1976-2006; we repeated the analysis for 3 shorter periods: 1976-1989, and 1989-1995, periods where sheep declined at different rates (Holl et al. 2004, Holl and Bleich 2009); and 1995-2006, when the sheep population increased. We used linear regression to evaluate the influence of density on lamb recruitment, with adult female density as the independent variable. The number of females was determined using the observed age and sex ratios obtained during the surveys and the reconstructed population estimates (Holl and Bleich 2009). This analysis did not include 1976-1984, when recruitment was associated with early winter precipitation and low temperatures and precipitation during the spring birthing season (Holl et al. 2004). We also used correlation to determine the relationship between mule deer HSF and the reported buck harvest during 1976-2006. We repeated that analysis during 2 shorter periods, 1976-1989 and 1989-2006. The reported buck harvest was also staggered 3 years to represent fawn production 3 years earlier to determine if changes in mule deer HSF were associated with earlier fawn recruitment.

Response of Recruitment to Precipitation

We used precipitation as an index of annual nutrient availability in forage (McKinney et al. 2006). We used correlation and regression analyses to test for a relationship between nutrient availability during pregnancy (total precipitation October-March) and observed fawn and lamb recruitment rates during 1985-2004.

Acceptance of Statistical Tests

All statistical tests were considered to be significant when $\alpha \leq 0.05$, except for the relationship between reported buck harvest and mule deer HSF, when $\alpha = 0.1$ was accepted because an index of abundance was used and that index was staggered to represent events that occurred 3 years earlier.

RESULTS

Comparison of Bighorn Sheep Recruitment and Exponential Growth Rates between Burned and Unburned Ranges

Recruitment Rates.—Following the 1975 fire, recruitment rates of bighorn sheep at 1.5 years were lower on the burned range in Cattle Canyon (13 ± 10) than the unburned ranges (37 ± 11) ($P = 0.009$; Table 1) and at 2.5 years, recruitment rates were higher on the burned range (37 ± 23) than the unburned ranges (10 ± 6) ($P = 0.003$); there was no difference ($P = 0.99$) 3.5 years post-fire. No data on recruitment rates were available from the East Fork San Gabriel River immediately following the 1997 fire; however, there was no difference in recruitment rates ($P = 0.28$) between burned and unburned ranges 3.5 years post-fire. Although recruitment rates appeared higher on the Cucamonga subunit than on the unburned ranges at 1.5 years post-fire (76 ± 81 *vs*. 33 ± 24) and at 2.5 years (28 ± 16 *vs*. 22 ± 16), they were not statistically different ($P = 0.17$). There was no difference ($P = 0.82$) at 3.5 years post-fire (Table 1).

Exponential Rates of Increase.—From 1996-2006, the exponential rate of increase for bighorn sheep was 0.103 on the East Fork San Gabriel River winter-spring range following the 1997 fire and it was 0.133 in the Cucamonga subgroup (burned in 2003) during 1998-2006. Given these rates, the East Fork San Gabriel River population would double every 6.6 years and the Cucamonga subgroup would double

Table 1. Recruitment rates (LL:100EE) ± 95% confidence limits in burned and unburned winter-spring ranges following 3 fires in the San Gabriel Mountains, California.

Years Post-Fire	Years of Fires					
	1975		1997		2003	
	Cattle Canyon	Unburned Ranges	East Fork San Gabriel	Unburned Ranges	Cucamonga Subgroup	Unburned Ranges
1.5	13±10*	37±11*			76±81	28±16
2.5	37±23*	10±6*			33±24	22±16
3.5	36±20	36±10	14±21	43±34	62±32	68±49

* significant differences ($P < 0.05$) between burned and unburned ranges for each fire.

every 5.2 years. On the 2 unburned ranges, the exponential rate of increase was 0.022 and the population would be expected to double about every 32 years.

Responses of Bighorn Sheep and Mule Deer to Changes in Habitat Suitability Resulting from Wildfires

Bighorn Sheep.—During 1976-2006 HSF for bighorn sheep winter-spring ranges varied from 2,093 ha in 1976 to 2,837 ha in 1980, declined to 670 ha in 1994, and increased to 3,392 ha in 2003 (Figure 2).

The HSF increased as a result of large wildfires in 1975, 1980, 1997, and 2003. Although small wildfires in 1983 and 1984 burned portions (115 ha) of 2 winter-spring ranges, it did not result in a net increase in available habitat because larger quantities of habitat on other winter-spring ranges were simultaneously maturing and becoming less suitable for bighorn sheep. There was a significant correlation ($r_{29} = 0.414$, $P < 0.05$) between the HSF and population estimates during 1976-2006 (Figure 2).
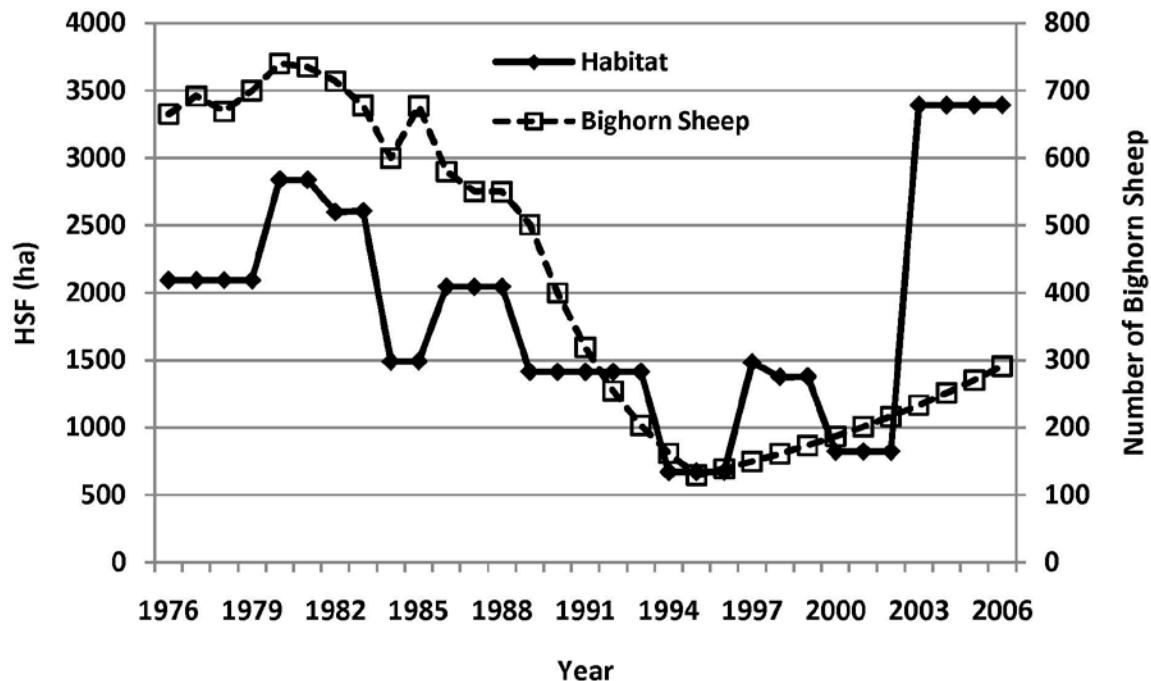

Figure 2. Changes in bighorn sheep population estimates and habitat suitability resulting from fire (HSF) during 1976-2006 in the San Gabriel Mountains, California.

When individual time periods were considered, the relationships between the HSF and population estimates improved during 1976-1989 ($r_{12} = 0.654$, $P < 0.01$), when the largest population estimate (740±49) was obtained, and during 1995-2006 ($r_{10} = 0.823$, $P < 0.01$), as the population increased from 130 in 1995 to 292±69 in 2006 (Fig. 2). There was no correlation between the HSF and bighorn sheep population estimates during 1989-1995 ($r_5 = 0.69$, $P > 0.05$) when the HSF remained unchanged from 1989-1993 and the bighorn sheep population declined from 501±30 to 203 animals (Figure 2); during 1994-1995 both the HSF and the sheep population estimates declined, culminating in 130 bighorn sheep. Thus, 80% of the population decline during 1989-1995 occurred when there was no change in the HSF, suggesting other factors were affecting the number of sheep.

During 1976-1979 mean densities were 16.6 ewes/km^2 HSF; densities increased to a peak of 21.3 ewes/km^2 in 1984, and then declined to 15.6 ewe/ km^2 and 5.0 ewe/ km^2 in 1986 and 1997, respectively, following wildfires; densities then increased to 17.9 females/ km^2 in 2002. In response to the 2003 wildfire, mean densities declined to 10.7 /km^2 during 2004-2006. During 1984-2006 there was a linear and negative relationship (slope = -1.21; $r^2 = 0.47$, $P < 0.05$) between lamb recruitment rates and ewe density (Figure 3).

Mule Deer.—The mule deer HSF was more variable during 1976-2006 (Figure 4) than the bighorn sheep HSF (Figure 2). The HSF increased in response to wildfires in 1975, 1979, 1988, 1997, and 2003 (Figure 4) and oscillated during 1985-2002. There was no relationship ($r_{29} = 0.04$, $P > 0.1$) between the HSF and reported buck harvest (Figure 4) during 1976-2006.

When shorter time periods were used and the reported harvest was staggered 3 years there was a relationship ($r_{15} = 0.51$, $P < 0.1$) between the HSF during 1973-1986 and the reported buck harvest during 1976-1989, indicating fawn recruitment was associated with changes in the HSF. That relationship did not occur ($r_{16} = 0.158$, $P > 0.1$) during 1989-2006, indicating other factors may have been associated with fawn recruitment.

Response of Recruitment to Precipitation

There was a linear relationship ($y = 10.3 + 0.34x$, $r^2 = 0.58$, $P = 0.004$) between precipitation during pregnancy and fawn recruitment during 1985-2004, while there was no relationship between precipitation and lamb recruitment during the same years ($r_{16} = 0.323$, $P > 0.05$) (Figure 5). Fawn recruitment rates were approximately 50% lower during periods of less than normal precipitation in 1990 (23) and 1999-2004 (20±4.4) when compared to the mean recruitment rate (47±3.4) during years of at least normal precipitation.
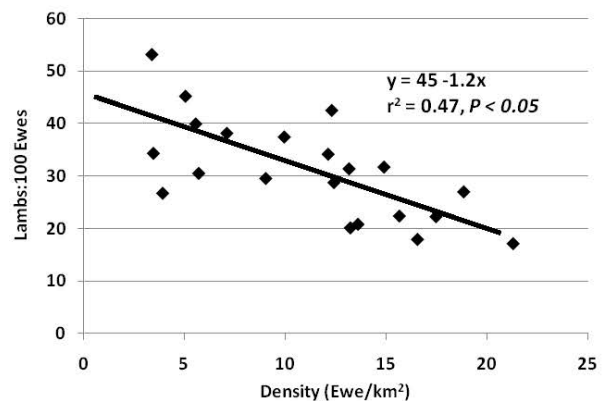

Figure 3. Relationship between ewe density and recruitment during 1984-2006 in the San Gabriel Mountains, California.
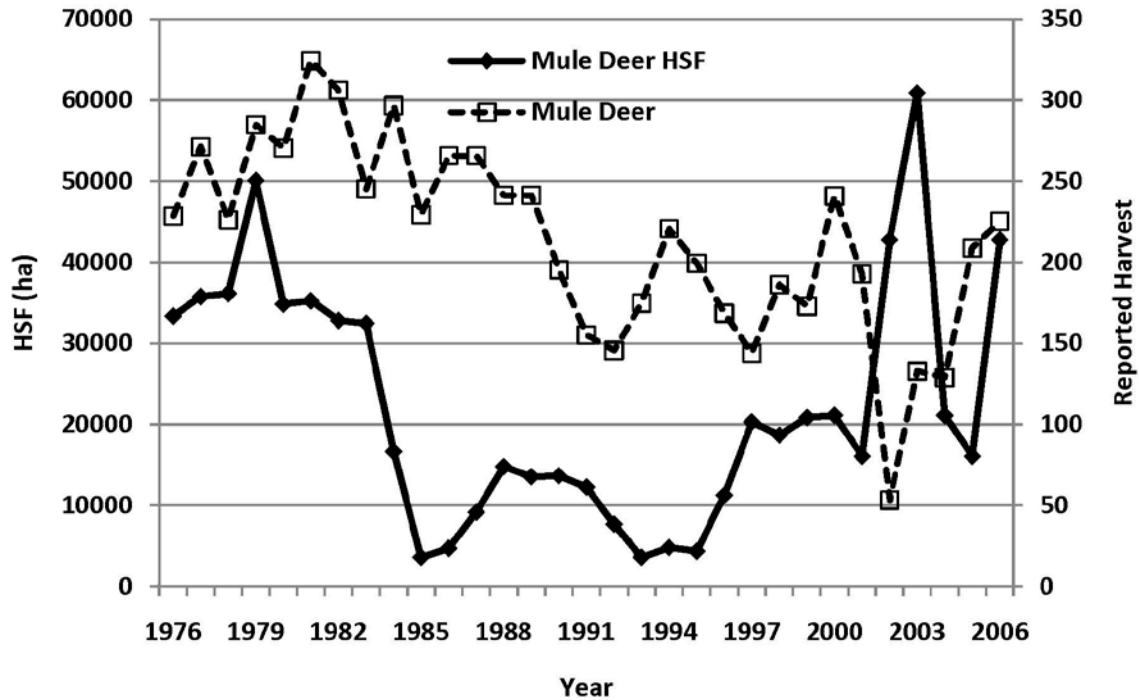
Figure 4. Relationship between mule deer abundance during 1976-1989 and habitat suitability resulting from fire 3 years earlier in the San Gabriel Mountains, California.
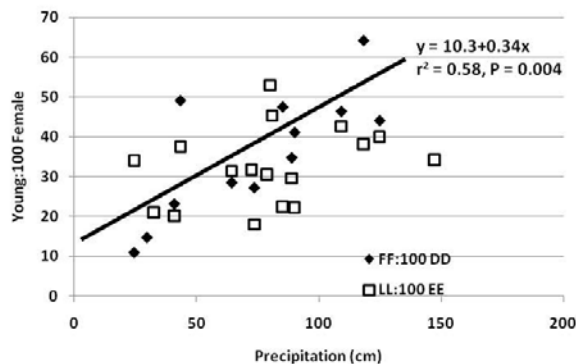

Figure 5. Relationship between precipitation during pregnancy and recruitment rates in mule deer and bighorn sheep during 1985-2004 in the San Gabriel Mountains, California.

DISCUSSION

Comparison of Bighorn Sheep Recruitment and Growth Rates between Burned and Unburned Ranges

Recruitment Rates.—Improved nutrition has been associated with increased recruitment in bighorn sheep (Seip and

Bunnell 1985, Blanchard et al. 2003, McKinney et al. 2006), and forage quality in chaparral improves for 2-3 years after fires (Biswell et al. 1952). Although we expected recruitment would be consistently higher on burned ranges for at least 2 years following fires, we detected that pattern only during the second year after the 1975 fire (Table 1). Small samples sizes ($n < 20$ females) in the East Fork of the San Gabriel River in 2001, Cucamonga Canyon in 2005, and on unburned ranges in 2007 may not have yielded representative estimates of recruitment rates; however, sample sizes were substantially larger ($n > 30$ females) for all other ranges and years, and likely had little influence on our ability to detect differences. Alternatively, intra-annual differences in the distribution of bighorn sheep may have had an important, but undetected, affect.

Earlier investigators (Weaver et al. 1972, Holl and Bleich 1983) noted that both resident and migratory bighorn sheep

occurred in the San Gabriel Mountains. Resident animals generally remain below 2,000 m elevation, while all migratory animals occupy summer ranges above 2,000 m. Vegetation associations change substantially above 1,850 m, and sheep that migrate to higher elevations can take advantage of differences in plant phenology and, presumably, more nutritional forage than animals remaining on lower elevation ranges (Hebert 1973, Wehausen 1983, Festa-Bianchet 1988). Our ability to detect differences in recruitment rates was confounded by sympatry between resident and migratory animals, which were indistinguishable during the annual aerial surveys on winter-spring ranges.

Exponential Rates of Increase.—Exponential rates of increase on burned ranges indicated bighorn sheep subgroups doubled every 5-6 years when compared with 32 years on unburned ranges, and the very low rate of increase on unburned ranges indicated that the majority of the population increase after 1997 was attributable to additional sheep on burned ranges. It is very unlikely that additional bighorn sheep on burned ranges was the result of immigration because bighorn sheep have high fidelity to seasonal ranges (Geist 1971), there are large patches of unsuitable and unoccupied habitat between winter-spring ranges (Holl and Bleich 1983), and available evidence indicates the San Gabriel Mountains are effectively isolated from other mountain ranges inhabited by bighorn sheep (Bleich et al. 1996, Epps et al. 2007). Short pulses of improved forage quality and recruitment on burned ranges would however, increase the number of animals and contribute to the higher rates of increase on those ranges.

Responses of Bighorn Sheep and Mule Deer to Changes in Habitat Suitability Resulting from Wildfires

Bighorn Sheep.—Wildfire changes the suitability and availability of bighorn sheep habitat (Stelfox 1976, Riggs and Peek 1980, Wakelyn 1987, Etchberger et al. 1989, Cain et al. 2005, Bleich et al. 2008) by reducing the canopy cover of shrubs and trees, which improves access and the field of vision of bighorn sheep (Risenhoover and Bailey 1980, Holl and Bleich 1983) which is required for the detection of predators. The HSF for winter-spring ranges used by bighorn sheep in the San Gabriel Mountains expanded and contracted during 1976-2006 as a result of wildfires and the HSF was positively associated with population changes in bighorn sheep during that period (Figure 2). When individual time periods were considered, the relationship between the HSF and bighorn sheep abundance improved during 1976-1989 and during 1995-2006; however, there was no relationship between HSF and abundance during 1989-1995.

During 1976-1989 the HSF initially improved as a result of wildfires in 1975 and 1980 and the largest population estimate, 749±49, was recorded in 1980 (Figure 2). After 1980 the HSF started to decline as a result of increased shrub growth and canopy cover in previously burned areas, and this corresponded with a decline in the abundance of bighorn sheep. During 1976-1982 adult survival was high, recruitment rates were influenced by precipitation and cold temperatures during the birthing season, and the exponential rate of increase (0.015) indicated the population was stable (Holl et al. 2004, Holl and Bleich 2009). Although small wildfires burned on winter-spring ranges after 1983 the HSF declined 46% during 1983-1989 (Figure 2), fewer sheep were observed in previously burned areas during the annual surveys (Holl et al. 2004), and the population estimates declined 23% during that period (Figure 2).

Between 1989 and 1995, there was no relationship between the HSF and bighorn sheep population estimates because the HSF remained unchanged during the first 4 years of that period while 80% of the sheep population decline during 1989-1995 occurred (Figure 2), indicating another factor was associated with the population decline.

The rate of the population decline during 1989-1995 was 4 times the rate of the decline during 1982-1989 (Holl et al. 2004, Holl and Bleich 2009), and it was characterized by the loss of adult sheep (Holl et al. 2004), which is uncommon (Gaillard et al. 2000, Harris et al. 2008); however, disease or large predators may account for much of the variation in adult survival (Gaillard et al. 2000). There is no evidence that disease influenced population changes in bighorn sheep in the San Gabriel Mountains (Holl et al. 2004). Based on the known demographic changes in the San Gabriel Mountains and observed declines in bighorn sheep resulting from mountain lion predation in nearby mountain ranges during a similar time period (Wehausen 1996, Hayes et al. 2000, Schaefer et al. 2000), it previously had been hypothesized that the bighorn sheep population decline during 1989-1995 was associated with mountain lion predation (Holl et al. 2004, Holl and Bleich 2009).

By 1995 the HSF and bighorn sheep population reached their lowest values (Figure 2). All previously burned areas had recovered and dense shrub cover would have substantially reduced the visual field of sheep and their ability to detect predators or move into adjacent habitat. Wakelyn (1987) and Etchberger et al. (1989) reported bighorn sheep abandoned seasonal ranges in the absence of fire in other mountain ranges. Yet, during the annual surveys in 1995 and 1996, sheep were observed on every winter-spring range except Cucamonga Canyon.

Similarly, during 1976-1983 an estimated 290 bighorn sheep inhabited the Iron Mountain and Twin Peaks subgroups (Holl and Bleich 1983) even though those 2 areas had not burned in more than 25 years. Thus, the lack of fires in the San Gabriel Mountains did not result in complete abandonment of all seasonal ranges. In the absence of fire, escape terrain (Holl 1982) remains suitable habitat providing a refuge in the San Gabriel Mountains, likely because the steep, rocky substrate limits the density of shrubs and does not eliminate the ability of bighorn sheep to detect predators. As a result, the majority of the population changes associated with fire-related habitat changes likely occurred because fire had a disproportionately greater effect on the suitability and availability of chaparral habitat adjacent to escape terrain. Wildfires in 1997 and 2003 increased the HSF, which was associated with an increase in the number of bighorn sheep during 1998-2006 (Figure 2; Holl and Bleich 2009).

The reduction in shrub canopy cover that resulted from the wildfires in 1975, 1980, 1986, 1997, and 2003 increased the field of vision of bighorn sheep and improved access into recently burned areas (Stelfox 1976, Smith et al. 1989, Holl et al. 2004, DeCesare and Pletscher 2006), which reduced sheep densities, presumably as they searched for higher quality forage (Biswell et al. 1952, Hobbs and Spowart 1984). Browse species compose approximately 60% of the annual diet of bighorn sheep in the San Gabriel Mountains (Perry et al. 1987); therefore, seedlings and basal sprouts from root burls, combined with increased availability of grasses and forbs that followed fires, likely resulted in a short-term improvement in the quality of their diets (Biswell et al. 1952, Taber and Dasmann 1958, Hobbs and Spowart 1984) and should have improved lamb recruitment. Although this was not detected when recruitment on

burned and unburned ranges was compared (Table 1), the number of bighorn sheep on burned ranges increased about 5 times faster than on unburned ranges.

During 1984-2006 there was a negative relationship between the density of adult females and recruitment rates (Figure 3). Density estimates are also ratios and are subject to the same concerns identified for age ratios (Caughley 1974, McCullough 1994, Harris et al. 2008), where changes in either the numerator (number of females) or denominator (area of habitat) can affect the ratio.

The highest density of ewes occurred in 1984. That peak resulted from a decline in the HSF during 1983-1984, rather than an increase in the number of ewes (Figure 2). Ewe densities generally declined during 1984-1997 as the number of ewes and the HSF declined (Figure 2), the latter a result of increased shrub cover. As ewe survivorship improved after 1995, density increased and recruitment rates declined until the 2003 fire increased the HSF, and thereby allowed sheep to redistribute themselves, reduce densities, and increase recruitment.

Mule Deer— Population estimates of mule deer were not available, but the reported buck harvest was correlated with the results of helicopter surveys and provides a reasonable index of changes in abundance in this mountain range (Holl et al. 2004). Annual changes in the HSF were not associated with the reported buck harvest, indicating habitat changes did not affect hunter success and minimized another potential source of bias that could have affected our analyses.

Black-tailed deer that occupy chaparral-dominated habitat increase production and survival of young for approximately 3 years post-fire (Taber and Dasmann 1957). During 1976-1989 the reported buck harvest was positively associated with the HSF 3 years earlier,

indicating the HSF was associated with fawn recruitment 3 years earlier. Thus, the population increase during 1976-1981, as indicated by the reported buck harvest for those years, resulted from an increase in fawn recruitment that was initiated by earlier in the HSF (Figure 4).

Between 1981 and 1989, the reported buck harvest indicated the deer population declined by approximately 26% (Figure 4). That population decline corresponded with a reduction in the amount of habitat that had burned and lower recruitment 3 years earlier, which is consistent with the decline in the number of black-tailed deer that occurred as chaparral matured (Taber and Dasmann 1957, 1958). Following 1989, the reported buck harvest and aerial survey data (CDFG files) indicated a sharp decline in the deer population. During 1990-1992, the reported buck harvest declined 40% from 1989 levels. Harvest data indicated that mule deer increased during 1993-2000 and then oscillated, but those changes were not related to habitat changes (Figure 4). Thus, factors other than habitat changes resulting from wildfires likely affected the mule deer population after 1989 (Figure 4).

Effects of Precipitation

During 1976-2004, fawn recruitment was directly affected by nutrient availability, as indexed by precipitation (Figure 5), and the lowest fawn recruitment rates occurred during 1989-1990 and 1999-2004, periods of lower than normal precipitation and when the HSF was not associated with the abundance of mule deer.

Mule deer commonly produce multiparous births (Anderson 1981), and nutrition affects ovulation and fetal rates, and fetal growth rates, in mule and white-tailed deer (*O. virginianus*). Females on lower nutritional planes produce fewer and smaller young (Taber and Dasmann 1957, 1958; Verme 1963, 1969). More recently,

fawn production and survival on arid southwest ranges has been linked to precipitation and forage production (Kucera 1988, Lawrence et al. 2004, Bender et al. 2007) and population declines in southeastern California (Pierce et al. 2000). Similar observations of the effects of drought on mule deer recruitment and abundance were also reported from Arizona (Kamler et al. 2002), New Mexico (Logan and Sweanor 2001), and Nevada (Sweitzer et al. 1997). Thus, a regional drought appears to have been associated with the decline or constrained growth in mule deer populations across the southwest during the 1990s.

There was no apparent relationship between lamb recruitment and precipitation (Figure 5). Browse species comprise most of the annual diets of mule deer and bighorn sheep in the San Gabriel Mountains (Cronemiller and Bartholomew 1950, Perry et al. 1987), and the timing of changes in the nutritional value of the annual diet of black-tailed deer in chaparral (Taber and Dasmann 1958) is identical to that for bighorn sheep in the San Gabriel Mountains (Perry et al. 1987). Young of both species are born April through June, with the majority in May (Cronemiller and Bartholomew 1950, Holl and Bleich 1983). Thus, differences in foraging strategies or the timing of births do not explain observed differences in responses to decreased levels of precipitation and nutrient availability.

Bighorn sheep produce a single young (Geist 1971) and the birth weight of that young is small in relation to maternal weight when compared to white-tailed or black-tailed deer (Robbins and Robbins 1979). Producing a single offspring that is small would be advantageous during periods of reduced nutrient availability; conversely, a smaller individual would have a larger surface area:volume ratio, which would be disadvantageous if it was cold and wet

during the birthing period (Holl et al. 2004). Although lack of precipitation in desert ranges affects nutrient availability and lamb recruitment (Leslie and Douglas 1979, Wehausen et al. 1987, Douglas 2001, McKinney et al. 2006), the San Gabriel Mountains are mesic and produce more biomass than those desert ranges; as a result, recruitment in bighorn sheep was less apt to be affected by changes in precipitation (an index to nutrient availability) than in arid desert ranges.

CONCLUSIONS

Wildfires on chaparral winter-spring ranges in the San Gabriel Mountains improved habitat suitability, resulting in reduced ewe densities that were associated with increased recruitment rates and bighorn sheep populations on burned ranges increased faster than populations on unburned ranges. Wildfire history was associated with the abundance of bighorn sheep during all years except 1989-1995, and with the abundance of mule deer during 1976-1989. Precipitation during pregnancy was associated with recruitment in mule deer, and drought years reduced recruitment and mule deer abundance during the 1990s, similar to what was observed in other mule deer populations in the southwest during that period.

In their review of temporal variation in the dynamics of ungulates Gaillard et al. (2000) identified 4 sources of temporal variation that influenced demographic responses in large herbivores: predictable seasonal environmental variation, unpredictable weather fluctuations, density-dependent responses, and changes in the behavior or abundance of predators. California's very predictable Mediterranean climate results in a similar annual cycle in forage quality in chaparral. In northern California, the crude protein content in chaparral browse consumed by black-tailed

deer peaked in April, then declined to its lowest quantity in September and gradually increased during winter fall and winter (Taber and Dasmann 1958). This is identical to the annual cycle of crude protein content in the diet of bighorn sheep in the San Gabriel Mountains (Perry et al. 1987). The predictability of the annual forage quality cycle corresponds to the timing and duration of the birthing season for mule deer and bighorn sheep (mid-April to early-June), which has little annual variability.

Unpredictable amounts of spring precipitation influence critical fuel moisture levels in late summer (Dennison et al. 2008) and warm fall winds influence wildfire behavior which directly affects habitat suitability and demographic responses of mule deer and bighorn sheep. Changes in habitat suitability resulting from wildfires may have the greatest influence on inter-year variability in mule deer and bighorn sheep in the San Gabriel Mountains. Unpredictable droughts influence recruitment and abundance of mule deer; however, variability in precipitation appears to have little influence on bighorn sheep, except when they are at high densities and precipitation and cold temperatures occur during the birthing season.

Predators, particularly mountain lions, increase demographic variability in mule deer and bighorn sheep. Variability in survivorship associated with predators is high in mule deer because they are the primary prey of mountain lions (Ballard et al. 2001). The available information indicates predation has had little influence on the abundance bighorn sheep in the San Gabriel Mountains (Robinson and Cronemiller 1954, Weaver et al. 1972, Holl and Bleich 1983, Holl et al. 2004) and predation may only have a substantial effect on the number of bighorn sheep after the mule deer population has declined (Sweitzer et al. 1997, Logan and Sweanor 2001, Holl

et al. 2004). The population decline in bighorn sheep during 1989-1995 that was hypothesized to have resulted from mountain lion predation (Holl et al. 2004) was preceded by the decline in mule deer that was associated with the rare alignment of few wildfires that reduced habitat suitability and a drought that reduced fawn recruitment.

MANAGEMENT IMPLICATIONS

For the past 50 years the management of large mammals in the San Gabriel Mountains has been limited to suppressing all wildfires in a fire-adapted ecosystem, a limited harvest of mule deer, and removal of 66 bighorn sheep for translocation. The decline of bighorn sheep during 1989-1995 led to their re-listing as a Forest Service Sensitive Species and the preparation of a restoration plan (US Forest Service et al. 2004).

Habitat changes resulting from fires clearly affect the distribution, productivity, and abundance of mule deer and bighorn sheep. Modeling has demonstrated that fire can significantly increase bighorn sheep habitat in the San Gabriel Mountains (Bleich et al. 2008) and our analysis demonstrated a similar relationship exists for mule deer. Bighorn sheep can be removed from the Sensitive Species list after demonstrating that a larger population can be sustained (US Forest Service et al. 2004). Although prescribed burns to improve habitat suitability and increase the number of bighorn sheep were identified in the restoration plan (US Forest Service et al. 2004), no prescribed burns have been implemented because the current local paradigm does not recognize prescribed fire as an effective tool to manipulate a fire-adapted ecosystem. Local perceptions and policies that constrain the use of prescribed burning or the use of natural fire to improve habitat suitability for mule deer and bighorn

sheep will have to be modified before the restoration goal can be achieved.

LITERATURE CITED

Anderson, A. E. 1981. Morphological and physiological characteristics. Pages 27-98 *in* O. C. Wallmo, editor. Mule and black-tailed deer of North America. University of Nebraska Press, Lincoln, USA.

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

Bender, L. C., L. A. Lomas, and J. Browning. 2007. Condition, survival, and cause-specific mortality of adult female deer in north-central New Mexico. Journal of Wildlife Management 71:1118-1124.

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.

Blanchard, P., M. Festa-Bianchet, J. Gaillard, and J. T.Jorgenson. 2003. A test of long-term fecal nitrogen monitoring to evaluate nutritional status in bighorn sheep. Journal of Wildlife Management 67:477-484.

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.

Bleich, V. C., J.D. Wehausen, J. D. 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.

Cain, J. W. III, H. E. Johnson, and P. R. Krausman. 2005. Wildfire and desert bighorn sheep habitat, Santa Catalina Mountains, Arizona. The Southwestern Naturalist 50:506-513.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York, USA.

Caughley, G. 1974. Interpretation of age ratios. Journal of Wildlife Management 38:557-562.

Cronemiller, F. P. and P. S. Bartholomew. 1950. The California mule deer in chaparral forests. California Fish and Game 36:343-365.

DeCesare, N. J. and D. H. Pletscher. 2006. Movements, connectivity, and resource selection of Rocky

Mountain bighorn sheep. Journal of Mammalogy 87:531-538

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

Douglas, C. L. 2001. Weather, disease, and bighorn lamb survival during 23 years in Canyonlands National Park. Wildlife Society Bulletin 29:297-305.

Epps, C. W., J. D. Wehausen, V. C. Bleich, S. G. Torres, and J. S. Brashares. 2007. Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44:714-724.

Etchberger, R. C., P. R. Krausman, and R. Mazaika. 1989. Mountain sheep habitat characteristics in the Pusch Ridge Wilderness, Arizona. Journal of Wildlife Management 53:902-907.

Festa-Bianchet, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75: 580-586.

Gaillard, J. M., M. Festa Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review Ecology and Systematics 31:367-393.

Geist, V. 1971. Mountain sheep: a study in behavior and evolution. University of Chicago Press, Chicago, Illinois, USA.

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

Harris, N. C., M. J. Kaufman, and L. S. Mills. 2008. Inferences about ungulate population dynamics derived from ratios. Journal of Wildlife Management 72:1143-1151.

Hayes, C. L., E. S. Rubin, M. C. Jorgensen, R. A. Botta, and W. M. Boyce. 2000. Mountain lion predation of bighorn sheep in the peninsular ranges, California. Journal of Wildlife Management 64:954-959.

Hebert, D. M. 1973. Altitudinal migration as a factor in the nutrition of bighorn sheep. Dissertation, University of British Columbia, Canada.

Hobbs, N. T. and R. A. Spowart. 1984. Effects of prescribed fire on nutrition of bighorn sheep and mule deer during winter and spring. Journal of Wildlife Management 48:551-560.

Holl, S. A. 1982. Evaluation of bighorn sheep habitat. Desert Bighorn Council Transactions 26:47-49.

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

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

Holl, S. A. and V. C. Bleich. 2009. Reconstructing the San Gabriel Mountains bighorn sheep population. California Fish and Game 1:77-87

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.

Kamler, J. E., R. M. Lee, J. deVos, Jr., W. B. Ballard, and H. A. Whitlaw. 2002. Survival and cougar predation of translocated bighorn sheep in

Arizona. Journal of Wildlife Management 66:1267-1272.

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

Keeley, J. E. and C. J. Fotheringham. 2001. Historic fire regimes in southern California shrublands. Conservation Biology 15:1536-1548.

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 Press, New York, USA.

Kucera, T. E. 1988. Ecology and population dynamics of mule deer in the eastern Sierra Nevada, California. Dissertation, University of California, Berkeley, USA.

Lawrence, R. K., S. Demarais, R. A. Relyea, S. P. Haskell, W. B. Ballard, and T. L. Clark. 2004. Desert mule deer survival in southwest Texas. Journal of Wildlife Management 68:561-569.

Leslie, D. M., and C. L. Douglas. 1979. Desert bighorn sheep of the River Mountains, Nevada. Wildlife Monographs 66:1-56.

Logan, K. E., and L. A. Sweanor. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, Washington, D.C., USA.

Longhurst, W. M., E. O. Garton, H. F. Heady, and G. E. Connolly. 1976. The California deer decline and possibilities for restoration. CAL-NEVA Wildlife Transactions 12:74-103.

Marshal, J. P., P. R. Krausman, V. C. Bleich, W. S. Ballard, and J. S. McKeever. 2002. Rainfall, El Niño, and dynamics of mule deer in the Sonoran Desert. Journal of Wildlife Management 66:1283-1289.

McCullough, D. R. 1994. What do herd composition counts tell us? Wildlife Society Bulletin 22:295-300.

McKinney, T., T. W. Smith, and J. C. deVos, Jr. 2006. Evaluation of factors potentially influencing a desert bighorn sheep population. Wildlife Monographs 164:1-36.

Minnich, R. A. 2001. An integrated model of two fire regimes. Conservation Biology 15:1549-1553.

Perry, W. P., J. W. Dole, and S. A. Holl. 1987. Analysis of the diets of bighorn sheep from the San Gabriel Mountains. California Fish and Game 73:156-162.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Selection of mule deer by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. Journal of Mammalogy 81:462-472.

Riggs, R. A., and J. M. Peek. 1980. Mountain sheep habitat-use patterns related to post-fire succession. Journal of Wildlife Management 44:933-938.

Riney, T. 1956. Differences in proportion of fawns to hinds in red deer (*Cervus elaphus*) from several New Zealand environments. Nature 177:488-489.

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 Biennial Symposium of the Northern Wild Goat and Sheep Council 2:18-28.

Robbins, C. T. and B. L. Robbins. 1979. Fetal and neonatal growth patterns and maternal reproductive effort in ungulates and subungulates. American Midland Naturalist 114:101-116.

Robinson, C. S., and F. P. Cronemiller. 1954. Notes on the habitat of desert bighorn in the San Gabriel Mountains. California Fish and Game 40:267-271.

Rupp, S. P., W. B. Ballard, and M. C. Wallace. 2000. A nationwide evaluation of deer hunter harvest survey techniques. Wildlife Society Bulletin 28:570-578.

Schaefer, R. L., S. G. Torres, and V. C. Bleich. 2000. Survivorship and cause-specific mortality in sympatric populations of mountain sheep and mule deer. California Fish and Game 86:127-135.

Seip, D. R., and F. L. Bunnell. 1985. Nutrition of Stone's sheep on burned and unburned ranges. Journal of Wildlife Management 49:397-405.

Smith, T. S., P. J. Hardin, and J. T. Flinders. 1989. Response of bighorn sheep to clear-cut logging and prescribed burning. Wildlife Society Bulletin 27:840-845.

Stephenson, J. R., and G. M. Calcarone. 1999. Southern California mountains and foothills assessment: habitat and species conservation issues. General Technical Report GTR-PSW-172, USDA, Forest Service, Pacific Southwest Research Station, Albany, California, USA.

Stelfox, J. G. 1976. Range ecology of Rocky Mountain bighorn sheep in Canadian national parks. Canadian Wildlife Service Report 39:1-50.

Sweitzer, R. A., S. H. Jenkins, and J. Berger. 1997. Near-extinction of porcupines by mountain lions and consequences of ecosystem change in the Great Basin desert. Conservation Biology 11:1-12.

Taber, R. D. and R. F. Dasmann. 1957. The dynamics of three natural populations of deer, (*Odocoileus hemionus columbianus*). Ecology 38:233-246.

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. California Department of Fish and Game, Game Bulletin 8:1-163.

U. S. 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. Angeles National Forest, Arcadia, California, USA.

Verme, L. J. 1963. Effects of nutrition on growth of white-tailed deer fawns. Transactions of the North American Wildlife and Natural Resources Conference 28:431-443.

Verme, L. J. 1969. Reproductive patterns of white-tailed deer related to nutritional plane. Journal of Wildlife Management 33:881-887.

Wakelyn, L. A. 1987. Changing habitat conditions on bighorn sheep ranges in Colorado. Journal of Wildlife Management 51:904-912.

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. 1983. White Mountain bighorn sheep: an analysis of current knowledge and management

alternatives. Administrative Report. Inyo National Forest, Bishop, California, 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.

Wehausen, J. D., V. C. Bleich, B. Blong, and T. L. Russi. 1987. Recruitment dynamics in a southern California mountain sheep population. Journal of Wildlife Management 51:86-98.