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A retrospective look at mountain lion populations in California (1906-2018)

JUSTIN A. DELLINGER* AND STEVEN G. TORRES†

California Department of Fish and Wildlife, Wildlife Investigations Lab, 1701 Nimbus Rd, Suite D, Rancho Cordova, CA 95670, USA

†Retired

**Corresponding Author: justin.dellinger@wildlife.ca.gov*

Mountain lion (*Puma concolor*) population management in California has varied widely over the past 100 plus years, ranging from a bounty system (1906-1963) to specially-protected status (1972-present). To elucidate how these different management approaches have influenced California's mountain lion populations, we estimated historical population trends by combining purposeful (i.e., bounty and depredation) and incidental (i.e., vehicle strike) mortality statistics with estimates of annual growth and mortality rates derived from the literature. We used a backwards population projection method to estimate annual abundance and population trends, starting with population sizes drawn randomly from a uniform distribution ranging from 1,000-5,000. These back-calculations suggest that the bounty was effective at reducing mountain lion populations, as all simulations indicated a statewide population decline during this period. Specially-protected status was also likely effective, as mountain lion populations appear to have increased statewide following cessation of the bounty period. These analyses demonstrate the effectiveness of various management approaches to influence mountain lion population trends for the intended results, and provide context for understanding historical aspects of mountain lion populations in California, which is unique from other areas given the species' specially-protected status here.

Key words: bounty, depredation, mortality, *Puma concolor*, vehicle strike

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Mountain lion (*Puma concolor*) population management in California has gone through many changes (Table 1), resulting from changing attitudes of public stakeholders, policy makers, and elected officials (Bruskotter and Shelby 2010; Davenport et al. 2010). Mountain lions were subject to a bounty system in California from 1906-1963 (Mansfield and Weaver 1989), with the amount paid per mountain lion varying over time and with sex

Table 1. Management status of mountain lions (*Puma concolor*) through time in California, USA.

Years	Status	per Male	per Female
1906–1916	Bounty	$20	$20
1917–1944	Bounty	$20	$30
1945–1963	Bounty	$50	$60
1964–1969	Vermin	NA	NA
1970–1971	Game	$1[a]	$1
1972–1986	Protected	NA	NA
1987–1990	Game	NA[b]	NA
1991–2018	Protected	NA	NA

[a]Price per hunting tag

[b]No hunting season occurred

(Table 1). In 1919, the California Department of Fish and Game (Department) employed the first full-time statewide lion hunter (McLean 1954), and the number of individuals employed for this purpose grew to a maximum of five in 1948. The Department employed at least one individual through 1959, prior to terminating the bounty program in 1963 (Nowak 1974). Records show that bounty hunters took 224 mountain lions on average each year, totaling 12,580 over the duration of the bounty system (Mansfield and Weaver 1989). After the bounty system ended in 1963, hunters could take mountain lions year-round without a bag limit or hunting license. In 1970 the Fish and Game Commission designated mountain lions as a game species, wherein a hunting license and tag were required for the 1970 and 1971 hunting seasons. In 1972, the state legislature enacted a moratorium on the hunting of mountain lions due to growing public concern over the status of the species in California (Fitzhugh and Gorenzel 1986). The moratorium expired in 1986 and ungulate conservation groups successfully lobbied to re-designate mountain lions as a game species. As a result, the Department began to develop regulations for harvest quotas and management zones, and to assess environmental impacts in compliance with the California Endangered Species Act (Mansfield and Weaver 1989). However, a majority vote by the citizens of California passed Proposition 117 (Fish & Game Code §4800-4809) in 1990, which classified mountain lions as a specially-protected mammal species. This unique status was a political designation, and not based on biological information regarding population abundance or trend. Thus, from 1990 to present, human-caused mountain lion mortalities have been limited to vehicle strikes, targeted removal under the authority of a depredation permit, poaching, public safety concerns, and take of mountain lions negatively impacting California bighorn sheep (Torres et al. 1996; Fish & G. Code §4801).

Mountain lions' specially-protected status has resulted in a spectrum of concerns from interested parties. On one end of the spectrum are ungulate conservation groups who have expressed concern that the mountain lion population may be increasing and thus negatively impacting deer (*Odocoileus hemionus*) herds due to high rates of predation (Proposition 197 [1996]; Walgamuth 2017). Conversely, predator conservation groups have suggested that a combination of mortality factors (e.g., habitat loss, degradation, and fragmentation; vehicle strikes; depredation take; disease; etc.) may be causing the state's mountain lion population to decline in numbers and genetic diversity to a level that may threaten the species' viability (Proposition 117 [1990]; Walter 2015). To address these concerns, wildlife managers and biologists must gain insight into historical trends and the contemporary abundance of mountain lion populations to make effective management decisions.

In light of the controversies regarding mountain lion status in California, the Department seeks to clarify the effects of historical management on mountain lion populations. For this purpose, we proposed the following hypotheses: 1) the statewide mountain lion population in California declined during the bounty period (1906-1963); and 2) the statewide mountain lion population in California increased during the period of increasing legal protections (1972-2018). We tested these hypotheses by analyzing historical statewide data on mountain lion mortalities within a discrete growth equation to estimate historical population trends. Our objectives were to estimate statewide population trends during and after the bounty period, and to elucidate how historical and current management policies have affected the statewide mountain lion population.

METHODS

Study area

We collected mortality data from California county courthouses; California Departments of Fish and Wildlife (Department), and Transportation (Caltrans); California Highway Patrol (CHP); and United States Department of Agriculture, Wildlife Services (USDA Wildlife Services). County courthouse and Department records supplied data on mountain lions removed during the bounty period, and included data from all counties except Imperial, Sacramento, San Francisco, Solano, and Sutter, from which no bounty records were available. CHP and Caltrans supplied statewide data on mountain lions killed due to vehicle strikes. Department and USDA Wildlife Services supplied statewide data on mountain lions removed due to depredation.

Data collection

We collected statewide data on mountain lions purposefully killed due to bounties, hunting, and depredations from 1906-2018 (McLean 1954; Fitzhugh and Gorenzel 1986; Mansfield and Weaver 1989), and on mountain lions incidentally killed due to vehicle strikes from 2009-2018 (Table 2). There were no data available on purposeful removals between the conclusion of the bounty system in 1963 and establishment of a hunting season in 1970, nor were accurate data available on sex and age of individuals for any animals (bountied, hunted, depredated, vehicle-killed) but the most recent depredations (2015-2017).

For all these data, we made a number of assumptions described here, which may variously have contributed to over- or under-estimates of the number of lions removed from the population. Throughout the time period of interest, mountain lions undoubtedly died due to additional human-related incidents (e.g., poaching). Because of a scarcity of accurate data on such incidents, we assumed that our bounty, hunting, depredation, and vehicle strike data represented the majority of human-caused mountain lion mortalities. This assumption may underestimate the number of individuals removed. In addition, bounty systems encourage

Table 2. Data on mountain lions (*Puma concolor*) purposefully (i.e., bounty, hunting, and depredation) and incidentally (i.e., vehicle strike) removed through time in California. Incidental removals 2015–2018 are raw data while incidental removals prior to that are derived based on the assumption of decreasing traffic volume backward through time.

Status	Year	# Purposefully Removed	# Incidentally Removed
Depredation	2018	100	56
	2017	87	70
	2016	120	47
	2015	101	49
	2014	90	52
	2013	68	51
	2012	77	61
	2011	105	55
	2010	108	50
	2009	103	57
	2008	123	61
	2007	137	51
	2006	128	56
	2005	125	59
	2004	133	56
	2003	111	57
	2002	124	51
	2001	121	57
	2000	151	56
	1999	120	48
	1998	123	52
	1997	104	47
	1996	110	48
	1995	117	52
	1994	124	45
	1993	76	46
	1992	83	52
	1991	74	47
	1990	76	51
	1989	76	45
	1988	61	44
	1987	50	48
	1986	45	40
	1985	58	47
	1984	37	44

Table 2 continued

Status	Year	# Purposefully Removed	# Incidentally Removed
	1983	26	42
	1982	18	48
	1981	12	46
	1980	12	48
	1979	21	40
	1978	8	36
	1977	7	36
	1976	6	44
	1975	2	44
	1974	3	37
	1973	4	40
	1972	6	42
Hunting	1971	35	41
	1970	83	36
Bounty	1963	99	33
	1962	115	38
	1961	144	36
	1960	127	39
	1959	112	37
	1958	136	35
	1957	157	39
	1956	165	33
	1955	188	34
	1954	155	36
	1953	188	35
	1952	167	31
	1951	140	33
	1950	202	35
	1949	228	29
	1948	188	35
	1947	199	35
	1946	213	34
	1945	152	34
	1944	177	29
	1943	155	29
	1942	159	30

Table 2 continued

Status	Year	# Purposefully Removed	# Incidentally Removed
	1941	236	29
	1940	224	28
	1939	291	28
	1938	252	27
	1937	221	29
	1936	185	31
	1935	249	27
	1934	225	32
	1933	268	23
	1932	313	27
	1931	292	26
	1930	293	24
	1929	297	23
	1928	339	26
	1927	247	24
	1926	253	26
	1925	240	27
	1924	279	28
	1923	230	23
	1922	302	21
	1921	252	25
	1920	238	22
	1919	263	22
	1918	192	23
	1917	171	24
	1916	181	25
	1915	170	23
	1914	196	23
	1913	232	22
	1912	253	21
	1911	270	21
	1910	322	20
	1909	360	22
	1908	443	20
	1907	117	23
	1906	118	23

inflated reporting (i.e., submitting animals for bounty in California while they were actually taken in a neighboring state), so bounty data may overestimate the number of individuals removed (Fitzhugh and Gorenzel 1986). However, it should be noted that the majority (>50%) of the bounty records submitted were by agency employees. Further, none of the border counties had high numbers of bounties paid relative to interior counties. As such, we assumed that these records are accurately reported and represent animals taken within California. There is also a likelihood that vehicle strike data are underreported. We assumed that the proportion of missing records is similar from year-to-year and does not account for a significant number of records in a given year. To account for potentially missing depredation reports, we compared Department records and USDA Wildlife Services records for 1998-2018. Discrepancies between the two sets of records were generally within ±10 individuals statewide, and occurred for a variety of reasons (e.g., lost paperwork, position vacancies, etc.). Where discrepancies existed between the two datasets, we used the higher of the two reported numbers to represent number of animals removed via depredation in the given year.

Population simulations

Using a back-calculation method to estimate the historical population of mountain lions in California, we began with a discrete growth equation, modified to include rates of human-caused mortality:

$$N_{t+1} = N_t\lambda_t - d_t - N_t\lambda_t m_t, \qquad (1)$$

where λ is the annual intrinsic growth rate, *d* is the combined number of individuals taken purposefully and incidentally per year, and *m* is the coefficient of additional mortality (e.g., intraspecific strife, poaching, and disease) per year (Mykra and Pohja-Mykra 2015). Estimating the trend of a population from one year to the next requires an estimate of potential annual growth and mortality. Based on results reported by Beausoleil et al. (2013), we established the mean intrinsic growth (λ) at 1.14 (14% annual increase) with a standard deviation of 0.03 to allow for annual stochasticity (Robinson et al. 2008; Cooley et al. 2009; Robinson and DeSimone 2011; Beausoleil et al. 2013). We estimated the number of mountain lions killed annually by vehicle strike from 2000-2014 (prior to available data) by using the mean number killed annually by vehicle strike from 2015-2018, with a standard deviation of ±10% to account for annual stochasticity. For every decade prior to this (e.g., 1990-1999, 1980-1989), we decreased the mean by 10% from the next most recent timespan (i.e., mean for 1990-1999 was 10% less than mean for 2000-2014), but held standard deviation at ±10%. We decreased the mean from current to past to simulate decreased vehicle traffic in the past, and thus decreasing likelihood of vehicle strike. We established the coefficient of additional mortality per year (*m*) at a mean of 0.10 with a standard deviation of 0.03 to allow for annual stochasticity in additional mortality factors (Robinson et al. 2008; Cooley et al. 2009; Robinson and DeSimone 2011; Beausoleil et al. 2013). For the years in which there were no take data (1964-1969), *d* is the average removal rate during the two hunting seasons (59 mountain lions/year), and we allowed annual population parameters to vary stochastically as with all other iterations. Thus, for each year that we simulated population abundance, we randomly drew values for λ and *m* from a normal distribution with a mean of 0.14 and 0.10, respectively, and a standard deviation of 0.03. To assess impacts of missing data on population trends, we estimated sensitivity of population simulations to changes in mean values of *λ* and *m* (see Supplementary Material).

For estimating population sizes via back-calculation, we transformed Equation 1:

$$N_{t-1} = (N_t + d_t)/[(1 - m_t)\lambda_t]. \quad (2)$$

We considered N_{t-1} to be the population size at the end of the year after accounting for annual growth, additional mortality, and individuals taken that year. We iterated the backwards equation annually starting with 2018 and ending with 1906. We randomly drew the initial population abundance at 2018 from a uniform distribution ranging from 1,000-5,000 individuals. We selected the upper limit of the uniform distribution from potential mountain lion densities previously identified within high, medium, and low suitability habitats across California (Torres et al. 1996; Table 3). These upper threshold values are within reported confidence intervals derived in other areas of the western United States (Cougar Management Guidelines Working Group 2005). We selected the lower limit of the uniform distribution from recently published results on effective population size (N_e) in regional mountain lion populations (Gustafson et al. 2018) and ratios between N_e/N (Frankham 1995). Together, the upper and lower thresholds likely contain the actual statewide abundance of mountain lions in California, particularly considering the estimated average adult mountain lion density across the western United States (1.6/100 km^2; Quigley and Hornocker 2010; Beausoleil et al. 2013), and the amount of mountain lion habitat in California (186,000 km^2; Torres et al. 1996). We also assessed sensitivity of population simulations to changes in starting values (see Supplementary Material).

After deriving initial abundance, we iterated back-calculations according to Equation 2 for 112 years (timespan from 1906-2018) with 1,000 replications, and values of λ and m varying stochastically according to mean and standard deviation values detailed above. We also generated minimum and maximum population trajectories with our simulations to illustrate the extreme limits within which California mountain lion populations may grow or decline. For the minimum population trajectory, we kept the annual growth rate constant at one standard deviation above the mean λ for a value of 1.17, and the additional annual mortality rate constant at one standard deviation below the mean of m for a value of 0.07. For the maximum population trajectory, we kept the annual growth rate constant at one standard deviation below the mean of λ for a value of 1.11, and the additional annual mortality rate constant at one standard deviation above the mean of m for a value of 0.13.

Table 3. Demonstration of systematically adjusted density values for each habitat suitability class and derived range of initial mountain lion population values for back calculation of mountain lion (*Puma concolor*) population projections.

Suitability	Habitat Suitability Score[a]	Size	Mountain Lion Density (animals/100km^2)[b]
High	>0.60	170,486 km^2	2.20
Medium	0.41–0.60	63,085 km^2	1.60
Low	0.20–0.40	24,641 km^2	1.00
None	<0.20	165,759 km^2	0.00

[a]Habitat suitability thresholds were on a scale of 0–1

[b]Densities of mountain lions (animals/100km^2) for each habitat suitability.

Sensitivity testing

Because each replicate began with a randomly drawn value, we estimated the sensitivity of population trend estimates to variation in input values. We thus derived the upper and lower 10% population values for each decade (beginning in 1910 and concluding in 2010) for all 1,000 replicates. Next, we estimated slopes of values between decades (e.g., 1910 to 1920) for those upper and lower 10% values, and tested for significant differences between them. For example, we estimated the slope between the upper 10% values for 1910 and 1920 to represent population trend between the two periods. We did the same for the lower 10% values in the same timeframe, and then statistically compared the two slopes using a Student's t-test (Mykra and Pohja-Mykra 2015). We elected to use conservatively high and low initial values, to maximize the possibility that the actual mountain lion population would be represented within these estimates. All non-significant ($\alpha > 0.05$) p-values thus provided increased confidence in the given range for mountain lion abundance for the given time period. We used Program R, version 3.1.2 (R Core Team 2014) for all statistical analyses.

Hypothesis testing

To test our two hypotheses, we determined the proportion of years among all simulations in which removal was above or below 14% of N_t. Removals from the simulated populations above this level would lead to a decline that presumably corresponds with a removal threshold for mountain lions in California above which populations would have declined (Cougar Management Guidelines Working Group 2005, Beausoleil et al. 2013). Removals from the simulated populations below 14% would lead to an increase that presumably corresponds with a removal threshold for mountain lions in California below which populations would have increased.

Results

Results of 1,000 replicates of back-calculations on mountain lion removal data consistently suggest a steady decline occurred in mountain lion populations from 1906 to the mid-1960s, followed by an increase until the mid-1990s, after which the population appears to have stabilized until about 2000. However, after 2000, our results diverged (Figure 1). Replicates with starting values in the low 1,000s exhibited a second population decline occurring in the early 2000s that continues until present. Replicates with starting values ranging from approximately 1,500 to 5,000 exhibited a slowing or stabilizing population growth rate from the late 1990s to mid-2000s, and a stable or increasing population growth rate, with population values comparable to the input values.

We found no significant differences between the slopes of the upper and lower 10-year population trends (the sensitivity analysis) from 1910 to 1980 (Table 4). However, after 1980 we detected significant differences in those slopes in the simulated data. This divergence began several decades after the conclusion of the bounty period, and was likely a result of the large range in starting values which itself was due to uncertainty about the current status of the mountain lion population across California. The closer the date a given annual population simulation was to the initial starting value, the greater influence that initial starting value had on the associated numeric value of that simulation. Thus, all simulations

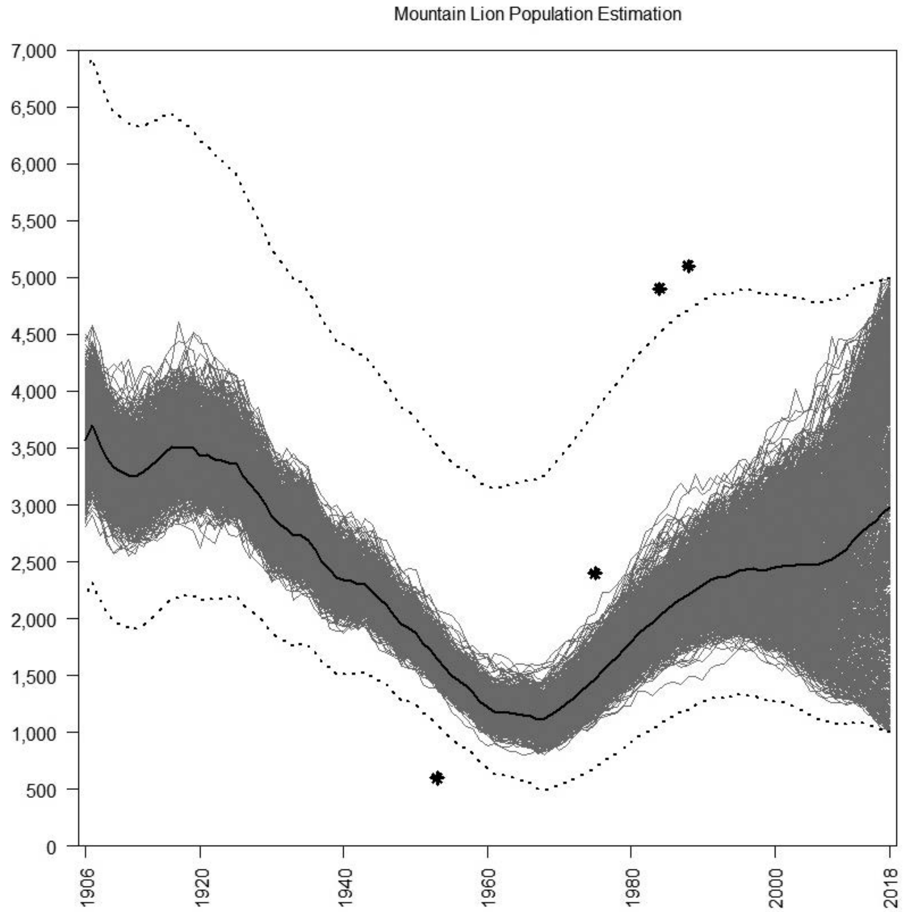

Figure 1. Mountain lion (*Puma concolor*) population simulation results for California from 1906-2018. Simulation results were yielded by running 1,000 iterations wherein a random number between 1,000-5,000 was selected as a starting population estimate. Back calculation of yearly population size to 1906 was then done using mountain lion demographic estimates derived from literature searches and mountain lion removal data from California. Previous mountain lion population abundance estimates reported by California Department of Fish and Game are represented by asterisks (*) symbols. Individual simulations are represented by gray lines. The mean for all simulations is represented by the bold black line. The maximum and minimum population simulations are represented by the dotted black lines. The upper dotted line was created by holding annual population growth constant at 1.17 (one standard deviation above the mean of 1.14) and additional annual mortality constant at 0.07 (one standard deviation below the mean of 0.10). The lower dotted line was created by holding annual population growth constant at 1.11 (one standard deviation below the mean of 1.14) and additional annual mortality constant at 0.13 (one standard deviation above the mean of 0.10).

Table 4. Statistical comparisons of slopes of simulated population trends over 10-year periods for the lower and upper 10% starting population values, respectively, using a Student's t-test. The first mean lower 10% value represents the mean of the lowest 10% of the simulated population estimates for the first year in the comparison. For example, the value 2,898 represents the mean value of the lower 10% of simulated population estimates for 1910, while the value 3,094 represents the mean value of the lower 10% of simulated population estimates for 1920. The same associations apply for the upper 10% column.

Years compared	Mean lower 10%	Mean upper 10%	t-score[a]	p-value
1910 & 1920	2,898; 3,094	3,816; 3,996	-0.34	0.74
1920 & 1930	3,094; 2,749	3,996; 3,527	-1.69	0.09
1930 & 1940	2,749; 2,139	3,527; 2,749	1.48	0.14
1940 & 1950	2,139; 1,729	2,749; 2,210	1.64	0.10
1950 & 1960	1,729; 1,177	2,210; 1,549	1.11	0.27
1960 & 1970	1,177; 927	1,549; 1,364	-1.68	0.09
1970 & 1980	927; 1,389	1,364; 1,984	-176	0.08
1980 & 1990	1,389; 1,840	1,984; 2,676	-2.48	0.01
1990 & 2000	1,840; 1,897	2,676; 3,103	-6.15	<0.01
2000 & 2010	1,897; 1,524	3,103; 3,685	-10.75	<0.01

[a]Degrees of Freedom = 3,996

support that the statewide mountain lion population experienced a decline during the bounty period and a subsequent increase (Table 4) after the bounty was ended.

DISCUSSION

The type of modeling we report here is not inherently tied to mountain lion populations, nor are such analyses new (Elton and Nicholson 1942; Jedrzejewski et al. 1996; Kojola 2005; Mykra and Pohja-Mykra 2015). This simple approach to using purposeful and incidental mortality data to infer historical population trends is an important tool for managers who lack adequate population information. However, the approach does have limitations, and its results cannot be assumed to represent precise population figures. In addition to the assumptions described previously, the data and our population modeling approach present limitations which preclude such precision. Neither the size and ecological diversity of California, nor the magnitude of anthropogenic changes to habitat that have occurred therein during the period of interest (Torres et al. 1996) are accounted for in our results. For example, although we did adjust for decreasing vehicle density going back in time, our estimates were limited by lack of accurate data. Nor did our estimates account for changes in road densities and other developments that may have affected lion densities and removal rates. Further, our model did not account for density dependent factors, including prey abundance, that may have affected our results. Our model treated all mountain lion removals as additive, which was likely not the case with the actual removals, at least not for all lion subpopulations (Lambert et al. 2006; Robinson et al. 2008; Cooley et al. 2009). Consequently, the actual rates of decline and subsequent increase were likely somewhat different than those we detected with our model. We suspect that density dependence was likely marginally important under intense removal during the bounty period but became more so as carrying capacity changed due to human-caused habitat conversion (Cougar Management Guidelines Working Group 2005). Finally, our model did not account for the disproportionate impact that mortalities of different sex and age classes have on population dynamics. However, detecting these fine-scale population effects were beyond the scope of this study, and despite the limitations discussed herein, our model provides important insight into the overall effects of historical policies and laws on the statewide mountain lion population in California.

To our knowledge, no population estimates were conducted on mountain lions in California during most of the bounty period. The first known estimate by McLean (1954) of 600 mountain lions in California was made 10 years prior to the end of the bounty period. The next estimate of approximately 2,400 was published nearly 10 years after the bounty period ended (Sitton et al. 1976). We were unable to determine how these two estimates were derived. Subsequent researchers reported the number of mountain lions in California at 4,100 - 5,700 individuals (California Department of Fish and Game 1984), in which Department staff averaged adult densities from various studies across suitable mountain lion habitat statewide. The minimum population estimate (5,100) reported in Mansfield and Weaver (1989) did not distinguish between high, medium, and low habitat suitability, and thus identified almost 25% more highly suitable habitat for mountain lions than Torres et al. (1996), and used a density estimate 1.8 times greater than our highest estimate (Table 3). Given the differences in how these various estimates were derived, we were unable to use our findings to support or dispute any of these previous estimates.

A simple calculation of average adult mountain lion density (1.6/100 km^2; Quigley and Hornocker 2010; Beausoleil et al. 2013) in the western United States, and a recent estimate of mountain lion habitat in California (165,350-170,085 km^2; Dellinger et al. in press) suggests that the statewide mountain lion population in California occurs within the 1,500-5,000 range. Recent work estimating the effective population size (that portion of the total population likely to contribute to the next generation – essentially the breeding individuals in a population) of mountain lions in California is approximately 400 (Gustafson et al. 2018) also suggests that California's statewide mountain lion population is most likely in the 1,500-5,000 range (Frankham 1995). However, none of the population estimates discussed here are based on systematic assessments of mountain lions. In the absence of such robust data, we present our simulations based on the data available to us.

The general agreement among the results of our simulations with respect to mountain lion population trends during the bounty period regardless of input value (Figure 1), and low variation in trend slopes (see Supplementary Material), suggests that our model is a reasonable estimation of mountain lion population trends for that period. Some researchers have suggested that the bounty had little to no impact on the statewide mountain lion population (Fitzhugh and Gorenzel 1986), likely because previous research suggested it could sustain 25-30% removal rates. However, our analyses suggest that removal rates in many years during the bounty period regularly exceeded the removal threshold of 14% from our simulated populations (Figure 2). A plot of the take data for which removals exceeded the estimated removal threshold of 14% suggests that during the bounty period the number of mountain lions taken exceeded the population's ability to replace itself (Figure 2).

Our simulations also suggest that mountain lion populations increased following the bounty period (Figure 1), and that removal was below the replacement threshold of 14%

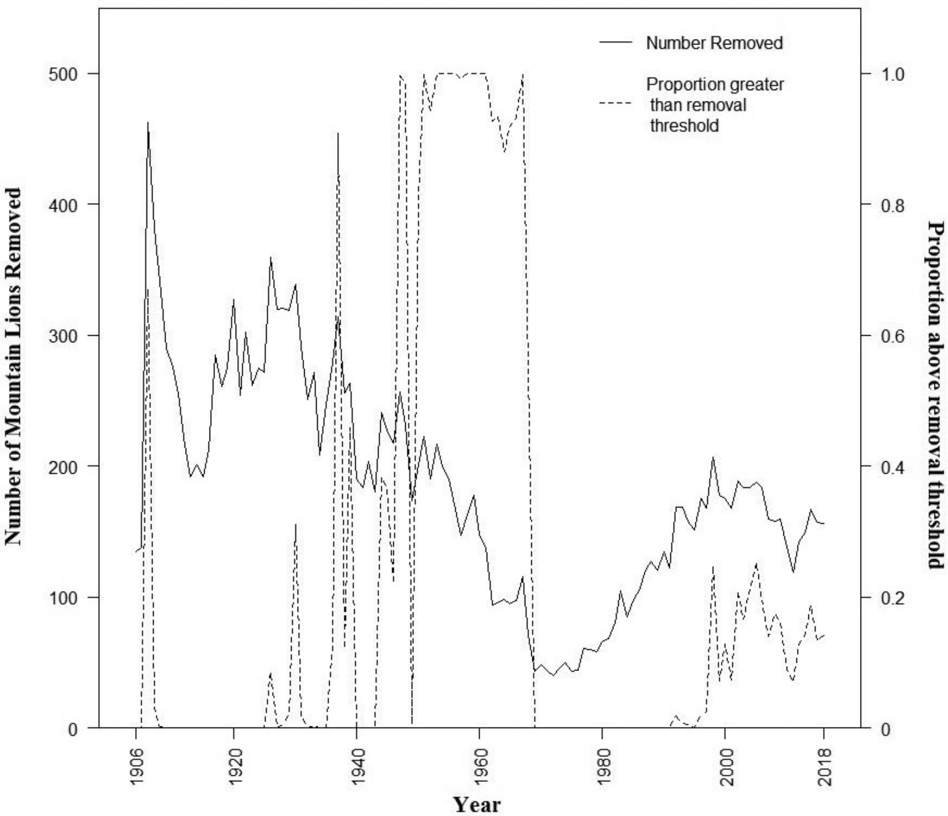

Figure 2. Mountain lion (*Puma concolor*) removal in California from 1906-2018 in relation to population simulation removal thresholds. Removal thresholds were determined from literature searches and set at 0.14 or 14% of the population. Likelihood of whether number of mountain lions removed in a given year (solid line) surpassed the removal threshold of 14% of the population was done by assessing proportion of all 1,000 simulations where removal > 0.14 x Nt (dotted line). The greater the proportion of instances where actual removal was greater than simulations for a given year, the greater the support for mountain lion populations having decreased during that given year (e.g., 1950-1970 in the figure).

(Figure 2), allowing the population to recover. Though our trend estimates began to diverge in the 1980s, the upward trend remained consistent until the 1990s (Table 4), after which our results were inconsistent, again likely due to the range in initial starting values. Further support for a rapid increase in the mountain lion population in the few decades following the end of the bounty period was an increase in distribution and number of mountain lions taken via depredation permit in California over the same time period (Torres et al. 1996). For example, mountain lions may have been extirpated from or severely reduced in the Santa Cruz Mountains based on the fact that only five animals were bountied in the Santa

Cruz Mountains, with the last one taken in 1923 (McLean 1954). Then it appears mountain lions subsequently recolonized the area following the bounty period based on the fact that there have been ≥12 mountain lion depredation events per year in the Santa Cruz Mountains in the last 10 years (CDFW 2019). This example demonstrates the ability of mountain lion populations to recover quickly following intense removal (Cougar Management Guidelines Working Group 2005; Quigley and Hornocker 2010). Release from incentivized and widespread intensive removal likely decreased overall anthropogenic mortality of mountain lions, increased their survival rates, and allowed the population to grow. This increase in number of mountain lions taken via depredation permit could have arisen in part due to increased human density, land-use changes, and an increase in development; however, increased human-carnivore conflict has been shown to increase with increasing carnivore population size (Torres et al. 1996; Thompson 2009; Vickers et al. 2015; Poudyal et al. 2016; Teichman et al. 2016). Further, Torres et al. (1996) demonstrated that most mountain lion depredations in California from 1972-1995 were not in counties with high human densities or development. This suggests that increases in mountain lion depredations could be the result of an overall increase in mountain lion populations. Additional research into how local mountain lion abundance relates to local depredation incidents and human density and development is needed to tease apart how these factors interact in California.

A logical explanation of our results is that California's mountain lion population was unable to withstand the high rates of removal under the bounty, causing their numbers to decline significantly from the early 1900s until well into the 1960s; after which they were released into an overabundant prey base, allowing their numbers to increase rapidly into the 1990s. During the 1960s, as the bounty on mountain lions ended, deer populations in California had peaked (Longhurst et al. 1976). During the decades following the 1960s, deer were declining due to a number of factors (Chapel and Rempel 1981; Neal et al. 1987; Loft and Bleich 2014), while the mountain lion population initially increased rapidly, and eventually came into equilibrium with its much-declined prey base after 2000.

We attribute the variability in our results for the most recent period (e.g., 2000-2018) to the broad range of input values (Tables 3, 4). Efforts to effectively assess mountain lion populations are lacking (Sitton et al. 1976; Weaver 1982; CDFG 1984; Fitzhugh and Gorenzel 1986; Mansfield and Weaver 1989), and that lack of effort is especially notable since the 1970s. Wildlife policies and laws are most effective when based on scientifically rigorous data. Given the diversity of stakeholder interests and agency issues related to managing and conserving mountain lions in California (Bruskotter and Shelby 2010; Davenport et al. 2010), our results highlight the need to remedy the knowledge deficit by significantly increasing our assessment efforts. This would give the Department the information they need to accurately assess the implications of the specially-protected status of mountain lions in California.

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Author Contributions:

Conceived and designed the study – JD & ST
Collected the data – ST
Performed the analyses – JD
Authored the MS – JD & ST
Critical revisions – JD

LITERATURE CITED

Beausoleil, R. A., G. M. Koehler, B. T. Maletzke, B. N. Kertson, and R. B. Wielgus. 2013. Research to regulation: cougar social behavior as a guide for management. Wildlife Society Bulletin 37:680–688.

Bruskotter, J. T., and L. B. Shelby. 2010. Human dimensions of large carnivore conservation and management: Introduction to the special issue. Human Dimensions of Wildlife 15:311–314.

California Department of Fish and Game (CDFG). 1984. Computer simulation model for mountain lions. California Department of Fish and Game, Sacramento, CA, USA.

California Department of Fish and Wildlife (CDFW). 2019. Table of mountain lion depredation permits issued by CDFW and number of mountain lions reported taken by permittees in California by county (2001–2018). Available from: http://nrm.dfg.ca.gov/ FileHandler.ashx?DocumentID=171192&inline

Chapel, M., and R. Rempel. 1981. Management plan for the North Kings deer herd. U.S. Forest Service, Fresno, CA, USA.

Cooley, H. S., R. B. Wielgus, G. M. Koehler, H. S. Robinson, and B. T. Maletzke. 2009. Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90:2913–2921.

Cougar Management Guidelines Working Group. 2005. Cougar management guidelines. Opal Creek Press, Salem, OR, USA.

Davenport, M. A., C. K. Nielsen, and J. C. Mangun. 2010. Attitudes toward mountain lion management in the Midwest: implications for a potentially recolonizing large predator. Human Dimensions of Wildlife 15:373–388.

Dellinger, J. A., B. Cristescu, J. Ewanyk, D. J. Gammons, D. Garcelon, P. Johnston, Q. Martins, C. Thompson, T. W. Vickers, C. C. Wilmers, H. U. Wittmer, and S. G. Torres. *in press.* Using mountain lion habitat selection in management. Journal of Wildlife Management.

Elton, C., and M. Nicholson. 1942. The ten-year cycle in numbers of the lynx in Canada. The Journal of Animal Ecology 11:215–244.

Fitzhugh, E. L., and W. P. Gorenzel. 1986. The biological status of the California mountain lion. Vertebrate Pest Conference 12:336–346.

Frankham, R. 1995. Effective population size/adult population size ratios in wildlife: a review. Genetic Research 66:95–107.

Gustafson, K. D., R. B. Gagne, T. W. Vickers, S. P. Riley, C. C. Wilmers, V. C. Bleich, B. M. Pierce, M. Kenyon, T. L. Drazenovich, J.A. Sikich, and W. M. Boyce. 2019. Genetic source-sink dynamics among naturally structured and anthropogenically fragmented puma populations. Conservation Genetics 20: 215–227.

Jedrzejewski, W., B. Jedrzejewska, H. Okarma, K. Schmidt, A. N. Bunevich, and L. Milkowski. 1996. Population dynamics (1869–1994), demography, and home ranges of the lynx in Bialowieza Primeval Forest (Poland and Belarus). Ecography 19:122–138.

Kojola, I. 2005. The biology of the wolf and the viability of the wolf population. Pages 8–5 in Management Plan for the Wolf Population in Finland. Ministry of Agriculture and Forestry, Helsinki, Finland.

Lambert, C. M. S., R. B. Wielgus, H. S. Robinson, D. D. Katnik, H. S. Cruickshank, R. Clarke, and J. Almack. 2006. Cougar population dynamics and viability in the Pacific Northwest. Journal of Wildlife Management 70:246–254.

Loft, E. R., and V. C. Bleich. 2014. History of the conservation of critical deer ranges in California: concepts and terminology. California Fish and Game 100:451–472.

Longhurst, W. M., E. O. Garton, N. F. Heady, and G. E. Connolly. 1976. The California deer decline and possibilities for restoration. Transactions of the Western Section of the Wildlife Society 16:74–101.

Mansfield, T., and R. Weaver. 1989. The status of mountain lions in California. Transactions of the Western Section of the Wildlife Society 25:72–76.

McLean, D. D. 1954. Mountain lions in California. California Fish and Game 40:147–166.

Mykra, S., and M. Pohja-Mykra. 2015. Back-calculation of large carnivore populations in Finland in 1865–1915. Annales Zoologici Fennici 52:285–300.

Neal, D. L., G. N. Stegar, and R. C. Bertram. 1987. Mountain lions: preliminary findings on home-range use and density in the central Sierra Nevada. Pacific Southwest Forest and Range Experimental Station, Research Note PSW-392, CA, USA.

Nowak. R. M. 1974. The cougar in the United States and Canada. United States Fish and Wildlife Service, Office of Endangered Species, Washington D.C., USA.

Poudyal, N., N. Baral, and S. T. Asah. 2016. Wolf lethal control and livestock depredations: counter-evidence from respecified models. PLOS ONE 11:e0148743.

Quigley, H., and M. Hornocker. 2010. Cougar population dynamics. Pages 59–75 in M.G. Hornockerand, and S. Negri, editors. Cougar ecology and conservation. University of Chicago Press, Chicago, IL, USA.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: https://www.R-project.org

Robinson, H. S., and R. M. DeSimone. 2011. The Garnet Range mountain lion study: characteristics of a hunted population in West-central Montana. Final report, Montana Department of Fish, Wildlife, and Parks, Wildlife Bureau, Helena, MT, USA.

Robinson, H. S., R. B. Wielgus, H. S. Cooley, and S. W. Cooley. 2008. Sink populations in carnivore management: cougar demography and immigration in a hunted population. Ecological Applications 18:1028–1037.

Sitton, L. W., S. Wallen, R. A. Weaver, and W. G. MacGregor. 1976. California mountain lion study. California Department of Fish and Game, Sacramento, CA, USA.

Teichman, K. J., B. Critescu, and C. T. Darimont. 2016. Hunting as a management tool? Cougar-human conflict is positively related to trophy hunting. BMC Ecology 16:44.

Thompson, D. J. 2009. Population demographics of cougars in the black hills: survival, dispersal, morphometry, genetic structure, and associated interactions with density dependence. Dissertation. South Dakota State University, Brookings, SD, USA.

Torres, S. G., T. M. Mansfield, J. E. Foley, T. Lupo, and A. Brinkhaus. 1996. Mountain lion and human activity in California: testing speculations. Wildlife Society Bulletin 24:451–460.

Vickers, T. W., J. N. Sanchez, C. K. Johnson, S. A. Morrison, R. Botta, T. Smith, B. S. Cohen, P. R. Huber, H. B. Ernest, and W. M. Boyce. 2015. Survival and mortality of pumas (*Puma concolor*) in a fragmented, urbanizing landscape. PLOS ONE 9:e0131490.

Walgamuth, D. 2017. California Deer Summer 2017: deer first. California Deer Association. Sacramento, CA, USA.

Walter, R. 2015. Cats in a cage. Sierra: the national magazine of the Sierra Club. Sierra Club, Oakland, CA, USA.

Weaver, R. A. 1982. Status of the mountain lion in California with recommendations for management. California Department of Fish and Game, Sacramento, CA, USA.

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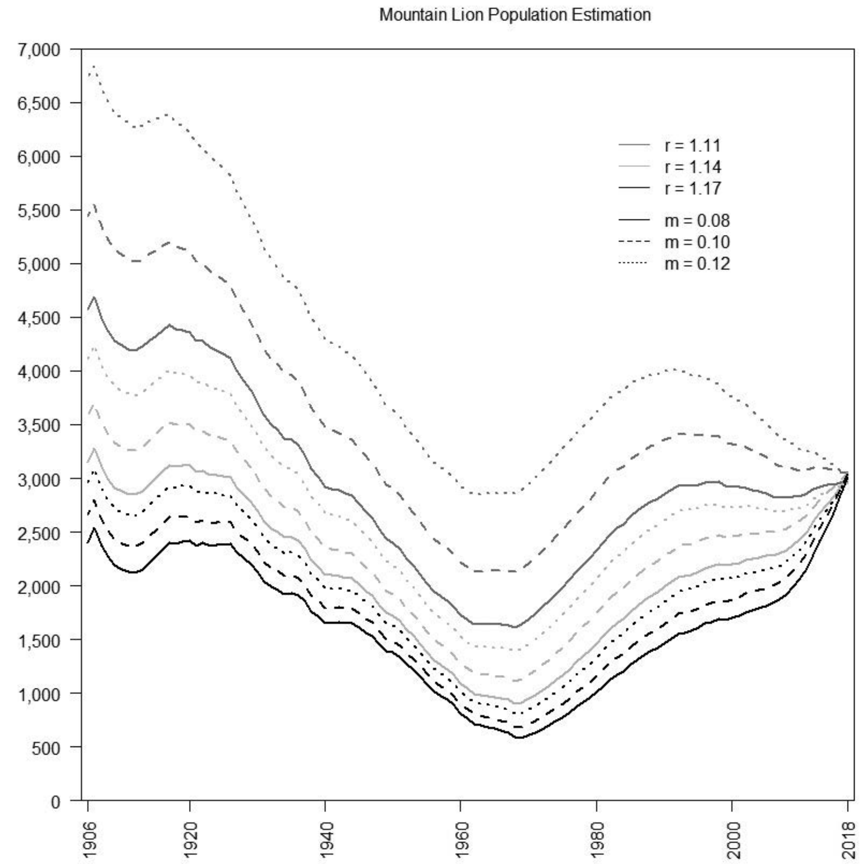
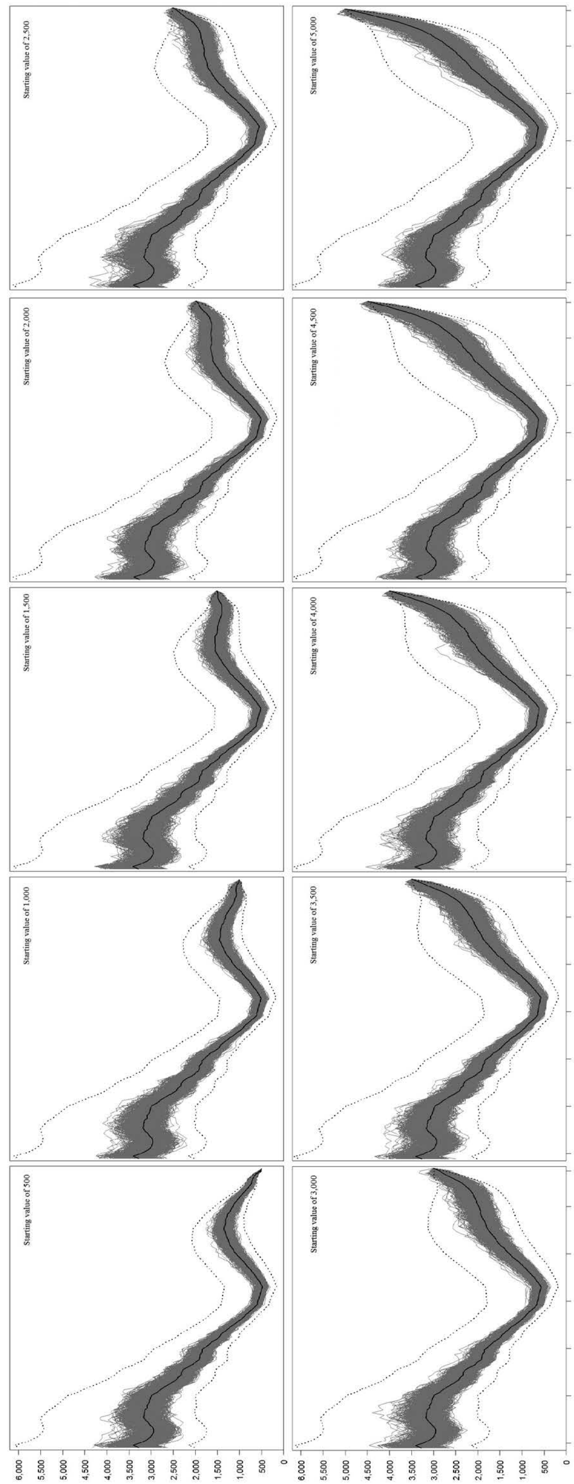
SUPPLEMENTARY MATERIAL

We estimated the sensitivity of population simulations to changes in annual population growth (λ) and additional annual mortality (m) rates. We allowed the input value to vary in a uniform distribution between 500 and 5,000 while changing the mean λ and m values. We set the mean value of λ variously at 1.11, 1.14 (used in main analyses), and 1.17, and that of m at 0.08, 0.10 (used in the main analyses), and 0.12. We conducted 1,000 simulations for each λ and m value, which resulted in 9 different groupings of 1,000 simulations. For example, one set of 1,000 simulations had a mean λ value of 1.11 and a mean m value of 0.08. Visual examination of the results demonstrated that changes to mean λ and m values, respectively, did change the results of our population simulations, but the population trends (i.e., overall decreasing during the bounty period and overall increasing post-bounty) were unchanged (Supplementary Figure 1).

We also estimated the sensitivity of our simulations to input population values. We used the parameterizations described in the manuscript but held the input value constant for 1,000 simulations. We did this for different input population values in intervals of 500. For example, we conducted 1,000 simulations wherein we held the input population value constant at 500. We then conducted another 1,000 simulations wherein we held the input population constant at 1,000. We did this at intervals of 500 up to a starting population value of 5,000. Visual examination of the results demonstrated that influence of starting value on simulated population trends decreased around the year 2000 (Supplementary Figure 2). Furthermore, starting population value did not change the overall trends of simulated populations during the bounty (i.e., decreasing mountain lion population size) or post-bounty up to the mid-1990s (i.e., increasing mountain lion population size).



Supplementary Figure 1.



Supplementary Figure 2.