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Temporal trends and drivers of mountain lion depredation in California, USA

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Abstract: Increasing human populations and expanding development across the globe necessitate continual progress in understanding and mitigating human–wildlife conflict. California, USA has the largest human population and at least half of the state is suitable mountain lion (*Puma concolor*) habitat. The juxtaposition of high human abundance within and adjacent to mountain lion habitat make California relevant for understanding human–large carnivore conflict. We compiled 7,719 confirmed incidents of mountain lions depredating domestic animals over a 48-year period (1972–2019) to examine temporal trends in mountain lion depredations as well as factors influencing annual depredation rates at the county level. Linear regressions demonstrated that the overall number of depredation events and those involving pets (e.g., dogs [*Canis lupus familiaris*] and cats [*Felis catus*]) and small hoofstock (primarily sheep [*Ovis aries*] and goats [*Capra aegagrus hircus*]) have increased significantly over time with small hoofstock comprising the majority of depredations. Poisson regression models revealed human density and agricultural productivity were negatively associated with increasing depredation rates while amount of suitable habitat and number of mountain lions removed in the previous year were positively associated with increasing depredation rates. In general, our results point to smaller-sized hoofstock operations in areas of suitable mountain lion habitat as key factors in predicting mountain lion depredations in California. Further, the permanent removal of offending individuals appears to increase the potential for conflict in the following year. Broadly speaking, improving husbandry standards for pets and small hoofstock living in areas occupied by large carnivores may be the most effective way to reduce human–predator conflict in California and elsewhere.

Key words: hoofstock, human–wildlife conflict, large carnivore, pets, *Puma concolor*

Large carnivore attacks on domestic animals are an annual and ubiquitous challenge for livestock producers and wildlife managers and can hinder conservation efforts across the globe (Treves and Karanth 2003, Woodruffe et al. 2005, Miller 2015). Given the large spatial requirements of large carnivores, increasing human population size and habitat fragmentation are likely to increase interactions with these species and exacerbate human–large carnivore conflicts (e.g., depredations and public safety threat; Michalski et al. 2006, Baruch-Mordo et al. 2008, de Souza et al. 2018). Long-term human–large carnivore conflict data can help inform local efforts to mitigate such conflict and communicate potential paths forward for similar efforts across the globe.

Mountain lion (*Puma concolor*) management in California, USA has been largely addressed within the realm of human–large carnivore conflict, making it unique amongst all the other states and provinces in western North America that manage mountain lions primarily via hunting (Torres et al. 1996). An intensive bounty period from 1907 to 1963 resulted in 12,580 individuals being purposely removed to protect domestic animals and promote wild ungulate populations (Dellinger and Torres 2020). Nine years later in 1972, temporary legislation was enacted that placed a moratorium on mountain

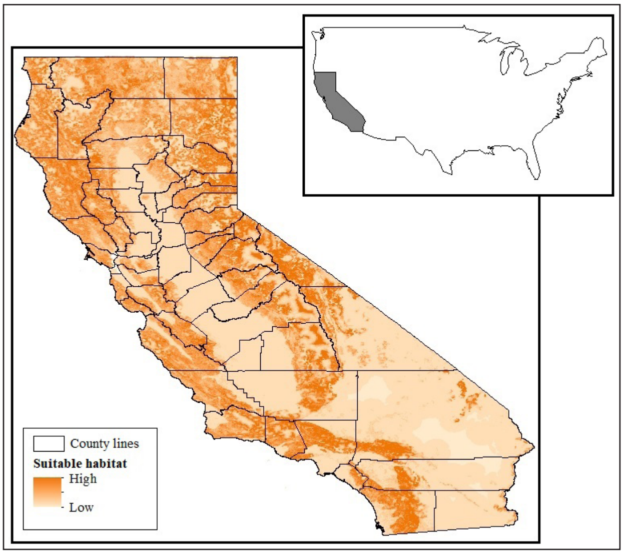

Figure 1. Location of California within the contiguous United States and a statewide display of all the counties and mountain lion (*Puma concolor*) habitat suitability across California. Habitat suitability is derived from Dellinger et al. (2020).

lion hunting. Then in 1990, California citizens voted into law a measure known as Proposition 117 (Fish and Game Code §4800–4809; Torres et al. 1996) that made mountain lions a specially protected mammal. One outcome of this rapid shift in mountain lion management was greater diligence in documenting human–mountain lion conflict. This is in part because the moratorium and subsequent special protection status meant that conflict data were the only type of annual broad-scale data that the California Department of Fish and Game (now California Department of Fish and Wildlife; CDFW) could readily collect on mountain lions from 1972 to the present. In addition, the special protection status legally mandated the CDFW to document mountain lion depredation events, which is the most common form of human–mountain lion conflict in California and the primary form of conflict focused on hereafter. This dynamic political history has resulted in California having a long-term broad-scale dataset for understanding trends in and factors influencing human–mountain lion conflict (Dellinger and Torres 2020).

Previous research has demonstrated that mountain lion depredations can occur in both rural and more developed landscapes with mountain lions depredating animals from agricultural operations and residential areas, respectively (Torres et al. 1996). Further, recent reports indicate that small hoofstock (e.g., sheep [*Ovis aries*] and goats [*Capra aegagrus hircus*]) are the most common domestic animals taken during depredation events (CDFW 2019). In all instances, offending mountain lions can be lethally removed during a 10-day period under authority of a CDFW permit issued to the property owner.

Recent research in the state of Washington, USA and in British Columbia, Canada has demonstrated that removal of mountain lions within a hunting framework does not reduce depredation events (Peebles et al. 2013, Teichman et al. 2016). In trying to build upon these previous research findings, we are using a uniquely long-term dataset on mountain lion depredations across California where hunting is not a part of the management framework. We evaluated temporal trends in mountain lion depredation as well as factors influencing mountain lion depredation rates. We hypothesized that increasing depredation rates would have a quadratic association with human density (i.e., highest depredation rates at intermediate human densities) and a positive linear association with increasing amount of suitable habitat and quality, number of hoofstock involved in agricultural operations present, and number of mountain lions removed the previous year.

Study area

We compiled existing CDFW mountain lion depredation data from 1972 to 2019 originating from an assortment of private, county, regional, state, federal, and tribal lands across the state of California (Figure 1), which encompasses an area of 423,970 km^2 with 8 recognized ecoregions (Sawyer et al. 2009). Across the state there is substantial variability in the level of human use and development (e.g., wilderness areas and locales immediately adjacent to and within large urban population centers; U.S. Census Bureau 2017). Further, the geographic extent of the dataset represented the diversity of ecoregions, which ranged from the Mojave Desert in southeastern California to temperate rainforests in the northwestern part of the state. The vari-

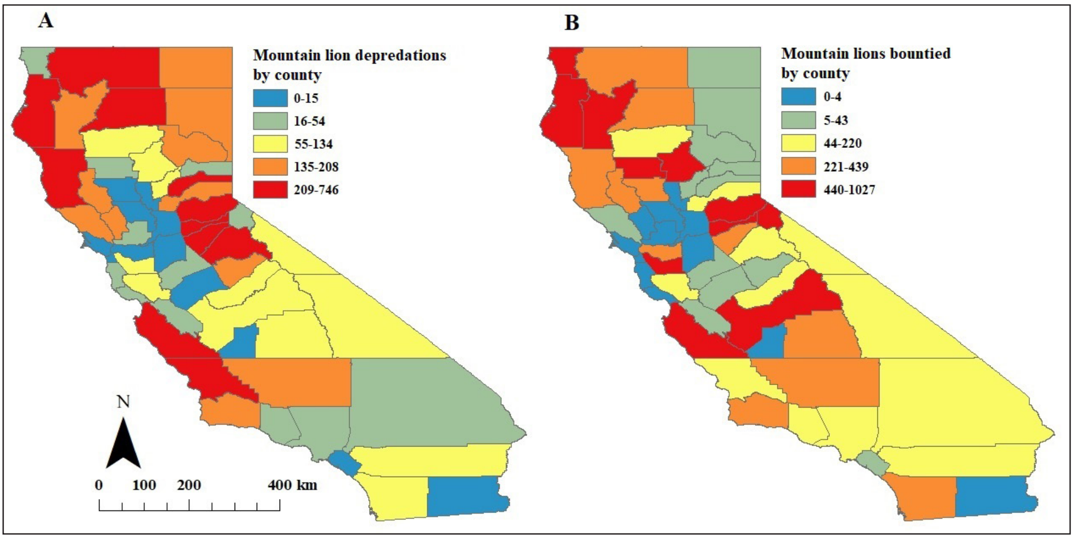

Figure 2. Spatial representation of (A) total number of confirmed mountain lion (*Puma concolor*) depredations by county in California, USA, from 1972 to 2019, and (B) total number of mountain lions bountied by county in California from 1906 to 1963.

ous ecoregions encompassed large gradients in physical attributes such as elevation (from sea level to ~4,000 m; U.S. Geological Survey 2017), seasonal precipitation (13.1–140.9 cm), and temperature (-15°C to 45°C). Seasonality varied greatly across the state. Interior areas of California experienced cooler summers and colder winters with large amounts of precipitation in the form of snow. Conversely, coastal areas experienced warm summers and cool winters with precipitation in the form of rain (Sawyer et al. 2009).

Methods

Data collection

Laws and regulations concerning mountain lion depredations in California have been constant since 1972. As such, data collection procedures for these events have been consistent. The only changes to data collection procedures for mountain lion depredations have been in relation to the level of specificity of information about a depredation event, a result of advances in technology. For example, from 1972 to 2010, the location of a depredation event was defined at the county level and reporting was done via submission of a paper form. From 2010 to 2019, detailing the location of a depredation has become more refined due to global positioning system technology and reporting was done electronically via CDFW's online Wildlife Incident Reporting system (https://apps.wildlife.ca.gov/wir).

The typical process for responding to and documenting information related to a mountain lion depredation is initiated when a property owner contacts the CDFW stating that they suspect a mountain lion has depredated 1 or more animals they own. A CDFW biologist or warden has 48 hours to respond and conduct a site visit to determine whether a mountain lion was the source of the damage. If the responding biologist or warden confirms the damage is due to a mountain lion, they collect pertinent site-specific information (e.g., species depredated and sometimes the number and type of other domestic animals present) and issue a depredation permit if requested by the property owner (Fish and Game Code §4800–4809). All depredation information is reported to the CDFW headquarters in Sacramento either via paper copy (prior to 2010) or electronic submission (2010–2019). Further, any mountain lion killed under authority of a depredation permit is documented in the depredation permit and the carcass is turned over to the CDFW and necropsied. It is important to note that a verified mountain lion depredation event did not always lead to lethal removal of a mountain lion under a depredation permit. Carcasses of killed mountain lions were sexed but due to the potential of inaccuracies in sexing individuals, we did not use this variable (Beausoleil and Warheit 2015). Thus, this on-site verification, data collection, and permitting system has helped create a standardized approach for documenting mountain lion depredation events. It is possible that during the phased transition from paper copies to electronic submissions that some depredation records were lost and that there was a subsequent underreporting of mountain lion depredations from 2006 to 2014.

For our analyses, the spatial resolution was the county in which the event occurred (Figure 2A). Further, for our analyses, domestic animals were grouped into 3 categories: pets (i.e., dogs [*Canis lupus familiaris*], cats [*Felis catus*], chickens [*Gallus gallus domesticus*], ducks [Anatidae], and turkeys [*Meleagris gallopavo*]), small hoofstock (i.e., pigs [*Sus scrofa*], goats, llamas [*Lama glama*], and sheep), and large hoofstock (i.e., cattle [*Bos taurus*] and horses [*Equus caballus*]). We grouped poultry ($n = 206$) in with more typical pets (e.g., dogs and cats; $n = 596$) due to limited number of records for these domestic animals. In addition to the on-site information collected for individual depredation events, we also collected data on human population size for each county and year (California State Association of Counties 2019), number of hoofstock (e.g., cattle, sheep, goats, etc.) in agricultural production for each county and year (California Department of Food and Agriculture 2020), amount of suitable mountain lion habitat in each county (Dellinger et al. 2020; Figure 1), total number of mountain lions bountied (i.e., proactive lethal removal reinforced via monetary incentives for each individual removed) in each county (Dellinger and Torres 2020; Figure 2B), and number of mountain lions lethally removed on depredation permits the previous year by county (Dellinger and Torres 2020). It is important to note that our estimation of number of hoofstock present annually in each county is likely an underestimation because the reports we gathered the data from likely do not contain smaller (hobby) operations. We tried to outreach pertinent groups to gather this data but did not find anything of use.

Data analysis

Individual mountain lion depredation events were used to understand temporal trends (increasing/decreasing/stable) in mountain lion depredations in California. Two linear regressions were conducted for each of the 3 types of domestic animals: one for temporal trend in overall annual number of depredations involving that category of domestic animal and another for temporal trend in proportion of overall annual number of depredations involving that category of domestic animal. Linear regressions involving annual proportions were arcsine square root transformed. We differentiated between raw annual numbers and annual proportion of depredations attributed to each type of domestic animal because the raw number of a specific category of domestic animal killed by mountain lions could increase annually, while the proportion of overall depredations consisting of that same category of domestic animal does not change. Following development of linear regressions, we then examined the R^2 value and slope of each linear regression to understand the strength and direction of the temporal trend, respectively.

We then assessed what variables were influencing mountain lion depredations in California. First, we processed the independent variables. Human population size data for each county and year were converted into humans per km² using the overall amount of land in each county. Number of domestic animals in agricultural production primarily included open range/pasture cattle and sheep. We tried to exclude feedlot animals as these animals are not likely at risk of being depredated by a mountain lion. However, the sources used to derive the data did not always differentiate between open range/pasture and feedlot animals (California Department of Food and Agriculture 2020). As with human populations, we converted number of domestic animals in agricultural production into a density estimate of domestic animals per km² (California Open Data Portal 2020). The amount of suitable mountain lion habitat in each county was used as a variable to represent the relative contribution of each county where mountain lions were likely present. The total number of mountain lions bountied in each county (from 1906 to 1963, which is the timespan of the mountain lion bounty period in California) was used as a proxy to represent the quality of mountain lion habitat in each county, whereby we assumed a high number of mountain lions bountied in a given county was likely due to long-term quality of mountain lion habitat in that county. All of these continuous variables (Table 1) were

Table 1. Predictor variables used in analyses of mountain lion (*Puma concolor*) depredation rates throughout California, USA, from 1972 to 2019. Mountain lions bountied per county was used as a proxy for habitat quality in each county.

Variable	Units	Representation	Source
Amount of suitable habitat	km^2	Scaled continuous	Dellinger et al. (2020)
Animals in agricultural production	Per km^2	Scaled continuous	California Department of Food and Agriculture (2020)
Mountain lions removed previous year	Numeric	Integer	Dellinger and Torres (2020)
Human density	Per km^2	Scaled continuous	California State Association of Counties (2019)
Mountain lions bountied per county	Numeric	Integer	Dellinger and Torres (2020)
Area of county	km^2	Natural log	California Open Data Portal (2020)

standardized by subtracting the mean from each value and dividing by the standard deviation (i.e., we placed continuous variables on the same scale) to render coefficient estimates derived from these variables easier to interpret and comparable to each other. We checked for collinearity among these variables. None of the continuous variables above had $|r| > 0.30$.

Next, individual mountain lion depredation events were totaled by year for each county to derive annual depredation rates by county. Counties without a depredation event in a given year did not have a corresponding depredation rate for that year. We used these depredation rates as the primary response variable to represent the intensity of depredations in a Poisson regression model framework. We used the scaled variables mentioned above as the independent variables. The global Poisson regression model included all continuous variables (Table 1) and a quadratic term for human density. We assessed the need for an offset in the global Poisson regression model. We set the natural log of the area of each county as the offset variable. An ANOVA comparison between a global Poisson regression model with and without an offset, respectively, revealed that the model without an offset had significantly lower residual deviance ($P < 0.001$). Thus, we used did not use an offset in our model selection process (Goedhart and ter Braak 1998). Akaike's Information Criterion corrected for small sample sizes (AIC_c) was used to determine the most parsimonious model from the global model and all possible subsets (Burnham and Anderson 2002). The most parsimonious models were those with the lowest ΔAIC_c and highest AIC_c weight (Arnold 2010). We used a log-link function to interpret coefficient estimates of the most parsimonious Poisson regression model to understand mountain lion depredation rates (Acharya et al. 2017).

We used Program R version 3.6 (R Core Team 2019) and associated package MuMIn (Barton 2019) for all statistical analyses and data management. We used ArcView GIS version 10.3.1 (ESRI, Redlands, California, USA) for visual representation of data and results. We used $P < 0.05$ to determine significance of an analysis or variable.

Results

We compiled 7,719 verified instances of mountain lion depredation events in California between 1972 and 2019 (Figure 2A) with 3,394 individuals lethally removed. Of the 7,719 confirmed mountain lion depredations 61.1% (n = 4,718) involved small hoofstock, 13.1% (n = 1,013) involved large hoofstock, and 10.4% (n = 802) involved pets, while 15.4% of reported depredation events (n = 1,186) did not have any information concerning what type of animal was killed or injured. Of small hoofstock depredated, sheep and goats accounted for 97.3% (n = 4,589). From 1972 to 2019, there was an increase (i.e., positive slope) in annual overall number of mountain lion depredations and for each type of domestic animal over time (Figure 3). However, the slope for mountain lion depredations on large hoofstock over time was

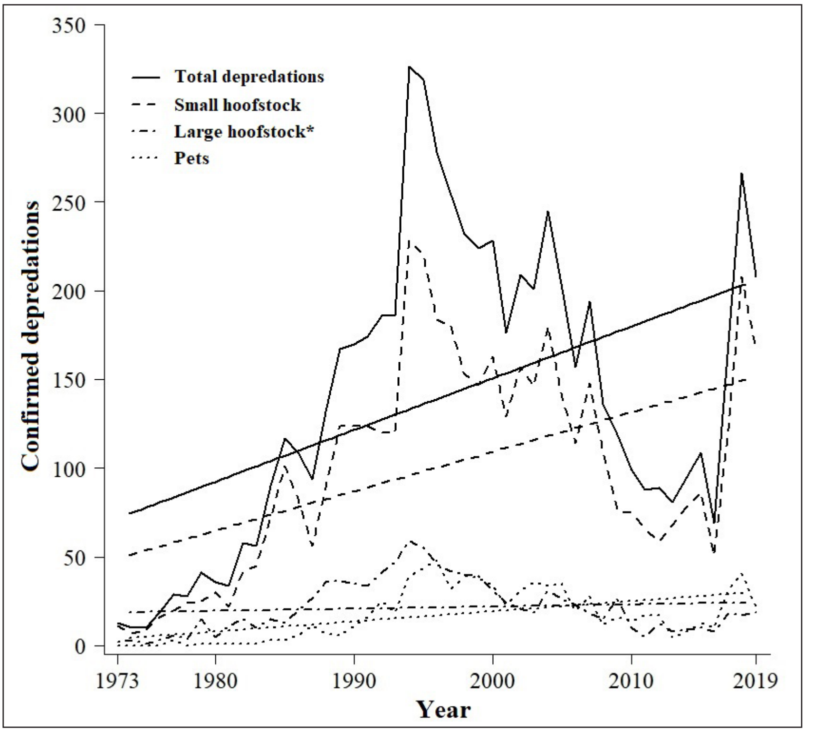

Figure 3. Number of annual confirmed mountain lion (*Puma concolor*) depredations overall and by domestic animal type overlaid with individual linear regression lines for each to understand trends in mountain lion depredations in California, USA from 1972 to 2019. The slopes for each of the 4 linear regressions was positive but the slope for large hoofstock was not significant at P = 0.05 (*). Pets included dogs (*Canis lupus familiaris*), cats (*Felis catus*), ducks (Anatidae), chickens (*Gallus gallus domesticus*), and turkeys (*Meleagris gallopavo*). Small hoofstock included goats (*Capra aegagrus hircus*), sheep (*Ovis aries*), pigs (*Sus scrofa*), and llamas (*Lama glama*). Large hoofstock included cows (*Bos taurus*) and horses (*Equus caballus*).

Table 2. Slope (m), standard error (SE), and P-values (P) for the individual linear regressions looking at annual trends in mountain lion (*Puma concolor*) depredations over time in California, USA, from 1972 to 2019. Linear regressions looked at overall trends in annual mountain lion depredations as well trends in number of annual mountain lion depredations by type of domestic animal: pets (i.e., dogs [*Canis lupus familiaris*], cats [*Felis catus*], ducks [Anatidae], chickens [*Gallus gallus domesticus*], and turkeys [*Meleagris gallopavo*]); small hoofstock (i.e., goats [*Capra aegagrus hircus*], sheep [*Ovis aries*], pigs [*Sus scrofa*], and llamas [*Lama glama*]); and large hoofstock (i.e., cows [*Bos taurus*] and horses [*Equus caballus*]). Further, linear regressions looked at trends in proportion of annual mountain lion depredations by type of domestic animal. We considered a linear regression with a positive slope with $P < 0.05$ as evidence of a significant increase in the annual number/proportion of mountain lion depredations in California, USA, from 1972 to 2019. We considered a linear regression with a negative slope with $P < 0.05$ as evidence of a significant decrease in the annual number/proportion of mountain lion depredations in California, USA, from 1972 to 2019.

Linear regression	m	SE	P
Overall annual depredations	2.915	0.825	<0.001
Annual pet depredations	0.571	0.135	<0.001
Annual small hoofstock depredations	2.223	0.566	<0.001
Annual large hoofstock depredations	0.122	0.161	0.454
Proportion depredations pets	0.008	0.001	<0.001
Proportion depredations small hoofstock	-0.001	0.001	0.578
Proportion depredations large hoofstock	-0.004	0.001	<0.001

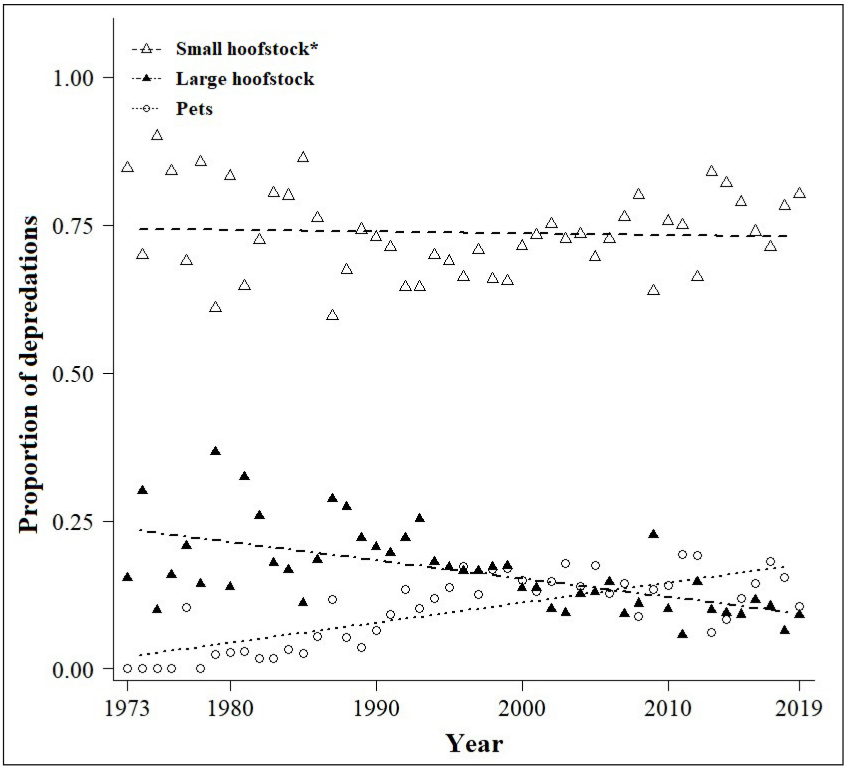

Figure 4. Proportion of annual confirmed mountain lion (*Puma concolor*) depredations involving each type of domestic animal overlaid with individual linear regression lines for each to understand trends in mountain lion depredations in California, USA from 1972 to 2019. Pets included dogs (*Canis lupus familiaris*), cats (*Felis catus*), ducks (Anatidae), chickens (*Gallus gallus domesticus*), and turkeys (*Meleagris gallopavo*). Small hoofstock included goats (*Capra aegagrus hircus*), sheep (*Ovis aries*), pigs (*Sus scrofa*), and llamas (*Lama glama*). Large hoofstock included cows (*Bos taurus*) and horses (*Equus caballus*). The slope for annual proportion of depredations involving pets was positive while the slope for large hoofstock was negative. The slope for small hoofstock was negative but was not significant at $P = 0.05$ (*).

not significant (Table 2). There was a decrease in proportion of annual overall mountain lion depredations over time involving both small and large hoofstock but only the slope for large hoofstock was significant. Conversely there was a significant increase in proportion of overall mountain lion depredation events over time involving pets (Figure 4; Table 2). These results support our first hypothesis where we predicted that mountain lion depredations would increase over time but not uniformly across types of domestic animals.

The 7,719 confirmed mountain lion depredations were used to derive 1,456 annual depredation rates by county from 1972 to 2019. Poisson modeling results and AIC_c model selection revealed 4 models with $\Delta AIC_c < 5$. The most parsimonious model was the global model, which was 1.8 times more likely to be the best model according to AIC_c weights (Table 3). Mountain lion depredation rates were positively associated with the amount of suitable mountain lion habitat within a county, number of mountain lions removed during the bounty period from a county, and year. Further there was a positive relationship between number of mountain lions lethally removed the previous year in a county and the number of mountain lion depredation events the following year. Number of domestic animals involved in agricultural production was negatively associated with mountain lion depredation rates such that larger operations suffer proportionately less depredation than smaller operations. Additionally, there was a quadratic relationship between mountain lion depredation rates and human density such that the depredation rate decreased more rapidly as human density increased compared to a simple

Table 3. Comparison of change in Akaike's Information Criterion corrected for small sample sizes (ΔAIC_c), AIC_c weights, and number of parameters (*K*) of the most parsimonious Poisson model for understanding annual mountain lion (*Puma concolor*) depredation rates at the county level throughout California, USA, from 1972 to 2019. The table below only represents models with an AIC_c weight >0.05 and ΔAIC_c <5. Covariates included number of mountain lions bountied in a county from 1906 to 1963 (BNTY), annual number of domestic animals in agricultural production by county (COM_AG), number of mountain lions removed the previous year on depredation permits by county (RM_PREV_YR), amount of suitable habitat in a county (SUIT_HAB), year (YR), natural log of the area of a county (AREA), and annual human density by county (HD). The global model was found to be the most parsimonious model (i.e., lowest ΔAIC_c and highest AIC_c weight).

Model[a]	ΔAIC_c	Weight	*K*
BNTY + COM_AG + RM_PREV_YR + SUIT_HAB + YR + AREA + HD + HD^2	0	0.44	8
BNTY + COM_AG + RM_PREV_YR + SUIT_HAB + YR + AREA + HD	1.19	0.24	7
BNTY + COM_AG + RM_PREV_YR + SUIT_HAB + YR + HD + HD^2	1.24	0.23	7
BNTY + COM_AG + RM_PREV_YR + SUIT_HAB + YR + HD	3.19	0.09	6

Table 4. The most parsimonious Poisson model for understanding annual mountain lion (*Puma concolor*) depredation rates at the county level throughout California, USA, from 1972 to 2019. Coefficient estimates (β), standard error (SE), and *P*-value are presented for each variable present in the most parsimonious Poisson model. Covariates included number of mountain lions bountied in a county from 1906 to 1963 (BNTY), annual number of domestic animals in agricultural production by county (COM_AG), number of mountain lions removed the previous year on depredation permits by county (RM_PREV_YR), amount of suitable habitat in a county (SUIT_HAB), year (YR), natural log of the area of a county (AREA), and annual human density by county (HD).

Variable	β	SE	*P*
BNTY	0.119	0.019	<0.001
COM_AG	-0.061	0.017	<0.001
RM_PREV_YR	0.086	0.005	<0.001
SUIT_HAB	0.186	0.036	<0.001
YR	0.006	0.002	<0.001
AREA	0.032	0.032	0.321
HD	-0.218	0.048	<0.001
HD^2	0.018	0.011	0.088

negative linear relationship between human density and mountain lion depredation rate. Though the global model was the most parsimonious model, the natural log for the area of the county and the quadratic term for human density were not significant (Table 4). More specifically, coefficient estimates demonstrated that mountain lion depredation rates increased 9% for every mountain lion removed on a depredation permit the previous year (Figure 5A). Mountain lion depredation rates increased 13% for every ~250 additional mountain lions that were historically reported bountied in a county (Figure 5B). Again, this metric was used as an index of long-term mountain lion habitat quality in that county. Finally, mountain lion depredation rates increased 20% for every ~1,800 km^2 of suitable mountain lion habitat present in a county (Figure 5C). These results partially support our second hypothesis where we predicted that increasing depredation rates would have a quadratic association with human density (i.e., highest depredation rates at intermediate human densities) and a positive linear

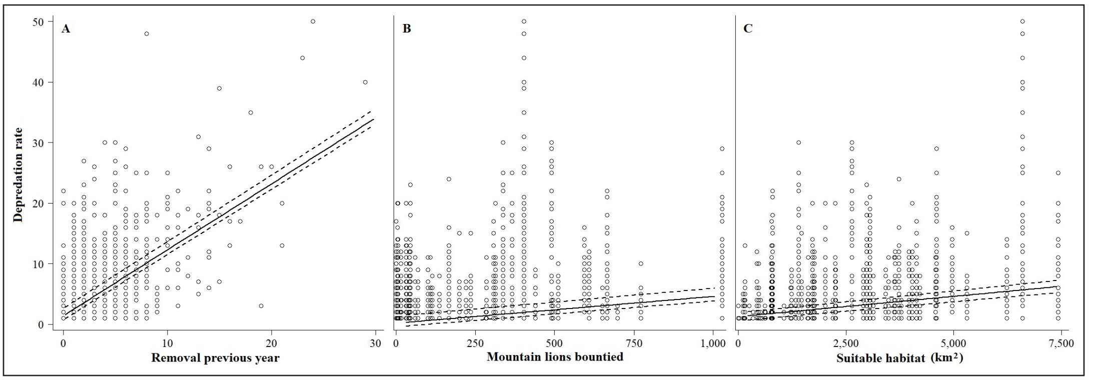

Figure 5. Predicted depredation rates (solid lines) and associated 95% confidence intervals (dashed lines) as they relate to factors influencing annual confirmed mountain lion (*Puma concolor*) depredation rates by county in California, USA from 1972 to 2019. We derived predicted depredation rates using a log-link function to interpret coefficient estimates from the most parsimonious Poisson model for understanding factors influencing annual confirmed mountain lion depredation rates by county. Mountain lions bountied was the total number of mountain lions bountied from 1906 to 1963 per county and was used as a proxy for quality of suitable habitat in each county.

association with increasing amount of suitable habitat and quality, number of domestic animals involved in agricultural production, and number of mountain lions removed the previous year.

Discussion

We examined the temporal trends in mountain lion depredation events as well as factors influencing annual mountain lion depredation rates in California using a dataset compiled from 1972 to 2019. We demonstrated that mountain lion depredations have increased over time and are most often associated with small hoofstock and pets secondarily, primarily sheep and goats (Torres et al. 1996; Table 2). Mountain lions most often depredated small hoofstock and are increasingly depredating pets (Figures 3 and 4). Further, we verified a suite of variables were associated with changes in annual mountain lion depredation rates at the county level (Table 4). In general, our work points to presence/quality of mountain lion habitat and wildlife management actions as primary drivers predicting mountain lion depredation rates (Cougar Management Guidelines Working Group 2005, Robinson et al. 2008, Zarco-Gonzalez et al. 2013). The lack of a relationship between mountain lion depredation rates and intermediate human density could be due to the scale of our analyses being too coarse (Teichman et al. 2013).

An increase in overall annual number of mountain lion depredations from 1972 to 2019 is not surprising given that human populations have increased from 1972 to 2019 (20.7–39.9 million people; California State Association of Counties 2019), which has resulted in increased development in and adjacent to suitable mountain lion habitat (Burdett et al. 2010, Smith et al. 2016, Zeller et al. 2017). Further, there is evidence that the mountain lion population statewide has increased from the 1970s to 2019 (Dellinger and Torres 2020). Intuitively, an increasing mountain lion population, in the presence of a human population that has doubled in the past 20 years, increases the probability of these 2 parties being near one another more and invariably leading to an increase in conflict between humans and mountain lions (Torres et al. 1996, Hiller et al. 2015). Our results agree with other studies wherein mountain lion depredations were shown to have increased in the past few decades (Torres et al. 1996, Ruth and Murphy 2010). Though we found a significant increase in overall annual mountain lion depredations in California from 1972 to 2019, the increasing trend was driven by mountain lions increasingly depredating small hoofstock, primarily sheep and goats, and pets secondarily, but not large hoofstock such as cattle (Table 2; Figures 3 and 4). Our results are similar to other research demonstrating large hoofstock weighing >136 kg (>300 pounds) were infrequently depredated by mountain lions while small hoofstock are more commonly depredated by mountain lions (Shaw 1983, Rosas-Rosas et al. 2008). Given that there has been a decrease in agricultural production involving both small and large hoofstock in California (California Department of Food and Agriculture 2020), increasing depredations involving small hoofstock is noteworthy. It is likely that increasing depredations involving small hoofstock involves smaller (hobby) operations. It is also possible that the increase in number of pets depredated annually could simply be due to an increase in human population size and thus an increase in number and distribution of pets.

The idea that an increase in annual number of depredations on small hoofstock over time is primarily related to smaller (hobby) operations is supported by our modelling efforts to understand factors influencing mountain lion depredation rates. Specifically, we found a negative relationship between agricultural productivity (i.e., number of domestic animals involved in agricultural production by county, primarily cattle and sheep) and mountain lion depredation rates, which agrees with previous research on factors influencing mountain lion depredation rates (Zarco-Gonzalez et al. 2013; Table 4). This negative relationship and an increase in annual number of depredations on small hoofstock over time jointly suggests small-scale small hoofstock operations consisting of sheep and goats play a key role in mountain lion depredations in California. The association between mountain lion depredations and small-scale small hoofstock operations, especially those composed of sheep and goats, has been suggested elsewhere (Torres et al. 1996, Cougar Management Guidelines Working Group 2005, Orlando 2008, Vickers et al. 2015, Moss et al. 2016). The U.S. Department of Agriculture ([USDA] 2019) report states that 69% of all sheep and goat operations in California have <25 animals. Further, 51% of all sheep and goat operations in California utilize <4.05 ha (<10 acres) of land (USDA 2019). Given the small number of animals and land involved in a majority of such operations, it is conceivable that more effective (e.g., night penning or electric fencing) and less expensive improvements (e.g., repairs to fencing and enclosure facilities) to husbandry methods can be employed to mitigate the likelihood of future mountain lion depredations (Mazzolli et al. 2002). Currently, 78% of all sheep and goat operations in California make <$5,000 in profit per year (USDA 2019). This low profit margin has perhaps influenced the fact that from 2004 to 2014 the percentage of all sheep and goat operations utilizing nonlethal measures (e.g., guard dogs and night penning) to mitigate depredation has increased from 32–59% (USDA 2015). Because depredation results in economic loss as well as loss of future genetic potential of livestock, continued efforts to mitigate depredations could be beneficial for all operations, including smaller operations with limited profit margins, while also conserving mountain lion populations at the wildland–urban interface.

While the positive relationship between both amount of suitable mountain lion habitat (Figure 5C) and number of mountain lions bountied (used herein as a proxy for habitat quality; Figure 5B), respectively, per county and mountain lion depredation rates is intuitive, it reinforces the idea that where large carnivores are present, conflict with domestic animals is likely to occur (Michalski et al. 2006, Rosas-Rosas et al. 2008, Ruth and Murphy 2010). This aspect of mountain lion depredation is especially pertinent to California as ~40% of the state is considered suitable mountain lion habitat and many of the nearly 40 million residents live in or near suitable mountain lion habitat (Dellinger et al. 2020). Thus, wildlife agencies and other vested parties (e.g., non-governmental organizations, Cooperative Extension, etc.) should work to better inform local residents about both the distribution and abundance of large carnivores to increase awareness about the likelihood of large carnivore conflict (Baruch-Mordo et al. 2008). Local residents can then better determine whether they need to employ husbandry techniques to reduce the likelihood of large carnivore depredations (Mazzolli et al. 2002). However, such lines of thought necessitate demonstrating the efficacy of mitigation measures and the economic value of taking proactive measures to mitigate the likelihood of large carnivore depredations (Conforti and de Azevedo 2003).

The positive relationship between the number of mountain lions lethally removed 1 year and the increase in depredations the following year (Figure 5A; Table 4) can seem counterintuitive. Lethal removal of resident adults can create vacancies and increase immigration rates of subadult males (Robinson et al. 2008, Peebles et al. 2013). Subadult mountain lions are more likely to use areas closer in proximity to people (Kertson et al. 2013) and are less likely to have refined hunting skills causing them to more readily take easily killed prey such as domestic animals (Ruth and Murphy 2010). These factors predispose subadult mountain lions, especially males, to be more likely to depredate than adults (Torres et al. 1996, Linnell et al. 1999, Hiller et al. 2015, Logan 2019). While consistent and reliable data on sex and age of animals removed for depredation were not available for the majority of our dataset, more recent efforts to collect data on mountain lions removed for depredation in California indicates that subadult and dispersal age males (≤3 years old) represent a large proportion (41% of all animals and 60% of all males removed from 2016 to 2019) of the animals removed (CDFW, unpublished data). Removals can thus create a negative-feedback loop that leads to increasing conflict and lethal removal, which could begin to negatively impact the mountain lion population via reduced gene flow and population viability (Hiller et al. 2015, Vickers et al. 2015, Benson et al. 2019). Thus, maintaining an older age structure by reducing lethal removal of resident adults could mitigate depredations (Logan 2019). Our results agree with previous findings that lethal removal of mountain lions is positively associated with increasing depredation rates (Cooley et al. 2009, Peebles et al. 2013, Teichman et al. 2016), but the coarse scale at which we detected such a relationship was surprising. However, it is important to point out that such scenarios are most likely to occur within large contiguous blocks of suitable habitat that support populations large enough to produce excess individuals (i.e., a source population) that can fill in areas of vacated habitat (Robinson et al. 2008, Cooley et al. 2009). Also, removal of a depredating animal, which can create a brief reprieve for the affected property owners, followed by improved husbandry practices, could mitigate the potential for subsequent increases in depredation rates (Mazzolli et al. 2002, Guerisoli et al. 2017).

We acknowledge that there are likely other important factors influencing mountain lion depredation rates in California, probably the most important of which is ratio of wild prey to domestic animals (Ruth and Murphy 2010). Annual county and statewide data on wild prey abundance encompassing this time frame were not available, but it has been shown that increasing availability of wild prey relative to domestic animals decreases utilization of domestic animals by large carnivores (Shaw 1981, Polisar et al. 2003, Llanos and Travaini 2020). Thus, in some areas where native prey is less abundant, depredation may not be limited to subadult animals as mentioned above but rather something all demographic classes do (Kertson et al. 2013, Moss et al. 2016, Logan 2019). A similar scenario where depredations are related to wild prey abundance is in areas with migratory prey. Dellinger et al. (2018) reported that removal for depredation purposes was the primary source of mortality for mountain lions that did not follow migratory mule deer to summer range; these removals most often occurred in early summer following mule deer [*Odocoileus hemionus*] migration to higher elevations. Regardless of the ratio of wild prey to alternative food sources such as domestic animals, the opportunistic dietary patterns of mountain lions suggest a secondary food source is still likely to be consumed at some point if that secondary food source is regularly present within a mountain lion's home range and vulnerable to predation (Torres et al. 1996, Cougar Management Guidelines Working Group 2005). Though this further argues for long-term solutions to mitigate depredations such as improved husbandry practices, we also recognize that some large carnivores can become habitual depredators irrespective of abundance of wild prey (Linnell et al. 1999). Selective removal of these conflict individuals may be justified to reduce local conflict (Anderson et al. 1992, Treves and Naughton-Treves 2005, Rosas-Rosas et al. 2008). However, selective removal means that animals involved in conflict are readily identifiable and not likely to be confused with other local individuals. Regardless, it is likely that increasing abundance of wild prey can benefit large carnivores and simultaneously reduce depredation rates (Janeiro-Otero et al. 2020).

We acknowledge that large carnivore depredations involve more than environmental variables and are often influenced by strongly held human perceptions and values (Dickman et al. 2013). Though we do not discount these social aspects, we encourage all involved to seek to address the matter with viable long-term solutions that can promote co-existence between people and large carnivores (Carter and Linnell 2016). Long-term solutions like improved husbandry techniques for pet owners and smaller operations (Torres et al. 1996, Mazzolli et al. 2002) might result in less lethal removal of depredating individuals (Teichman et al. 2016). Local governments at the county, city, or township level could implement animal husbandry ordinances to help encourage residents to properly house and take care of their animals to mitigate depredation events. The ability to obtain a depredation permit to lethally remove could then be tied to whether a resident is in compliance with such an ordinance. However, coexistence also means an adaptive approach wherein removal might be warranted in some situations (e.g., operations financially impacted by losses or areas with individual large carnivores engaging in conflict; Treves and Naughton-Treves 2005) to: (1) support economic viability of livestock operations that serve to maintain critical wildlife habitat and (2) decrease antipathy of local residents toward large carnivores. Long-term solutions to achieve coexistence should also include greater evidence-based research on efficacy of various husbandry practices and mitigation measures to reduce depredations (van Eeden et al. 2018).

Management implications

Our study of temporal trends in and factors influencing mountain lion depredation rates highlights key factors for potentially mitigating depredation rates. Wildlife agencies should communicate with pet owners and small-scale small hoofstock operations, primarily those with sheep and goats, living in or near areas of suitable mountain lion habitat to support animal husbandry practices that proactively reduce conflict. Suggestions to effectively improve animal husbandry could just involve putting animals in enclosures nightly or require more advanced approaches like electric fencing. We also think local governments could possibly become more involved to help encourage residents to provide more adequate shelter and overall accommodations to help mitigate occurrence of depredation events. Additionally, wildlife agencies should continue to research effective means of deterring mountain lions from depredating to reduce lethal removal of depredating animals and resulting conflict. Most significantly, it appears that if small-scale agricultural operations and pet owners can improve animal husbandry standards with the purpose of mitigating depredation, depredation rates throughout California could decrease substantially and maybe even more than might be expected, as depredation rates are positively influenced by previous lethal removal. Whatever the long-term approach to reducing conflict, coexistence cannot be achieved without effective and proactive measures to address large carnivore conflict. Reducing conflict would not only benefit landowners via keeping their domestic animals alive, but it would also promote an older age structure in mountain lion populations adjacent to human development, which in turn would promote gene flow and population viability in such areas.

Depredation by mountain lions is increasing in all the western states (Apker 2017). As evidenced by California, the definitive increase in human development proximate to mountain lion habitat ensures that these conflicts will continue. Different than removals as a result of regulated harvest, depredation removals increasingly occur in landscapes that are fragmented and otherwise compromised by increased human activity. Addressing depredation conflicts, solutions, and potential impacts to mountain lion populations necessitates that accurate data collection and reporting standards are followed. This is fundamental to determining best management practices, and we recommend that states adopt standardized protocols for issuing depredation permits and recording depredation events.

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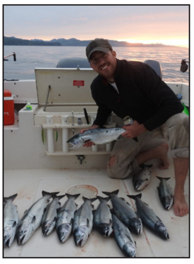

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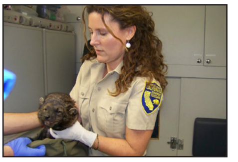

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