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Evaluation of Key Scientific Issues in the Report, "State of the Mountain Lion—A Call to End Trophy Hunting of America's Lion"

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By James W. Cain III and Michael S. Mitchell

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International System of Units to U.S. customary units

Multiply	By	To obtain
Length		
meter (m)	3.281	foot (ft)
kilometer (km)	0.6214	mile (mi)
Area		
square kilometer (km^2)	0.3861	square mile (mi^2)

Abbreviations

HSUS Humane Society of the United States
MCP Minimum convex polygons
USGS U.S. Geological Survey

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Abstract

In their recently published report, *State of the Mountain Lion: A Call to End Trophy Hunting of America's Lion*, the Humane Society of the United States suggested that mountain lion (*Puma concolor*) hunting should be abolished in the United States. The report claims this recommendation is based on scientific arguments that demonstrate the overharvest of mountain lions throughout much of their current range in the United States. We reviewed the science presented by the Humane Society to support their call for the cessation of mountain lion hunting. Rather than provide a rigorous assessment of the peer-reviewed scientific literature and available data on mountain lion ecology, population dynamics and management, the report uses a fundamentally unscientific approach that starts with an *a priori* assumption that hunting is detrimental to the long-term persistence of mountain lion populations, then attempts to use scientific arguments to support this value-based position. The report frequently ignores or selectively interprets relevant peer-reviewed literature, weakening the scientific credibility of the report. The report relies on imprecise and inadequate demographic measures, questionable data, and simplistic methodologies to derive dubious estimates of potential lion densities; it compares these estimates to various measures produced by State agencies (which themselves vary in reliability as estimates of abundance) to purportedly illustrate the detrimental effects of hunting. The approach used in the report to support the predetermined supposition that mountain lion populations are over-hunted fails to serve as a scientifically defensible foundation for management recommendations range-wide or at the State level.

Introduction

The U.S. Geological Survey, Cooperative Fish and Wildlife Research Unit Program (CRUP) provides scientific guidance, technical training, and workforce development to program cooperators (PL 86-686, Cooperative Research Units Act). Principal program cooperators are Department of the Interior agencies and state fish and wildlife agencies. A key role of the CRUP is to provide science support to program cooperators, which takes many forms including technical support on important fish and wildlife management issues. This includes meeting requests by cooperating agencies to peer review the scientific basis and merit of gray literature reports (reports not published in the peer-reviewed literature) that may have significance to their management programs. Consistent with the mission of the USGS, CRUP scientists provide objective and independent scientific reviews of such reports. Peer reviews focus on the strengths and weaknesses of referenced scientific information, interpretation, and assumptions, and make no assessments of policy or recommendations for natural resource management. This report represents such an effort, performed at the request of cooperating agencies.

The Humane Society of the United States (HSUS) recently published a report calling for the end of mountain lion (*Puma concolor*) hunting in the United States based on several scientific arguments (Humane Society of the United States, 2017). These arguments range from citing available literature on demography, ecology, and sociality of mountain lions, to the presentation of potential habitat and population sizes across 16 States where breeding populations exist. The U.S. Geological Survey (USGS) reviewed the science presented in the Humane Society of the United States (2017), focusing on subjects key to the conclusions of the report.

Positions stated in the Humane Society of the United States (2017) are based on human values, in this case an opposition to "trophy hunting" in general and specifically the harvest of mountain lions. Although inherently subjective, these values are as legitimate as those of any other stakeholder in the effective conservation of wildlife in the United States. The report cites numerous polls to illustrate that these values are shared by a diversity of people. Indeed, these values may be increasingly prevalent in the United States as constituencies that have traditionally taken part in hunting and fishing decline (Manfredo and others, 2003; but see Butler and others, 2003 for an alternative finding).

All decisions in wildlife management are based on human values, including the value placed on science. Care must be taken, however, when scientific arguments are used to support recommendations based on other values. Science is easily misused on behalf of non-scientific agendas, becoming a seemingly objective but diversionary proxy for the subjective values behind the agendas (Mitchell and others, 2018). The HSUS report falls short on four standards that would lend it scientific credibility: (1) an assumption that hunting limits mountain lion populations, (2) pertinent scientific literature either was ignored or selectively cited and interpreted, (3) imprecise and inadequate demographic measures were used to illustrate the detrimental effects of hunting, and (4) a scientifically inadequate estimate of potential lion densities was used to argue that hunting keeps densities of mountain lions below acceptable limits.

Presumption That Hunting Limits Mountain Lion Populations

It is human nature to seek evidence to support a value or belief (that is, confirmation bias; Kahneman, 2011). Humane Society of the United States (2017) begins with the supposition that hunting is limiting growth and threatening long-term persistence of mountain lion populations, then attempts to build a scientific case to support this belief; seeking evidence to argue a preconceived conclusion is inherently unscientific (Platt, 1964; Romesburg, 1981, 2009; Sells and others, 2018). The report cites but then ignores factors other than hunting that could influence lion populations across their range (that is, habitat loss and fragmentation, poaching, disease, starvation, inbreeding, intraspecific strife,

poisoning, and climate change; Humane Society of the United States, 2017, p. 36–37). The scientific remedy for confirmation bias is to evaluate the evidence for alternative explanatory causes for observed phenomena (Sells and others, 2018). Without an objective evaluation of all factors potentially influencing mountain lion populations, it cannot be concluded that hunting is the dominant limiting factor, as the report claims. The evidence needed to objectively evaluate factors influencing demography of mountain lions is rare and sparse across the full range of mountain lion populations in the United States. An analysis of all available information almost certainly would have shown much more ambiguous and uncertain patterns than the report currently presents.

Selectively Cited and Interpreted Literature

The report cites numerous peer-reviewed publications to support its recommendation against hunting of mountain lions. In building this case, the report frequently fails to reference relevant publications offering contrary conclusions, or offers selective interpretations, thereby failing to thoroughly assess all pertinent results, assumptions, and critical caveats detailed in the original peer-reviewed papers. Selective use of peer-reviewed scientific literature is misinformative, particularly for readers unfamiliar with published research, which diminishes the credibility of the report.

For example, the report repeatedly claims that trophy hunting is the most important threat to the persistence of mountain lion populations. This claim generally is not supported by the peer-reviewed literature. Research has shown that hunting mortality is additive for mountain lion populations and thus has the potential to cause declines where hunting is high and sustained, but these populations are highly resilient and can recover quickly (Lindzey and others, 1992; Logan and Sweanor, 2001; Stoner and others, 2006; Robinson and others, 2014). Therefore, even heavy hunting does not inevitably cause irretrievable declines in mountain lion populations. Importantly, there is broad consensus among wildlife ecologists that habitat loss, degradation, and fragmentation are the primary threats to the survival of most wildlife species in the United States (Wilcove and others, 1998); mountain lions are no exception. Habitat loss and habitat fragmentation, including the effects of habitat alterations on prey species, are considered the most important threats to persistence of mountain lions (Logan and Sweanor, 2001; Pierce and Bleich, 2003, Cougar Management Guidelines Working Group, 2005; Anderson and others, 2009; Negri and Quigley, 2009).

Humane Society of the United States (2017) also states unequivocally that ungulate populations are food limited and that predator removal has little effect on the productivity of ungulate populations. Whether or not an ungulate population is nutritionally limited or whether predation may be a compensatory or additive source of mortality depends on population size relative to carrying capacity (Ballard and others, 2001; Bowyer and others, 2014; Monteith and others, 2014; Bergman and others, 2015). When populations are at or above carrying capacity, animals tend to be in poor nutritional condition, produce small offspring, and are strongly susceptible to predation or mortality due to effects of severe weather or disease; predation on these populations often is compensatory (Bergman and others, 2015). Controlling predators when ungulate populations are near carrying capacity typically has little influence on population growth (Ballard and others, 2001; Bergman and others, 2015). However, ungulate populations below carrying capacity generally are composed of individuals in good nutritional condition that produce more offspring that likely have higher survival rates than populations near or above carrying capacity (Bowyer and others, 2014, Monteith and others, 2014, Bergman and others, 2015); predation on these populations often is additive. The review on mule deer (*Odocoileus hemionus*) and black-tailed deer (*O. h. columbianus*) by Forrester and Wittmer (2013) and other publications cited in Humane Society of the United States (2017) (Watkins and others, 2001; Pojar and Bowden, 2004; Bishop and others, 2009) to support the blanket claim of food limitation in ungulates, suggests that

many of these studies were of populations at or near carrying capacity. Low abundance commonly typifies ungulate populations of serious management concern. When population abundance is low and well below carrying capacity, moderate predation rates can hamper recovery even if other limiting factors are alleviated, thus precluding recovery of the population (Ballard and others, 2001). For example, predation by mountain lions was reported to contribute to declines of small populations of desert bighorn sheep (*Ovis canadensis nelsoni* and *O.c. mexicana*; Wehausen, 1996; Ernest and others, 2002) or to hamper recovery efforts (Hayes and others, 2000; Kamler and others, 2002; Rominger and others, 2004). All these peer-reviewed papers describe results that are contrary to the claim in Humane Society of the United States (2017) that mountain lions have no effect on bighorn sheep populations, but none of these publications were cited in the report.

In another example, citing Collins and Kays (2011), Coltman and others (2003), and Monteith and others (2013) the HSUS report claims that hunter harvest has led to evolutionary changes in behavior and morphology, compromising the ability of ungulates to adapt to changing conditions. Collins and Kays (2011) reviewed literature about the cause of mortalities for medium- and large-size mammals. They concluded that humans cause most of the mortality (that is, 51.8 percent versus 48.5 percent due to natural causes), but they do not, as implied in the HSUS report, provide any data demonstrating evolutionary changes due to human-caused mortalities in general or hunting. Coltman and others (2003) and Monteith and others (2013), provide data more directly related to potential changes in morphology of ungulates in response to human harvest. However, the bighorn sheep population studied by Coltman and others (2003) was subjected to unlimited harvest of legal rams, unlike the more conservative harvest limits imposed by management agencies for most populations across the species' range (Heffelfinger, 2018). Additionally, the Coltman and others (2003) study did not account for the effects of population density, nutrition, maternal effects, or shifting age distributions due to harvest on changes in average horn size of the population. Some of these factors have a stronger effect on ungulate morphological characteristics than purported genetic changes due to selective human harvest (Coltman, 2008; Monteith and others, 2013; Traill and others, 2014; Douhard and others, 2017; Heffelfinger, 2018). Therefore, Humane Society of the United States (2017) selectively cites literature to support its premise while avoiding mention of the ongoing and rigorous debate among ecologists about the evidence for evolutionary consequences of trophy hunting (Coltman and others, 2003; Darimont and others, 2009; Traill and others, 2014; Heffelfinger, 2018).

Imprecise and Inadequate Demographic Measures

Identifying a measurable demographic parameter for understanding and managing large carnivores is notoriously difficult because they occur at low densities, range widely, and are highly elusive. Scientific careers have been built on the challenges of understanding demography of animals much easier to study. This challenge becomes much greater when imprecise concepts and definitions are used. Terms such as population size, trend, census, abundance, estimates, habitat, density, home range, and mortality have precise scientific definitions but are used loosely, inconsistently, and sometimes interchangeably throughout Humane Society of the United States (2017). For example, figures and discussion of mountain lion mortality in appendix B are misleading. The text reports *trophy hunting mortality* (presumably including animals killed through legal harvest) as a percentage of *total human-caused mortality* (presumably including vehicle collisions, depredation removals, poaching, and other factors), then inappropriately draws conclusions that *trophy hunting mortality* parallels *human-caused mortality* and *total overall mortality* (presumably including all forms of mortality such as starvation, intraspecific killings, and other mortality sources). Associated figures suggest a comparison between *trophy hunting mortality* and *total mortality* (presumably the same as *overall mortality*). Overall or total

mortality do not equate to total human-caused mortality and the report offers no evidence of having obtained or generated estimates of total or overall mortality. This imprecise terminology can lead to subjective, divergent inferences about the effects of hunting on mountain lion populations. Comparing hunting mortality to all human-caused mortality is not informative if, as appears to be the case, most human-caused mortality is produced by hunting. Conversely, comparing hunting mortality to overall mortality can produce information highly useful for managing harvested species (that is, whether hunting mortality is compensatory or additive; Robinson and others, 2014). Because of the inconsistencies in terminology, the HSUS report presents evidence only for the former comparison but appears to reach conclusions as if based on the latter, selectively leading the reader to an erroneous inference.

The most fundamental demographic measure for understanding and managing populations arguably is abundance. Estimates of abundance can represent a key bottom line that is central to most management questions—how many animals are there and how has that changed over time? In the absence of such information, it is difficult to understand population dynamics and how they are influenced by a variety of factors, including hunting. Humane Society of the United States (2017) makes the case that such understanding is an important component of harvest management, finding fault with state agencies for making harvest decisions based on less reliable data such as harvest returns (although offering no financially or logistically feasible solutions to the problem). However, Humane Society of the United States (2017) makes the same error for which it criticizes the state wildlife management agencies: without knowing annual abundance it uses annual harvest data to support the claim that hunting has an unacceptably detrimental effect on populations of mountain lions. Without credible evidence that hunting is associated with declines in abundance, it is impossible to make the argument that hunting or any other factor is responsible for declines in population, the central argument put forth in the report. Even if, for example, hunting mortality comprises most of the mortality, unless it is known whether total mortality is sufficient to cause declines in abundance, the conclusion that hunting mortality has deleterious demographic consequences is logically indefensible. Importantly, even if hunting mortality is associated with a decline in abundance its meaning must be interpreted according to management objectives that states seek to achieve through harvest. If the objective is to reduce the size of the mountain lion population through regulated hunting, then hunting mortality should, by design, be associated with a decline in abundance.

Inadequate Estimate of Potential Lion Densities

In an attempt to build further support for the position that mountain lions are overharvested Humane Society of the United States (2017) constructed a simple habitat-based model to estimate potential mountain lion abundance. These estimates of potential lion abundance were compared to a variety of estimates used by State wildlife management agencies, and the report concluded that almost all States are overharvesting mountain lions. The report describes abundance estimates as "most suitable density" (p. 6), "potential optimal abundance" (p. 25), and "healthy densities" (p. 6). However, these terms have no precise, operational definitions in the fields of population and wildlife ecology and the report does not offer any definitions. Without an established operational definition, the biological meaning of each those terms is not clear, making their interpretation subjective based on the reader's personal values and knowledge of population ecology. The use of vague terms obscures the questionable assumptions and methodological approaches behind the estimation of potential lion abundance in the report.

Comprehensive habitat modeling when coupled with rigorous estimates of abundance and other demographic parameters (for example, productivity and recruitment) can provide meaningful information for managing wildlife (Mitchell and Hebblewhite, 2012). A credible population or habitat modeling effort includes a rigorous assessment of the accuracy of the underlying data, assumptions made when using the data, and the assumptions inherent to the models used. Model prediction results are then tested (that is, evaluating how well model predictions fit independent data) or validated (for example, cross validation). Furthermore, when presenting a point estimate of abundance (or any other estimated parameter of interest), an estimate of precision or uncertainty should accompany the estimate. The modeling presented in Humane Society of the United States (2017) does not meet any of these criteria, and that failure compromises the validity of the resulting abundance estimates.

Overall, the data and modeling approach used to estimate potential mountain lion density in the report are problematic. There are critical issues with the nature of prey data selected, the use of relatively small female home range sizes for delineating habitat classifications, vague classifications of habitat quality, use of a fixed lion density estimate across the western United States, questionable assumptions in the modeling process, and the use of the derived abundance estimates without an assessment (either formal or informal) of associated uncertainty.

Although mountain lions occupy a wide range of environments, prey abundance, vegetation, and topographic features that contribute to hunting success, and human disturbance commonly are considered important habitat components wherever mountain lions occur (Seidensticker and others, 1973; Logan and Irwin, 1985; Lindzey, 1987; Laundré and Hernández, 2003; Robinson and others, 2015). Informed selection of available geospatial data for habitat modeling is primarily based on the questions or hypotheses of interest that the modeling is intended to address. The selection criterion for data used to model habitat and prey characteristics in Humane Society of the United States (2017) was based on coverages that were consistently available across the western United States, rather than the data needed to accurately capture the broad variation in critically important habitat components across the diversity of ecoregions occupied by mountain lions. The model used for the HSUS report attempted to account for the effects of topographic variation, prey, and human disturbance; vegetation cover data and their potentially important contribution to stalking cover were omitted from the modeling. The limits imposed by data availability and completeness on comprehensively modeling important habitat characteristics across broad geographic extents hampers all habitat modeling (Barry and Elith, 2006). Any habitat modeling effort, therefore, makes two critical assumptions: (1) available data are sufficient to model key habitat characteristics, and (2) the inability to model habitat characteristics for which no data are available does not biologically invalidate model predictions. A scientifically credible habitat model requires a forthright discussion of these assumptions, as well as a discussion of the potential for bias in model predictions if any assumptions are violated.

Prey data used in the model were obtained from the U.S. Geological Survey National Gap Analysis Program (2011a, b) for bighorn sheep (*O. canadensis*) and elk (*Cervus elaphus canadensis*); mule deer and black-tailed deer data were obtained from Utah State University (2005). These data represent estimated distributions or maps of areas where conditions have the potential to be occupied by these prey species (that is, potential habitat). Distribution models of potential habitat for mule deer, elk, and bighorn sheep are poor substitutes for actual data on prey abundance and availability. The distribution model data do not depict the biologically meaningful spatial variation in abundance of prey species, nor do they always represent the actual distribution of extant populations of prey across their range. Density of prey throughout the distributional ranges was assumed to be constant, ignoring spatial variation in density of ungulate populations. For example, mule deer distribution data clearly designate substantial areas as "limited range" that are occupied only occasionally or by small populations (Utah State University, 2005). Similarly, the modeling referenced in Humane Society of the United States

(2017) equates low density mule deer populations in the Desert Southwest and high density populations in Montana and Wyoming, leading readers to assume density of mule deer is constant across their range, thus serving as a spatially consistent source of prey for mountain lions.

Critically important, the distribution ranges do not necessarily reflect the actual distributions of prey populations. For example, the bighorn sheep data used in the modeling included broad areas where no bighorn sheep populations currently exist (Western Association of Fish and Wildlife Agencies 2016; fig. 1). The data produced by USGS and Utah State University are not themselves problematic, but the assumption that the data provide a reliable depiction of the prey resources needed to support a lion population is. Accounting for the wide spatial variation in prey abundance within the boundaries of the distribution ranges would provide more meaningful information on the spatial variation in mountain lion densities that certainly exist on the landscape (for example, Carbone and Gittleman, 2002; Karanth and others, 2004).

Additional issues with two assumptions made in the geospatial modeling warrant discussion. Briefly, the basic modeling approach assigned a weighted sum to each pixel based on values for prey, terrain ruggedness, and human footprint. The pixels were partitioned along a habitat quality gradient ranging from non-habitat to optimal, and considered only the highest three habitat classes (average, good, optimal) to be capable of supporting mountain lions (Humane Society of the United States, 2017). The estimates of habitat areas for each state (that is, the total area from which the abundance estimates were derived) were based on a moving window approach in which each focal cell was assigned a habitat value based on the majority habitat value of the pixels within the moving window. A primary flaw was the assumption that a single value for mountain lion density would be accurate for estimating abundance across the western United States. Empirical estimates of mountain lion density vary widely across the United States (0.3–2.2 adults/100 km^2), mostly due to differences in prey abundance and habitat conditions (Seidensticker and others, 1973; Logan and others, 1986; Anderson and others, 1992; Ross and Jalkotzy, 1992; Beier and Barrett, 1993; Lindzey and others 1994; Logan and others, 1996; Spreadbury and others, 1996; Pittman and others, 2000; Logan and Sweanor, 2001). Because different ecoregions have inherently different capacities to support mountain lion populations, the use of a single density value both over- and under-estimates potential mountain lion abundance in different parts of their range. Moreover, the assumption that a 5-km moving window represents the typical home range radius (about 78.5 km^2) for an adult female mountain lion does not withstand scrutiny. Although female home ranges (estimated as 90–100 percent kernel density functions or minimum convex polygons [MCP]; Worton, 1989) less than or equal to 78.5 km^2 are reported in the peer-reviewed literature (Logan and others, 1986; Hopkins, 1989; Spreadbury and others, 1996; Logan and Sweanor, 2001), much larger home ranges have been reported in many areas, commonly in excess of 140–250 km^2 (for example, Hemker and others, 1984; Neal and others, 1987; Pence and others, 1987; Anderson and others, 1992; Ross and Jalkotzy, 1992; Beier and Barrett, 1993; Pierce and others, 1999; Pittman and others, 2000; Dickson and Beier, 2002; Grigione and others, 2002). If a larger home range size was used for the moving window, many areas ultimately classified as average habitat would have been more likely to have been classified into one of the lower habitat classes, thus resulting in a lower abundance estimate. Home range size in mountain lions is strongly inversely related to prey abundance or density (Grigione and others, 2002). Therefore, potential errors generated due to fixed, small home ranges and fixed lion density would be exacerbated in areas characterized by low prey abundance, lower lion densities, and larger mean home range sizes. Finally, any estimate of density, abundance, or any other estimated parameter, almost without exception, needs to be accompanied by an estimate of precision or uncertainty.
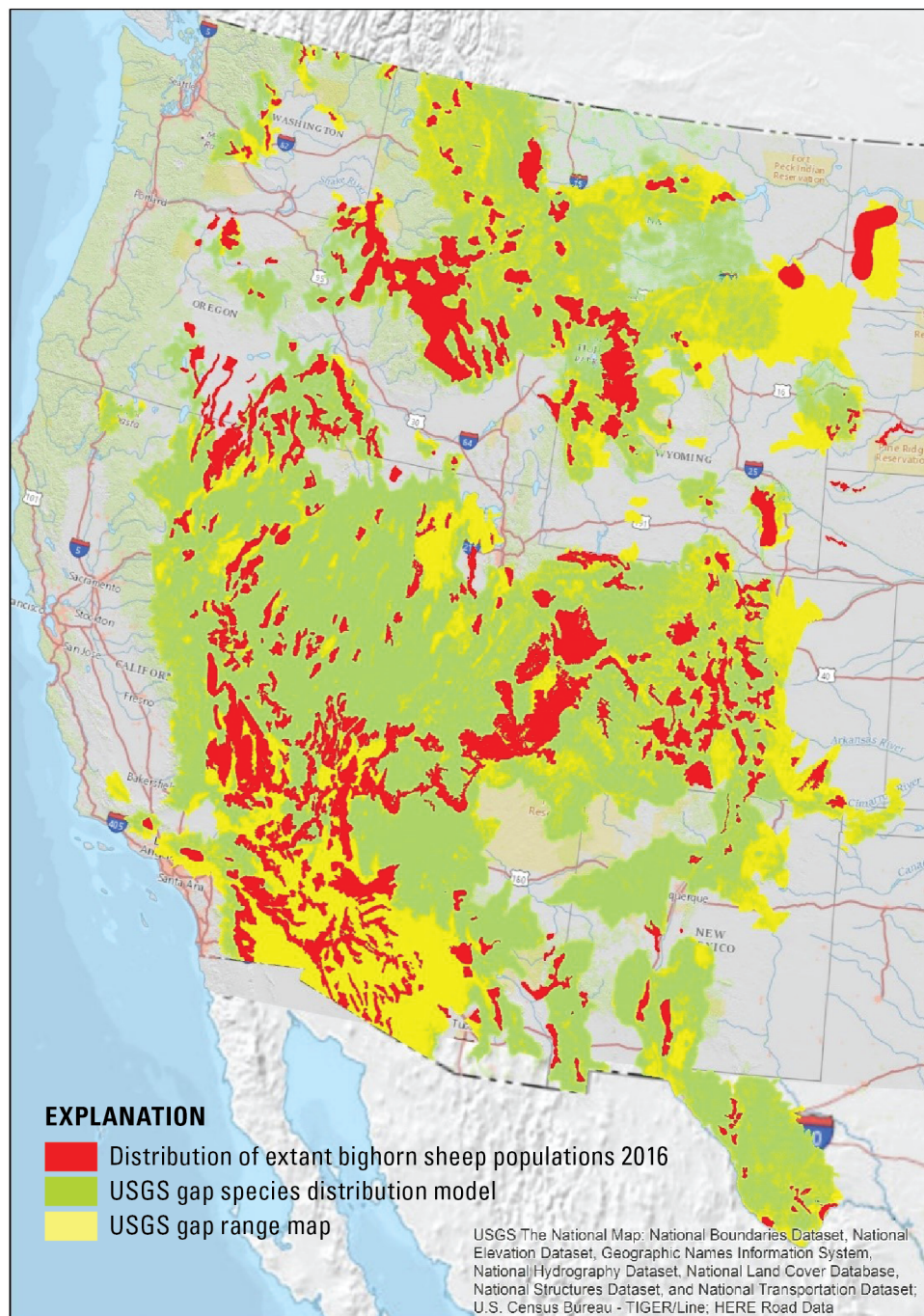
Figure 1. USGS GAP range map and USGS Gap species distribution model used in the Humane Society of the United States (2017) mountain lion report to depict bighorn sheep availability as prey for mountain lions in the Western United States. The actual distribution of extant populations of bighorn sheep (Western Association of Fish and Wildlife Agencies. 2016) is superimposed on the GAP range map and distribution model.

Potential habitat or presence of critically important habitat components (for example, prey, stalking cover) can be modeled if accurate data upon which to build the model are available. Habitat quality (that is, the extent to which habitat characteristics contribute to fitness; Mitchell and Hebblewhite, 2012), however, is best determined based on demographic rates of the species of interest (Van Horne, 1983; Johnson, 2007). Instead, Humane Society of the United States (2017) identifies potential mountain lion habitat using predetermined categories that are based on a vague conceptualization of the number of lion territories (for example, "Good—many lions can occupy as home range, can support a breeding population;" Humane Society of the United States, 2017, p. 25) that could exist in a given area. The categorical classifications of mountain lion habitat quality are based on the summation of habitat characteristic scores used in the geospatial habitat model and are based on neither demographic attributes nor peer-reviewed research. To be most informative for estimating statewide abundances, habitat modeling is best coupled with estimates of mountain lion abundance or demographic rates (for example, survival) derived from field studies on lion populations spanning the range in habitat conditions depicted in the geospatial model.

Authors of Humane Society of the United States (2017) indicated that population estimates used by state agencies do not provide information appropriate to making management decisions. In reaching conclusions about over-harvest, however, the state estimates presented in the report (modified to represent adults only based on age ratio data from a single population in New Mexico, Logan and Sweanor, 2001) were quantitatively compared to the estimated potential population sizes derived from the models presented in the report. This reasoning is difficult to understand. If the density and abundance estimates used by state agencies for management of mountain lion populations are inherently flawed, then those data probably do not serve as a good benchmark for comparison to estimates derived from modeling used for the report. When combined, the uncertainties in the variety of abundance estimates used by states, the assumptions made when modifying those estimates to represent only adult animals, and the unassessed uncertainties of estimating potential abundance based on their simplistic habitat model, comparisons of state estimates and those produced as part of Humane Society of the United States (2017) does not support the conclusion that mountain lions are generally overharvested and should be protected.

Management Implications

Humane Society of the United States (2017) argues against hunting of mountain lions based on human values, while attempting to demonstrate scientific support for those values. The science used to support the foregone conclusion that mountain lions generally are over-hunted is of insufficient logical and methodological rigor to be credible. Importantly, the unsubstantiated contentions distract from two important points made in the report that are difficult for anybody to argue: (1) parts of American society are decreasingly tolerant of hunting mountain lions and (2) harvest decisions made by state agencies would benefit from more rigorous measures of population estimation. Few managers would disagree with either of those points. The question then becomes what are the realistic approaches management agencies can take to address them. Failing to adapt to societal changes can lead to loss of management authority by state agencies (for example, ballot initiatives that led to the ban on mountain lion hunting in California; Bleich and Pierce, 2005), but the reasonable means of adaptation may be unclear. Management of mountain lion hunting would be more transparent and quantitatively defensible if it were based on rigorous population estimates, but reasonable means of support and methodological approaches for doing such monitoring are yet to be discovered or widely adopted. Quasi-scientific arguments based on preordained, value-based conclusions are not likely to provide clarity to either of these issues.

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