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Analyses of national mountain lion harvest indices yield ambiguous interpretations

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Abstract

1. Wildlife managers make difficult decisions about how best to ensure sustainable wildlife populations. This is especially contentious in the absence of accurate abundance data. Currently, many managers rely upon harvest metrics to monitor mountain lion abundance and to set management objectives.
2. We analysed mountain lion harvest data from 2005 to 2016 across 10 U.S. states to determine mountain lion metapopulation trends.
3. Our results were ambiguous and suggested conflicting population trends. Three hunting metrics indicated that the metapopulation was declining, two metrics could be interpreted as support for either an increasing or decreasing metapopulation and one metric indicated that the mountain lion metapopulation was stable.
4. This ambiguity may indicate that some metrics better reflect carnivore abundance than others or that harvest metrics are a poor method for monitoring carnivore abundance. This is a concern because ambiguity in population trends may also fuel conflict between different stakeholder groups with different views of mountain lions.
5. To avoid future ambiguity and to mitigate dissension among stakeholders, state agencies might consider a collaborative integrated population model to monitor mountain lions at a national scale.

KEYWORDS
abundance, carnivore, harvest metrics, Puma concolor, wildlife management

1 | INTRODUCTION

Successful large carnivore management weighs varied stakeholder values and beliefs, social tolerance for wildlife and the real and perceived risks of living with these species (Lamb et al., 2020; Lüchtrath & Schraml, 2015; Mitchell et al., 2018; Skrbinšek et al., 2019). Wildlife managers make difficult decisions about how best to maintain recreational hunting and ensure sustainable wildlife populations held in public trust, all while balancing, and sometimes deflecting political will and the influences of different stakeholder groups (Beausoleil et al., 2021; Fuller et al., 2020; Lute et al., 2020). These decisions are more difficult where abundance estimates for carnivores are lacking (Beausoleil et al., 2021; Mitchell et al., 2018). For many carnivores, it remains difficult to quickly and robustly estimate their abundances, which sometimes fuels speculation about the mechanisms driving human–carnivore conflict (Beausoleil et al., 2021) and the effects of legal

TABLE 1 Harvest metrics and expected trends of each metric reflecting decreasing, stable and increasing mountain lion populations based on Barnhurst (1986), Anderson and Lindzey (2005) and Wolfe et al. (2016)

Metric	Population decreasing	Population stable	Population increasing
%Subadult males[a]	Decreasing proportion of the harvest	Stable proportion of the harvest	Consistent or increasing proportion of the harvest
%Adult males	Decreasing proportion of the harvest	Stable proportion of the harvest	Consistent or increasing proportion of the harvest
%Subadult females	Increasing proportion of the harvest	Stable proportion of the harvest	Consistent or decreasing proportion of the harvest
%Adult females[b]	Increasing proportion of the harvest	Stable proportion of the harvest	Consistent or decreasing proportion of the harvest
Mean age of all cats killed	Decreasing average age	Stable average age	Increasing or stable average age
% subadults (of both sexes) versus adults	Increasing proportion of the harvest	Stable proportion of the harvest	Consistent or decreasing proportion of the harvest

[a]A low subadult male harvest may indicate a depressed mountain lion population rather than a trend (Anderson & Lindzey, 2005).
[b]Female harvest is expected to rise after impacts of harvest are already apparent in other age and sex classes (Anderson & Lindzey, 2005), but their relative abundance in the population has also been shown to decrease under increased harvest pressure as well, exhibiting contrary patterns to what is reported above in this table (Cooley et al., 2009).

hunting on carnivore population dynamics and persistence (e.g. mountain lion, *Puma concolor*; Cain & Mitchell, 2018; Humane Society of the United States [HSUS], 2017).

Mountain lion hunting results in additive mortality (Heurich et al., 2018; Wolfe et al., 2015), meaning that animals killed by hunters are unlikely to die from other causes if not for being harvested. At local scales and across short-time frames, hunting can dramatically influence the abundance and structure of mountain lion populations (Cooley et al., 2009; Proffitt et al., 2020; Stoner et al., 2006). However, at larger scales (e.g. across a state or country's population) and across longer time periods, dispersal behaviours and metapopulation dynamics appear to buffer their populations against the long-term effects of hunting, at least in terms of the number of mountain lions on the landscape (Robinson et al., 2008; Stoner et al., 2006; Sweanor et al., 2000).

There has been considerable investment in developing techniques to determine mountain lion abundance at local scales, with varied success: track counts (Alibhai et al., 2020), telemetry studies (Beausoleil et al., 2021), genetic mark-recapture using scat-detecting dogs, hair snares or biopsy darts (Davidson et al., 2014), motion-triggered cameras and space-to-event models (Loonam et al., 2021), among others. Wildlife managers also collect index or harvest data at larger scales to monitor mountain lion populations and to aid them in designing and assessing the success of their management objectives (Wolfe et al., 2016).

Wildlife managers interpret mountain lion harvest metrics to infer population dynamics based upon the assumption that individual mountain lions experience different vulnerabilities to hunters, especially hound hunters. More specifically, the assumptions are as follows: (1) hunters prefer male mountain lions over female, (2) hunting regulations generally protect females accompanied by kittens, and (3) different mountain lion sex- and age-classes exhibit different behaviours that influence their vulnerability to hunters patrolling roads to locate mountain lion footprints (Anderson & Lindzey, 2005; Barnhurst, 1986; Table 1). For example, subadult male mountain lions should be the most vulnerable to hunters patrolling roads because of obligate male dispersal and the longer dispersal distances exhibited by males over females. Not all harvest metrics, however, reliably mirror population trends, and many deliver low power when trying to detect changes in population abundance (Wolfe et al., 2016).

In this paper, we conducted analyses of mountain lion hunting data collected by western U.S. wildlife agencies from 2005 to 2016 to assess trends that might provide insights into the status of the larger U.S. mountain lion metapopulation. In the absence of better data, harvest metrics are the only tool currently at our disposal to assess the state of the U.S. mountain lion metapopulation (Wolfe et al., 2016).

2 | MATERIALS AND METHODS

2.1 | Data description

We gathered harvest data from 10 U.S. state agencies (Table 2) on mountain lions legally killed by licensed hunters. Some state agencies share mountain lion harvest data on websites easily accessible to the public and others do not. In areas where data were not accessible, we contacted agency biologists and requested harvest data information personally.

Data were collected on an annual basis for the years 2005–2016, and either included total males and females harvested, or where available, the number of adult males, adult females, subadult males and subadult females harvested, and the average age of harvested animals. Not all states had complete data for each metric (Table 2), and different states managed the species differently across time and jurisdictions (e.g. some had female sub-quotas). In the event of incomplete data, only the metrics that a given state reported were used in the appropriate analyses. Oregon and Washington did not permit hound hunting over this time period, which is the predominant method of

TABLE 2 Summary of data collected from state agencies and designation of inclusion of each state into our analyses: Average age of mountain lions harvested within a given age class by year (2005–2016), number of males and females harvested by year (2007–2015; data were excluded in 2005–2006 and 2016 due to incomplete data across states), and number of adult males, adult females, subadult males and subadult females harvested by year (2007–2015; data excluded as above)

State	Average age of each age/sex class harvested (2005–2016)	Total males and females harvested (2007–2015)	Total for each age/sex class harvested (2007–2015)
Colorado	✓	✓	✓
Idaho	✓	✓	✓
Montana		✓	
Nevada	✓	✓	✓
New Mexico		✓	
North Dakota	✓	✓	✓
Oregon	✓	✓	✓
Utah		✓	
Washington	✓	✓	✓
Wyoming	✓	✓	✓

mountain lion hunting in the USA and Canada (Beausoleil et al., 2008). The method of hunting can influence the age and sex classes harvested. For example, hound hunters preferentially select males over females and presumably older over younger animals (Martorello & Beausoleil, 2003). California was excluded because it does not host legal mountain lion hunting, and Texas was excluded because the state classifies mountain lions as nongame species and does not require any reporting of animals killed.

2.2 | Data analysis

First, we analysed the trend in harvest age over time using a generalized linear mixed model. Our base model regressed harvest age as a function of the fixed effects of year and age class, and their interaction; years ranged from 2005 to 2016, and class was one of four categories (adult male, adult female, subadult male, and subadult female). We also included a random intercept for state to account for interstate variability in baseline harvest age. To obtain a traditional *p*-value, we used a normal distribution to approximate these values from the provided *t*-values.

Some states reported the number of harvested individuals by sex (n = 9 states; Table 2), while others also reported the number of harvested individuals by age and sex class (n = 6 states; Table 2). We attempted both a linear and quadratic function of the year; the quadratic function was used to test a curvilinear rather than linear response. We used Akaike information criterion (AIC) corrected for small sample sizes (AICc) to determine our top model (Burnham & Anderson, 2002). Models with ΔAICc $<$ 2 were considered to have equivalent support, and models with ΔAICc $>$ 2 to have less support.

We also analysed trends in sex-specific proportions of annual harvest (2007–2015), and, where available, each age and sex class (adult males, adult females, subadult males, and subadult females). Data were again pooled across states such that there was a single proportion for each sex or age class by year. Data analysis proceeded in a logistic regression framework, with each proportion fitted to the year separately. We fit linear functions of the year only to the response. All analyses were conducted in Program R (R Core Team, 2019); mixed models were run in package lme4 (Bates et al., 2015).

2.3 | Interpreting harvest trends

Based upon Barnhurst (1986), Anderson and Lindzey (2005) and Wolfe et al. (2016), we summarize the predicted relationships between harvest metrics commonly collected by state agencies and mountain lion population trends in Table 1.

3 | RESULTS

There were 22,691 mountain lions (9133 females, 13,558 males) reported harvested in 10 U.S. states from 2007 to 2015 (Elbroch et al., 2022). We did not detect any change in the average age of mountain lions killed in any age class over time (all *p*-values $>$ 0.6) (Table S1 and Figure S1 in the Supporting Information). When age classes were ignored, we did not detect any changes in the proportions of overall males to females harvested over time (p = 0.94; Table S2 in the Supporting Information). When age class was included, we detected significant trends in proportional changes in age-sex classes of mountain lions harvested over time (all $p < 0.002$) (Table S3 in the Supporting Information). In particular, there were increases in the proportion of subadult males and subadult females harvested over time with concomitant decreases in the proportion of adult males and subadult females harvested (Figure 1).

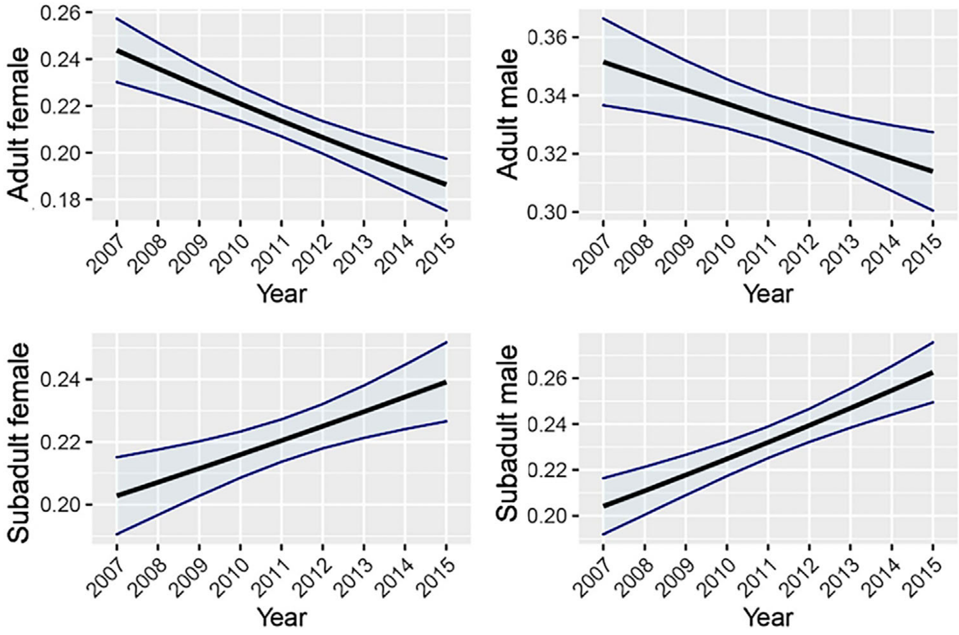

FIGURE 1 Modelled trends in the proportion of each age-sex class in harvested mountain lions from 2007 to 2015 in seven western USA states (Colorado, Idaho, North Dakota, Nevada, Oregon, Washington, Wyoming) using a generalized linear model and associated confidence intervals

4 | DISCUSSION

We found ambiguity when interpreting harvest indices to determine the current population trend for the U.S. mountain lion population. Three hunting metrics indicated that the metapopulation was declining (declining adult male harvest, increasing subadult female harvest and increasing overall subadult harvest). Two metrics could be interpreted as support for either an increasing or decreasing metapopulation (increasing subadult male harvest and decreasing adult female harvest) (Anderson & Lindzey, 2005; Barnhurst, 1986; Cooley et al., 2009). One metric, the average age of cats harvested over time, indicated that the mountain lion metapopulation is stable. The average age of mountain lions killed across the west during the study period remained at approximately 3.26 years, which is only slightly below the average age of mountain lions in "lightly hunted" populations (Cooley et al., 2009). This ambiguity in harvest trends may indicate that some metrics better reflect carnivore population dynamics than others (Robinson & DeSimone, 2011; Wolfe et al., 2016), or that harvest metrics are a poor method for monitoring carnivore abundance, or that harvest indices are better suited for monitoring smaller geographies because of variability in ecology and hunting regulations and more. This ambiguity may also fuel conflict between different stakeholder groups with different views of mountain lions (e.g. elk and mountain lion hunters; Mitchell et al., 2018, mountain lion advocates and agency biologists; Cain & Mitchell, 2018; HSUS, 2017).

There is some evidence that hunting increases the percentage of young mountain lions in populations, and our results suggest that this may be occurring within the U.S. metapopulation. These changes may impact mountain lion social systems that negatively impact mountain lion abundance or fitness (Elbroch et al., 2017; Maletzke et al., 2014; Packer et al, 2009) and may impact human–mountain lion interactions as well (e.g. decreasing human safety and increasing conflicts with livestock; Mattson et al., 2011; Peebles et al., 2013). Mountain lion populations, however, can recover from heavy hunting pressure in as little as 2–7 years (Anderson & Lindzey, 2005; Proffitt et al., 2020; Stoner et al., 2006), if they are connected to other mountain lion populations that support immigration.

Currently, mountain lion management is not conducted at the national scale, but maintaining an awareness of metapopulation trends may be useful for wide-ranging species that occur at low densities. As hunting metrics provide ambiguous or unreliable indicators of mountain lion population dynamics or abundance (Robinson & DeSimone, 2011; Wolfe et al., 2016), we suggest that state wildlife managers consider collaborating on an integrated population model approach to monitor U.S. mountain lions. Integrated population models can include multiple types of data and are particularly well suited to analysing variable, sparse datasets and creating precise parameter estimates (Arnold et al., 2018; Horne et al., 2019). To build such a model, analysts would require states to collect the same harvest data – specifically age- and sex-specific harvest metrics, and consistent metrics for hunter effort and success (while accounting for variation due to local hunting regulations) – in combination with survival probabilities for representative individuals tracked in ongoing research projects across states (e.g. Montana Fish, Wildlife & Parks, 2019).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Mark Elbroch and Hugh Robinson conceived the project. Connor O'Malley gathered the data, and Lisanne Petracca analysed the data. All authors wrote the manuscript.

DATA AVAILABILITY STATEMENT

Data archived with Figshare: https://doi.org/10.6084/m9.figshare.19641381 (Elbroch et al., 2022).

PEER REVIEW

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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