

Estimating Mountain Lion Abundance in Arizona, 2004-2016 Using Harvest Records

Comment [ERubin1]: Perhaps consider something like "Estimating Mountain Lion Abundance in Arizona Using Harvest Records"

F. Peck, A. Howard, M. Clement, E. Rubin
Arizona Game and Fish Department

INTRODUCTION

Monitoring the status of wildlife populations is an important component of wildlife management, especially for species managed for harvest. In many cases, it is possible and sufficient to monitor the status of a population using data on numbers, ages, and sex of individuals harvested. This approach has been used by the Arizona Game and Fish Department (AZGFD) in monitoring populations of mountain lions (*Puma concolor*) at a statewide scale. Managers have collected age and sex data on harvested animals via mandatory check-in by hunters, and have used these data collectively to monitor the general status of the population to guide sustainable harvest of this species. Anderson and Lindzey (2005) evaluated this approach experimentally in Wyoming and concluded that age and sex data on harvested mountain lions could be used effectively to inform an adaptive management framework for managing harvest thresholds. (has anyone else used this for same purpose for lions?, if so add citations as appropriate)

Although AZGFD has effectively used this approach to guide decisions related to mountain lion harvest, harvest data have only been used to monitor mountain lion population trends, and not to generate absolute population estimates. However, to address additional management needs, such as those related to predator-prey relationships, and to address stakeholder questions about the number of mountain lions in the state, managers sought an absolute population estimate for mountain lions in Arizona.

Estimates of population size have previously been generated for mountain lions via a variety of techniques. A common approach for generating an absolute population estimate has been the application of mark-recapture techniques using actual capture of mountain lions (Lambert et al. 2006), or via genetic "marking" and "recapture" using tissue, scat, or hair samples (Russell et al. 2012, Davidson et al. 2014,

[Beausoleil et al. 2016](#)). Other researchers have generated a minimum population estimate via genetic sampling of scat or hair ([Gilad et al. 2011](#), [Naidu et al. 2011](#), [Sawaya et al. 2011](#)), unique identification of tracks ([Germaine et al. 2000](#), [Rosas-Rosas and Bender 2012](#)), or identification of mountain lions via use of remote cameras ([Smythe 2008](#), [Rosas-Rosas and Bender 2012](#)).

While these methods have become well established, they are labor intensive and generally require extensive field work for data collection. Yet, they have been successfully implemented, typically within a particular geographic area (e.g., a mountain range) or within a single population ([Laundré et al. 2007](#), [Kelly et al. 2008](#), [Negrões et al. 2010](#)). Often, multiple years of data collection are necessary for producing an estimate that may quickly be outdated, requiring additional large investments to provide updated estimates. These shortcomings made these methods impractical for our needs. In Arizona, mountain lions are found in nearly all parts of the state, and the AZGFD sought a method for estimating population size for the entire state. In addition, we sought a method that allowed population estimates to be updated annually, to maximize their use in guiding management decisions and setting yearly harvest thresholds.

To accomplish this goal, we applied virtual population analysis (VPA), also known as cohort analysis, in an age-structured population reconstruction method using harvest data from 2004 through 2016 to generate population estimates for mountain lions in Arizona. VPA was first used in fisheries management where catch data are accessible but other traditional methods of abundance estimation are difficult to apply (Fry 1949, Gulland 1965, Skalski et al. 2005). In recent years, population reconstruction methods have been used to examine population trends in a variety of species such as greater sage-grouse (*Centrocercus urophasianus*; [Broms et al. 2010](#)), martens (*Martes americana*; [Skalski et al. 2011](#)), and turkeys (*Meleagris gallopavo*; [Clawson 2015](#)). When auxiliary data such as overall survival rates and information on cause of mortality have been incorporated into the analysis, these methods have also been used to generate absolute population estimates ([Gove et al. 2002](#), [Broms 2007](#), [Clawson et al. 2013, 2016](#)). The objective of this project was to generate absolute statewide population estimates for mountain lions in Arizona using available harvest data and information on survival and cause-specific mortality.

METHODS

Data

We used age-at-harvest data for mountain lions collected by AZGFD during 2004-2016. In Arizona, successful hunters are required to register harvested mountain lions within 10 days of harvest, at which time a premolar tooth is pulled. Hunters were required to mail teeth to AZGFD during 2004-2005 and to physically check-in animals with AZGFD during 2006-2016. Age-at-harvest was determined using cementum annuli analysis conducted by Matson's Laboratory (Manhattan, Montana). In addition, livestock operators are required to report depredation-related removals of mountain lions to AZGFD, although teeth are generally not collected from these animals. Mountain lions are occasionally removed due to public safety concerns, and these are also reported to AZGFD. Mountain lions killed by vehicles, recovered from poachers, or otherwise encountered after death are intermittently reported to AZGFD. For this study, we constructed the age-at-harvest data solely from hunter-harvested, depredation-related, and public-safety removal mountain lions because they are consistently reported to AZGFD. We excluded other categories because they were not reliably reported and our analysis methods assume that harvested animals are reported accurately. However, we accounted for these additional categories of mountain lion losses by incorporating estimates of non-harvest mortality rates into our analyses.

We used data on the fate of mountain lions fitted with Global Positioning System (GPS) collars to generate survival estimates. A total of 137 animals were monitored by AZGFD and other researchers between July 2003 and October 2017 during several independent studies in Arizona. Animals were collared in 8 of 15 counties in Arizona. When a collar emitted a mortality signal or GPS data indicated a mortality, researchers investigated to assign a cause of death to the animal.

We also obtained estimates of non-harvest mortality rates from published literature covering hunted mountain lion populations in the Southwest USA. We used scientific search engines to locate peer-reviewed papers that provided estimates of non-harvest mortality rates among hunted populations of mountain lions. We excluded studies of non-hunted populations because we were interested in populations in which mortalities were due to both harvest and non-harvest causes. Similarly, we excluded studies from outside Arizona, southern

Comment [ERubin2]: You may be able to improve on the wording in this sentence, but my point for this addition is to make sure that reader doesn't think that we ignored these lion losses. It also provides a transition to the next paragraph.

Comment [ERubin3]: Instead of "survival", would it be accurate to say "non-harvest mortality rates" (this would also then be consistent with the next paragraph)

California, Nevada, Utah, Colorado, New Mexico, and west Texas because mountain lion mortality causes and rates could differ substantially in dissimilar habitats.

Analysis

We used a virtual population analysis to estimate abundance from age-at-harvest data and survival estimates, using methods developed by Gulland (1965). Essentially, the population is divided into harvest-mortality and non-harvest-mortality animals, with the assumption that all harvest-mortality animals are reported to AZGFD, while non-harvest-mortality animals are typically unreported. We estimated abundance by summing the number of harvest-mortality animals, and then used survival estimates to adjust this tally to account for non-harvest-mortality animals.

Under this approach, harvest data were organized into a year by age-at-harvest table. From 2006 to 2016, 75% of animals were aged, while during 2004-2005, only 47% of animals were aged. We assumed that the unaged animals were a random sample of all animals, and therefore we completed the life table by assigning ages to the unaged animals according to the age distribution of the aged animals reported in each year. We then summed harvest data within each cohort to obtain year- and age-specific abundance estimates harvest estimates.

For incomplete cohorts, it is necessary to estimate the number of animals alive in the most recent year (2016). To do this, we first estimated the harvest mortality rate for age class j ,

$$\hat{M}_j = \sum_i h_{i,j} / \sum_i \hat{N}_{i,j}$$

where $h_{i,j}$ is the number of harvested animals in year i and age class j , and $\hat{N}_{i,j}$ is the estimated size of the cohort. For the incomplete cohorts, we then estimated cohort size using the known harvest data and the estimated harvest mortality rate, so that

$$\hat{N}_{last,j} = h_{last,j} / \hat{M}_j$$

where 'last' indicates the most recent year. Once cohort size is estimated for incomplete cohorts, annual abundance of harvest-mortality animals can be estimated by summing across cohorts within each year to obtain annual abundance of harvest mortality animals. These abundance estimates are often termed minimum known

Comment [ERubin4]: Just wondering.... Did we use the age distribution from each year to do this (or with years combined)? Reason I ask is that I was reading Anderson and Lindzey 2005 and they mentioned that age composition of harvest changed under different hunt strategies. If we had changes in hunt pressure from year to year, this could have had effect on age composition from year to year.?

Comment [AH5]: We used the age distribution from each year

Comment [ERubin6]: ok

Comment [ERubin7]: Is this wording correct? Seems that a tally just tells us what was harvested. Or is this sentence perhaps simplifying and combining several steps? If it is indeed generating an "abundance" then is this just an abundance if harvest was the only cause of mortality?

Comment [ERubin8]: "...of harvest-mortality animals" only?

population estimates, but in this case, we excluded known individuals with mortality types that are not consistently reported, such as vehicle collisions and poached animals. Thus, these abundance estimates are less than the minimum known population.

The above abundance estimates are clearly lower than the true abundance because they are based only on harvested animals. To increase the accuracy of these estimates, we adjusted the year by age-at-harvest table to account for additional mortality of non-harvested animals. For the oldest age class, we assumed that total mortality is 1 and we adjusted the harvest to estimate cohort size according to

$$\hat{N}_{i,old} = \frac{h_{i,old}}{\left(\frac{\mu_{H,old}}{\mu_{H,old} + \mu_N} \right)}$$

where ‘old’ indicates the oldest age class, μ_N is the instantaneous ‘natural’ (non-harvest) mortality rate, and μ_{H_j} is the instantaneous harvest mortality rate, which is estimated by $-\ln(1 - M_j)$. It should be evident that a higher non-harvest mortality rate yields a higher estimated cohort size. For all other age classes, $\mu_{H_{j-1}}$ is estimated (using numeric methods) from

$$\frac{N_{i,j}}{h_{i-1,j-1}} = \frac{(\mu_{H_{j-1}} + \mu_N) e^{-(\mu_{H_{j-1}} + \mu_N)}}{\mu_{H_{j-1}} (1 - e^{-(\mu_{H_{j-1}} + \mu_N)})}$$

and cohort size during the previous year, $N_{i-1,j-1}$, is estimated from

$$N_{i-1,j-1} = N_{i,j} e^{(\mu_{H_{j-1}} + \mu_N)}$$

Again, the larger μ_N , the more that the counts of harvested animals need to be adjusted to account for non-harvest mortality, resulting in a larger estimated cohort size. Again, for incomplete cohorts, the number of animals alive in the most recent year must be estimated from harvest and non-harvest mortality rates (see Skalski et al. 2005 for details). After generating year- and age-specific abundance estimates, annual abundance can be obtained by summing across cohorts.

Comment [ERubin9]: For all animals (including harvest and non-harvest animals?) And should this be “non-harvest” rather than “natural”?

Comment [AH10]: It is referring to non-harvest mortality rate but Skalski uses the terminology “instantaneous natural mortality rate.” If we are reporting it from Skalski, quoting him, and using his formula and symbols, can we change it? If we do change it, do we need to add a note referencing how it is referred to in the Skalski literature?

Comment [ERubin11]: See if my addition of quotes and “non-harvest” in parentheses helps.

These calculations required that we have an estimate of the non-harvest mortality rate. We obtained one estimate of the non-harvest mortality rate from the 137 mountain lions fitted with GPS collars in Arizona. We used a nest survival model to estimate daily survival rates for mountain lions (Johnson 1979, Rotella 2016). We then converted the daily survival estimate to an annual mortality rate and used this in the Gulland estimator described above. Because we were interested in non-harvest mortality, we right-censored harvested animals, as well as capture mortalities and animals removed to support a bighorn sheep reintroduction project. We estimated survival rates using the RMark package (Laake 2013) to interface with Program MARK (White and Burnham 1999) in Program R (R Core Team 2016). We also generated abundance estimates using survival rates and non-harvest mortality rates from previously published research on hunted populations in the Southwest USA.

RESULTS

During 13 years (2004-2016), 3,835 harvest mortalities were reported to AZGFD. Considering only these harvested animals, the minimum known population has increased by 1.4% per year over the past 13 years, with an average of 1,299 animals (Figure 1). However, this number excludes both a small number of reported mortalities due to vehicle strikes and poaching, and an unknown number of other non-harvest mortalities.

Using the nest survival analysis, we estimated that the annual non-harvest mortality rate for 137 animals with GPS collars was 19.1% per year (SE = 3.6%). Using this value for μ_N in the Gulland estimator increased the estimate of the average population size to 2,683 (Figure 1). Our literature search revealed four previous studies that provided mountain lion mortality data from hunted populations in the Southwest (Cunningham et al. 2001, Stoner et al. 2006, McKinney et al. 2009, Young et al. 2010; Table 1). A review of these published estimates of non-harvest mortality rates yielded estimates between 9.0% and 18.0% (Table 1). We used these values to generate additional estimates of abundance (Figure 1). [The 16 mountain lions reported in McKinney et al. \(2009\) represent a subset of our larger dataset.](#)

Comment [ERubin12]: I'm not seeing this in the graph. There are periods when the estimate appears to be decreasing (e.g., between 2006 and 2012, and again after 2015). I'm assuming that the '1.4% per year' may have come from fitting a regression line to these data?...If so, is this the slope of that line?
If so, would it be more accurate to say something like "Considering only these harvested animals, abundance estimates averaged 1,299 animals during 2004-2016 and increased from an estimated X animals in 2004 to X animals in 2016, representing an average increase of 1.4% per year"?

DISCUSSION

The availability of age-at-harvest data makes age-structured population reconstruction methods appealing where traditional population estimation techniques are impractical. When considering only data from harvested animals, our analyses indicated that during 2004 – 2016 the average population of mountain lions was 1,299 animals with a slightly increasing population trend. However, this number is known to underestimate the population because it doesn't account for mountain lions that died of non-harvest causes (Skalski et al. 2005). We therefore incorporated information on non-harvest mortality to increase accuracy of our estimate (Gulland 1965, Skalski et al. 2005). Using mortality data from collared mountain lions, the average population size during this same period is 2,683 mountain lions, also showing a slowly increasing trend with the population approaching 3,006 animals in recent years. Additional abundance estimates generated with published mortality data from prior studies in Arizona and other parts of the Southwestern USA fell between these two values (Figure 1).

Data from collared animals and published mortality data came from various geographic areas, from studies implemented for other purposes. Patterns of mortality likely differ among populations of mountain lions, based on hunter access and other risk factors; however, using a range of documented non-harvest mortality rates, our analysis provides strong evidence that the mountain lion population in Arizona has averaged between 1,299 and 2,683 during the past 13 years. Importantly, our analyses suggest that the population has been stable, and possibly increasing slightly, indicating that the population, at a state-wide scale, has been harvested at sustainable levels.

Recent advances in population reconstruction modeling (Clawson et al. 2015, 2016) will allow us to further refine our population estimates over time while continuing to make use of harvest data collected on an annual basis. The incorporation of updated data on natural (non-harvest) mortality rates has been shown to

Comment [ERubin13]: Please see question about this in the results section.

Comment [AH14]: Would this be a good place to also mention that future estimates could apply sex-specific and age-specific survival rates?

Comment [ERubin15]: I'm not really sure, but I'd guess that we'd be limited more by our data rather than by the available methods. We'd still need to have good survival data (from the field) for males and females, as well as different age classes? (...no reconstruction models will provide a substitute for good field data)

Unless there additional methods that would allow us to use our existing dataset in additional ways to get these sex- and age-specific rates? Matt, what do you think?

increase the precision of abundance rates (Clawson et al. 2013, Clawson 2015), while additional years of harvest data will also result in improved population estimates for this long-lived species (Skalski et al. 2005). Future estimates would also be improved by the incorporation of auxiliary survival data collected at the same spatial extent as our intended area of inference. Our current statewide estimate is based on a range of survival estimates from studies conducted in smaller geographies within and outside of Arizona, but future estimates including those for specific management units, would best be generated using survival data representing the same geographic area (Gove et al. 2002).

MANAGEMENT IMPLICATIONS

Virtual population analysis can be conducted annually to incorporate current harvest data to update abundance estimates. It can be tailored to the specific harvest and auxiliary data that wildlife management agencies have available and can be used to evaluate and refine management approaches.

Hunter harvest data are easy to collect, relatively low cost, and frequently collected by wildlife managers (Skalski et al. 2005). However, there are some limitations to applying VPA to age-at-harvest data. For a longer lived species such as mountain lions, more recent cohorts will not have entirely passed through the population so final cohort abundance must be estimated. Therefore, the earlier years of cohort data will be more complete than more recent years, making estimates generated from earlier years of harvest data more accurate than those generated with recent (less complete) years of data.

Population reconstruction models provide a convenient and flexible framework for estimating abundance at large spatial scales such as in our study, where other traditional approaches such as mark-recapture methods may not be practical. Our analyses produced a statewide estimate that will be useful in monitoring statewide trends in population abundance but may not be appropriate for making inferences at a smaller scale. However, mountain lion management generally occurs at smaller geographic scales, such as zones or game management units. It may therefore be useful to estimate abundance based on more spatially

refined harvest units in which informed management decisions can be made. In Arizona, the use of VPA will be investigated to estimate abundance of mountain lions within smaller geographic areas, such as mountain lion management zones, to inform management decisions at the most appropriate scale.

Acknowledgements

Data were kindly provided by Dave Conrad, Brian Jansen, Andrew Jones, and Dan Sturla from AZGFD, Kirsten Ironside from U.S. Geological Survey, and Kerrie Nicholson from University of Arizona. Financial support for the development of the mountain lion VPA methodology that we used was provided by AZGFD. XX. AZGFD, provided helpful comments on an earlier draft of this paper.

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Comment [ERubin16]: Check the journal instructions for format of citations. Typically, the title of the paper only has a capital at the beginning of the first word (no other caps). Also, journal info usually looks more like: ".....Journal of Mammalogy 89(2):408-418" Sometimes they don't want the issue number ("2" in this situation) (I'd suggest fixing formatting throughout the lit cited)

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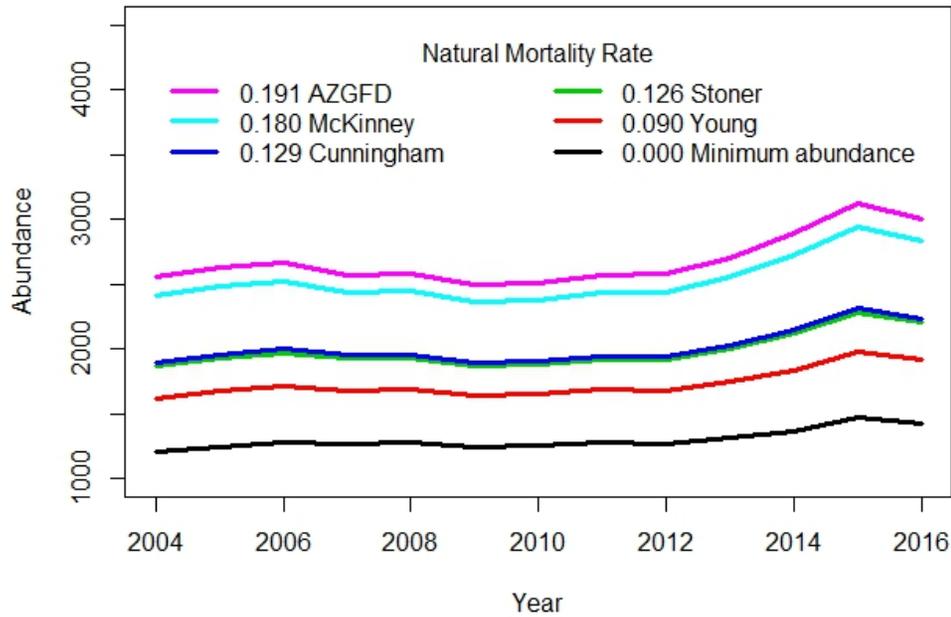
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Table 1: Sources of estimates of non-harvest mortality rates.

Source	Location	No. of lions	Non-harvest mortality rate	Notes
Cunningham et al. 2001	SE Arizona	24	12.9%	
Stoner et al. 2006	S-Central Utah	110	12.6%	We combined estimates from two study sites.
McKinney et al. 2009	N-Central Arizona	16	18.0%	We combined estimates from two study sites.
Young et al. 2010	W Texas and SE New Mexico	60	9.0%	We combined estimates from three study sites.

Figure 1: Estimated abundance of mountain lions (*Puma concolor*) in Arizona, 2004-2016, using a range of non-harvest mortality rates.



Comment [ERubin17]: A couple of comments:
 1. Need to change the title of the graph to "non-harvest" (within the graph) or take it out completely because the legend will include this information.
 2. In the graph, I'd also suggest changing the "0.000 Minimum abundance" line to something else because we already stated in the text that we believe that this is lower than a minimum estimate. Perhaps something like "0.000 (estimate if harvest was the only cause of mortality)"? ...or maybe you can come up with something better.
 3. I'd suggest being consistent in how the mortality rates are shown. For example, here the AZGFD rate is shown as 0.191, while in the text it's referred to as "19.1%".

DRAFT