Estimating Mountain Lion Abundance in Arizona, 2004-2016

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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. Lindzey et al. (1992) and Anderson and Lindzey (2005) evaluated this approach experimentally in Utah and 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 quotas.

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 mark-recapture techniques using actual capture of mountain lions (Ross and Jalkotzy 1992, Lindzey et al. 1994, Lambert et al. 2006), or via genetic “marking” and “recapture” using tissue, scat, and/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. Previous applications have typically been limited to 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). For long-term monitoring efforts, the costs of these intensive methods are prohibitive. 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 frequently updated annually, to maximize their use in guiding management decisions in a timely manner 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 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 and maintained 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. Tooth submission was voluntary from 2003-2004, but mandatory during 2006-2016. 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. A smaller number of 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. Instead, we accounted for these additional categories of lion losses by incorporating estimates of non-harvest mortality rates into our analyses.

We also used data on the fate of mortality data from 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 with the expectation that mortality rates would differ from those in Arizona. Similarly, we excluded studies from outside Arizona, southern California, Nevada, Utah, Colorado, New Mexico, and west Texas because on the grounds that 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 preliminary year- and age-specific abundance estimates that do not yet account for non-harvested animals.

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 $j$,

$$
\hat{M}_j = \frac{\sum h_{x,j}}{\sum \hat{N}_{x,j}}
$$
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
\[
\hat{N}_{\text{last},j} = h_{\text{last},j} / \hat{M}_j
\]
where ‘last’ indicates the most recent year. Once cohort size is estimated for incomplete cohorts, abundance can be estimated by summing across cohorts within each year to obtain annual abundance of harvest-mortality animals only. These abundance estimates are often termed minimum known 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 inflated 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 inflated the harvest to estimate cohort size according to
\[
\hat{N}_{\text{old}} = \frac{h_{\text{old}}}{\mu_{H_{\text{old}}} + \mu_N}
\]
where ‘old’ indicates the oldest age class, $\mu_N$ is the instantaneous ‘natural’ (non-harvest) mortality rate, and $\mu_{H_j}$ 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, $\mu_{H_{i+1}}$ is estimated (using numeric methods) from
\[
\frac{N_{i,j}}{h_{i+1,j}} = \left(\mu_{H_{i+1}} + \mu_N\right)e^{-\left(\mu_{H_{i+1}} + \mu_N\right)}
\]
where $N_{i,j}$ 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.
and cohort size during the previous year, \( N_{t,j-1} \), is estimated from

\[
N_{t+1,j-1} = N_{t,j}e^{(\mu_{t+1} - \mu_t)}
\]

Again, the larger \( \mu_t \), the more that the counts of harvested animals need to be inflated-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.

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 big-horn 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 U.S.

RESULTS

Over 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 \( \ln(1-0.191) \) for \( \mu_o \) 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 (xxx, xxx, xxx; Table 1). A review of these published estimates of non-harvest mortality rates yielded estimates ranging between 9.0% and 18.0% (Table 1). We used these to generate additional estimates of abundance (Figure 1).

**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 improve our estimates (Gulland 1965, Skalski et al. 2005). Using mortality data from collared mountain lions, the average estimated population size during this same period is 2,683 mountain lions. Our results suggest, also showing a slowly increasing trend with the estimated population approaching reaching 3,060 animals in the most recent years. Additional abundance estimates generated with published mortality data from published prior studies in Arizona and other parts of the U.S. Southwestern population estimates 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 we estimate that the mountain lion population in Arizona has averaged between 1,299 and 2,683 during the past 123 years. Importantly, our analyses demonstrate we 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 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).

We believe our approach was useful for initial model development, and offers a foundation on which future modeling efforts can be built. While there are some limitations with using harvest only data, this estimate currently provides the best scientifically sound statewide estimate of abundance and will be useful in monitoring population status and trends. When paired with additional auxiliary information, the abundance estimate should become more reliable and precise. Our next step will likely involve the consideration of models that incorporate additional inputs such as reporting rates and hunter effort, and offer the potential to estimate sex- and age-specific survival rates.
additional parameters of interest such as survival rates, annual recruitment, and harvest probabilities. Though this model only uses one survival rate for both sexes and all age classes, we know that survival varies for males and females across age classes (Feeske et al. 2011, Ruth et al. 2011, Clark et al. 2014). Future models could apply sex-specific and age-specific survival rates to generate a more robust abundance estimate.

The non-harvest natural mortality rate we generated from data on collared animals in the annual mortality analysis for Arizona was higher than estimates we included from other southwestern states, however, it is consistent with non-harvest natural mortality rates reported from Arizona (Table 1; Cunningham et al. 2001, McKinney et al. 2009). Although we produced abundance estimates using other non-harvest natural mortality rates to show the likely range of abundance, we feel confident that the estimated abundance using Arizona non-harvest natural mortality rates most likely represents mountain lion abundance statewide. We also believe the model to be reliable in predicting changes to the population because the observed decrease in abundance from 2006-2012 coincides with an increase in hunter harvest trends from 2005-2011.

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 generally already 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. For newly proposed Mountain Lion Management Zones in which harvest thresholds will be established,

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 rigorous surveys or long-term, expensive mark-recapture methods may not be practical. It also allows wildlife managers to monitor changes in abundance over time and predict population trajectory by estimating both past and present population abundance (Clawson et al. 2016). Hunter harvest data are easy to collect, relatively low cost, and can provide crucial information on survival, recruitment, sex and age composition, and abundance (Skalski et al. 2005). Population reconstructions methods can be used in conjunction with indices or radio-telemetry studies to refine the accuracy of abundance estimates and investigate the effects of management actions.

Virtual population analysis can be conducted annually, or any other desired length of time, to incorporateing 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. In Arizona, VPA is currently underway to estimate abundance for newly proposed

Comment [ERubin58]: It does not provide survival data (especially not for the non-harvest component)
Comment [ERubin59]: ? as demonstrated by us (and previous researchers)?
Comment [ERubin60]: Indices for what?
Comment [ERubin61]: Perhaps give an example!
Mountain Lion Management Zones in which harvest thresholds will be set for each management zone based on abundance estimates in each zone.

Acknowledgements

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Literature Cited


Vol. 78, No. 6, pp. 1104-1114.


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

<table>
<thead>
<tr>
<th>Source</th>
<th>Location</th>
<th>No. of lions</th>
<th>Non-harvest mortality rate</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cunningham et al. 2001</td>
<td>SE Arizona</td>
<td>24</td>
<td>12.9%</td>
<td></td>
</tr>
<tr>
<td>Stoner et al. 2006</td>
<td>S-Central Utah</td>
<td>110</td>
<td>12.6%</td>
<td>We combined estimates from two study sites.</td>
</tr>
<tr>
<td>McKinney et al. 2009</td>
<td>N-Central Arizona</td>
<td>16</td>
<td>18.0%</td>
<td>We combined estimates from two study sites.</td>
</tr>
<tr>
<td>Young et al. 2010</td>
<td>W Texas and SE New Mexico</td>
<td>60</td>
<td>9.0%</td>
<td>We combined estimates from three study sites.</td>
</tr>
</tbody>
</table>
Figure 1: Estimated abundance of mountain lions (Puma concolor) in Arizona, 2004-2016, using a range of non-harvest mortality rates.

Comment [MC66]: Eventually, let me know if journal allows color, what file formats they accept, and what resolution/dimensions they require.

Comment [MC67]: See next page for alternate figure.

Comment [ERubin68]: 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%”.

Comment [MC69]: “Non-harvest Mortality Rate” is intended to be the legend title, not the figure title. I could add a box around the legend, although I generally find that busy-looking.
Figure 1: Estimated abundance of mountain lions (Puma concolor) in Arizona, 2004-2016, using a range of non-harvest mortality rates.