INTRODUCTION

One of the most challenging aspects of mountain lion (*Puma concolor*) management is that abundance and density are difficult to estimate because of their elusive behavior, solitary nature and propensity for nocturnal movements. In Arizona, their distribution in rugged terrain and wide dispersal across the state make them a difficult population to study at large spatial scales. The high cost of field-intensive, long-term research projects is another limitation, making efforts to count every mountain lion logistically impractical or economically prohibitive. As an alternative to direct counts, indices and noninvasive sampling are widely used as alternative methods to survey mountain lion populations. Track counts, remote cameras, and genetic analysis of scats have been used to estimate local abundance in Arizona (Germaine et al. 2000, Smythe 2008, Naidu et al. 2011), but there are limitations to extrapolating these estimates to the statewide population (Long et al. 2003, CMGWG 2005, Choate et al. 2006). Consequently, wildlife managers may use expert opinion, numbers of mountain lion sightings, depredation incidents, and harvest as proxies for population size and trend (Martorello et al. 2006). However, these are not ideal methods for evaluating mountain lion populations because sighting reports can be unreliable and harvest information generally are not sensitive to small-to-moderate population changes over a short period of time.
In Arizona, statewide mountain lion abundance and survival is poorly understood and studies of survival and abundance have been limited in scope and sample size. Cunningham et al (2001) estimated low rates of survival (0.62) for a heavily exploited population of radio-collared mountain lion adults for southeastern Arizona and found it was one of the lowest in the country. McKinney et al (2009) compared estimated rates of survival in radio-collared mountain lions in 2 different study sites in north-central Arizona for 2006 and 2007. Survival rates ranged from 0.50 to 1.0 during that time period with combined rates of survival for the two years estimated at 0.40 for the Payson site and 0.55 for the Prescott site (McKinney et al 2009).

Given the shortcomings of indices and the increased public scrutiny of wildlife management, there is a need for reliable and affordable techniques to monitor population trends for mountain lions, especially for those in hunted populations (e.g., Anderson and Lindzey 2005). Currently, in Arizona, sex and age structure derived from harvested mountain lions is used to monitor trends in age and sex ratios but modern analytical developments offer additional opportunities for assessment (Gove et al. 2002, Skalski et al. 2005b). In this paper, we use statistical population reconstruction models of Fry (1949) and Gulland (1965) as reported by Skalski (2005a & b) using age-at-harvest data from 2004 through 2015 to estimate a range of total abundance for mountain lions statewide.

Statistical population reconstruction (SPR), also known as cohort analysis, is an age-structured population reconstruction method that uses age-at-harvest data to reconstruct cohort abundance over time and sums across cohorts to estimate animal abundance (Skalski 2005b). SPR was first used in fisheries management where catch data are accessible but other traditional methods of abundance estimation are difficult to apply. More recently, SPR has been applied to a variety of mammals including mountain lions (Clawson), black bear (Skalski 2005b), martens, (Skalski 2011), elk (Gove et al. 2002), moose (Ueno et al 2009), and black-tailed deer (Skalski et al 2005c).
METHODS

Data

We used age-at-harvest data for mountain lions collected and maintained by AZGFD from 2003-2016. 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 2003-2005, but mandatory from 2006-2016. Age-at-harvest was determined using cementum annuli analysis (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 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.

We also used mortality data from GPS-collared mountain lions to generate survival estimates. A total of 143 GPS collars were affixed to 137 animals by AZGFD (and XXX) between July 2003 and October 2017 during several independent studies in Arizona. Animals were collared in XX of 15 counties in Arizona. When a collar emitted a mortality signal, staff investigated and assigned a cause of death to the animal.

We also obtained estimates of natural 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 natural mortality rates among wild populations of mountain lions. We excluded studies of non-hunted populations 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 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 natural-mortality animals, with the assumption that all harvest-mortality animals are reported to AZGFD, while natural-mortality animals are unreported. We can estimate abundance by summing the number of harvest-mortality animals, and then use survival estimates to inflate this tally to account for natural-mortality animals.

Under this approach, harvest data was organized into a year by age-at-harvest table. From 2004 to 2016, 74% of animals were aged, while in 2003, only 1.4% 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. We then summed harvest data within each cohort to obtain year- and age-specific abundance 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 $j$,

$$\hat{M}_j = \frac{\sum h_{i,j}}{\sum \hat{N}_{i,j}}$$

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

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

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. 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 account for this, we inflated the year by age-at-harvest table to account for non-harvested animals. For the oldest age class, we assume that total mortality is 1 and we inflate the harvest to estimate cohort size according to

$$\hat{N}_{old} = \frac{h_{old}}{\mu_{H}_{old} + \mu_N}$$

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

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

and $N_{j+1,j-1}$ is estimated from

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

Again, the larger $\mu_N$, the more that the counts of harvested animals need to be inflated to account for natural 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 natural 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 require that we have an estimate of the natural mortality rate. We obtained one estimate of the natural mortality rate from the 143 GPS collars deployed by AZGFD. 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 natural mortality, we right-censored harvested animals, as well as capture mortalities and 26 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).

RESULTS
Over 14 years, 3,976 harvest mortalities were reported to AZGFD. Considering only these harvested animals, the minimum known population has been relatively steady over the past 14 years, averaging 1,213 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 natural mortalities.

Using the nest survival analysis, we estimated that the annual natural mortality rate for 137 animals with GPS collars was 19.1% per year (SE = 3.6%). Using this value for \( \mu_n \) in the Gulland estimator increased the estimate of the average population size to 2,451 (Figure 1). A review of published estimates of natural mortality rates yielded estimates between 9.0% and 18.0% (Table 1). We translated these into additional estimates of abundance (Figure 1).

DISCUSSION
Annual survival estimates in the current study were found to be higher than those reported for Arizona by either Cunningham et al (2001) or McKinney et al (2009). The sample size in the current study represents the statewide harvest of mountain lions for 2004–2016 of 204-304 mountain lions with a mean annual harvest of 253 mountain lions, compared to 24 lions reported by Cunningham et al (2001) and 16 lions in the McKinney et

Annual survival estimates and a range of abundance were calculated for mountain lions statewide from 2004–2016. Annual survival estimates were similar for males and females and are within range of those reported for other states by Cunningham et al (2001). The range of annual survival rates reported by Cunningham et al (2001) is found in Table 4.

While there are some limitations with using harvest only data, these estimations currently provide previous unknown statewide estimates of abundance and survival and will be useful in monitoring population trends. The availability of age-at-harvest data makes population reconstruction methods appealing where mark and recapture and visual count surveys are difficult, impractical, or impossible.

The abundance estimates from the Fry VPA analysis tend to underestimate abundance so these estimates are thought to be conservative and represent minimum numbers. The value of these estimates lies in providing a baseline for monitoring trend and informing management.

Anderson and Lindzey (2005) reported that while research suggests that mountain lion populations can sustain harvest rates of up to 20-30%, harvest effects will differ depending on the age and sex of mountain lions removed. Harvest of males and sub-adult females will have less of an impact on the population because males are replaced by immigration while females are replaced by female young produced in the population.

In this analysis, only hunter harvest mortality is reviewed. Reviewing 2003–2015 for mountain lion mortalities other than hunter kills (i.e., Department nuisance removals, reported natural mortality, vehicle mortalities, and
illegal kills), these other mortalities accounted for less than 1% of total mountain lion mortality (Table 6). Mortality type as a function of survival may provide additional information on which to make informed mountain lion population management decisions.

**MANAGEMENT IMPLICATIONS**

Population reconstruction models provide a flexible framework for estimating abundance at large spatial scales, where traditional surveys or long-term, expensive mark-recapture methods may not be practical. It also allows wildlife managers to monitor changes in abundance over time 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, 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.

SPR models can be tailored to the specific harvest and auxiliary data that wildlife management agencies have available.

Population reconstruction can be conducted annually, or any other desired length of time, incorporating current harvest data to update abundance estimates. It can be used as an additional tool to monitor changes in mountain lion populations from year-to-year and to refine management approaches. In Arizona, SPR is currently underway to estimate abundance and survival rates for newly proposed Mountain Lion Management Zones in which harvest thresholds will be set for each management zone based on zone population estimates.
Literature Cited


Table 1: Sources of estimates of natural mortality rates.

<table>
<thead>
<tr>
<th>Source</th>
<th>Location</th>
<th>No. of lions</th>
<th>Natural 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, 2003-2016.