Mountain Lion Predation of Translocated Desert Bighorn Sheep in Arizona

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Abstract
We analyzed data for 422 unmarked and 369 radiocollared desert bighorn sheep (Ovis canadensis) translocated into vacant historical habitats in 12 Arizona locations between 1979 and 1995. We evaluated factors potentially influencing predation of radiocollared desert bighorn sheep by mountain lions (Puma concolor) by determining relationships between predation rates, number released, size of releases, escape terrain, available terrain (escape terrain as a percentage of area with slopes ≥40°), habitat quality associated with release locations, and mule deer (Odocoileus hemionus) and predator abundance. We hypothesized that numbers of radiocollared animals released, quality of habitat and available terrain associated with release locations, and relative abundance of mule deer influenced predation of translocated desert bighorn sheep by mountain lions. (WILDLIFE SOCIETY BULLETIN 34(6):1255–1263; 2006)

Key words
Arizona, bighorn sheep, habitat, mountain lion, mule deer, Odocoileus hemionus, Ovis canadensis, predation, Puma concolor, reintroduction, translocations.

Desert bighorn sheep (Ovis canadensis) translocation programs in North America were initiated in the 1950s to augment and reestablish populations in areas of their historic range (Krausman and Shackleton 2000). Most reintroductions in Arizona, USA, have occurred since 1979 (Kamler et al. 2002). In general, many translocations have been successful but others have failed, and causes of failure are poorly understood (Douglas and Leslie 1999, McKinney et al. 2003). Disease, dispersal, predation, and presence of cattle have been cited as potential causes of translocation failures (Rominger et al. 2004). Also, habitat quality potential varies considerably among locations selected for translocations (Cunningham 1989), possibly further affecting restoration efforts.


Our objective was to evaluate factors potentially influencing mountain lion predation of radiocollared desert bighorn sheep translocated into vacant historical habitats in Arizona. Information about variables affecting predation ostensibly would benefit management efforts to restore extirpated desert bighorn sheep populations.

Study Areas
We compiled data for 12 areas comprised of mountain ranges where unmarked and radiocollared desert bighorn sheep were translocated in Arizona between 1979 and 1995 (Tables 1, 2). Locations of central, northeast, northwest, and southwest regions where translocations occurred in this study were presented previously (Kamler et al. 2002). We combined translocations into 2 regions: central–southwest (C–S) and northwest–southeast (N–S), based on regional differences in survival and mountain lion predation of bighorn sheep (Kamler et al. 2002) and vegetation types where translocations occurred (Table 1). Moreover, preliminary analyses indicated likely differences between these regions for mountain lion and mule deer harvest data and mule deer surveys (Arizona Game and Fish Department [AZGFD] 2004), thus suggesting regional differences in abundance.

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Table 1. Locations of desert bighorn sheep translocations for central-southwest (C–S) and northwest-southeast (N–S) regions, mountain ranges, number of releases (no. releases), years, and vegetation types in which releases occurred in Arizona, USA, between 1979 and 1995.

<table>
<thead>
<tr>
<th>Region</th>
<th>Mountain range</th>
<th>No. releases</th>
<th>Years of releases</th>
<th>Vegetation type</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Granite Wash</td>
<td>1</td>
<td>1994</td>
<td>Upper Sonoran Desert scrub</td>
</tr>
<tr>
<td></td>
<td>Sauceda</td>
<td>1</td>
<td>1993</td>
<td>Upper Sonoran Desert scrub</td>
</tr>
<tr>
<td></td>
<td>Peloncillo</td>
<td>2</td>
<td>1986, 1990</td>
<td>Chihuahuan Desert scrub</td>
</tr>
</tbody>
</table>

Translocation areas included in our analyses (Tables 1, 2) were Black, Buckskin, Gila Bend, Granite Wash, Harcuvar, Mazatzal, Sauceda, and Superstition mountains (C–S region), and Galilio, Peloncillo, and Virgin mountains, Grand Wash Cliffs, Kanab Creek, Paria River, and Vermillion Cliffs (N–S region). Number of releases, years, and vegetation types in which releases occurred varied among translocation sites (Table 1). We categorized Black, Buckskin, and Harcuvar mountains, and Paria River and Vermillion Cliffs, as single translocation sites (Tables 1, 2) due to proximity of mountain ranges or release sites to each other. Mazatzal and Superstition mountains also were adjacent to each other but we assumed movements of desert bighorn sheep and mountain lions between these areas were restricted by a series of reservoirs along the Salt River (McKinney et al. 2001, AZGFD 2005) and kept them as discrete populations. We assumed desert bighorn sheep populations inhabiting mountain ranges >15 km apart were fragmented by distance and represented discrete populations (i.e., they were not metapopulations characterized by intermountain movements of sheep [Bleich et al. 1990, 1996]).

In general, vegetation in Upper Sonoran Desert scrub regions was diverse and dominated by taller plant growth forms than other areas of our study. Vegetation in Great Basin Desert scrub and Mojave Desert scrub regions was characterized by relatively low diversity of plant species and predominantly low plant growth forms. Vegetation in Chihuahuan Desert scrub regions tended to be relatively diverse and may have more abundant taller plant growth forms than regions other than Upper Sonoran Desert scrub (Brown 1994; Table 1). Selection of translocation sites was based on rankings of local habitat characteristics, including available water, cover, habitat discreteness, human disturbance, potential interspecific competition, and topography (Cunningham 1989, Kamler et al. 2002). Translocations of desert bighorn sheep in Galilio and Virgin mountains involved release from enclosures (Cunningham et al. 1989), but translocations at all other sites incorporated direct releases into selected habitats.

Methods
Adult or yearling desert bighorn sheep were captured between 1979 and 1995 by darting, drop-netting, or aerial net-gunning (deVos et al. 2000). We analyzed deaths of translocated radiocollared desert bighorn sheep due to mountain lion predation in relation to numbers of translocated radiocollared desert bighorn sheep, escape terrain, and available terrain (escape terrain area as a percentage of area with slopes ≥40%) within the 2 regional groups (Table 2), as

Table 2. Locations of desert bighorn sheep translocations for central-southwest (C–S) and northwest-southeast (N–S) regions; mountain ranges, number of unmarked (TR), radiocollared (RC), and total animals released, mortalities due to mountain lions (MM); escape terrain area (ET; km²), and available terrain (PL; escape terrain area as a percentage of areas with slopes ≥40%) in Arizona, USA, 1979–1995.

<table>
<thead>
<tr>
<th>Region</th>
<th>Mountain range</th>
<th>TR</th>
<th>RC</th>
<th>Total</th>
<th>MM</th>
<th>ET</th>
<th>PL</th>
</tr>
</thead>
<tbody>
<tr>
<td>C–S</td>
<td>Black-Butchskin-Harcuvar</td>
<td>28</td>
<td>41</td>
<td>69</td>
<td>9</td>
<td>73.2</td>
<td>25.9</td>
</tr>
<tr>
<td></td>
<td>Gila Bend</td>
<td>29</td>
<td>18</td>
<td>47</td>
<td>0</td>
<td>62.4</td>
<td>31.3</td>
</tr>
<tr>
<td></td>
<td>Granite Wash</td>
<td>13</td>
<td>17</td>
<td>30</td>
<td>4</td>
<td>18.6</td>
<td>44.2</td>
</tr>
<tr>
<td></td>
<td>Mazatzal</td>
<td>28</td>
<td>23</td>
<td>51</td>
<td>7</td>
<td>14.9</td>
<td>28.0</td>
</tr>
<tr>
<td></td>
<td>Sauceda</td>
<td>16</td>
<td>30</td>
<td>46</td>
<td>7</td>
<td>65.9</td>
<td>25.2</td>
</tr>
<tr>
<td></td>
<td>Superstition</td>
<td>105</td>
<td>53</td>
<td>158</td>
<td>10</td>
<td>51.9</td>
<td>41.5</td>
</tr>
<tr>
<td></td>
<td>Galilio</td>
<td>38</td>
<td>31</td>
<td>69</td>
<td>4</td>
<td>1.4</td>
<td>25.9</td>
</tr>
<tr>
<td>N–S</td>
<td>Grand Wash Cliffs</td>
<td>55</td>
<td>28</td>
<td>83</td>
<td>2</td>
<td>837.7</td>
<td>80.5</td>
</tr>
<tr>
<td></td>
<td>Kanab Creek</td>
<td>32</td>
<td>31</td>
<td>63</td>
<td>2</td>
<td>176.9</td>
<td>53.2</td>
</tr>
<tr>
<td></td>
<td>Paria River-Vermillion Cliffs</td>
<td>36</td>
<td>16</td>
<td>52</td>
<td>0</td>
<td>80.6</td>
<td>63.3</td>
</tr>
<tr>
<td></td>
<td>Peloncillo</td>
<td>4</td>
<td>42</td>
<td>46</td>
<td>4</td>
<td>17.6</td>
<td>33.3</td>
</tr>
<tr>
<td></td>
<td>Virgin</td>
<td>38</td>
<td>39</td>
<td>77</td>
<td>5</td>
<td>188.9</td>
<td>43.8</td>
</tr>
<tr>
<td>Totals :</td>
<td></td>
<td>422</td>
<td>569</td>
<td>971</td>
<td>54</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
well as in relation to regional indices of habitat quality of release locations and abundance of mountain lions and mule deer. We limited analyses of deaths associated with mountain lion predation or other causes to data from radiocollared desert bighorn sheep.

About 47% of translocated desert bighorn sheep were radiocollared prior to release and generally were located at least once per month following release using aerial telemetry. Radiocollars were equipped with mortality sensors; dead animals were located as soon as possible and cause of death was determined based on examination of carcasses (Kamler et al. 2002).

We defined escape terrain as slopes ≥60% plus a contiguous 150-m buffer zone (McCarty and Bailey 1994, Douglas and Leslie 1999) with 40–60% slopes, and we defined available terrain as areas of potentially suitable terrain available to desert bighorn sheep. We quantified these parameters using a Geographic Information System (McKinney et al. 2003).

Harvest levels and permits issued for mule deer within game management units (AZGFD 2004, 2005) were based on results of standardized annual surveys (Rabe et al. 2002). We indexed relative abundance of mule deer and hunting pressure (Marshall et al. 2002) using sport harvest and hunting permits issued, respectively, between 1979 and 1995 in each region. Data for calculating indices of mule deer abundance and hunting pressure were based on harvests, number of hunter days, and hunting permits issued in game management units associated with each region (AZGFD 2004; AZGFD, unpublished data). Annual mule deer hunting seasons were between late October and late November (AZGFD 2005). We analyzed previously reported results of track surveys conducted between 1986 and 1999 (Shaw et al. 1988, Cunningham et al. 1995, Beier and Cunningham 1996, McKinney et al. 2006) to index relative mountain lion abundance by regions.

We used standard linear regression models to determine relationships between deaths of marked animals due to mountain lion predation numbers of radiocollared animals released, and escape and available terrain. We used 2 × 2 contingency tables and Yates’ corrected chi-square analyses or the Fisher exact test, 2-tailed t-tests, and 90% confidence intervals (CI; McBride et al. 1993, Zar 1999, Johnson 2009, Vaske et al. 2002) to compare sex ratios and sizes of desert bighorn sheep releases, proportions of radiocollared individuals released, mortalities due to mountain lions, and escape and available terrain.

We also used 90% CI and t-tests to compare habitat evaluation scores for release locations (AZGFD, unpublished data) calculated following Cunningham (1989), abundance of mule deer (harvest/100 hunter days, harvest/permit/yr), hunting pressure (permits issued), and mountain lion track densities between regions. We estimated effect sizes following Gliner et al. (2001) and Vaske et al. (2002). We calculated Akaike’s Information Criterion (AIC; Anderson et al. 2000) for models evaluating relationships between number of radiocollared animals killed by mountain lions versus number of radiocollared animals translocated for all locations combined and C–S and N–S regions.

Calculation of AIC values for different data sets does not allow selection of a best approximating model or ranking of models between data sets (Anderson and Burnham 2002). Akaike’s Information Criterion can be viewed as a model selection routine, or it might be viewed as a form of sensitivity analysis or estimation of magnitude of effects (Guthery et al. 2005). Information-theoretic methods such as AIC avoid statistical hypothesis testing and focus on relationships of variables and estimation of effect size and measures of precision, providing concepts of best inference relative to a given data and the set of a priori models (Anderson et al. 2000).

We analyzed data from 791 desert bighorn sheep (422 unmarked and 369 radiocollared) translocated between 1979 and 1995 (Table 2); 46 translocations averaged 17.8 animals (range = 1–46; SD = 9.52), 11.6% of releases consisted of ≤5 animals, and 52.2% of releases consisted of <20 animals. We analyzed data from 22 translocations (11–46 radiocollared sheep/release; 1–8 M, 7–39 F) between November 1980 and November 1995 in the C–S region, and from 24 translocations (1–31 radiocollared sheep/release; 0–9 M, 0–17 F) between November 1979 and November 1995 in the N–S region.

Results

We estimated 14.6% (54/369) of radiocollared animals died due to mountain lion predation (Table 2); 75.0% (39/52) were killed ≤1 year of release. Most known causes of death from factors other than sport hunting were due to predation by mountain lions (64% of deaths), followed by accidents and natural causes (20%), disease (11%), and bobcat (Lynx rufus) or coyote (Canis latrans) predation (5%). Mountain lions accounted for 88% of predation-related deaths. Numbers of animals killed by mountain lions were positively correlated with numbers of radiocollared desert bighorn sheep released (F1, 10 = 7.64, r2 = 0.433, P = 0.020, b = 0.63; AIC = 24.52) for all locations combined, and for C–S (F1, 4 = 8.83, r2 = 0.6881, P < 0.042, b = 0.83) and N–S (F1, 4 = 16.14, r2 = 0.8014, P < 0.016, b = 0.9) regions separately. Comparison of associations between these variables for the regions using AIC suggested the C–S region model (AIC = 11.47) might provide a better separation of information (structure of relationship) and noise (residual variation left unexplained; Anderson et al. 2000) but does not indicate priority of an approximating model, compared to the N–S region model (AIC = 19.83).

Similar proportions of translocated desert bighorn sheep were radiocollared (Yates corrected χ2 = 0.42, df = 1, P > 0.515) in the C–S (49.7%) and N–S (50.1%) regions. Total number of radiocollared desert bighorn sheep released was comparable in C–S (n = 182) and N–S (n = 187) regions (Table 2). Mean numbers of animals per release did not differ (t = 1.169, df = 41, P > 0.249) between C–S (mean = 21.1, 90% CI = 17.3–24.9, CV = 0.48) and N–S (mean = 15.9, 90% CI = 13.4–18.5, CV = 0.52) regions. Percent of
releases comprised of ≤5 animals tended to be lower (Fisher exact test, \( P = 0.061 \)) in the C–S region (0%) than in the N–S region (11.6%), but percent of releases comprised of <20 animals for these regions did not differ (45.0 and 60.0%, respectively; Fisher exact test, \( P > 0.752 \)).

The sex ratio for translocated animals was lower (Yates corrected \( \chi^2 = 3.78, \text{df}=1, P < 0.052 \)) in the C–S region (105:311 M:F) than in the N–S region (119:256 M:F). Proportions of radiocollared males and females killed by mountain lions did not differ for all translocations (Fisher exact test, \( P > 0.195 \)) or within regions (Fisher exact test, \( P ≥ 0.174 \)), and females comprised 93% and 76% of kills made by mountain lions in the C–S and N–S regions, respectively. The number of radiocollared desert bighorn sheep killed by mountain lions (Table 2) was greater (Fisher exact test, \( P < 0.002 \)) for the C–S region (20.3%) than for the N–S region (9.1%).

Mean escape terrain was more than 4-fold higher in the N–S region (mean = 217.2 km\(^2\), SE = 128.13, 90% CI = 41.0–475.4 km\(^2\)) than in the C–S region (mean = 47.8 km\(^2\), SE = 10.23, 90% CI = 27.2–627.6 km\(^2\)), but means did not differ (\( t\)-test with separate variance estimates: \( t = 1.318, \text{df} = 5.06, P = 0.244 \); \( F \) ratio of variances = 156.96, \( P < 0.001 \)). Mean available terrain tended to be lower (\( t\)-test with separate variance estimates: \( t = 1.956, \text{df} = 6.02, P = 0.094 \); \( F \) ratio of variances = 5.99, \( P < 0.072 \); effect size = 1.00) in the C–S region (mean = 32.7%, \( SE = 3.35, 90\% \text{ CI} = 25.9–39.4\% \)) than in the N–S region (mean = 50.0%, \( SE = 8.20, 90\% \text{ CI} = 35.5–66.5\% \)). Mean areas of escape and available terrain for all locations combined were 132.5 km\(^2\) (90% CI = 13.3–251.7 km\(^2\); \( CV = 0.58 \)) and 43.8% (90% CI = 34.6–53.1%; \( CV = 2.47 \)), respectively, and these parameters for all locations combined were positively correlated with each other (\( F_{1,10} = 10.16, r^2 = 0.5039, P < 0.01, b = 0.71 \)).

Numbers of radiocollared desert bighorn sheep killed by mountain lions were not correlated with escape terrain area (Table 2) for all locations combined (\( F_{1,10} = 0.79, r^2 = 0.0732, P > 0.395, b = -0.28 \)) or for C–S (\( F_{1,4} = 0.07, r^2 = 0.0165, P > 0.808, b = 0.13 \)) and N–S (\( F_{1,4} = 0.21, r^2 = 0.0498, P > 0.670, b = -0.23 \)) regions. Numbers of radiocollared desert bighorn sheep killed by mountain lions tended to be positively correlated with available terrain area (Table 2) for all locations combined (\( F_{1,10} = 3.44, r^2 = 0.2558, P < 0.094, b = -0.51; AIC = 28.12 \)), but not for the individual regions (\( F_{1,4} = 3.6, r^2 ≤ 0.4739, P = 0.13, b ≤ -0.08 \)).

Mean habitat evaluation score for release locations tended to be lower (\( t = 1.856, \text{df} = 9, P < 0.097, \text{effect size} = 1.04 \)) in the C–S region (mean = 42.9, SD = 6.12, 90% CI = 38.4–47.4) than in the N–S region (mean = 49.0, SD = 2.94, 90% CI = 45.5–52.5). Mean harvest of mule deer/100 hunter days between 1979 and 1995 was nearly 2-fold higher (\( t\)-test with separate variance estimates: \( t = 5.846, \text{df} = 20.75, P < 0.001 \); \( F \) ratio of variances = 6.587, \( P < 0.001 \); effect size = 1.42) in the N–S region (mean = 8.61/100 hunter days, SD = 2.415, 90% CI = 7.58–9.63/100 hunter days) than in the C–S region (mean = 4.93/100 hunter days, SD = 0.941, 90% CI = 4.53–5.33/100 hunter days). Mean number of mule deer hunting permits issued was higher (\( t = 6.152, \text{df} = 32, P < 0.001, \text{effect size} = 1.45 \)) for the C–S region (mean = 4,127 permits, SD = 788.96, 90% CI = 3,793–4,461 permits) than for the N–S region (mean = 2,529 permits, SD = 724.36, 90% CI = 2,222–2,836 permits). Mean number of mule deer harvested per year did not differ (\( t = 0.403, \text{df} = 32, P = 0.696 \)) between the C–S region (mean = 772/yr, SD = 162.96, 90% CI = 650–788/yr) and the N–S region (mean = 753/yr, SD = 193.51, 90% CI = 640–804/yr). Mean mule deer harvested per permit per year differed (\( t\)-test with separate variance estimates: \( t = 5.294, \text{df} = 23.03, P < 0.001 \); \( F \) ratio of variances = 4.432, \( P < 0.006 \); effect size = 1.54) between the C–S region (mean = 0.13/permit/yr, SD = 0.03, 90% CI = 0.17–0.20/yr) and the N–S region (mean = 0.3/permit/yr, SD = 0.07, 90% CI = 0.27–0.32/permit/yr).

We analyzed mountain lion track survey data for 10 locations (55 transect routes; 147 km surveyed) in the C–S region, and 9 locations (78 transect routes; 293 km surveyed) in the N–S region. Mean track densities (tracks/km) did not differ (\( t\)-test with separate variances: \( t = 0.744, \text{df} = 11.52, P > 0.471 \)) between C–S (mean = 0.09 tracks/km, SD = 0.113, 90% CI = 0.027–0.159 tracks/km) and N–S (mean = 0.06 tracks/km, SD = 0.041, 90% CI = 0.039–0.099 tracks/km) regions.

**Discussion**

Mountain lions are likely the only predators capable of causing substantial mortality in bighorn sheep populations that occupy suitable habitats (Sawyer and Lindzey 2002). Mountain lion predation appears to have hampered desert bighorn sheep translocation efforts in Arizona, Colorado, New Mexico, Texas, and Utah (Krausman et al. 1999, Rominger et al. 2004). Survival of radiocollared bighorn sheep in Arizona declined between 1992 and 1997 compared to earlier periods in Central and Southwest, but not in Northwest and Southeast regions of the state. Mountain lions accounted for 95% of predation-related mortalities among all regions between 1979 and 1995. Mountain lion predation increased during 1992–1997, compared to earlier periods, in Central, Southeast, and Southwest, but not in Northwest regions (Kamler et al. 2002). Releases in both regions consisted of similar proportions of radiocollared individuals.

We found that mountain lion predation accounted for deaths of >14% of radiocollared desert bighorn sheep between 1975 and 1995. Overall, most known causes of mortality (64%) were from mountain lion predation, which accounted for 88% of predator-related deaths. Our results suggest that predation of radiocollared desert bighorn sheep in C–S (20%) and N–S (9%) regions generally were within reported ranges of predation in extant and translocated populations. Mountain lion predation as cause of death of radiocollared desert bighorn sheep in extant populations ranged from about 23–90% (Bristow and Olding 1998, Rominger and Weisenberger 1999, Schaefer et al. 2000).
Logan and Sweanor 2001), and ranged from about 20–39% of translocated radiocollared bighorn sheep (Creeden and Graham 1997, Kamler et al. 2002, Rominger et al. 2004). Mortalities due to mountain lion predation were independent of abundance of the predator, sex of prey, size of releases, and escape terrain. Wildlife managers use sport and depredation harvests and track surveys to index trends of mountain lion populations, but track surveys may provide the better method (Beier and Cunningham 1996). However, sample sizes for the track surveys we analyzed might be adequate to detect only large differences (e.g., >30%) in relative abundance of mountain lions (Beier and Cunningham 1996). Assuming the track surveys we analyzed were representative of regional abundance, we suggest relative abundance of mountain lions likely was not a factor affecting regional differences in predation of desert bighorn sheep. Other surveys using searches for tracks and other signs, trained hounds, and remote cameras suggested very low abundance of mountain lions in the southwestern portion of the Southwest region, but presence of mountain lions was documented in Hacaruvar and Saucedo mountains (Germaine et al. 2000), where desert bighorn sheep were translocated during the present study.

Consistent with our findings, predation of desert bighorn sheep by mountain lions might be independent of predator abundance (Logan and Sweanor 2001). Predation, thus, may be more a function of learned behavior by individual predators (Hoban 1990, Ross et al. 1997, Logan and Sweanor 2001, Ernest et al. 2002) and relative availability of prey, primarily mule deer (Leopold and Krasuman 1986, Rominger and Weisenberger 1999, Rosas-Rosas et al. 2003, Rominger et al. 2004). Mountain lions killed radiocollared female and male desert bighorn sheep in our study in proportion to availability and did not select for prey of either sex. Results of most studies indicate similar numbers of kills of female and male desert bighorn sheep by mountain lions (Bristow and Olding 1998, Hayes et al. 2000, Schaefer et al. 2000, Logan and Sweanor 2001). However, prey selection of bighorn sheep by mountain lions may differ among studies in different locations, and prey-class vulnerability might be a function of behavior of individual predators (Ross et al. 1997, Mooring et al. 2004).

About half of the releases in our study consisted of <20 desert bighorn sheep per release, below the recommended level of ≥20 animals/ translocation in direct releases (Rowland and Schmidt 1981, Wilson and Douglas 1982). Numbers per release of <20 animals were not different between regions. Vigilance of individual bighorn sheep decreases when they are in groups of >5, but collective vigilance of the group increases. Individual vigilance increases in groups of <5 animals, but risk of predation is greater for smaller groups and is greatest for groups of <5 animals (Berger 1978, Mooring et al. 2004). No releases of ≤5 animals occurred in the C–S region, where predation of radiocollared desert bighorn sheep by mountain lions was higher, compared to the N–S region, where predation was lower but 20% of releases consisted of ≤5 animals. Thus, releases of group sizes ≤5 and <20 animals likely did not influence regional differences in mountain lion predation.

Bighorn sheep anti-predator strategy consists largely of placing visual obstacles in the path of pursuing predators, a strategy that closely links their distribution to narrow areas around escape terrain (Geist 1999, Krausman et al. 1999). This strategy likely is most effective against coursing predators, such as wolves (Canis lupus; Geist 1999) and coyotes (Bleich 1999). In contrast, mountain lions are stalking and ambushing predators that can use rugged cliffs, shrubs, and trees as visual cover when stalking prey—suggesting escape terrain might provide limited benefit to bighorn sheep in avoidance of predation by mountain lions (Mooring et al. 2004). Lack of correspondence between mountain lion predation and escape terrain in our study also might have derived from differences between use of escape terrain by recently translocated animals, compared to apparent use by established populations (McKinney et al. 2003). Only Galvuro Mountains provided <15 km² of escape terrain suggested as a minimum requirement for translocating desert bighorn sheep into vacant, historically occupied habitats (McKinney et al. 2003). Use of escape terrain by translocated desert bighorn sheep, particularly ≤1 year postrelease, probably primarily reflected use of comparatively limited, localized areas independent of total escape terrain in a mountain range. Escape terrain had low priority in a model of critical habitat for desert bighorn sheep in southern California (Turner et al. 2004).

In contrast to mountain lion abundance, sex of prey, size of releases, and escape terrain, results led us to believe number of radiocollared animals released, habitat quality associated with release locations, available terrain, and abundance of mule deer likely were variables that affected regional differences in mountain lion predation of translocated radiocollared desert bighorn sheep. Numbers of radiocollared desert bighorn sheep killed by mountain lions in our study were positively correlated with numbers of collared animals translocated for all locations combined and for C–S and N–S regions separately, suggesting mountain lion predation was a function of numbers of marked animals translocated. However, mountain lions killed more radiocollared animals in the C–S region than in the N–S region. Higher predation in the C–S region was associated with fewer releases of <5 bighorn sheep, and lower indices of available terrain, habitat quality, and mule deer abundance, compared to the N–S region.

We are unable to definitively explain the positive correlations between numbers of radiocollared desert bighorn sheep translocated and predation by mountain lions, and for regional differences in mortalities due to predation. We postulate that higher numbers of animals released ostensibly corresponded with increased exposure to predators. Broad exploratory and movement patterns following reintroductions might influence predation of translocated desert bighorn sheep by mountain lions within both regions. Most animals killed by mountain lions in our study died <1
year postrelease. Desert bighorn sheep often explore, travel long distances, or disperse from release sites within the first several months to a year following translocations, and movements may be extensive (Remington and deVos 1985, Cunningham et al. 1989) through areas that may or may not include escape terrain (Elenowitz 1984) or comparatively dense brush (deVos et al. 1981, deVos 1982, Remington 1983). This behavior ostensibly influences vulnerability of translocated desert bighorn sheep to predation by mountain lions (Rominger and Weisenberger 1999, Mooring et al. 2004), as well as coyotes (Bleich 1999).

Generally poorer habitat quality associated with translocation sites possibly was a factor contributing to higher predation in the C–S region than in the N–S region. Vegetation cover is a component of Cunningham’s (1989) habitat-rating system, and greater abundance of brushy, shrubby terrain contributes to a lower habitat-quality rating. Reduced visibility by bighorn sheep due to encroachment of large shrubs and trees, which likely were more abundant in habitats where desert bighorn sheep were translocated in the C–S region (Brown 1994), ostensibly contributed to a higher level of predation in the C–S than in the N–S region (Krausman et al. 1999, Rominger and Weisenberger 1999, Rominger et al. 2004).

Although we found available- and escape-terrain were positively correlated with each other, only available terrain likely was a factor affecting mountain lion predation. However, in our models of mountain lion predation for all locations combined, available terrain had lower priority than numbers of radiocollared animals released. Available terrain tended to be negatively correlated with number of bighorn sheep killed by mountain lions for all release locations combined, and tended to be lower in the C–S region, where mountain lion predation was higher, compared to the N–S region, where predation was less. Results suggested a tendency for mountain lion predation of radiocollared desert bighorn sheep following translocations to increase in areas with less available terrain. Explanation for this relationship is uncertain, but might involve a tendency for increased post-translocation movements of animals into unfavorable habitats when available terrain is comparatively low. Conditions such as greater distance from, or higher densities of taller vegetation away from escape terrain likely would increase predation risk if animals ventured into such areas.

Consistent with differences in available terrain in C–S (<33%) and N–S (50%) regions in our study, indices of abundance of total desert bighorn sheep, females, and lambs in 14 populations in Arizona also increased with greater areas of available terrain (McKinney et al. 2003). Also consistent with our indices of escape terrain and available terrain, desert bighorn sheep tend to be found most often <100 m from escape terrain and on slopes ≥40%, although this varies among studies, and they may be found on slopes that are less steep (Wakeling and Miller 1989, McCarty and Bailey 1994, Bristow et al. 1996, Etchberger and Krausman 1999).

Because higher available terrain indicates a greater landscape proportion of escape terrain, we suggest our findings (present data; McKinney et al. 2003) are consistent with a broadly accepted perception that escape terrain is a critical habitat component for desert bighorn sheep populations (Douglas and Leslie 1999, Krausman et al. 1999). Definitions of escape terrain in studies of desert bighorn sheep vary and potentially confound interpretations of relative importance, but escape terrain generally incorporate slopes ≥60% as a criterion (McCarty and Bailey 1994).

Mule deer occur throughout Arizona, except for the extreme southwestern corner of the state (Hoffmeister 1986), and are the primary prey of mountain lions (Anderson 1983, Iriarte et al. 1990). We assumed harvest indices provided valid measures of relative abundance of mule deer (Marshall et al. 2002), and these indicated lower abundance of mule deer in the C–S region than in the N–S region. More hunting permits were issued and more days were spent hunting in the C–S region, but sport harvest per 100 days and number of mule deer harvested per permit were higher in the N–S region. Total sport harvest of mule deer did not differ by region, indicating hunting effort was greater, but success per unit effort was lower, in the C–S region than in the N–S region.

Relative availability of mule deer also might influence predation of desert bighorn sheep by mountain lions (Leopold and Krausman 1986, Rominger and Weisenberger 1999, Rosas-Rosas et al. 2003). Effects of mountain lion predation on bighorn sheep potentially are limited to areas where bighorn sheep and mule deer are sympatric and where mule deer densities are adequate to provide a primary prey (Schaefer et al. 2000). In contrast, predation by mountain lions may not be a substantial mortality factor for bighorn sheep if densities of mule deer are above some threshold (Schaefer et al. 2000; references therein). Higher mountain lion predation of bighorn sheep in Arizona was associated with declining mule deer populations (Kamler et al. 2002).

Predation of bighorn sheep by mountain lions also appeared to increase with declining mule deer abundance in California (Holl et al. 2004), and mountain lion predation rates on desert bighorn sheep likely increased following decline of a mule deer population in New Mexico (Logan and Sweanor 2001). Relative scarcity of mule deer in relation to bighorn sheep in Mexico also might have caused mountain lions to shift to bighorn sheep as an alternative food source (Rosas-Rosas et al. 2003). Thus, we hypothesize that numbers of radiocollared animals released, habitat quality, available terrain on release locations, and abundance of mule deer influenced predation of translocated desert bighorn sheep by mountain lions.

Other variables we were unable to measure in our study also might have contributed to regional differences in mountain lion predation of translocated radiocollared desert bighorn sheep. Drought ostensibly results in removal of cattle and less abundant native prey, potentially resulting in mountain lions prey-switching to desert bighorn sheep (Rominger et al. 2004). Regional differences also might
occur in human development and activities (Krausman et al. 1999, Papouchis et al. 2001), possibly affecting abundance and exposure of desert bighorn sheep to predation.

Recent studies suggested mountain lion reductions might benefit small populations of bighorn sheep. Based on Monte Carlo simulations incorporating fecal DNA data, removal of 1–4 mountain lions/year in a 5-year period effectively reduced extinction risk for populations comprised of ≤30 female bighorn sheep (Ernest et al. 2002). Lethal removal of 12 mountain lions over 4 years in central Arizona was associated with lower predation of radiocollared animals, and higher indices of lamb production (lams counted/survey hr) and productivity (lams/100 F) of a small (<90) desert bighorn sheep population in central Arizona, despite continual years of drought (McKinney et al. 2006). Compared to predation of radiocollared desert bighorn sheep by mountain lions during 3 years prior to mountain lion reductions (67%), predation during 4 years following reductions (25%) declined. Compared to average lamb production (mean = 0.2/hr; range = 0–0.4/hr) and productivity (mean = 7 lams/100 F; range = 0–18.4 lams/100 F) during 4 years prior to reductions, these indices during 4 years following reductions increased >4-fold (mean production = 1.2/hr; range = 0.5–1.6/hr; mean productivity = 41 lams/100 F; range = 24–73 lams/100 F). In contrast, removal of 20 mountain lions between 1980 and 1983 in New Mexico apparently did not reduce the number of mortalities related to mountain lion predation in a population of about 20–30 desert bighorn sheep (Hoban 1990).

Management Implications

Assuming similar predation on uncollared and radiocollared animals (Rominger and Weisenberger 1999), we suggest predation by mountain lions was a substantial source of mortality among translocated desert bighorn sheep between 1979 and 1995, at least in some locations in Arizona. Conservation and management of mountain lions and their prey are ecologically complex issues involving biological, professional, and socio-political considerations (Ross et al. 1996, Douglas and Leslie 1999, Ballard et al. 2001, Casey et al. 2005). Understanding cause-specific mortality and survivorship in bighorn sheep populations likely would be useful in development of management objectives for re-establishing populations on vacant native ranges (Schaefer et al. 2000). Translocation of desert bighorn sheep likely would benefit from closer scrutiny of philosophy and protocols of management (Douglas and Leslie 1999) and ecological variables associated with proposed release sites (present data; McKinney et al. 2003). Our findings are in contrast to previous recommendations (Rowland and Schmidt 1981, Wilson and Douglas 1982) that direct translocations should consist of single groups of ≥20 desert bighorn sheep. Despite present findings, translocating desert bighorn sheep into smaller areas of habitat or escape terrain also likely is a dubious approach to achieving successful restoration (Douglas and Leslie 1999, McKinney et al. 2003). Moreover, our results suggest further research is needed to evaluate habitat quality, available terrain associated with release locations, and abundance of mule deer as factors potentially influencing predation by mountain lions and selection of sites for reintroductions of desert bighorn sheep.

Although controversy exists regarding predator control (Ballard et al. 2001), we propose translocation of desert bighorn sheep and localized, short-term removal of mountain lions potentially are viable tools in the conservation and management of these species. We suggest sport and depredation harvests of mountain lions, in the absence of specific harvest quotas such as recently enacted (AZGFD 2005), likely are inadequate to affect mountain lion abundance and predation of desert bighorn sheep on our study areas and in Arizona. Consistent with previous suggestions (Douglas and Leslie 1999, Kamler et al. 2002, Rominger et al. 2004), we propose management intervention of mountain lion predation on a case-by-case basis might benefit translocations of desert bighorn sheep in areas where habitat might be potentially unsuitable, or where populations of mule deer intrinsically are low or have undergone substantial decline.

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