AGE STRUCTURE, SURVIVAL, AND MORTALITY OF MOUNTAIN LIONS IN SOUTHEASTERN ARIZONA

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ABSTRACT—Reliable estimates of survival and mortality rates for mountain lions (Puma concolor) have been difficult to obtain because of their low densities and secretive behavior. We estimated annual survival and cause-specific mortality rates for a heavily exploited mountain lion population in southeastern Arizona from February 1991 to April 1994. We monitored 24 adult radio-collared mountain lions weekly. We used MICROMORT to determine daily, annual, and overall survival rates. Radio-collared mountain lions had low annual survival (0.62). Depredation control was the leading cause of mortality. Survival rates of female (0.67) and male (0.58) lions did not differ. Because of the high mortality in the area of depredation control, this area may represent a mortality sink.

RESUMEN—La medida de estimación segura de la supervivencia y mortalidad de grandes carnívoros como el león de montaña (Puma concolor) ah sido difícil de obtener por la baja densidad y el comportamiento secreto. Estimamos la supervivencia anual y la causa específica de la medida de mortalidad de una población de León de Montaña muy explotada en el sureste del estado de Arizona demes de Febrero 1991 a Abril 1994. Vigilamos 24 leones de montaña equipados con collares de frecuencia de radio, una vez por semana. MICROMORT fue usado para determinar la medida de supervivencia diaria, anual, y sobrtotal. Leones de montaña equipados con collars de frecuencia de radio en el área del estudio tuvieron una supervivencia anual baja (0.62). El control de depredación fue la mayor causa de mortalidad. La medida de supervivencia de las hembras (0.67) y machos (0.58) leones no diferenciaron. Porque la alta mortalidad en el área de depredacion controlada, creemos que esta área pueda representar una depreion en el nirel mortalidad.

In North America efforts to eradicate mountain lions (Puma concolor) began with the arrival of European settlers and their livestock. Control efforts were highest in Arizona between 1947 and 1969 when the legislature offered a bounty and 5,400 mountain lions were killed ($\bar{x} = 245$/year; Phelps, 1989). When mountain lions were classified as a game species in 1970, 4,962 mountain lions were harvested ($\bar{x} = 240$/year, range = 120 to 316) from 1970 until 1988 (Phelps, 1989). Depredation kills continued and 251 were taken from 1987 to 1993. The combined mean annual harvest (1970 to 1993) was only 5 less/year than the mean annual harvest when the bounty was offered.

During 1987, the Klondyke-Bonita Cattle Growers Association of southeastern Arizona reported that mountain lions killed more calves than in previous years. Consequently, they contracted with the Animal and Plant Health Inspection Service (APHIS), United States Department of Agriculture, to control mountain lions. From 1987 through 1989, 57 mountain lions were killed in an area of ca. 1,000 km². Ensuing public articles resulted in negative criticism of the control operation (B. Burkhart: Rancher, United States hunters kill wildlife without rein by State. Arizona Republic, 25 June 1989). Between 1988 and 1993, an additional 32 mountain lions were killed in or near (<10 km) the control area by sport hunters, and 26 more were killed in depredation cases. Ignoring natural mortality, 115 moun-
March 2001  Cunningham et al.—Survival of mountain lions  77

Fig. 1—Study area boundaries where mountain lion survival and cause-specific mortality rates were examined from February 1991 to April 1994 in southeastern Arizona.

mountain lions were killed in the Aravaipa-Klondyke area from 1988 to 1993.

The combined depredation control and sport hunting indicated the mountain lion population in the Aravaipa-Klondyke area appeared to be experiencing high mortality. Consequently, we estimated mountain lion survival and cause-specific mortality rates, and age structure in this population in southeastern Arizona during February 1991 through April 1994, and compared our findings with those obtained elsewhere in North America.

MATERIALS AND METHODS—We studied the mountain lion population in a 4,035 km² area in southeastern Arizona. The Aravaipa-Klondyke study area included most of the Aravaipa Creek watershed, portions of the San Carlos Indian Reservation, the Turnbull-Santa Teresa Mountain complex, much of the Galiuro Mountains, Aravaipa Canyon and Valley, and a small portion of the Eastern Pinaleño Mountains. We captured and radio-collared mountain lions from 3 areas (Fig. 1) with different programs for mountain lion control and management: 1) mountain lion depredation control and sport hunting (Commercial livestock section—1,150 km²); 2) no depredation control or mountain lion hunting (San Carlos Apache Indian Reservation—1,272 km²); and 3) only sport hunting (1,627 km²).

Elevations ranged from 750 to 2,300 m, with steep mountain ranges characterized by steep slopes, narrow canyons, and rugged cliffs. These formations merged downslope to comparatively level terraces.

<table>
<thead>
<tr>
<th>Interval</th>
<th>Males</th>
<th>Females</th>
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<tr>
<td></td>
<td>Survival rate</td>
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<tr>
<td>Autumn</td>
<td>1.0000</td>
<td>0.0000</td>
</tr>
<tr>
<td>November</td>
<td>0.9285</td>
<td>0.0686</td>
</tr>
<tr>
<td>Winter</td>
<td>0.6756</td>
<td>0.1000</td>
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<tr>
<td>Summer</td>
<td>0.9317</td>
<td>0.0663</td>
</tr>
<tr>
<td>Annual</td>
<td>0.5844</td>
<td>0.1054</td>
</tr>
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</table>

Results—We captured 24 adult mountain lions (≥1 year of age). Sex ratio of adults (13 males:11 females) was not different from 50:50 ($\chi^2 = 0.08, P = 0.77$). However, lions killed for depredation control were mostly males (16 males:7 females), but not different ($\chi^2 = 1.87, P = 0.17$) from 50:50 because of small sample size. More males were killed in the depredation program ($\chi^2 = 3.49, P = 0.12$) than those represented in the capture. The sex ratio of lions killed statewide for depredating cattle (31 males:15 females) during 1990 to 1995 was skewed towards males ($\chi^2 = 5.79, P = 0.02$).

Mean ages of captured adult mountain lions was 3.2 years versus 4.5 years for those killed for depredation control (no kittens were killed as part of depredation control). Age structure between the 2 groups was not different ($\chi^2 = 3.49, df = 4, P = 0.48$).

Radio-collared lions were monitored for survival for 10,132 radiodays (Table 1). Three lions died as a result of capture-related mortality and 3 males dispersed (dispersal rate = 0.185 ± 0.011); no females dispersed. Depredation control ($n = 8; rate = 0.197 ± 0.062$) was the largest cause of mortality. Other causes of mortality included sport harvest ($n = 2; rate = 0.083 ± 0.057$), intraspecific strife ($n = 2; rate = 0.051 ± 0.035$), and drowning ($n = 2; rate = 0.049 ± 0.033$). Because of small sample size, our power to detect differences between treatments was inadequate. Consequently, years were pooled, and we compared survival and cause-specific mortality estimates for all radio-collared mountain lions for each sex among seasons by Ztests (Nelson and Mech, 1986).

Female survival during winter (0.814 ± 0.097) was lower ($Z = 2.0, P < 0.05$) than dur-
ing autumn (1.00 ± 0.00); survival during other seasons did not vary (Table 1). Male survival was also lowest during winter (0.676 ± 0.1), and was different from November (0.929 ± 0.067; Z = 2.1, P < 0.05) and summer (0.932 ± 0.066; Z = 2.2, P < 0.05) survival rates. Overall, female (0.665 ± 0.124) and male (0.584 ± 0.105) annual survival rates did not differ (Z = 0.51, P = 0.53). Annual adult survival averaged 0.620 ± 0.077.

Overall survival for the 19 mountain lions monitored in the area of depredation control and sport hunting area was 0.55 ± 0.21 and depredation was the highest cause-specific mortality (0.35 ± 0.3). All male mountain lions monitored in this area dispersed (n = 3) or were killed in depredation cases (n = 6) and lived from 1 to 18 months before being killed. Mean annual survival of male mountain lions where depredation and sport hunting occurred was 0.44 ± 0.22, and the only cause of mortality was depredation. Only 2 of 8 females were killed in depredation cases in this area (0.2 ± 0.4); 1 was killed by a sport hunter (0.05), and another was killed by another mountain lion (0.05). Of the 6 mountain lions monitored where there was no control or sport hunting, annual survival was 0.53 ± 0.5; 1 was killed by another mountain lion, and 2 died in a flood.

DISCUSSION—This annual mountain lion survival rate (0.62) estimated for the heavily exploited population in southeastern Arizona was one of the lowest found in the literature (Table 2). Since the early 1970s the population we studied had a high mortality rate, with as many as 15 mountain lions killed annually for depredation control, in addition to sport kills and natural mortality (Cunningham et al., 1995). Survival analyses conducted elsewhere did not identify depredation control as a mortality factor; in southeastern Arizona, 8 of 14 mortalities were a result of depredation control efforts.

It is commonly held that sport hunting is the primary cause of mortality in hunted cougar populations (Ruth et al., 1998). Other than mortality due to unknown causes, Ruth et al. (1998) identified hunting as the primary cause of death in adult lions translocated to an area allowing sport harvest, although the human-related mortality rate (0.25) was similar to the rates due to intraspecific strife, prey capture, and bacterial infections (range 0.17 to 0.18). Adult lion mortality due to sport harvest in southeastern Arizona was lower (0.08) than that reported by Ruth et al. (1998). Our estimated mortality rate due to depredation control (0.35 in areas where depredation control was practiced) is greater than their reported human-related rate.

In unhunted populations, evidence indicates that intraspecific strife is the primary cause of lion mortality. Ruth et al. (1998) documented mortality rates from 0.08 to 0.19 in an unhunted lion population in New Mexico and in an isolated natural population, Sweanor (1990) reported that 94% of all lion deaths were from natural mortality, primarily from intraspecific strife (38%). In southern California, where there is no sport hunting, annual adult survival was estimated at 75% (P. Beier and R. Barrett, in litt.).

Hopkins (1989) reported that the average age of males (3.1 years) and females (4.3 years) in an unexploited population was higher than those found in moderately or heavily exploited populations. We did not find a similar difference; average age of captured adult males and

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**Table 2—Annual survival rates of mountain lions in the United States.**

<table>
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<tr>
<th>Location</th>
<th>Conditions</th>
<th>Survival rate</th>
<th>Reference</th>
</tr>
</thead>
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<tr>
<td>Arizona</td>
<td>Sport hunt/depredation control</td>
<td>0.55</td>
<td>This study</td>
</tr>
<tr>
<td>Utah</td>
<td>Sport hunt</td>
<td>0.68</td>
<td>Robinet et al., 1997</td>
</tr>
<tr>
<td>Nevada</td>
<td>Sport hunt</td>
<td>0.73</td>
<td>Ashman et al. unpubl. rep., 1983</td>
</tr>
<tr>
<td>Wyoming</td>
<td>Sport hunt</td>
<td>0.73–1.00</td>
<td>Logan et al., 1986</td>
</tr>
<tr>
<td>Utah</td>
<td>Unhunted</td>
<td>0.72</td>
<td>Lindsey et al., 1988</td>
</tr>
<tr>
<td>California</td>
<td>Unhunted</td>
<td>0.75</td>
<td>P. Beier and R. Barrett In litt.</td>
</tr>
<tr>
<td>Colorado</td>
<td>Unhunted</td>
<td>0.88</td>
<td>Anderson et al., 1992</td>
</tr>
<tr>
<td>New Mexico</td>
<td>Unhunted</td>
<td>0.86</td>
<td>Ruth et al., 1998</td>
</tr>
</tbody>
</table>
females was 2.7 and 4.1 years, respectively, whereas average age of depredation kills was 4.5 and 3.9 years, respectively. The age distribution of lions killed for depredations in our study areas was not different ($\chi^2 = 1.11$, $P = 0.77$) from that found in unexploited populations (Hopkins, 1989; Anderson et al., 1992; K. Logan, L. Sweanor, J. Smith, B. Spreadbury, and M. Hornocker, New Mexico Department of Game and Fish, in litt.). Possible explanations for the relatively old age distribution in this heavily exploited population include either a shifting of older age residents from adjacent areas in response to more favorable prey densities, and transients, particularly males, can be >3 years of age before establishing a territory in a large contiguous population (Cunningham et al., 1995).

We do not know if this mountain lion population can sustain the high mortality rates we observed. We believe the area is maintained by immigration, and represents a mortality sink (Pulliam, 1988). This constant immigration into the area could depress mountain lion populations nearby, and affect the social maintenance of territories and territory size. The effect on social maintenance of territories could be enhanced due to the increased risk of males in areas where depredation control is practiced. Fortunately, areas of high mountain lion removal such as in our study area are rare and fairly localized, and an overall statewide decline in mountain lion numbers has not been detected (Cunningham et al., 1995).

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LITERATURE CITED


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