MIGRATORY PATTERNS OF MOUNTAIN LIONS: IMPLICATIONS FOR SOCIAL REGULATION AND CONSERVATION

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We studied movements of mountain lions (*Puma concolor*) in the southern Sierra Nevada of California from 1992–1997. We observed two distinct patterns, which likely represent strategies of mountain lions for coping with variability in abundance of their primary prey, mule deer (*Odocoileus hemionus*). Some mountain lions migrated together, often slowly, following movements of mule deer from winter range toward the summer range of their prey. Those mountain lions remained together on the eastern scarp of the Sierra Nevada and overlapped in distribution throughout the year. Other mountain lions exhibited rapid movements to disjunct summer ranges, on the western side of the Sierra Nevada, shared with mountain lions that did not occur on their winter range. Mountain lions that moved more slowly and overlapped in distribution had large annual home ranges (95% adaptive kernel; $\bar{X}$ = 817 km^2), whereas mountain lions with distinct summer ($\bar{X}$ = 425 km^2) and winter ($\bar{X}$ = 476 km^2) distributions had smaller home ranges. Such disparate patterns of movement may lead to difficulties in sampling population size for mountains lions. Moreover, maintaining corridors that would allow for both patterns of movement may be critical for the conservation of these large felids. Finally, extensive overlap in the distribution of mountain lions, especially the association of one group of individuals on winter range and another on summer range for mountain lions with disjunct distributions, indicates a more flexible social system than previously described.

Key words: *Puma concolor,* mountain lion, home range, migration, conservation, behavior, social organization

Mountain lions (*Puma concolor*) that feed on nonmigratory populations of ungulates can have distributions and sizes of home ranges that change little over time (Hopkins, 1989; Sweanor, 1990). Nonetheless, populations of mountain lions that feed on migratory mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) exhibit seasonal movements, particularly elevational shifts, with those primary prey (Anderson et al., 1992; Rasmussen, 1941; Seidensticker et al., 1973). Most periodic movements noted in those studies, however, were gradual, and seasonal home ranges of mountain lions usually remained contiguous. Little attention has been given to the relatively long-range migrations made by some mountain lions within subpopulations or the potential significance of those movements between subpopulations.

Social regulation of mountain lions may occur in populations with high densities of prey as a result of territorial behavior among resident adults (Lindzey et al., 1994; Seidensticker et al., 1973). Those studies proposed that populations of mountain lions often exhibited a land-tenure system of resident adults that shared space but avoided each other temporally. Hornocker (1969) termed that behavior, mutual avoidance. In those systems, resident adults had overlapping home ranges but did not allow younger mountain lions that were transient to establish residency unless a vacant home range became available. Thus, density of mountain lions was independent of the density of their primary prey (Seidensticker et al., 1973). Such intrinsic limitation of the population, however, is reliant on a system where individual mountain lions are familiar with other conspecifics with which they share space. Under a land-tenure system, spatial arrangement and social behavior of mountain lions would be expected to be relatively stable. For populations of mountain lions that are dependent on a migratory prey base, however, such a social system could pose problems when prey leave an area.

For many species, migratory behavior has evolved in response to seasonal changes in availabilities of habitat and food (French et al., 1989). In ungulates, mixed strategies of migration occur within populations as a result of variation in food availability in different areas among years (Loft et al., 1984; Nicholson et al., 1997). Because populations of deer can comprise individuals with different migratory patterns, mountain lions also may have evolved flexibility in social behavior that allows them to cope with changes in prey density.

Migratory behavior in mountain lions may have important implications for management and conservation of this large felid. Track censuses often have been proposed for mountain lions as a reliable method for detecting trends in population change (Beier and Cunningham, 1996; Van Dyke et al., 1986; Van Sickle and Lindzey, 1992). An understanding of differences in migration strategies within a population or between subpopulations is imperative for such techniques to provide accurate information.

We quantified timing of migration in mountain lions and tested for differences in size and distribution of their home ranges in summer and winter. In addition, we described several strategies of movement by mountain lions within a single subpopulation and tested for differences in the size of home ranges by animals following those disparate patterns. We also discuss potential implications of home-range dynamics in mountain lions for social regulation and conservation of this solitary carnivore.

MATERIALS AND METHODS

Study area.—Round Valley, located on the eastern side of the Sierra Nevada, a major mountain range in California (37°24′N, 118°34′W), was the winter range for a migratory population of mule deer. Most of those deer migrated to the west side of the Sierra Nevada in spring and returned to Round Valley each autumn (Kucera, 1992). The crest of the Sierra Nevada provided a distinct boundary between the east and west sides of that mountain range, with many peaks > 4,000 m above mean sea level. Migration of deer occurred via several mountain passes > 3,000 m. Most deer moved to summer ranges over the crest of the Sierra Nevada in mid-June and returned to winter range by mid-November. The White Mountains, ca. 25 km E of Round Valley, also rise to 4,000 m and were inhabited by a resident population of mule deer.

Analyses of home ranges.—We monitored the population of mountain lions associated with the deer herd in Round Valley from February 1992 to October 1997. We captured 21 adult mountain lions using hounds or snares (Davis et al., 1996; Pierce et al., 1998) and fitted them with radio-telemetry collars during November 1991–May 1995. We used a fixed-wing aircraft to locate mountain lions each week. A maximum density of 10 adults (ca. 1 mountain lion/25 km^2) was recorded within the boundary of the study area in 1992–1993. Density of mountain lions was likely highest in winter 1991–1992 before several adults died. These deaths occurred prior to our collaring all known individuals, and we could not confirm their presence on the study area during aerial-telemetry flights; therefore, we did not include that period in our analysis of mountain lion density. All methods used in this research were approved by the Institutional Animal Care and Use Committee at the University of Alaska Fairbanks.

The CALHOME (Kie et al., 1996) program was used to calculate 95% home ranges using the adaptive-kernel method (Worton, 1989) for nine adult mountain lions with locations ($\bar{X}$ = 29.2, SD = 5.8) that spanned ≥12 months. For females that made extensive seasonal movements, we estimated annual home ranges using the first location of an individual on winter range (east side of the Sierra Nevada) through the last location of that individual on summer range (west side of the Sierra Nevada, or in the White Mountains). For some of those females, analysis of home range resulted in separate 95% contours for winter and summer. Therefore, discontinuities between home ranges in winter and summer were not the result of pre-selecting dates but were based on adaptive-kernel analyses. For instances where mountain lions had disjunct home ranges, we tested for differences in sizes of winter and summer home ranges using the Wilcoxon matched-pairs signed-ranks test (Siegel, 1956).

Some females followed the beginning of the deer migration N but remained on the east side of the Sierra Nevada throughout summer. In most instances, there were not dramatic movements to and from seasonal home ranges, and those females periodically returned to winter range during summer. Because no distinct migrational movements were identified, analyses of annual home ranges were based on the first location obtained in November through the last one recorded in the following October. That period coincided with the arrival of deer on winter range. For periods that did not span 12 months prior to November or following October, data were excluded. Two males also were included in the analyses using the same criterion.

Percent overlap of seasonal home ranges was measured for females that had discontiguous seasonal home ranges on opposite sides of the Sierra Nevada and returned to those home ranges in consecutive years. Percent overlap was calculated as the area of overlap for two consecutive seasonal home ranges, divided by the area of the smallest of the two home ranges. We calculated that measure using 95% contours from 2 consecutive years for one female and 4 consecutive years for the other.

RESULTS

Mountain lions exhibited two distinct patterns of movement in response to migration of mule deer. Some mountain lions moved gradually, remaining on the eastern scarp of the Sierra Nevada and often having home ranges that overlapped throughout the year. Analysis indicated a single annual home range for those mountain lions. Other mountain lions made two long-range movements each year, also corresponding with the migration of the deer herd. Those mountain lions moved across the crest of the Sierra Nevada or to the White Mountains. Analysis of home ranges for that pattern of movement generally defined two distinct areas, one each for summer and winter. Those mountain lions that crossed the crest of the Sierra Nevada or migrated to the White Mountains likely overlapped with other subpopulations of mountain lions known to inhabit that region of their summer distribution.

Five of nine mountain lions moved north (three females and one male) or south (one male) with the deer herd as it dispersed from Round Valley to summer range. One of those females did not return to the winter range during one summer and had disjunct home ranges in summer and winter. Movements were gradual for four individuals and did not result in discontiguous home ranges between seasons in eight of nine instances; the male that moved southward had distinct summer and winter home ranges in 1 of 4 years. Mean (± *SD*) size of annual home ranges was 817 ± 379 km^2. Three female mountain lions followed the migration routes of the deer in spring through high mountain passes, and established summer ranges west of the crest of the Sierra Nevada (Figs. 1a, 1b, and 1d). A fourth female moved eastward in spring after leaving Round Valley and established a home range in the White Mountains during summer (Fig. 1c). The following year, that female switched her pattern and moved N of Round Valley, had a single annual home range and raised a litter of young (Bleich et al., 1996). That female remained in close proximity to other females inhabiting the east side of the crest of the Sierra Nevada during summer.

Timing of migration by mountain lions corresponded with the migration of mule deer. All four mountain lions that made extensive movements (Fig. 1) migrated by

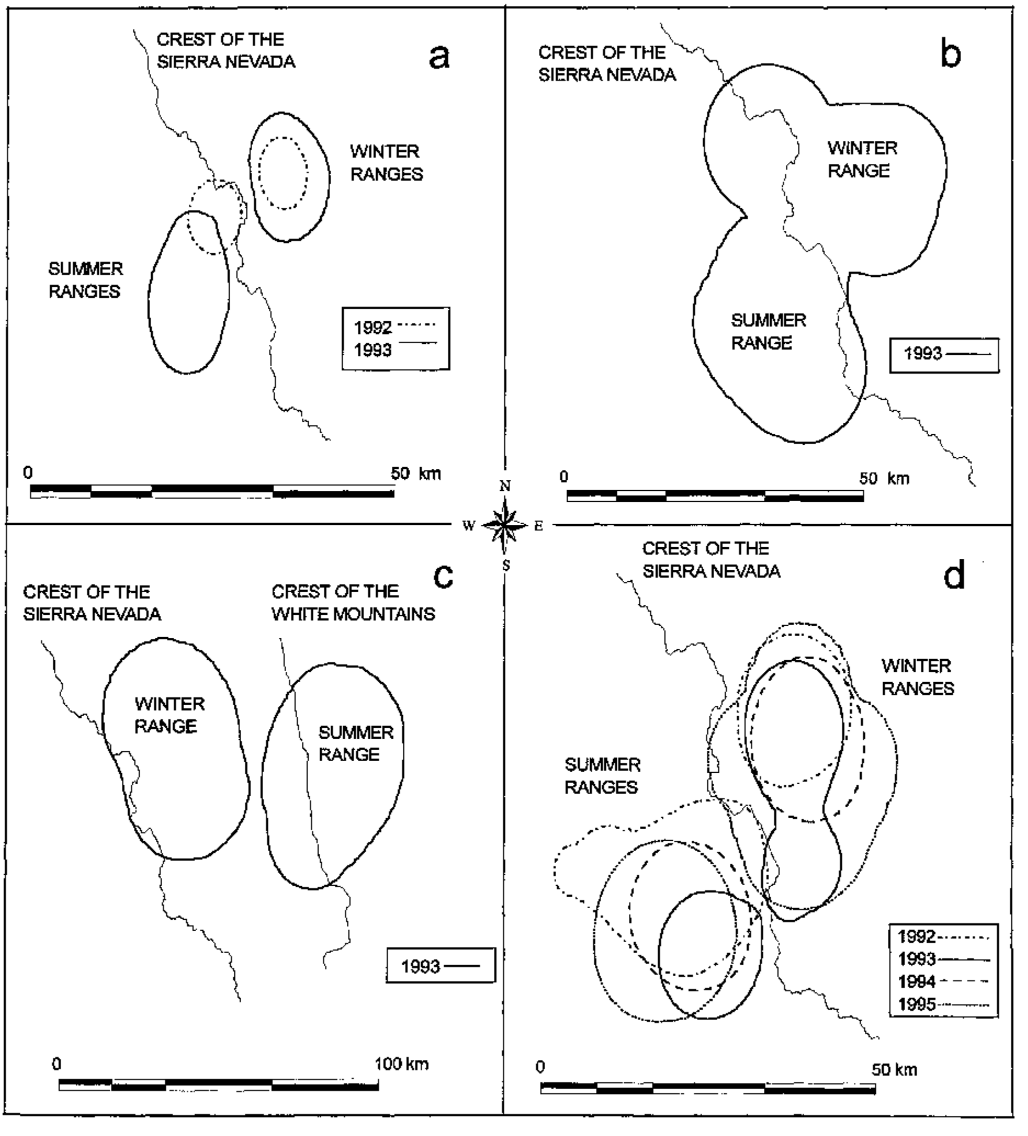

Fig. 1.—Winter and summer home ranges (95% adaptive kernels) for four female mountain lions (a, b, c, d) that migrated from winter range in Round Valley, California, to summer ranges on the west side of the crest of the Sierra Nevada and the White Mountains. For clarity, only 4 of 6 consecutive years are shown for the female in Fig. 1d.

July and returned to Round Valley by November every year, except one individual that crossed the crest of the Sierra Nevada in December 1993 and August 1994. Of the three female mountain lions that migrated westward over the Sierra Nevada, two traveled with single male offspring.

Seven of nine migrations of mountain lions over the crest of the Sierra Nevada resulted in winter and summer home ranges that were not contiguous (Fig. 1), and movements of those mountain lions occurred after migrations of deer in autumn and spring. Mean ($\pm$ *SD*) size of summer (292 ± 120 km^2) and winter (307 ± 152 km^2) home ranges for two mountain lions with disjunct seasonal ranges on opposite sides of the Sierra Nevada did not differ significantly ($Z = -0.169$, $d.f. = 6$, $P = 0.87$). Mean ($\pm$ *SD*) size of summer (425 $\pm$ 475 km^2) and winter (476 $\pm$ 465 km^2) home ranges for all mountain lions with disjunct ranges also did not differ ($Z = -0.612$, $d.f. = 9$, $P = 0.54$). The two mountain lions that crossed the crest of the Sierra Nevada and returned to summer home ranges in consecutive years exhibited strong home-range fidelity in summer and winter (Figs. 1a, and 1d). Overlap of home ranges was 33% in summer and 100% in winter for one of those females. Mean ($\pm$ *SD*) overlap for the other female was 71 $\pm$ 15% for summer, and 83 $\pm$ 15% in winter.

Both males included in analyses also remained on the east side of the Sierra Nevada throughout summer. One moved northward and had a single annual home range that overlapped those of the females that remained on the east side. One repeatedly moved southward along the Sierra Nevada and into the Owens Valley adjacent to the east side of those mountains.

Discussion

Our results indicate that mountain lions that depend on migratory prey may have multiple strategies of migration that allow them to cope with changing densities of prey. Mountain lions that wintered with a migratory deer herd on the east side of the Sierra Nevada exhibited two general patterns of movement. Most remained on the east side of the Sierra Nevada during summer, extending their winter range but returning to it periodically throughout the year. Most mountain lions exhibiting that pattern of movement had singular annual home ranges that tended to overlap those of other lions. Because those mountain lions moved together with the herd of mule deer and remained in close proximity to one another, they may not have interacted with mountain lions from other winter ranges. Mountain lions that migrated to the west side of the Sierra Nevada or the White Mountains tended to make long-range movements that resulted in distinct summer and winter ranges. Three mountain lions that migrated over the crest of the Sierra Nevada and one that migrated to the White Mountains became members of different subpopulations during summer and winter. Furthermore, the female that migrated to the White Mountains in 1 summer changed her pattern of movement and overlapped extensively with mountain lions on the east scarp of the Sierra Nevada the following summer. Although sample size of locations was too small for making inferences about home-range sizes for some individuals, our results demonstrated distinct patterns in movement among mountain lions and indicated multiple patterns of migration and flexibility in social behavior in response to changing densities of prey.

Track censuses have been proposed as a meaningful method for estimating trends in populations of mountain lions throughout much of their range (Beier and Cunningham, 1996; Currier, 1976; Koford, 1978; Van Dyke et al., 1986), including the eastern Sierra Nevada (Smallwood, 1994). Where some mountain lions migrate seasonally and others do not, investigators cannot be certain of the population being monitored; survey results also may vary with season and, hence, lead to spurious conclusions. The potential for mountain lions to migrate needs to be considered in planning such surveys.

Knowledge and understanding of migration patterns have fundamental importance for conservation of mountain lions. Migration is an adaptive strategy that likely evolved in response to variability in the environment (Baker, 1978). Multiple strategies, where some segment of a population migrates while another remains resident, have been observed for mule deer (Nicholson et al., 1997), and that same behavior was evident among mountain lions inhabiting Round Valley. Therefore, viability of some populations of mountain lions may rely on seasonally distinct geographic regions that allow individuals to cope with environmental fluctuations. Furthermore, because migration often requires suitable habitat for movement between seasonal ranges, maintenance of corridors for migration by mountain lions may be essential for maintenance of some subpopulations, as has been suggested for dispersal corridors for mountain lions in southern California (Beier, 1993, 1995, 1996). Moreover, gene flow among populations of mountain lions may be as dependent on patterns of migration of adults as it is on dispersing juveniles. Thus, migratory behavior by this large felid may play a critical role in metapopulation structuring (Levins, 1970).

Several mountain lions repeatedly migrated into areas that they had left vacant for >6 months. During summer, home ranges of those individuals were in areas inhabited by subpopulations of mountain lions that spent each winter in areas isolated from Round Valley (Bleich and Taylor, 1998; Torres et al., 1996). In winter, those individuals reestablished home ranges in Round Valley among mountain lions with which they had not interacted throughout summer. Extensive movements of mountain lions suggest that the social system thought to play a role in regulating populations of mountain lions (Seidensticker et al., 1973) may be far more flexible than previously recognized. Extensive overlap of home ranges of mountain lions occurred on a seasonal basis. Migratory populations of prey and their resultant shifts in density likely caused numbers of mountain lions to fluctuate seasonally.

Factors promoting social regulation (Watson and Moss, 1970) may operate differently in populations of mountain lions that feed on migratory prey compared with populations where densities of prey do not vary seasonally. In situations such as our study area, mountain lions can reach high densities and potentially have a strong influence on populations of mule deer (Bleich and Taylor, 1998). Research on the potential for social regulation to limit densities of mountain lions must include detailed information about distribution of their primary prey (Anderson et al., 1992). Whether the patterns of distribution for mountain lions we observed can lead to social regulation requires further study, but these patterns certainly raise questions about existing paradigms of social behavior of mountain lions.

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