
Cougar Dispersal Patterns, Metapopulation Dynamics, and Conservation

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Abstract: *We examined cougar (Puma concolor) dispersal, emigration, and immigration in the San Andres Mountains, New Mexico, from 1985 to 1995 to quantify the effects of dispersal on the local population and surrounding subpopulations. We captured, tagged, and radio-collared animals to detect the arrival of new immigrants and dispersal characteristics of progeny. We found that cougars in southern New Mexico exhibited a metapopulation structure in which cougar subpopulations were separated by expanses of noncougar habitat and linked by dispersers. Of 43 progeny (n = 20 males, 23 females) studied after independence, only 13 females exhibited philopatric behavior. Males dispersed significantly farther than females, were more likely to traverse large expanses of noncougar habitat, and were probably most responsible for nuclear gene flow between habitat patches. We estimated that an average of 8.5 progeny (i.e., cougars born in the study area) successfully emigrated from and 4.3 cougars successfully immigrated to the San Andres Mountains each year. Concurrently, an average of 4.1 progeny were recruited into the San Andres cougar population. Protected cougar subpopulations can contribute to metapopulation persistence by supplying immigrants to surrounding subpopulations that are affected by fragmentation or offtake by humans. Cougar population dynamics and dispersal behavior dictate that cougar management and conservation should be considered on a regional scale.*

Patrones de Dispersión de Jaguares, Dinámica Metapoblacional y Conservación

Resumen: *Examinamos la dispersión, emigración e inmigración del jaguar (Puma concolor) en las montañas de San Andrés, Nuevo México de 1985 a 1995 para cuantificar los efectos de dispersión de la población local y de subpoblaciones adyacentes. Capturamos, marcamos e instalamos radiocollares en animales para detectar el arribo de nuevos inmigrantes y las características de dispersión de la progenie. Encontramos que los jaguares en el sur de Nuevo México exhibieron una estructura de metapoblación en la cual las subpoblaciones estuvieron separadas por extensiones de hábitat sin jaguares y unidas por dispersores. De 43 descendientes (n = 20 machos, 23 hembras) estudiados post-independencia, solo 13 hembras exhibieron conducta filopátrica. Los machos se dispersaron significativamente más lejos que las hembras, estuvieron más inclinados a atravesar extensiones largas de hábitat sin jaguares y probablemente fueron los más responsables del flujo nuclear de genes entre parches de hábitat. Estimamos que un promedio de 8.5 descendientes (por ejemplo, jaguares nacidos en el área de estudio) emigraron exitosamente de, y 4.3 jaguares inmigraron exitosamente hacia las montañas de San Andrés cada año. Al mismo tiempo, un promedio de 4.1 descendientes fueron reclutados dentro de la población de jaguares de San Andrés. Las subpoblaciones protegidas de jaguares pueden contribuir a la persistencia de la metapoblación al proporcionar inmigrantes a las subpoblaciones adyacentes que son afectadas por la fragmentación o eliminación por humanos. Las dinámicas poblacionales y la conducta de dispersión de los jaguares indican que el manejo y la conservación de jaguares deberían ser considerados a escala regional.*

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Introduction

Cougars (*Puma concolor*) once ranged throughout North America. By the turn of the twentieth century, however, humans had virtually extirpated cougars in eastern North America and in the West relegated them to the most remote habitats (Young 1946; Nowak 1976). Recent recovery of the cougar throughout much of its western range can be attributed to regulated hunting of the species since the mid-1960s, the presence of large tracts of relatively undisturbed habitat, and pathways for dispersal.

Because vast areas (>100,000 km²) of wild lands may be required for long-term viability of large carnivores (Shaffer 1987), and because North American parks and wilderness areas do not encompass such large areas (Noss et al. 1996), rebounding cougar populations may become threatened by anthropogenic habitat fragmentation. Where cougar habitat is naturally or artificially fragmented, cougars may exhibit a metapopulation structure, defined as a "network of semi-isolated populations with some level of regular or intermittent migration and gene flow among them, in which individual populations may go extinct but can then be recolonized from other populations" (Meffe & Carroll 1997:678). In such instances, deterioration of landscape linkages or patches may isolate and increase the extinction risk of subpopulations and may consequently degrade the persistence of the metapopulation. Hence, it is important to determine the juxtaposition of subpopulations that function as sources or sinks, the degree of natural dispersal between subpopulations, and the effectiveness of potential dispersal barriers, be they natural or human-made.

Some information exists on cougar dispersal distances (Anderson et al. 1992; Ross & Jalkotzy 1992) and on cou-

gar use of corridors (Beier 1995). No research, however, has quantified the effects of cougar dispersal on demographics or evaluated the relative importance of individual subpopulations to cougar metapopulations. We hypothesized that the basin and range structure of southern New Mexico resulted in a naturally occurring cougar metapopulation. Consequently, our objectives were (1) to describe the dispersal characteristics of cougars born in a large, relatively isolated study population, (2) to assess the importance of dispersers to other subpopulations, and (3) to determine the importance of immigrants to the study population. Our research provides the only long-term information on the relationship of a study population of cougars to surrounding subpopulations prior to any large-scale, human-caused habitat fragmentation.

Study Area

The 2059-km² study area was located in south central New Mexico and encompassed the entire San Andres Mountains (Fig. 1). The mountains lie at the northern edge of the Chihuahuah Desert, rise from 1280 to 2730 m in elevation, and have a semi-arid climate. Rugged topography supplies stalking and denning cover for cougars. The mountains contain numerous natural springs, four native ungulate species, and a variety of vegetation, from desert scrub and grasslands at lower elevations to mountain mahogany (*Cercocarpus montanus*) and piñon-juniper (*Pinus-Juniperus* spp.) woodlands at higher elevations. In contrast, the flat desert basins are drier (Ares 1974), support much lower plant diversity (primarily desert scrub such as creosote [*Larrea divaricata*] and

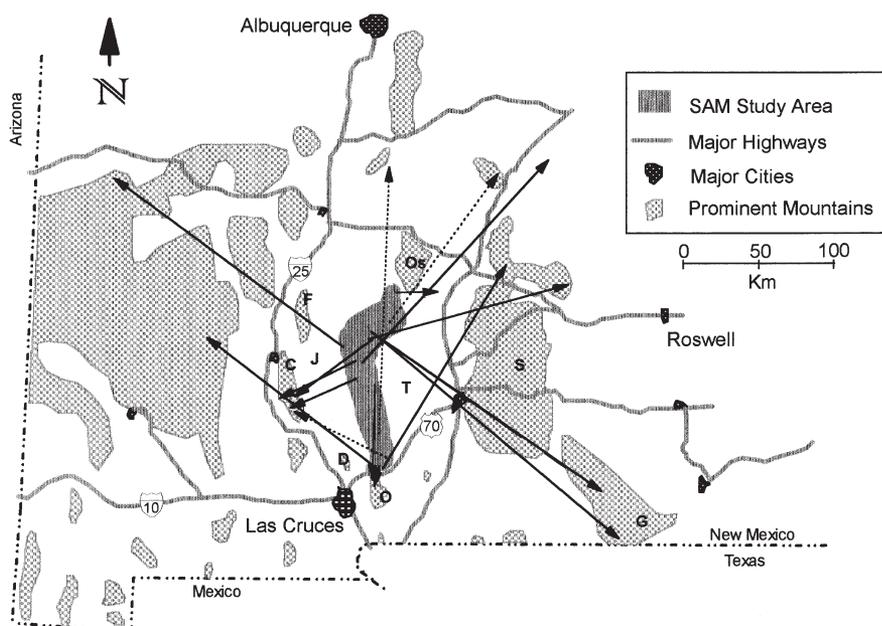


Figure 1. Dispersal directions, distances, and endpoints for 16 cougars from the San Andres Mountains (SAM) study area in New Mexico to areas outside the study area. Thirteen of the cougars were born on the study area (solid lines), and three had origins outside the study area (dotted lines). Movements were based on a cougar's natal home range center or its capture site to its independent home range center, mortality site, or last location. Letters depict mountain ranges (C, Caballo; D, Dona Ana; F, Fra Cristobal; G, Guadalupe; O, Organ; Os, Oscura; S, Sacramento) or basins (J, Jornada del Muerto; T, Tularosa).

mesquite [*Prosopis glandulosa*]), and do not support any significant numbers of native ungulate prey.

The San Andres Mountains are almost completely within White Sands Missile Range (WSMR) and under jurisdiction of the U. S. Army. Because access and activities are restricted by WSMR, the area is relatively undisturbed by humans. Consequently, these mountains probably represent the largest block of relatively pristine Chihuahua Desert habitat in the American Southwest.

The San Andres Mountains measure over 127 km long by 9–30 km wide and are part of a broken chain of mountains that extend into the Sierra Oscura to the north and terminate in the Organ Mountains to the south (Fig. 1). The Sierra Oscura cover approximately 670 km² and are connected to the San Andres Mountains by the Little Burro Mountains, a 27-km² corridor of rolling hills. The Organ Mountains, which contain about 270 km² of cougar habitat, are separated from the San Andres Mountains by a six-lane highway. Two large desert basins flank the study area: to the west, the Jornada del Muerto spans about 55 km at its widest point, and to the east, the Tularosa Basin spans about 97 km. The Dona Ana (25 km²), Caballo (200 km²), and Fra Cristobal (100 km²) mountains are the closest mountains west of the San Andres Mountains. The Rio Grande and more expansive and contiguous cougar habitat lie farther west. The Sacramento Mountains, a block of cougar habitat covering more than 6200 km², flank the eastern edge of the Tularosa Basin.

The San Andres Mountains cougar population was part of a larger subpopulation consisting of the Organ, San Andres, and Oscura mountains, referred to as the San Andres chain. Four resident adult cougars (two males, two females) had home ranges that included portions of the Oscura Mountains north of the study area, and two resident cougars (one adult male, one subadult female) had home ranges that overlapped the Organ Mountains south of the study area (Logan et al. 1996). No resident cougars had home ranges that extended more than 1–2 km from mountainous terrain into the surrounding desert basins, and cougars were never documented emigrating to other subpopulations once they became breeding adults.

Cougar hunting was prohibited on the San Andres Mountains during the study, but 50 cougars were removed from the study area through hunting and control efforts during the 5-year period prior to our research. We translocated another 13 cougars from a treatment area in the southern half of our study area during a 6-month period from 1990 to 1991 to simulate a control effort (Logan et al. 1996). Consequently, we were studying the dynamics of a rebuilding population. The study population showed an increasing trend: annual numbers from 1989–1995 ranged from 25 to 42 adult cougars, and corresponding densities were 1.2–2.0 adult cougars per 100 km². Observed annual exponential rates of increase for the treatment area ranged from 0.21 to 0.28, whereas

rates of increase in a northern reference area, where cougars were not removed, declined over time from 0.17 to 0.05. Sex ratios ranged from 0.6 to 1.1 adult males per adult female (Logan et al. 1996:99).

Methods

Field Study

We studied cougar population dynamics in the San Andres Mountains from 1985 to 1995. To accurately determine study population immigration, progeny recruitment, and emigration, we attempted to capture and mark all cougars, including subadults and cubs, so we could quantify cub and subadult survival and distinguish between progeny (i.e., cougars born in the study area) and immigrant recruits. We operated 16 camps in the study area, from which we systematically searched for, captured, and radiolocated cougars on a year-round basis. Around each camp, we set foot-hold snare lines (Schimetz/Aldrich Spring Activated Animal Snare) to capture independent cougars and large cubs. Once we had accounted for all cougar sign based on captures and radiotelemetry, we moved to the next camp. Our search and snaring efforts encompassed the entire San Andres Mountains.

The capture protocol for snared cougars is outlined by Logan et al. (1999). During the study we spent 40,533 snare days (one snare set for 1 day) at 1211 sites to capture 108 cougars 210 times. We tried to avoid recaptures unless radiocollars needed replacement. All snared cougars were ear-tagged, radiocollared (Telonics, Inc., Mesa, Arizona 85204), and marked with a uniquely coded, permanent ear tattoo.

The behavior of radiocollared adult females, including associations with males and subsequent localizing of activities at nurseries, indicated when cubs were born. We attempted to hand-capture and mark all cubs within observed litters when they were 21–72 days old. We hand-captured 163 cubs 186 times, 30 of which were later recaptured in snares. Some cubs, primarily females, were fitted with expandable radiocollars. Transmitters were equipped with mortality sensors. Fates of tagged cubs without radiocollars were determined by following other radiocollared family members. Subsequent visual observations of the family or attrition in track sets indicated whether cubs had survived.

We obtained over 13,000 locations on 126 radiocollared cougars during weekly flights and daily ground surveys. Characteristics of dispersing cougars, including direction and distance traveled, were obtained through radiotelemetry and tag returns. The New Mexico Department of Game and Fish informed us of tagged cougars killed outside the study area for sport or to protect livestock.

During the 10-year study, we captured 241 cougars 396 times. Another 54 cougars were detected but never

captured and marked. The majority of unmarked cougars were cubs ($n = 46$); of these, we knew that 13 died before independence and 9 were still dependent at the close of the study. Of the remaining 8 unmarked cougars, 4 were found or reported dead at ages ranging between 12 and 30 months, 2 were detected as new immigrants at the close of the study, and 1-2 (both females) successfully produced cubs (we visually observed one set of offspring). Intensive capture, mark, recapture techniques, radiotelemetry, and examination of cougar ages at first capture indicated that, beginning with 1988, an average of 95% of adults present in the San Andres Mountains each year were marked (Logan et al. 1996).

We use the following definitions in this paper. The three broad cougar age classes were cubs dependent on their mothers; subadults independent but not yet of breeding age; and resident adults that maintained home ranges in which they bred. Cubs became independent subadults when they no longer associated with their mothers; exact ages of independence could be determined only for radiocollared individuals. A disperser was a subadult that established a home range after becoming independent that overlapped <5% of its natal home range (based on the 90% minimum convex polygon) or was last located (due to death or transmitter loss) outside its natal area. All other independent progeny were considered philopatric. Dispersal began when a subadult made its first movement outside its natal home range without returning. Immigrants originated from outside the San Andres Mountains and then established residency on the study area. Recruits consisted of immigrants and progeny born in the San Andres Mountains that entered the resident adult segment of the study population. Progeny that dispersed completely outside the study area were emigrants.

Data Analysis

We calculated all dispersal distances and azimuth directions using Universal Transverse Mercator (UTM) grid coordinates (White & Garrott 1990). We determined dispersal distances and directions of study area progeny by calculating the straight-line distance and angle of direction from the arithmetic center of a progeny's natal home range (natal center) to the arithmetic center of its independent home range (independent center). When complete dispersal information was unavailable, we calculated dispersal distances and directions based on one of the following combinations: natal center to mortality site or last location, or capture site to independent center, mortality site, or last location.

We estimated home ranges using the minimum convex polygon (MCP, Hayne 1949) method in program CALHOME (Kie et al. 1994). We calculated each natal home range center using all telemetry locations obtained on a cub and its mother during the 12-month pe-

riod after the cub was born. A progeny's independent home range center was determined by radio locations from a 12-month period after it showed site attachment to an area. We also calculated the number of home range diameters crossed during individual dispersal movements (effective dispersal; Shields 1982). We calculated sex-specific home range diameters as the diameter of a circle with area equal to the average annual home range size for adult male and female cougars on the study area (Logan et al. 1996:157-158). We used the 100% MCP because exploratory movements may result in successful breeding encounters. We calculated the diameters for adult male and female home ranges (HR) as if home ranges were circular with diameter d :

$$d = 2\sqrt{\text{HR}/\pi}.$$

We tested the research hypothesis that the movements of dispersers from natal home ranges to independent home ranges would have a bimodal, north-south distribution that followed the orientation of the San Andres and the adjacent Organ and Oscura mountains. Directional data from dispersers were transformed to unimodal data and subjected to Raleigh testing (Zar 1984). We also tested for differences in dispersal distances of males and females using Wilcoxon rank sum tests (Zar 1984).

Tagged and detected progeny born from 1 February 1988 through 23 February 1993 (interval 1) were used to calculate recruitment and emigration rates for the 5.1-year period 1 February 1990 to 23 February 1995 (interval 2). These intervals were chosen because any surviving, untagged cubs born prior to 1988 would have had sufficient time to emigrate or be recruited prior to 1990. Also, because an average of 95% of the adult study population was marked each year beginning with 1988, we were able to detect all subsequent immigrants and cub births. Surviving cubs born during interval 1 would all reach 2 years of age (when cougars reach adulthood; Logan et al. 1996) during interval 2 and thus would be either recruits or emigrants.

Recruitment was determined through capture, mark, and recapture efforts. Except for three cases in which genetic (i.e., parentage analysis via 10 felid microsatellite loci; M. Culver, personal communication) and/or ground-tracking information indicated that previously unmarked subadults were progeny of resident females, all untagged subadults or adults captured during interval 2 were classified as immigrants. Emigration was estimated by first calculating the emigration rate (ER) of tagged cubs:

$$\text{ER} = \frac{\text{STC} \times \text{SSR} - \text{PR}}{\text{TC}}, \quad (1)$$

where STC is the number of tagged cubs from interval 1 that survived to independence, SSR is the subadult survival rate based on the finite rate of survival of a radiocollared sample of 9 males and 16 females monitored

from independence until they either died as subadults or became adults (Logan et al. 1996); PR is the number of progeny recruited into the adult San Andres Mountains population during interval 2, and TC is the total number of cubs tagged during interval 1.

Although we believe we detected all cubs born during interval 1, we were not able to tag all of them. Therefore, the emigration rate obtained for the tagged sample in equation 1 was applied to all cubs detected during that period:

$$\text{Successful emigrants per year} = \frac{\text{DC} \times \text{ER}}{5.1 \text{ years}}, \quad (2)$$

where DC is the number of cubs detected (tagged and untagged) during interval 1, and 5.1 years is the amount of time in interval 2. This way, we were able to estimate the number of successful emigrants (i.e., emigrants that survived to adulthood) leaving the study area on an annual basis.

Results

Fates of Tagged Progeny

We documented the fates of 43 progeny after they became independent. Age at independence averaged 13.7 ± 1.6 SD months ($n = 12$), and age at dispersal averaged 15.2 ± 1.6 SD months ($n = 8$) for progeny radio-tracked during the period before and after independence (Logan et al. 1996). Twenty-seven progeny dispersed from their natal home ranges. Of those, 6 males and 6 females moved minimum distances of 47.1 and 5.6 km, respectively, before establishing adult home ranges within the study area; another 10 males and 3 females emigrated

(Fig. 1). Two other males were dispersing within the San Andres Mountains when another cougar killed one and the other shed his radiocollar at the study area's southern border. Because the latter cougar was never recaptured on the study area, he either died or emigrated.

Sixteen of 43 progeny did not disperse from their natal areas. Two subadult males and 1 subadult female were killed by adult male cougars shortly after independence and at younger ages (14.3, 14.6, and 15.0 months) than the mean age of dispersal onset. Based on the behavior of surviving tagged subadults, we assumed that the 2 males probably would have dispersed and possibly emigrated if they had not been killed. Thirteen females exhibited philopatry. These 13 females, along with 4 dispersing females that established home ranges adjacent to their mothers, formed eight female matrilineages, which we defined as composed of genetically related females (i.e., mothers, daughters, siblings) with home ranges that abutted or overlapped.

Of 34 progeny tracked to independent home ranges or adult mortality sites, males dispersed significantly farther than females (Table 1). On average, males moved 8.1 times the distance of females from natal to independent centers. The longest documented dispersal movement was that of a 47-month-old male killed 214.9 km from his natal center. No female progeny were known to disperse farther than 78.5 km, but a 2-year-old female, whose origin we believe was outside the study area, traveled 118.2 km from her capture site to her last telemetry location outside the study area.

Based on the average annual home range size of adult male and female cougars (187.1 and 73.5 km², respectively; Logan et al. 1996), effective dispersal for 13 male progeny averaged 7.0 male home range diameters (range =

Table 1. Post-independent dispersal distances of cougars born in the San Andres Mountains, New Mexico ($n = 40$) and cougars with origins outside the San Andres Mountains ($n = 3$) 1986–1994.

Distance estimator ^a	Female dispersal distance (km)			Male dispersal distance (km)		
	n	\bar{x} (SD)	range	n	\bar{x} (SD)	range
Progeny						
NAC to IAC ^b	7	28.3 (26.1)	5.6–78.5	8	101.3 (57.7)	47.1–192.5
NAC to IAC (P)	12	3.2 (2.6)	0.7–9.9	0		
NAC or CS to AMS	0			5	139.8 (68.7)	56.0–214.9
CS to IAC	1	36.6		0		
CS to IAC (P)	1	2.2		0		
NAC or CS to LLS or SMS ^c	1	76.6		5	67.2 (37.5)	53.1–133.8
—						
Total ^d	21	13.1 (19.5)	0.7–78.5	13	116.1 (62.5)	47.1–214.9
Origin outside study area						
CS to LL or IAC	2	96.3 (31.0)	74.4–118.2	1	175.7	

^aOrigins and endpoints of distance estimators: NAC, natal home range arithmetic center; IAC, independent home range arithmetic center; P, remained philopatric; CS, capture site (CS for progeny was within the natal home range); AMS, adult (≥ 24 months old) mortality site; LLS, last location as a subadult; SMS, subadult mortality site; LL, last location, status unknown.

^bMales dispersed significantly farther than females ($T = 35$, $p < 0.025$).

^cNot included in analyses of sex-related dispersal distances.

^dMales dispersed significantly farther than females ($Z = 4.55$, $p < 0.001$). Total includes only those cougars that probably completed their natal dispersal moves and those that were philopatric into adulthood. We assumed that cougars that had reached adulthood prior to death or loss of radio contact had completed their dispersal moves, whereas subadults had not.

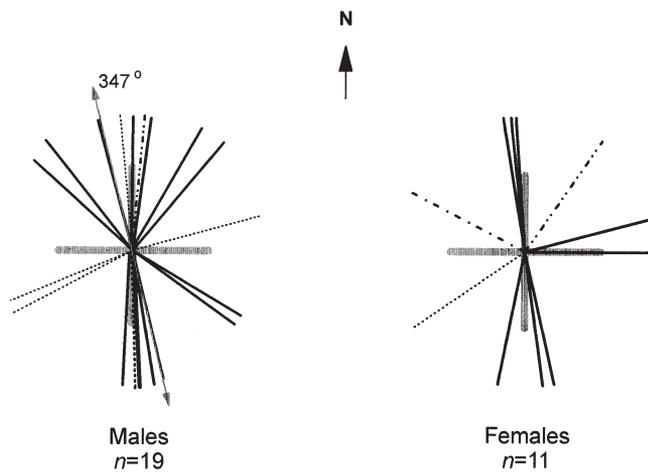


Figure 2. Dispersal directions for 30 cougars away from their natal home ranges or capture sites in the San Andres Mountains, New Mexico, to their independent home ranges, mortality sites, or last locations. Solid lines indicate direction of progeny (13 males, 8 females) that completed their natal dispersal moves, whereas dotted lines indicate progeny (5 males, 1 female) that either died or shed their radiocollars prior to reaching adulthood. Dot-dashed lines show dispersal directions for 3 cougars (1 male, 2 females) that were not born in the study area.

3.1–14.0 diameters). In contrast, 21 female progeny, including dispersing and philopatric females, effectively dispersed an average of 1.4 female home range diameters (range = 0.1–8.1).

Dispersal directions for male progeny were bimodally distributed ($n = 13$, $Z = 4.06$, $p = 0.015$) with a diameter line oriented at 347° (Fig. 2). Dispersal directions for females were random ($n = 8$, $Z = 1.44$, $p = 0.263$), but six of eight females dispersed along the north-south orientation of the San Andres Mountains, and one of two that dispersed east remained within the contiguous habitat of the study area (Fig. 2). Nevertheless, dispersing cougars (primarily males) still reached habitats throughout southern New Mexico (Fig. 1).

Recruitment and Emigration

From 1 February 1990 through 23 February 1995, 21 progeny (4 males, 17 females) were recruited into the San Andres Mountains population, for an average of 0.8 male and 3.3 female progeny recruits per year. During the same time period, 22 immigrants (14 males, 8 females), averaging 2.7 males and 1.6 females per year, were recruited into the study area (Table 2). At least 62% of progeny recruits (1 male, 12 females) and 45% of immigrant recruits (5 males, 5 females) produced offspring.

We estimated emigration based on mortality and recruitment rates of 114 marked cubs (51 males, 63 females) out of 137 progeny born on the study area from 1 February 1988 to 23 February 1993. Of the 114 marked cubs, 36 (16 males, 20 females) died as cubs. Using our calculated subadult survival rate of 0.56 for males and 0.88 for females (Logan et al. 1996) and subtracting the successful recruits (4 males, 17 females), we estimated that 36.4 marked cubs (15.6 males, 20.8 females) successfully emigrated. Assuming an even sex ratio for the 23 unmarked cubs (Logan et al. 1996), we estimated total successful emigration (marked + unmarked cubs) for the 5.1-year period (interval 2) at 43.7 progeny (19.1 males, 24.6 females), or 8.5 progeny (3.7 males, 4.8 females) per year. Of the estimated 65 progeny that survived to adulthood (44 emigrants + 21 recruits), about 68% (83% of males and 59% of females) emigrated (Table 2).

Bias in Emigration Estimates

The 43 progeny we followed after independence supplied information on subadult survival rates and on dispersal age, direction and distance but could not give us complete information on emigration. We knew that 33 of the 43 tagged progeny survived to adulthood. Of those, 7 of 13 males (54%) and 1 of 20 females (5%) successfully emigrated (24% in aggregate); the other 25 (76%) were recruited into the San Andres Mountains population. The low percentage of emigrants found for the tagged sample (24%) versus the one estimated by equations 1 and 2 (68%) is probably a consequence of

Table 2. Rates of recruitment and emigration for cougars in the San Andres Mountains, New Mexico.

	No. cougars in 5.1-year period		n/year/100 km ²		n/G/100 km ² ^a		Percentage of progeny surviving to adulthood	
	male	female	male	female	male	female	male	female
Total recruitment	18	25	0.17	0.24	0.41	0.58		
Immigration	14	8	0.14	0.08	0.34	0.19		
Progeny	4	17	0.04	0.16	0.09	0.39	17	41–67
Emigration ^b	19.1	8.4–24.6	0.18	0.08–0.23	0.44	0.19–0.56	83	33–59

^aG, or generation time, was the average age at which females gave birth to their first litters in the study area and equalled 29 months (Logan et al. 1996).

^bThe observed subadult female survival rate of 0.88 (maximum estimate) and the observed subadult male survival rate of 0.56 (minimum estimate) were used to calculate a range of female emigration rates.

recapture bias. Because we tried to recapture all progeny that were recruited into the adult study population, and because most of the subadults we radiocollared were philopatric females, the tagged sample was biased toward recruits. We were able to determine the fate of emigrants only when they were radio-monitored into adulthood or when their deaths were reported. Nevertheless, equations 1 and 2 probably overestimate the percentage of surviving females that successfully emigrated (59%) because we calculated emigration rate using an estimate of subadult female survival (88%) based on 16 radiocollared females, none of which dispersed outside the study area. This survival rate might be optimistic because females that disperse across the matrix (areas where cougars cannot survive; McCullough 1996a) may experience higher mortality than those that stay within contiguous habitat. If we assume that subadult females had the same survival rates as subadult males (0.56), only 1.6 females would have emigrated successfully each year. Consequently, only 33% of surviving females would have emigrated (Table 2).

Movements across Potential Barriers

Of 43 progeny for which we collected post-independence movement information, 25 remained within the San Andres Mountains into adulthood, at least 4 died as subadults within the study area, and 2 established residency in adjacent habitat south of the study area (i.e., Organ Mountains). Although none of the 43 established residency in adjacent habitat north of the study area (Oscura Mountains), the use of the Oscura Mountains by study area residents and dispersers suggests that some of the other surviving progeny may have done so.

The expansion of U.S. Highway 70 from 4 to 6 lanes in 1993 further weakened the connection between the San Andres and Organ Mountains. At least seven cougars successfully crossed U.S. Highway 70 prior to its expansion, including four dispersing male subadults, two residents that frequently traveled between the study area and Organ Mountains, and one study area resident that made occasional explorations south of the highway. After expansion, the only documented highway crossings were of two males (one tagged adult, one unmarked subadult) struck and killed by vehicles. No radiocollared cougars with home ranges abutting the widened highway ($n = 5$) were documented crossing it.

Eleven of 43 cougars dispersed outside the San Andres chain (Fig. 1). Of those, 5 males successfully crossed the Tularosa Basin, which was the widest span of noncougar habitat adjacent to the San Andres Mountains. One female dispersed 37 km into the Tularosa Basin, where she established a large home range (215 km², 90% MCP) within a recent lava flow. The area contained scarce prey resources and may have necessitated a larger home range than the

average of 46 km² (90% MCP) for an adult female in our study area (Logan et al. 1996). Five cougars (four males, one female) dispersed west across portions of the Jornada del Muerto. Of these, three were still subadults and were in the closest available cougar habitat west of the study area (Caballo Mountains) when they died or dropped their radiocollars; the other two successfully crossed the Rio Grande and Interstate 25 to larger expanses of cougar habitat. Most emigrants traveled north or south along the habitat corridor provided by the San Andres and adjacent Organ and Oscura Mountains, then used other habitat patches, when available, to link their dispersal moves (Fig. 3). Movements across wide expanses (>50 km) of inhospitable habitat were generally completed in short time periods (<7 days) and appeared to be unidirectional.

Discussion

Cougar Dispersal and Philopatry

In North American cougar populations, dispersing cougars typically leave their natal areas when they are 10–33 months old (Hemker et al. 1984; Maehr 1990; Ross & Jalkotzy 1992; Beier & Barrett 1993; this study) and before they are sexually mature (Anderson et al. 1992; Logan et al. 1996). Like most polygynous mammals (Greenwood 1980), males disperse more often and consistently farther than females (Anderson et al. 1992; this study). Anderson et al. (1992) reported maximum dispersal distances of 274 and 140 km for males and females, respectively, for a sample of 65 North American cougars from different study populations. The record distance is that of a male who dispersed 483 km from his natal area in northern Wyoming to his mortality site west of Denver, Colorado (Logan & Sweanor 2000). Dispersal appears to be independent of density in male cougars (Seidensticker et al. 1973; Logan et al. 1986; Ross & Jalkotzy 1992; Logan et al. 1996) and at least partially independent of density in females (Logan et al. 1996).

Female cougars often exhibit philopatry (Ross & Jalkotzy 1992; Lindzey et al. 1994; this study). In the un hunted San Andres Mountains cougar population, female philopatry resulted in the formation of matriline. Male philopatry has been documented only in Florida, where severe habitat restrictions apparently force male panthers (*P. c. coryi*) to return to the vicinity of their natal areas after frustrated dispersal attempts (Maehr 1997).

The cougar population in the San Andres Mountains was comprised of adult males with territories that overlapped, on average, home ranges of 5 adult females and their cubs. As young became independent, some were recruited into the local population and others emigrated, becoming potential recruits in other subpopulations (Logan et al. 1996). Total re-

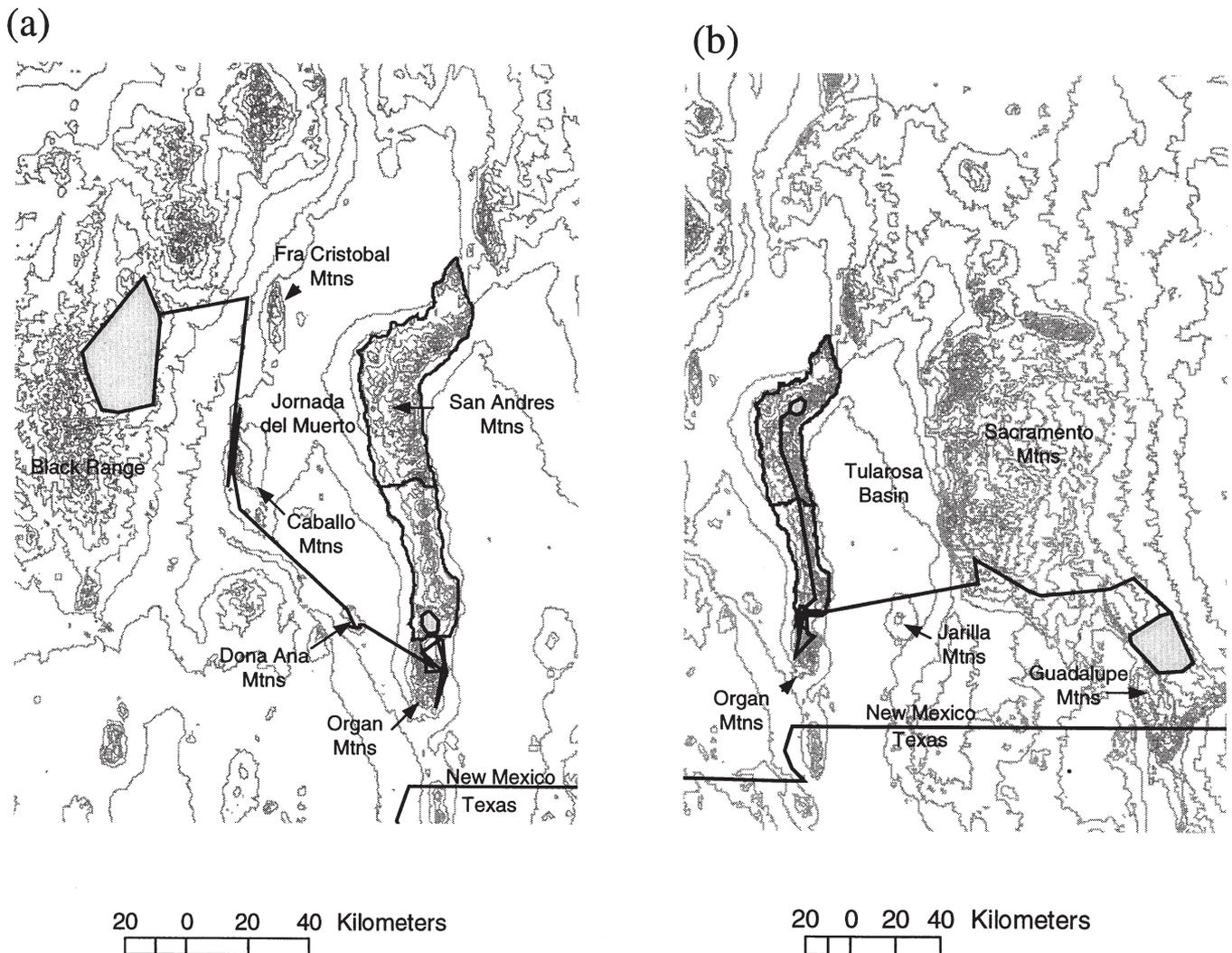


Figure 3. Example of two dispersing male cougars that used the San Andres Mountains and other habitat patches along dispersal routes from natal home ranges to independent home ranges. After leaving their natal home ranges (a) M26 and (b) M82 spent 1.5 and 4.3 months, respectively, within the San Andres Mountains chain. Upon leaving the study area and until they established independent home ranges, M26 and M82 were located, on average, every 5 days and 12 days, respectively. Entire dispersal took 3.6 months for M26 and 7.8 months for M82 to complete.

recruitment almost equaled successful emigration (8.4 recruits versus 8.5 emigrants per year).

Metapopulation Dynamics

The cougar population structure in southern New Mexico generally meets the definition of a metapopulation (Meffe & Carroll 1997). The cougar population occurs in habitat patches separated by desert basins, or matrix, and linked by dispersers. Each patch experiences different environmental conditions, prey characteristics, and human hunting pressures that can generate variable demographics among subpopulations. The small size of some of the patches subjects them to increased extinction risk.

As for our study population, the stability and growth of surrounding subpopulations probably are most dependent on the recruitment of female progeny and male immigrants. In the San Andres Mountains, 68% of the female recruits were born on the study area, whereas 78% of the male recruits were immigrants. This reflects the greater philopatric tendencies and shorter dispersal distances of females, and the obligatory, long-distance dispersal tendencies in males. The reproducing immigrants that we observed demonstrated that some dispersing cougars breed in other subpopulations.

Emigration probably influences genetic structure in cougar subpopulations throughout southern New Mexico. Given the tendency of males to disperse long distances and across matrix, it is likely that nuclear gene

flow between widely separated subpopulations occurs primarily through the movements of males. Radiotelemetry data on a sample of study area progeny indicated that most (18 out of 21 females, 8 of 13 males) did not disperse more than five home-range diameters, the distance that may be necessary to disrupt genetic adaptations to regional conditions (Shields 1982). The few progeny that did disperse longer distances could have been vital in promoting an outcrossing population structure (Templeton 1987). High rates of gene flow among populations are possible in carnivores that disperse long distances and exhibit high rates of dispersal (Wayne & Koepfli 1996). Moreover, the immigration rates observed in the San Andres Mountains (Table 2) greatly exceeded the one to five per generation suggested by genetic theory to ensure effective transfer of genetic variation (Crow & Kimura 1970; Lacy 1987). Hence, cougar populations in southern New Mexico may exhibit little genetic subdivision.

If dispersal between subpopulations is as high as that found for the San Andres Mountains, the system may be less a metapopulation than a single extinction-resistant, or patchy, population (Harrison 1991). In this case, there is little potential for extinction of discrete subpopulations. Even so, the structure found in southern New Mexico, where subpopulations are linked by dispersers, can have important consequences. Exchange between subpopulations can reduce the size of each subpopulation necessary to maintain viability (Beier 1993). In addition, environmental variation is not as powerful an extinction force when populations are spread across space (Shaffer 1987; Noss et al. 1996).

If dispersal is hampered, either because of distance or barriers between patches, subpopulations in small patches can suffer high probabilities of extinction, from genetic, demographic, or environmental stochasticity or catastrophes (Shaffer 1987). For example, from 1985 to 1995 the San Andres chain (about 3,000 km² of cougar habitat) probably supported 36–60 adult cougars (based on the range of densities found on the study area) and an effective population size (N_e) as low as half the adult density (Nunney & Elam 1994). Smaller subpopulations (e.g., those of the Caballo and Fra Cristobal mountains) would have an even lower N_e . Without gene flow via dispersal, such patches may eventually lose all genetic variability and thus the capability to adapt to altered environmental conditions (Chepko-Sade et al. 1987). Genetic stochasticity (i.e., loss of heterozygosity and inbreeding depression) may enhance the risk of extinction (Saccheri et al. 1998), at least in populations that have recently declined in size and that lack histories of severe fluctuations (Gilpin 1987; Lande 1988).

The effects of demographic and environmental factors on population persistence have been simulated by Beier's (1996) cougar population viability model. The model, which included demographic and environmental com-

ponents, indicated that, for a 98% probability of 100-year persistence, critical patch size was between 1000 and 2200 km². Based on Beier's model and the demographic data we collected during our research, the San Andres chain is large enough to withstand the threat of extinction for 100 years. Smaller patches of cougar habitat have high probabilities of extinction, however. For example, 12 of 100 simulated populations for land areas of 270 km² (size of the Organ Mountains) went extinct over a 100-year period, even when the productive population parameters and high immigration rates for cougars on the San Andres Mountains were used.

Although larger habitat patches (e.g., the Sacramento Mountains) may not experience the extinction and recolonization events necessary for a strictly defined metapopulation (Levins 1970), gene flow can still be restricted and patches with negative growth rates probably will have to be rescued (Brown & Kodric-Brown 1977) by adjacent patches with positive growth rates. The Sacramento Mountains may have experienced such a rescue. Bounties and unregulated hunting had confined cougars in New Mexico mainly to the remote mountains west of the Rio Grande by the 1940s (Young 1946). Regulations on cougar offtake since 1972 probably allowed remaining cougars to produce emigrants that recolonized or stabilized patches east of the river, including the Sacramento Mountains.

Implications for Conservation

In the Southwest, cougars may exist in metapopulations. Consequently, the long-term survival of cougar subpopulations is probably dependent on the movement of cougars between habitat patches. Because cougars disperse across management-unit boundaries, cougar management prescriptions executed on one management unit could affect cougar population dynamics on other units within cougar dispersal range and beyond. High human offtake of cougars from local populations could contribute to a source-sink structure (Hanski & Simberloff 1997), and overharvest in too many patches could destabilize the metapopulation. Considering metapopulation dynamics is an important step in understanding how human and natural processes, such as offtake, prey declines, disease, habitat loss, and fragmentation, influence cougar conservation in the Southwest.

During our research, the San Andres Mountains were a refuge (protected from human-caused mortality) and a source of emigrants that subsequently were recruited into other cougar subpopulations. Hence, refuges can function as robust, biological savings accounts that contribute to population resistance, and resilience (Weaver et al. 1996) in the face of management mistakes in exploited subpopulations, fragmentation, or natural stochastic events (McCullough 1996b).

Smaller habitat patches (e.g., those of the Fra Cristobal and Caballo mountains) that are within cougar dispersal distance may facilitate numerical and genetic flow to more distant habitat patches. Female dispersers that cannot reach distant patches may be able to disperse to closer, stepping-stone populations and subsequently produce young that disperse to more distant patches. Dispersing males can use intervening patches as links in single dispersal events.

We did not identify distinct habitat corridors connecting the San Andres chain with other habitat patches. Instead, the broad, wild-land matrix surrounding the San Andres chain poses few dispersal barriers other than sheer distance. The low human density in southern New Mexico results in few artificial barriers to dispersal; consequently, emigration from the study area may resemble prehistoric dispersal patterns. As the human population in the region increases from about two people per square kilometer (U.S. Bureau of the Census 1996), protected corridors will be needed. Such corridors are important for cougars inhabiting patches that have been semi-isolated by the urbanization of southern California (Beier 1995).

Increasing isolation is already apparent within the San Andres Mountains chain. The expansion of U.S. Highway 70 reduced cougar movements between the San Andres and Organ mountains. A completely severed corridor could result in extinction and poor chances for recolonization of the Organ mountains because female emigration from distant habitat patches to the east and west is unlikely. Human development along Interstate 25, the Rio Grande, and the west fronts of the Caballo and Sacramento mountains may also begin to curtail dispersal between the San Andres Mountains and surrounding blocks of cougar habitat.

The consequences of accelerating human development include habitat fragmentation, increasing incidents of encounters between cougars and humans, increasing removals of nuisance cougars, increasing cougar deaths from vehicle collisions, and disruption of natural dispersal patterns. For example, California, with the greatest human density of the Western states (over 78 people per square kilometer; U.S. Bureau of the Census 1996), also has the highest rates of cougar-human encounters (Torres et al. 1996) and poor dispersal success in some areas (Beier 1995). In Florida, where human densities exceed 101 people per square kilometer, collisions with vehicles are second only to intraspecific strife as a major cause of panther deaths (Maehr 1997). Long-term cougar management planning should include identification and maintenance of potential dispersal corridors before they succumb to development.

Detrimental demographic and genetic effects are expected where human development has caused fragmentation and isolation of habitat patches. In the Santa Ana Mountains of California, highways and suburbs resulted

in such low rates of exchange, a study population of seven females lacked a breeding male for 12 months (Padley 1990; Beier & Barrett 1993). In addition, Beier (1993, 1996) predicted that unless connectivity within and beyond the Santa Ana Mountains was maintained, the population would become extinct. In the most extreme case known for the species, isolation may have resulted in effective philopatry in male Florida panthers (Maehr 1997). This will likely exacerbate inbreeding depression and random genetic drift (Hedrick 1995). The high immigration rates found for the San Andres Mountains suggest that cougars in southern New Mexico do not form genetically discrete subpopulations, but support for this hypothesis will have to await genetic studies.

Agencies that manage cougars in fragmented habitats need to identify and map subpopulations that are sources, sinks, and vulnerable to extinction because of small size or poor connectivity. Long-term monitoring of trends in key source and vulnerable subpopulations could help managers determine how human offtake affects metapopulation dynamics and how developments may degrade habitat and corridors. Corridors linking patches of interest could be identified by radiotracking movements of dispersing subadults.

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