

Metapopulation Models, Tenacious Tracking, and Cougar Conservation



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In 1987, the California Department of Fish and Game (CDFG) and the University of California began a 5½ year study to document the home range, density, movements, food habits, reproduction, survival, and related parameters for cougars (*Felis concolor*) in the southern third of the Santa Ana Mountains of southern California. When he hired me to lead this study in early 1988, Dr. Reginald Barrett ruefully quipped that urban growth in the study area was so rapid that I would “document the demise of this cougar population.” Over the next few months, this remark seemed like a prophecy. After the death of the territorial male in February 1988, there was no reproductive activity among the seven radio-tagged females and no evidence of a breeding male in the study area for 12 months (Padley 1990). These females were visiting one another at intervals that seemed to coincide with estrus cycles (Padley 1990), provoking among the field crew a spate of ribald humor that gradually segued into anxiety. Increasingly concerned, I expanded the study in early 1989 to include the entire mountain range and was relieved to note reproduction among the cougars to the north. Also at this time two young males settled into the original study area and the females promptly stopped visiting one another and started bearing cubs.

The optimism created by the 1989 birth pulse was soon tempered by the high mortality observed in the new cohort and, moreover, by an awareness that in less than 5 years urban sprawl could completely isolate the population and internally fragment at least one large piece of habitat from the core area. I believed that maintaining connectivity within and beyond the Santa Ana Mountains would allow this population to persist and that unless habitat areas functioned spatially as a metapopulation, this population was doomed.

1996. In: D.R. McCullough, ed. *Metapopulations* 293
and *Wildlife Conservation*. Island Press, Covelo,
California. 429 pp.

But 2 years of data provided only biological anecdotes to support this view, and I did not know if my hunch was correct or, if it was correct, which metapopulation configurations would persist or fail. If those with power over land use decisions were to be persuaded to limit urban growth, I would need scientific evidence that was both rigorous and easily understood. In particular, I would need:

1. A population viability analysis (PVA) that would predict the fate of a cougar population under various scenarios, highlighting two elements at the heart of metapopulation dynamics—patch size and patch connectivity. The emphasis on these elements was crucial because these are the two factors controlled by land use decisions. Patch area is controlled by restricting human development; connectivity is controlled by protecting corridors for wildlife movement to adjacent populations. Although the predictions of my model would also depend on age-specific survival rates, carrying capacity, subroutines for various types of stochasticity, and the functions relating vital rates to density, planning commissioners might be distracted by these aspects of population ecology. To get their attention and keep it, I needed to highlight the extent to which the population's fate depended on land use decisions.
2. A PVA model that simulated cougar population dynamics realistically. Erroneous model predictions can arise from two interacting sources: uncertainty in parameter estimates (which I address via sensitivity analyses—making predictions under both high and low estimates for poorly known parameters) and oversimplification of a species' life history (which I minimize by species-specific algorithms). Because huge profits for developers are at stake, biologists representing development interests could rightly argue that planners should not rely on a model that ignores certain aspects of cougar life history, such as the cougar's ability to shorten the interbirth interval from about 24 months (when cubs survive to dispersal) to as little as 4 months (if cubs die early). Indeed a generic model that was too pessimistic might not only limit development unfairly but also cause a cougar population to be written off as a "hopeless case." Generic models could also be too optimistic; by accounting only for females, for instance, a model would fail to predict the lack of reproduction observed when males were absent in 1988. Because the consequences of error were so severe, I wanted the model to be as objective and realistic as possible.
3. Data on corridor use. My data on the local population and published values were available to estimate most vital rates, but I had no data

on cougar immigration. In this landscape, dispersing cougars would immigrate via narrow habitat corridors or not at all. I expected the model to show that immigration was critically important to the metapopulation. Thus, it would be crucial to know whether dispersing cougars would immigrate via such corridors into semi-isolated habitat patches and to know where corridors should be retained in the landscape.

Meeting these three needs became the focus of the past 3 years of the research effort. This chapter recapitulates my published descriptions of the population viability analysis (Beier 1993) and cougar use of corridors (Beier 1995). In addition, I partition stochastic variation in observed survival rates into environmental and demographic components, apply the model to another cougar metapopulation (in and near the Santa Monica Mountains), and discuss the successes and failures of this metapopulation analysis and fieldwork in helping to conserve the Santa Ana Mountains metapopulation.

Methods

I modeled population trajectories under various levels of habitat area and immigration. Also, I used radio tracking to estimate population parameters, ~~and~~ document movement between habitat patches, and identify travel routes and potential habitat corridors for the Santa Ana Mountain cougar metapopulation.

Simulation Model

I did not directly model the dynamics of an entire cougar metapopulation. Instead, the model simulated the trajectory of a subpopulation linked to adjacent populations via several levels of immigration. Linked Leslie matrices for males and females were used to model the Allee effect, make vital rates depend on the density of same sex individuals, and allow for sex-biased immigration. Additional subroutines introduced demographic and catastrophic stochasticity into survival and fecundity rates.

For each combination of input conditions, I simulated a 100-year population trajectory 100 times, recording the number of runs on which the population went extinct, mean population size in year 100, and other summary statistics. I set the initial number of adults (animals ≥ 2 years of age) at carrying capacity (with equal numbers in each year class) and initial numbers of 0-year-olds and 1-year-olds at 50 and 25 percent, respectively, of the total number of adult females. This initial age distribution represents a population that had stable reproductive and survival rates for the decade before the start

of the simulations. Because all models are simplifications and thus prone to error, and because I ran only 100 simulations per combination of input conditions, I considered any extinction risk of 2 percent or greater to be significant and unacceptable.

The factors controlled by land use decisions were area of habitat and level of immigration. I ran simulations starting with 200 km² of habitat and in increments of 200 km² until the extinction risk declined to zero. No estimates of immigration rates for cougars were available. Therefore, in addition to simulating no immigration (no corridor), I simulated the three lowest levels of immigration that would qualify the area as part of a metapopulation (that is, interacting with adjacent groups of conspecifics): one male immigrant per decade, two males per decade, and three males plus one female per decade. If these levels had no influence on population persistence, I planned to simulate higher immigration rates. The sex bias in these immigration rates reflects the fact that males are more likely than females to disperse out of their natal mountain range (Ashman et al. 1983; Anderson et al. 1992).

For each combination of habitat area and level of immigration I simulated the population dynamics under many combinations of estimates for life history and environmental attributes (Table 13.1). Because male and female equilibrium densities and juvenile survival rates are hard to estimate, may vary geographically, and have a profound influence on the results, the simulations used 36 permutations of values for these parameters. I used separate estimates of carrying capacity for adult females and males because social intolerance among adult females (calibrated to prey abundance and influenced by vegetation and topography) is thought to regulate their density, whereas territoriality among males (competing for access to females) regulates male density (Seidensticker et al. 1973).

The model included subroutines to simulate density dependence (Table 13.2), including an Allee effect, inhibition of reproduction for the youngest females when the population exceeded carrying capacity, enhancement of survival rates at low density, and decline in survival rates (especially for juveniles and dispersers) at high density. Lacking empirical data, I chose the survival rate functions for their computational simplicity (Beier 1993). However, I tested various alternative functions for density dependence in survival rates and found that neither risk of extinction nor ending population size varied among them (Beier 1993). Extinction risk was markedly higher in preliminary analyses with density-independent survival rates, but this approach also produced ending population sizes (for populations that survived) that far exceeded carrying capacity (Beier 1993).

Most studies report adult sex ratios skewed toward females; at some age, therefore, survival rates of males must be lower than those of females.

TABLE 13.1.

Values for biological parameters used in simulating cougar population dynamics

Parameter	Values used
Mean litter size	2.8 ^a
Juvenile survival rate ^b	0.65 for females, 0.60 for males 0.75 for females, 0.70 for males
Adult survival rate ^c	0.75 0.85
Probability that a resident female bears a litter in a given year	For 0- and 1-year-old females: 0% For 2-year-old females: <40% For older females: 0% if litter from previous year survived 1 year; 100% if litter from previous year died
Maximum life span	12 years
Carrying capacity (breeding adults per 100 km ²)	Sex ratio of 2 adult females per adult male: 0.4 females, 0.2 males 0.6 females, 0.3 males 0.8 females, 0.4 males 1.0 females, 0.5 males 1.2 females, 0.6 males Sex ratio of 3-4 adult females per adult male: 0.8 females, 0.2 males 1.2 females, 0.4 males Sex ratio of ~1 adult female per adult male: 0.4 females, 0.4 males 0.8 females, 0.6 males

Source: Anderson (1983), Anderson et al. (1989), Ashman et al. (1983), Beier and Barrett (1993), Currier et al. (1977), Eaton and Velandar (1977), Hemker et al. (1984), Hemker et al. (1986), Hopkins (1981), Hopkins (1989), Hornocker (1970), Lindzey et al. (1988), Logan et al. (1986), M. Jalkotzy and I. Ross, (Calgary, Alberta, unpublished data), Murphy (1983), Neal et al. (1987), Quigley et al. (1989), Robinette et al. (1961), Robinette et al. (1977), Seidensticker et al. (1973), Shaw (1977), Sitton and Wallen (1976), Young (1946), with justifications for specific values given by Beier (1993).

Note: Survival and breeding probabilities are for a population at carrying capacity and were modified as indicated in Table 13.2.

^aA value of 2.4 produced population sizes much smaller than carrying capacity, even when used together with optimistic estimates for other parameters. A value of 3.2 produced about the same extinction risk as a value of 2.8.

^bBoth sexes 0 and 1 year old and males 2 years old.

^cFemales ≥ 2 years old and males ≥ 3 years old.

TABLE 13.2.

Density-dependent relationships used in simulating cougar population dynamics

Vital rate	Relationship to density	Rationale
Litter size	Density independent	Low cost of gestation (92 days, 500-g neonate mass).
Probability that a resident female will breed	When $NF > KF$, 20% of resident females in excess of K breed; youngest females assigned to nonbreeding status.	Young females reproduce only after home range establishment (Seidensticker et al. 1973).
Probability that a resident female will breed	Allee effect: ^a When $NM < KM$ (some male territories are vacant), % of NF breeding is multiplied by: $1 - [(KM - NM) \cdot 1.15^{(KM - NM) / KM}]$ $= S(KF/NF)^{0.5}$, truncated to values between 0.3 and 0.9	To reflect our 1989 observations. Because territory of each adult male increases by 15% for each "deficit male," the effect is very mild except at very low N .
Survival rate, 0-year-olds (M, F) and 1-2-year-old F	$= S(KF/NF)^{0.5}$, truncated to values between 0.3 and 0.9	To reflect competition among mothers and dispersing females.
Survival rate, 1-year-old males	$= \text{minimum of } S(KF/NF)^{0.5} \text{ or } S(KF/NF)^{0.5} (KM/NF)^{0.5}$, truncated to values between 0.3 and 0.9	To reflect competition among mothers for food resources as well as mortality due to adult males during dispersal.
Survival rate, 2-year-old males	$= S(KM/NM)^{0.5}$, truncated to values between 0.3 and 0.9	To reflect mortality due to adult males during dispersal.
Survival rate, females >2 year old	$= S(KF/NF)^{0.25}$, truncated to values between 0.5 and 0.95	To reflect competition among mothers and dispersing females.
Survival rate, males >2 years old	$= S(KM/NM)^{0.25}$, truncated to values between 0.5 and 0.95	To reflect competition among males for territories and access to females.

Note: S = annual survival rate at carrying capacity, KF and KM = carrying capacity for breeding males and females, respectively, and NF and NM = number of ≥ 2 -year-old females and males, respectively.

^a Formula was incorrectly typeset in Beier (1993).

Robinette et al. (1977), Ashman et al. (1983), Lindzey et al. (1988), and Anderson et al. (1989) did not report sex differences in adult survival rates, however, nor did I document them in this population (Beier and Barrett 1993). Therefore, the model included a small difference between the sexes in juvenile survival rates, with the sex-specific subroutines for density dependence (Table 13.2) creating further sex differences in survival rates (especially for juveniles) to maintain the specified adult sex ratio.

I included two of the three types of stochasticity commonly included in simulation models (Table 13.3). Catastrophic stochasticity was included to reflect low-frequency, high-magnitude events such as prolonged droughts or severe epidemics that might cause large reductions in prey numbers. I modeled this variation by decreasing carrying capacity by 20 percent for a 3-year period starting every 25 years. Because demographic stochasticity arises from binomial processes (such as surviving or dying, breeding or not breeding, being born male or female), I modeled it by applying the appropriate probability to each simulated cougar (Table 13.3). If the survival rate for yearling

TABLE 13.3.

Stochasticity in population parameters used to simulate cougar population dynamics

Population parameter	How stochasticity was modeled	Type of stochasticity
Survival rate	Each animal in an age class survived with probability = density-dependent survival rate.	Demographic
Primary sex ratio	Each newborn had 50% chance of being male.	Demographic
Litter size	Each litter had 2, 3, or 4 cubs, with probabilities appropriate to the specified mean litter size.	Demographic
Immigration rate	Each year 1 male or female immigrated with probability = $0.1 \cdot$ specified number of immigrants per decade, and immigrants were assigned to the 1-year, 2-year, or 3-year age class with probability = 0.3, 0.5, and 0.2, respectively.	Demographic
Probability that a resident female bred	Each female bred with probability = density-dependent probability of breeding for that age class.	Demographic
Carrying capacity	20% decrease in carrying capacity in years 25–27, 50–53, 75–77. ^a	Catastrophic

Note: Demographic stochasticity was achieved by applying the appropriate age- and sex-specific binomial probabilities to each animal.

^a Extinction risk did not decrease when a 0% decline was simulated; nor did it increase when a 40% decline was used.

males was 0.60 and there were two yearling males in a given year, for example, all outcomes (2, 1, or 0 survivors) were possible (with binomial probabilities 0.36, 0.48, and 0.16, respectively) in a biologically realistic manner.

Environmental stochasticity, a third type of variation relevant to PVA, reflects low-magnitude, year-to-year variation in survival rates for all individuals resulting from fluctuation in food crops, subepidemic diseases, poaching, and similar factors. I attempted to estimate the magnitude of environmental stochasticity from the observed month-to-month variation in survival rates of radio-tagged cougars. In the absence of a catastrophe, this variation can come from only two sources: variation due to sampling a small population with a given probability (that is, demographic stochasticity) and variation in that probability of survival (that is, environmental stochasticity) (Lacy 1993). Therefore, I estimated environmental stochasticity by comparing observed variation to the variation due to demographic stochasticity. The variance of 64 monthly survival rates for adults (mean = 97.51 percent) was 25.6 (SD = 5.06 percent). The variance expected if the observed variation were based solely on demographic stochasticity was 30.5, yielding an estimate of zero (rounding -4.9 to the nearest feasible value) for variance due to environmental stochasticity. To further explore this issue I examined the frequency distribution of adult survival rates under the assumption that environmental stochasticity contributed to the observed month-to-month variation (Table 13.4). This Monte Carlo sample contained significantly fewer outcomes near the true mode and significantly more outcomes <0.80 (a monthly rate never observed in the field). Thus, incorporating environmental stochasticity into my PVA would have reduced the realism of the model and predicted higher extinction risks.

Fieldwork in the Santa Ana Mountains

Study Area. The cougar metapopulation in the Santa Ana Mountains of southern California consists of about 20 adults on about 2070 km² of habitat with a tenuous linkage to a larger population in the Palomar Range (Figure 13.1) (Beier and Barrett 1993). The surrounding urban areas do not offer even marginal cougar habitat. About 1270 km² of this habitat (61 percent) is protected from urban uses, primarily within lands owned by the U.S. Forest Service and U.S. Navy (Beier 1993). Of the protected land, about 1114 km² forms a contiguous block (the "protected core area"); if all private lands were developed, the other 154 km² of protected land would be isolated into fragments unusable by cougars. The terrain is rugged and elevation varies from zero to 1680 m. Vegetation includes chaparral, coastal scrub, oak (*Quercus agrifolia* and *Q. engelmannii*) woodlands, annual grasslands, and small areas of coniferous forest on high-elevation, north-facing slopes. Few drainages have

TABLE 13.4.

Relative frequency (%) of monthly survival rates for adult cougars in the Santa Ana Mountains (1987–1992) compared to that expected if environmental stochasticity (ES) is absent or accounts for half of the observed monthly variation

Monthly survival rate	Observed frequency	Expected frequency with demographic stochasticity <i>and...</i>	
		No ES ^a	ES accounting for 50% of observed variance ^b
0.0–0.8	0/64 = 0.0%	1.7	5.5
0.801–0.85	1/64 = 1.6%	2.8	3.2
0.851–0.9	10/64 = 15.6%	11.8	14.6
0.901–0.95	2/64 = 3.1%	1.4	1.9
0.951–1.0	51/64 = 79.7%	82.3	74.8

Note: Survival rate was computed as the number of cougars alive at the end of the month divided by the number alive at the start of the month (mean 7.9; range 5 to 12 animals at start of month). Expected frequencies were generated by repeated sampling, applying to each animal alive at the start of a month either a constant survival probability of 0.9751 (“no ES”) or a probability from a normal distribution with mean 0.9751 and SD = 0.0358 (“ES accounting for 50% of observed variance”).

^a Did not differ from observed frequency distribution, two-sample Kolmogorov-Smirnov test, $P = 0.06$. Standard deviation of 0.0552 was nearly the same as the observed SD of 0.0506.

^b Differed from observed frequency distribution, two-sample Kolmogorov-Smirnov test, $P < 0.0005$. Standard deviation of 0.732 was larger than the observed SD of 0.0506.

perennial aboveground water flow, but seeps and springs are well distributed throughout the range.

Because mule deer (*Odocoileus hemionus*) accounted for 81 percent of the prey biomass consumed (Beier and Barrett 1993), deer density probably was the ultimate determinant of carrying capacity. There were 2.3 to 4.6 deer per square kilometer in the Santa Ana Mountains (Beier and Barrett 1993). Hunting (legal and illegal combined) took less than 5 percent of the adult deer a year in one study area in the northeastern corner of the range (Environmental Science Associates 1992).

The human population of the eastern half of Orange County and the western sixth of Riverside County is projected to grow from 1.15 million in 1987 to 2.09 million by 2010 (Anonymous 1989). Most growth is expected to occur, not within existing cities, but via “planned communities” built in

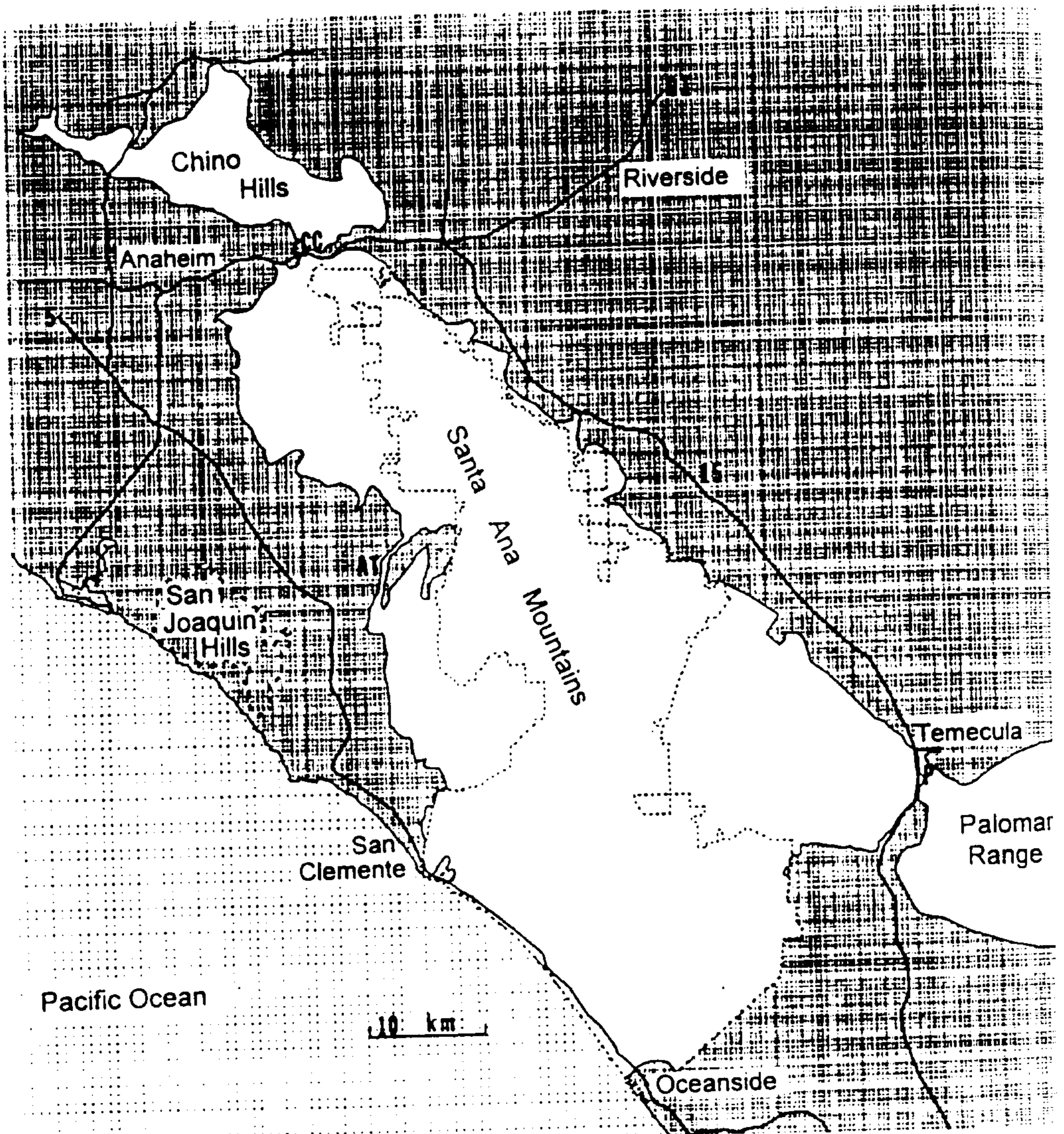


Figure 13.1. Map of the study area in Los Angeles, Riverside, Orange and San Diego counties, California. All highways (numbers) shown are six- to ten-lane freeways. The unshaded area includes 2070 km² of cougar habitat in the Santa Ana Mountains (including the Chino Hills) and a portion of the larger habitat area in the adjacent Palomar Range (east of Interstate 15). The center of the Santa Ana mountain range is about 65 miles southeast of Los Angeles and about 60 miles north of San Diego. The dotted line encloses the protected core area (seven interconnected protected parcels totaling 1114 km²). Urban (nonhabitat) areas are indicated by dense stippling with the dashed line enclosing the 75 km² of suitable habitat in the San Joaquin Hills (cougars recently extinct). Three habitat corridors are designated CC (Coal Canyon), AT (Arroyo Trabuco), and P (Pechanga).

privately owned open-space areas, including some of the best cougar habitat. Such rapid growth causes the outright loss of several square kilometers of habitat a year in Orange and Riverside counties. In addition, some wildlands are lost to the cougar population because they become isolated by freeways and other development. After urbanization isolated a 75-km² fragment of cougar habitat (Figure 13.1: San Joaquin Hills) in the late 1970s, for example, cougars became extinct there between March 1987 and June 1990 (Beier and Barrett 1990).

Radio Telemetry. I captured and radio-tagged 21 adult and 11 juvenile cougars from 1988 to 1992 (Beier 1995; Beier et al. 1995; Figure 13.2). To document travel paths, I monitored animals overnight, determining the focal animal's location by ground triangulation every 15 minutes from before sunset until after sunrise on each of 178 tracking sessions (Beier et al. 1995). Cougars traveled an average of 5.4 km per night (Beier et al. 1995). I radio-tracked adults and juveniles to document the routes by which cougars traveled from the protected core area to smaller protected parcels surrounded by private land. These smaller parcels (15,448 ha total) included six regional parks, one state park, three private reserves, and a university field station. To document use of corridors for dispersal, I followed the dispersal movements of the nine radio-tagged juveniles (all that survived to dispersal age) in relation to three potential corridors and several habitat peninsulas (Beier 1995). I identified the three potential corridors (Figure 13.1: Coal Canyon, Pechanga, and Arroyo Trabuco) before radio-tracking the dispersers. These areas were not designed as wildlife movement corridors, but were simply habitats made linear by urban growth.

The Coal Canyon Corridor (1.5 km long) provided the only potential habitat link between the Chino Hills and the rest of the Santa Ana Mountains (Figure 13.3). Most of the corridor was occupied by two shrubless golf courses and a horse stable devoid of understory. It was crossed by an eight-lane freeway (State Route 91) with heavy night traffic that precluded any at-grade road crossing. The only potential freeway undercrossings were a vehicle underpass (not used at night but devegetated, brightly lit, and noisy at all hours) and a 2.6 × 3.3 m concrete box culvert 200 m long.

The Pechanga Corridor (4 km long) was the last potential habitat link between the Santa Ana Mountains and the Palomar Range. It was crossed by a six-lane freeway (Interstate 15) and contained two golf courses. Although a bridge over the Santa Margarita River provided a quiet, well-vegetated, and relatively dark freeway undercrossing, a cougar using this underpass must also cross more than 400 m of golf course and skirt two fences along a golf driving range. The corridor was bordered by tract homes and contained an

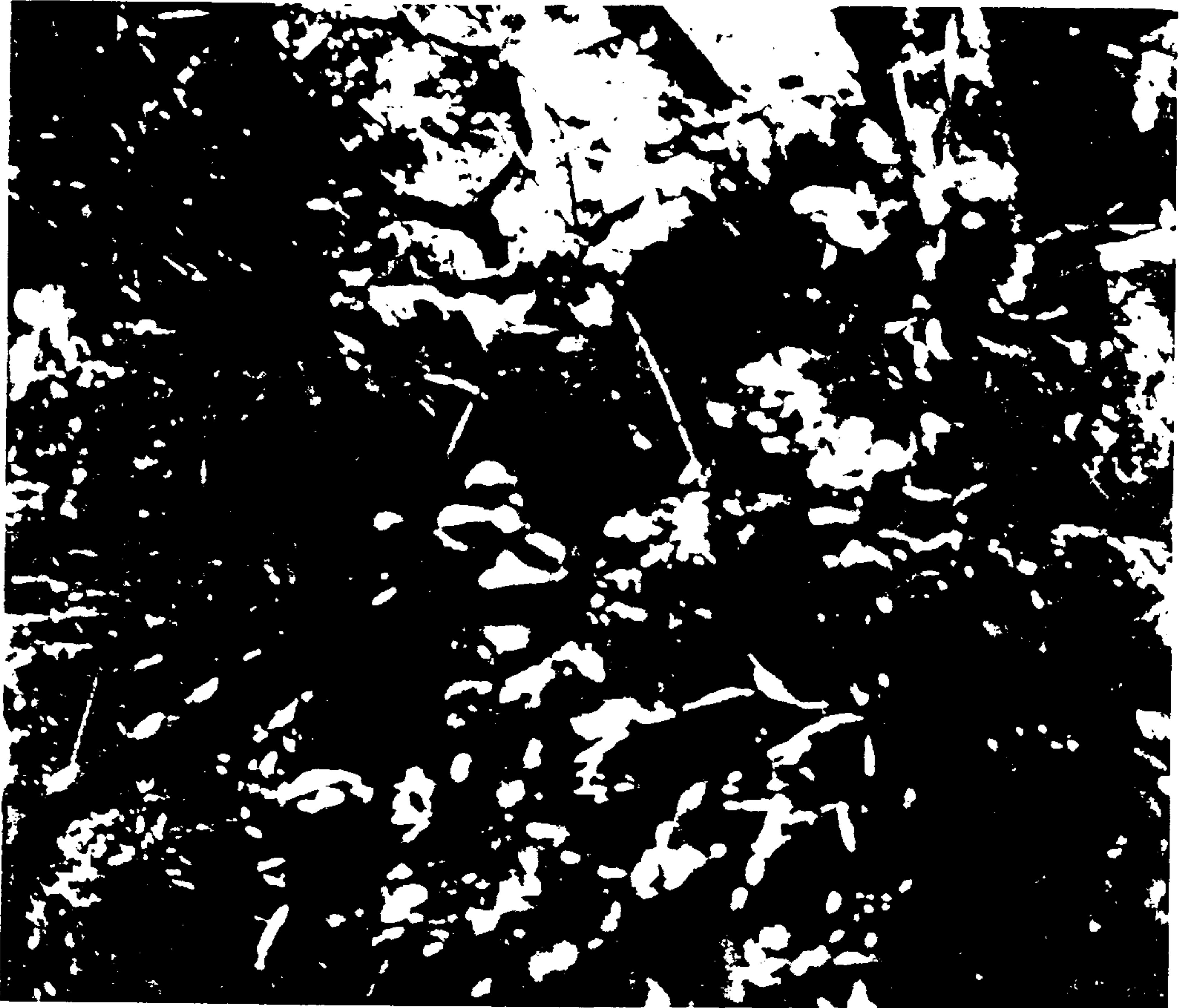


Figure 13.2. Female cougar F6 at capture in May 1989.

abandoned rock quarry, a two-lane paved road, several residences, and a concrete embankment on one side of the main watercourse.

The Arroyo Trabuco Corridor (6 km long) was 400 to 600 m wide and lined with tract homes. Steep bluffs (20 to 70 m deep) minimized urban vistas, noise, and light pollution in the arroyo, and the dominant vegetation was an oak-sycamore (*Platanus racemosa*) riparian forest. Unlike the other two corridors, the arroyo was not the sole link between the large habitat area at either end (Figure 13.1).

I estimated survival rates for radio-tagged adults (≥ 2 -year-old animals with stable home ranges) and juveniles (dependent young and dispersers lacking a stable home range) by using 1-month time intervals and the product limit procedure with staggered entry (Pollock et al. 1989). The product of 12 monthly rates yielded an estimate of annual survival rate, and the average of these running products yielded a single point estimate. I computed population density by applying mark-recapture estimators to the numbers of cougars tagged and the numbers of tagged and untagged animals killed on depredation or by vehicles in three half-year periods. Because road surveys for

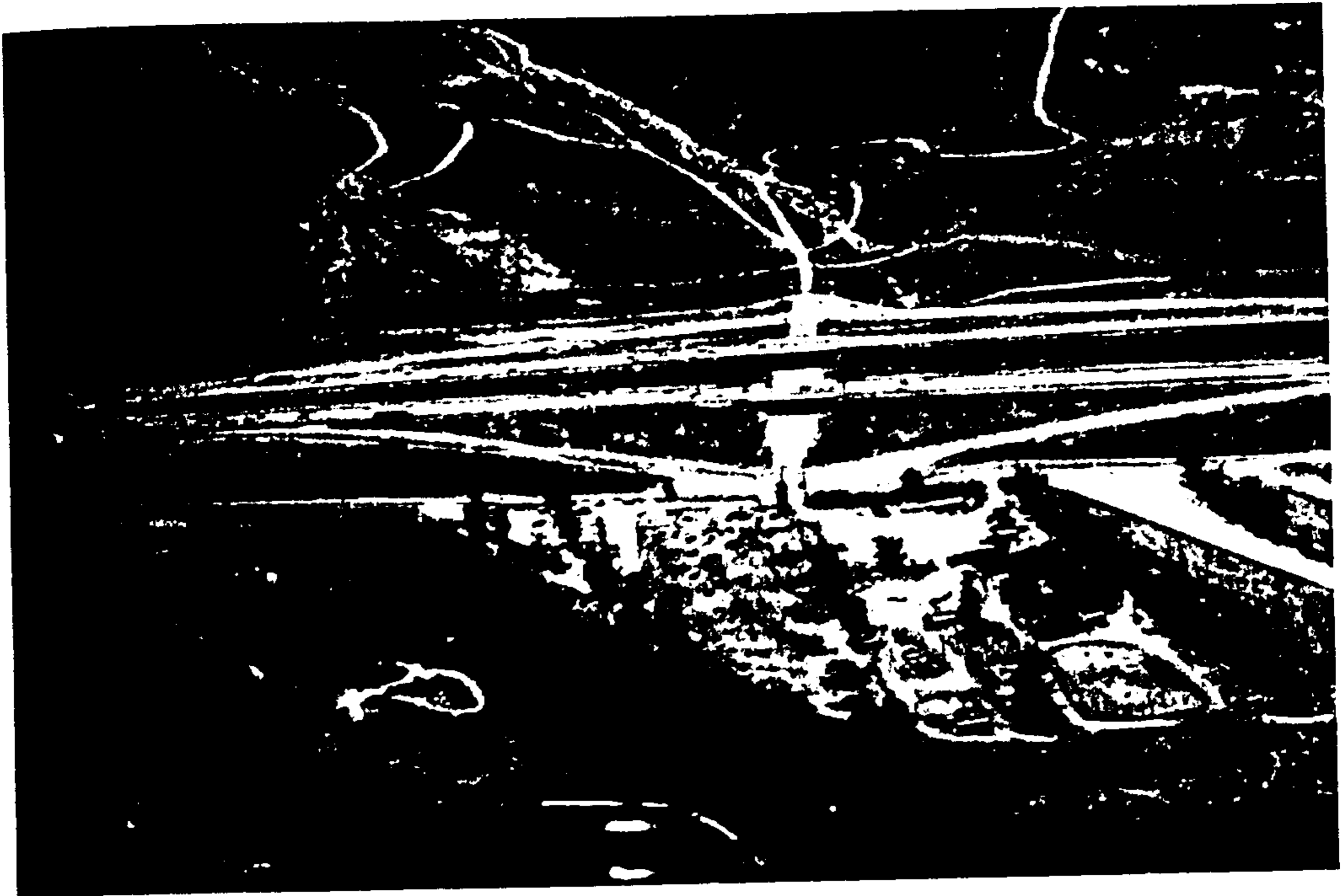


Figure 13.3. The Coal Canyon Corridor, looking southward from the Chino Hills. From the mouth of Coal Canyon (top of photo), northbound cougars had to walk under State Route 91, through an equestrian center (bare areas), and then across the Santa Ana River (hidden in the riparian forest running from left center to lower right) and a golf course (lower left) to reach the southern edge of the Chino Hills (just below bottom of photo).

cougar tracks suggested that approximately 10 percent of suitable habitat lacked resident females, and because female home ranges overlap broadly, I estimated carrying capacity for females as 20 percent higher than the maximum calculated density.

Results and Discussion

Both the model results and the field data emphasize the importance of movement corridors to maintenance of the Santa Ana and Santa Monica cougar metapopulations. I describe my efforts to bring this information to bear on the land use decisions of the different jurisdictions within this area.

Population Model

One does not need a model to make the point that patch size and connectivity are important for keeping cougars on the landscape. These landscape features are inherent in the metapopulation concept. The value of the model

is that it permits us to estimate which combinations of patch size and connectivity will conserve a cougar population, given our best estimates for that population's carrying capacity, survival rates, and other parameters. In this model, as expected, both area of habitat and the presence (or quality) of an immigration corridor influenced the probability of extinction (Figure 13.4; for other results see Beier 1993). Despite variation in biological parameters, at least 98 percent of simulated populations persisted for 100 years when there was more than 2200 km² of habitat available, except under the most pessimistic estimates of biological parameters (carrying capacity of no more than 0.4 adult female and 0.2 adult male per 100 km² in concert with adult survivorship ≤ 0.75). With only 1000 km² of habitat and no immigration, simulated populations had 98 percent persistence under only the most optimistic estimates of biological parameters (carrying capacity greater than 1.0 adult female and 0.5 adult male per 100 km² in concert with adult survivorship ≥ 0.85 and juvenile survivorship ≥ 0.65). Thus in the absence of an immigration corridor, the critically small habitat area lies between 1000 and 2200 km². Within this range, the critical size depended on demographic parameters.

Immigration improved the probability of survival at surprisingly low levels—as low as one male per decade. For any combination of biological parameter estimates, the critical habitat area was 200 to 600 km² smaller with an immigration corridor than without. I simulated only three low levels of immigration, and certainly a corridor allowing more immigration would make even smaller areas viable. Thus in areas where isolation or fragmentation of a cougar population appears imminent, protecting and enhancing any remaining corridor is a valuable measure.

These minimum habitat areas (1000–2200 km², depending on carrying capacity and vital rates) would hold 15 to 20 adult cougars—far fewer than necessary to preserve genetic variability over several centuries (Franklin 1980). Lacking a quantitative way to model how inbreeding would increase extinction risk, I relied on the generalization that small populations will succumb to demographic events before inbreeding becomes a problem (Lande 1988), and my model ignored this risk. Mills and Smouse (1994), however, argue convincingly that moderate levels of inbreeding depression can influence population persistence in the first few generations after habitat fragmentation and isolation. I, therefore, stress that the minimum areas suggested by this model will not guarantee survival of a cougar population. In cases where no immigration corridor is provided, populations confined to such small areas will require monitoring and perhaps periodic introduction of new genetic material by translocation.

These minimum areas (and the number of cougars they contain) are

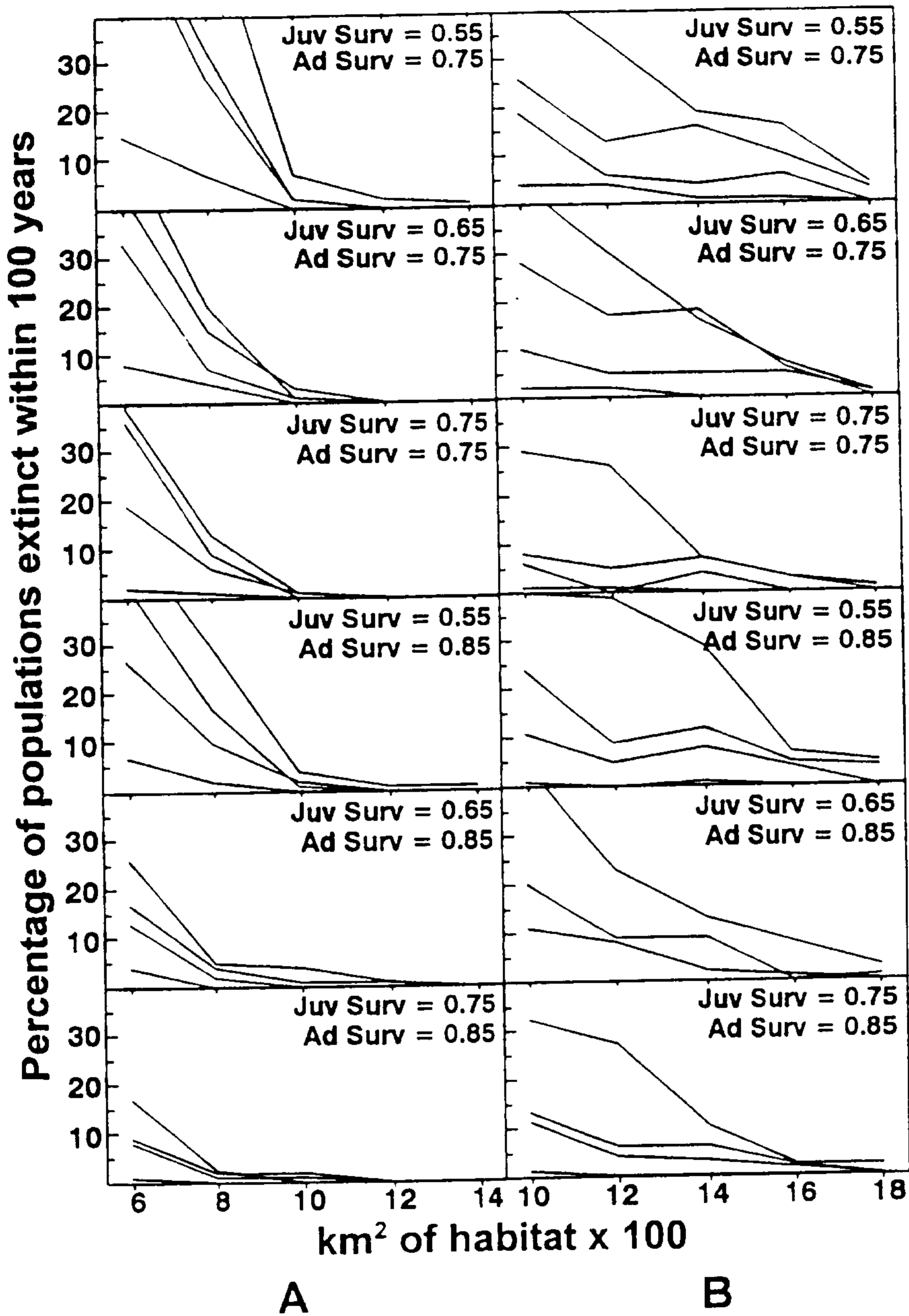


Figure 13.4. Effect of habitat area and immigration on cougar population persistence given (A) a carrying capacity of 0.8 breeding adult female and 0.6 breeding adult males per 100 km² or (B) a carrying capacity of 0.8 breeding adult female and 0.2 breeding adult male per 100 km². In each graph the top through bottom lines indicate the percentage of simulated populations that went extinct when the numbers of immigrants per decade were 0, 1 male, 2 males, or 3 males and 1 female, respectively. Juv Surv (juvenile survival rate) and Ad Surv (adult survival rate) are defined in Table 13.1.

comparable to the minimum area and number suggested by Shaffer (1983) for grizzly bears. Both my model and Shaffer's are species-specific and incorporate density dependence. Moreover, both produce minimum areas and populations much smaller than predicted by analytic models (for example, Belovsky 1987), simulation models lacking density dependence (for example, Ginzburg et al. 1990), or models that incorporate fewer subroutines to mimic cougar life history (Seal and Lacy 1989, although their model also models inbreeding depression and uses lower survival and reproductive rate estimates). It is tempting to favor models that call for protecting larger areas on the grounds that they are more "conservative," but such models have two drawbacks. First, in the long run they undermine the credibility of conservation biology and PVA especially when populations persist under conditions that such models predict will lead to rapid extinction. Second, to the extent that such analyses misclassify viable populations as "hopelessly" small, they can be a *less* conservative approach.

The modeling exercise yielded two results relevant to how stochasticity is incorporated into PVA models. First, natural catastrophes of moderate severity (up to 40 percent loss of carrying capacity), frequency (every 25 years), and duration (3 years) had little impact on extinction risk and were not apparent in graphs of population trajectory (Beier 1993). Shaffer (1983) similarly concluded that catastrophes are unimportant to the population dynamics of grizzly bears. Second, observed variation in survival rates was attributable entirely to demographic stochasticity; thus environmental stochasticity (ES) appeared trivial or absent in this population. Although ES, if it exists, can greatly increase extinction risk (Shaffer 1987; Lande 1993) and many PVAs therefore include subroutines for it, I am unaware of previous attempts to empirically measure ES for a PVA or (except for Lacy 1993) to partition observed variance between demographic stochasticity and environmental stochasticity. Although ES is probably important for populations of small-bodied or herbivorous animals (more at the mercy of weather and other transient phenomena) and is obviously important for exploited populations, it should not be incorporated blindly into all PVA models.

Applying the Model to the Santa Ana Mountains

I estimated the carrying capacity for the Santa Ana Mountains as 0.80 breeding female and 0.30 breeding male per 100 km². The mean annual survival rate was 0.74 for adults (0.9751 per month, SD = 0.0502, *n* = 64 months) and 0.48 for juveniles (0.9403 per month, SD = 0.1045, *n* = 34 months). Using these estimates, the model predicted that the cougar population in the Santa Ana Mountains is clearly endangered. Although there is low (less than two percent) risk of extinction in the next 100 years with the cur-

rent 2070 km² of habitat and no immigration, every parcel of habitat lost increases the risk of extinction (Figure 13.5). Consistent with our field observations in 1988, the model also predicted frequent local shortages of breeding males and an unstable sex and age structure under current conditions. If the population is confined to the 1114-km² block of contiguous protected lands, extinction risk rises to approximately 65 percent; an immigration corridor, necessarily including some lands now in private ownership, greatly improves the prognosis.

Applying the Model to the Santa Monica Mountains

Urban sprawl has created a second cougar metapopulation to the north of the study area in the Santa Monica Mountains (660 km²), Simi Hills (130 km²), and Santa Susana Mountains (contiguous with more than 5000 km² of cougar habitat) (Figure 13.6). Using the most optimistic published estimates for vital rates and carrying capacity, the model predicts that cougars would rapidly become extinct in both the Santa Monicas and the Simi Hills if these areas were isolated from the Santa Susanas. Edelman (1990) identified several potential movement corridors linking these areas (Figure 13.6), all on private land, and the Santa Monica Mountains Conservancy is actively working to

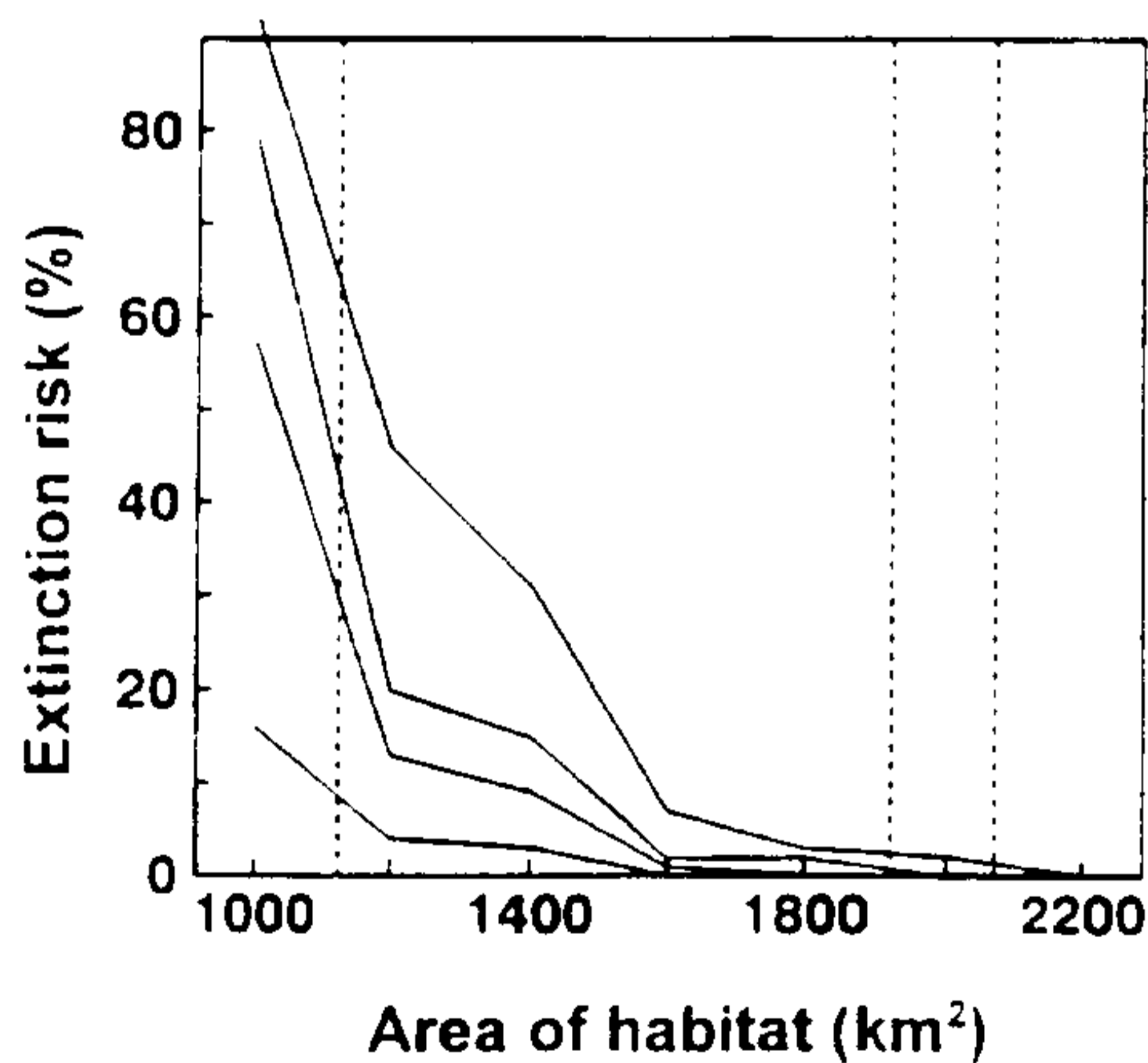


Figure 13.5. Extinction risk for the cougar population in the Santa Ana Mountains. The top through bottom lines give the percentage of simulated populations that went extinct within 100 years when the numbers of immigrants per decade were 0, 1 male, 2 males, or 3 males and 1 female, respectively. From right to left, the vertical lines indicate the total available habitat in 1992, the total habitat available if the Chino Hills (150 km²) is lost, and the total area of the protected and interconnected habitat block. Simulations were run with a carrying capacity of 0.80 breeding female and 0.30 breeding male per 100 km², an adult survival rate of 0.74, and a juvenile survival rate of 0.48.

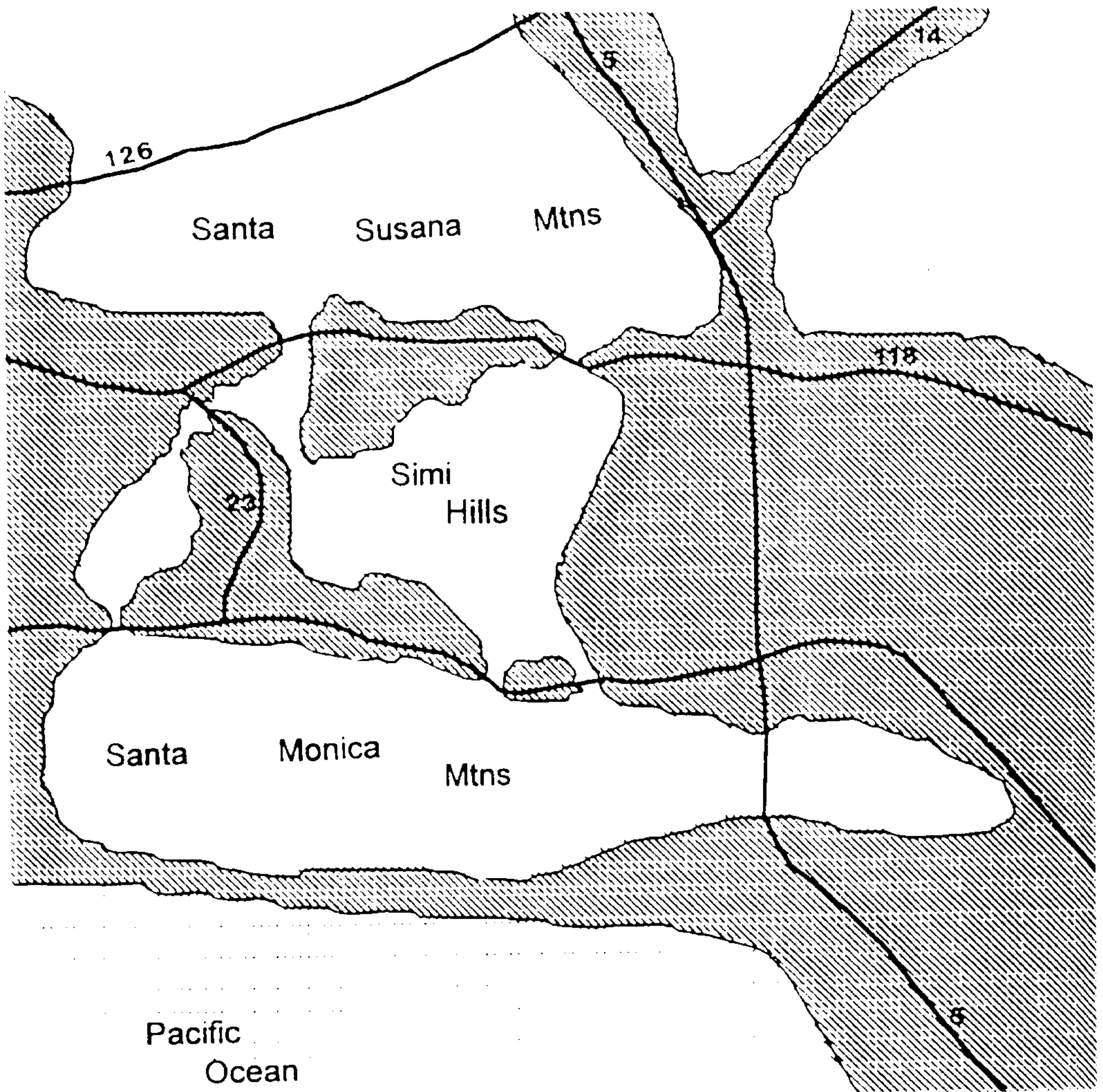


Figure 13.6. Map of the mountain ranges that lie just northwest of Los Angeles; all highways shown (numbers) are 4–12 lane freeways. All potential connections are threatened by urban development. The unshaded areas indicate cougar habitat in the Santa Monica Mountains (660 km²), Simi Hills (130 km²), Santa Susana Mountains (>2000 km², including contiguous areas to the north), and potential connections among these areas, in relation to urban areas (cross-hatched).

preserve these links. Because the average home range of an adult female cougar in southern California is about 110 km² (Beier and Barrett 1993), the Simi Hills are unlikely to support more than two adult female cougars and often may be unoccupied for several years after the death of resident females. Nonetheless, the offspring of resident females in the Simi Hills are the most likely immigrants to the Santa Monicas, even if the Simi Hills support breeding females less than 50 percent of the time. Thus, even if a formal

survey for cougars classifies the Simi Hills as "suitable but unoccupied" habitat in any given year, from the perspective of the metapopulation this habitat is as critically important as any occupied habitat.

Use of Corridors by Dispersers

I assessed corridor use from two perspectives. Both dramatically showed that cougars will disperse via habitat corridors in a landscape fragmented by urbanization and, moreover, that some dispersers will use corridors containing unnatural features such as golf courses and major freeways. First, from the perspective of the dispersers, five of the nine juveniles used corridors and one of them used two corridors (Table 13.5). Second, all three potential corridors were used. Three dispersers successfully used the Arroyo Trabuco. Two radio-tagged dispersers successfully used the Coal Canyon Corridor, a third was hit by a vehicle there, and tracks indicate that an uncollared juvenile also used the corridor. One disperser used the Coal Canyon Corridor more than 22 times over 19 months to establish a home range that included both the Chino Hills and the northern part of the Santa Ana Mountains (Beier 1995). Of the three dispersers encountering the Pechanga Corridor, one apparently did not enter it, another traversed it in a single night, and a third strayed from the corridor into a residential area where he was captured by animal control officers. Between October 1990 and December 1993, five unradioed cougars were killed by vehicles where I-15 crosses the Pechanga Corridor. Although my early observations (Beier 1993) led me to be pessimistic about the utility of this corridor, the five road-kills there suggest that successful crossings also are likely.

In addition, seven of the nine dispersers explored to the tips of habitat peninsulas, making a total of ten such forays averaging 2.9 km in one-way length (Table 13.5). All peninsulas extend into dense urban areas, and most were heavily used during the day by humans. Despite intense monitoring of 20 radio-tagged adults, there was no evidence that adult cougars visited any of the ten habitat peninsulas.

Travel Paths Likely to Become Corridors

In the Santa Ana Mountains, overnight radio monitoring identified 18 routes by which cougars traveled from the 1114-km² protected core area to the 11 regional parks and reserves surrounded by private land. Although only four of these routes had significant human intrusions in 1992, 17 (including these four) were threatened by proposed highway projects and anticipated urban development. The only secure connection was provided by the Santa Margarita River, which links the University of California Field Station to the protected core area.

TABLE 13.5.

Use of habitat corridors and peninsulas by dispersing juvenile cougars radio-monitored in southern California: 1990–1992

Disperser ^a	Corridor use		Peninsula use		Description of movement
	(successful unless otherwise noted)	Length (km)	Width (m)		
F17	None	1.1	50–250		Moved between horse stables, church, freeway (SR 91), and a 75-ha newly graded area to daybed at peninsula tip, <50 m from new housing tract in City of Anaheim.
M3	None	3.0	1000		Moved through mix of orchards and scrub into edge of residential area in City of Irvine. ^b
M5	1 km into Pechanga Corridor, detoured into peninsula	1.4	100–300		1. Partway into Pechanga Corridor, detoured into Temecula Creek habitat peninsula, walking 1.4 km to its tip and then into residential area in City of Temecula. ^b
		4.5	50–400		2. Explored Santiago Creek in Cities of Orange and Anaheim; daybedded in peninsula tip (10-ha riparian forest at Katella St.).
		1.5	50–100		3. Crossed 1 km of open terrain on three occasions to reach 50-ha riparian forest at Peters Canyon Reservoir and on one occasion continued an additional 500 m down canyon.
M6	Coal Canyon (≥22 crossings)				None.

M7	Encountered but did not use Pechanga Corridor				None.
M8	1. Arroyo Trabuco 2. Coal Canyon	1.0	30–400	1.0	1. Crossed under I-5 and spent 14 days in 350-ha riparian forest (“Trestles Beach”) in estuary of San Mateo Creek between City of San Clemente, freeway, and Pacific Ocean. 2. Crossed grassland at edge of Chino Hills and was killed at tip of peninsula trying to cross SR 60.
M10	1. Struck by vehicle in Coal Canyon Corridor 2. Arroyo Trabuco	2.3	1000	0.8	Used a small habitat peninsula west of Robbers’ Peak in the City of Anaheim; peninsula contained high-voltage power lines, water tanks, fire trails, and was heavily used by joggers.
M11	Arroyo Trabuco	>7	100–650		Followed San Luis Rey River (bordered by urban areas) under I-5 into City of Oceanside; at 0230 he was sighted three blocks from ocean, pursued, and shot by police.
M12	Pechanga Corridor	6.5	500–2000		During overnight monitoring, traveled the open grassy ridge separating cities of San Juan Capistrano and San Clemente, daybedding <30 m from I-5.

Note: All habitat peninsulas were bordered by freeways or densely populated urban areas. Despite intense monitoring, there was no evidence that any adult cougar used any of these habitat peninsulas.

^a F, M = female and male, respectively.

^b Freed by domestic dogs, captured, and released back to wild.

Bringing the Findings to Decision Makers

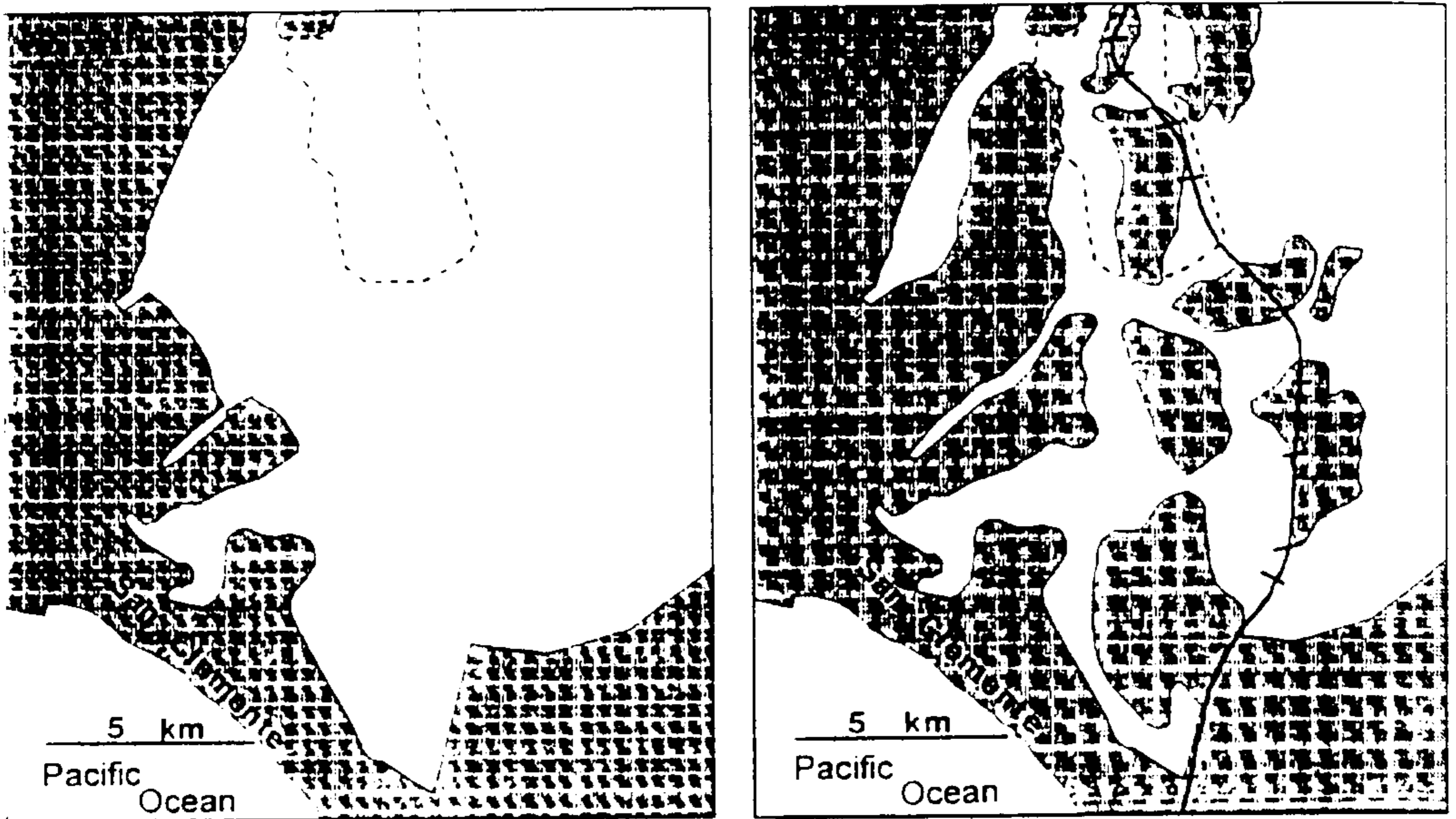
The model clearly showed that preserving the Pechanga Corridor is critically important to conserving the cougar population in the Santa Ana Mountains, and field data show that the corridor is usable. Although the five jurisdictions (City of Temecula, BLM, Pechanga Indian Reservation, and San Diego and Riverside counties) with authority over land use in the corridor do not coordinate their plans, Temecula has authority over the part of the corridor most threatened by urban encroachment. In 1992 I provided written reports and personally presented my findings to the city early in the process of drawing up its first land use plan. The city ignored this input, zoning almost all land into various urban uses, and has since approved every development proposal in its jurisdiction. Because it is possible to create a corridor outside the city limits, Temecula's response was legal under state environmental law. But now the only hope for this corridor lies in an effort by The Nature Conservancy to protect key parcels via purchase or easements.

The model convincingly predicted that loss of the Coal Canyon Corridor would guarantee the extinction of cougars from the 150 km² of habitat in the Chino Hills (Figure 13.1), reducing by 7.5 percent the total habitat available to the population and pushing the population toward the steeply rising part of the risk curve (Figure 13.5). The fieldwork showed that in fact the corridor was used. Because the local press covered these findings prominently in 1990 and 1991, local awareness was much greater than in Temecula (which is not served by its own print or broadcast media). Although less than 2 km long, this corridor is within the jurisdiction of three counties and two incorporated cities and is crossed by a state freeway. The City of Yorba Linda passed a resolution to preserve the part of the corridor in its jurisdiction so long as other jurisdictions kept it intact. But early in 1991, a developer proposed to build 1500 homes on a 150-ha parcel in the mouth of Coal Canyon in the city of Anaheim—a project that would sever the corridor. I provided information, attended meetings, and made three presentations to the city urging a scaled-back project. Anaheim delayed its decision several times to allow the developer to present alternatives to the Coal Canyon Corridor. In each case, I demonstrated that the alternative corridors were infeasible. Ultimately, Anaheim formally acknowledged that the project would destroy the corridor and “result in the loss of potential for a cougar population to occur in the Chino Hills.” When the city hinted it would approve the project anyway because other jurisdictions could destroy other parts of the corridor, supporters of the corridor urged Anaheim to enter into a Coordinated Resources Management Plan (CRMP), a voluntary legal mechanism for interjurisdictional cooperation, with the other parties. On 3 March 1992, the Anaheim City Council perfunctorily declined to initiate a CRMP and then, citing their lack of

authority over the entire corridor, unanimously approved the development project. Several groups, including the CDFG, sued Anaheim under the California Environmental Quality Act. Although the suit eventually failed, it delayed the project until a downturn occurred in the housing market. The developer is now willing to sell the parcel to the state if funding can be obtained.

Our field data may mitigate the impact of a proposed tollroad in southern Orange County that would slice through a pristine area with no human residents along its 21-km length (Anonymous 1990; Figure 13.7). All-night radio-tracking revealed the routes by which cougars traveled between the protected core area (east of the proposed road) and five smaller areas of dedicated open space west of the road. Although these routes now traverse pristine open space, they will become corridors (at best) as highway-induced growth removes the adjacent habitat. The regional transportation agency responded to this information by proposing bridged undercrossings at the most important crossing points (Figure 13.7), but preserving a corridor is not as simple as building a bridge at one point along the corridor. The agency has acknowledged that the tollroad, by providing "critical infrastructure to large expanses of open space," will induce massive urban growth (Anonymous 1990). (Under current policy, freeway access is a prerequisite for issuance of development permits.) Such growth could sever all of the wildlife corridors, rendering the underpasses pointless. Although state law requires mitigating the impacts of induced growth, the agency refused requests (from myself and CDFG) to purchase easements to the three most important corridors as mitigation for this induced growth. Because it was impossible to estimate the amount and location of induced growth, the agency argued that it was "speculative and infeasible" to mitigate for it and said that mitigation should occur in association with each proposed development project. Having repeatedly seen developers argue that it was "speculative and infeasible" to require them to preserve part of a corridor when the next project might destroy another section, I initiated a lawsuit on this issue with other plaintiffs in 1991. (The lawsuit was dropped when I moved out of the state.) The tollroad still lacks some of its environmental permits, which may present opportunities to deny or mitigate the project or use it as a means for obtaining comprehensive regional planning. I also provided findings on travel routes between the protected core area and the other six protected parcels to the appropriate agencies. This information caused the U.S. Forest Service to cancel a planned land swap and greatly improved the land use plan for one rural area (Anonymous 1991).

In early 1992, the Mountain Lion Foundation, relying on the quarterly reports from my study, filed a petition to list the cougar metapopulation in the



A. Potential reserve areas in 1994

B. Proposed reserve design

Figure 13.7. Maps of the reserve plan proposed for southern Orange County under the first attempt at a regional conservation plan. **A.** Unshaded area indicates distribution of potential reserve areas (including disturbed habitats such as annual grasslands and a small amount of agricultural land) in relation to urban areas (cross-hatched). **B.** The proposed NCCP reserve design. Additional cross-hatching indicates proposed urban developments. Heavy line indicates route of a proposed freeway; transverse bars indicate underpasses were planned to allow for cougar movements between the protected core area (east of the freeway alignment) and five smaller protected parcels to the west. The largest known concentration of the California gnatcatcher and the San Diego cactus wren (two primary target species of the NCCP) is indicated by the dashed line. Source maps: Habitat, Target Species, and Reserve Concept Maps, Dudek and Associates, Encinitas, California, dated 3 Oc-

Santa Ana Mountains and Chino Hills as endangered under the Endangered Species Act. The California Department of Fish and Game, which disagreed with the Mountain Lion Foundation on many issues, opposed the petition. After the initial headlines, the petition received little media attention, and the U.S. Fish and Wildlife Service delayed action for 30 months beyond the deadline for response. Then, in December 1994, the service rejected the petition.

In July 1991, the California gnatcatcher (*Polioptila californica californica*) was about to be listed as threatened under the Endangered Species Act, and the coastal cactus wren (*Campylorhynchus brunneicapillus sandiegensis*), the orange-throated whiptail lizard (*Cnemidophorus hyperythrus*), and the Santa

Ana Mountains cougar population were under consideration for listing. At this point the State of California initiated the Natural Communities Conservation Planning (NCCP) program (Anonymous 1993). In March 1993, the U.S. Fish and Wildlife Service accepted this effort as the vehicle for designating critical habitat for the gnatcatcher and for developing a biological reserve system for southern California that would prevent the need for listing other species.

The NCCP planning areas include the entire range of the Santa Ana Mountains cougar population. As part of the NCCP effort, a scientific review panel (SRP) was convened, composed of conservation biologists whose expertise included metapopulation dynamics. In August 1991 and again in January 1992, I pleaded with the SRP to make an explicit map of the reserve areas. I used as an example the three detailed maps provided by the northern spotted owl recovery team (Thomas et al. 1990), which realized that broad guidelines alone would be subject to interpretation unfavorable to the conservation of the species. The SRP responded that producing a map was not part of its mandate and assured me that the guidelines would be so explicit that CDFG, the lead agency, would be forced to map an effective reserve system. In November 1993, CDFG incorporated the SRP report, including seven "basic tenets of reserve design," into its NCCP Conservation Guidelines.

Subsequent events show that the SRP's faith in the implementation process was unjustified. California Department of Fish and Game has allowed landowners and developers to draw the map of the proposed reserve for southern Orange County. In fact, the map (Figure 13.7a) violates five of the seven basic tenets as follows (retaining the original numbering and wording):

- "2. *Larger reserves are better*" and "4. *Keep habitat contiguous.*" Two areas proposed for urban developments would fragment the largest known populations of gnatcatchers and cactus wrens in southern California. From a metapopulation perspective, these are clearly the main source populations for these two endangered species. Indeed, it would be difficult to draw a map that would inflict more discontinuity on these source populations.
- "5. *Link reserves via corridors.*" The proposed urban developments would prevent nonvolant animals from reaching over half of the underpasses proposed as mitigations for impacts to animal movement caused by the planned Foothill Tollroad (Figure 13.7b). The locations of these underpasses had been determined on the basis of my data on cougars traveling from the protected core area to five protected parcels west of the tollroad.
- "6. *Maintain reserve units that are biologically diverse . . . [including]*

other habitat types that occur in a mosaic with CSS." Virtually all rare grassland vegetation that occurs in a mosaic with coastal sage scrub is designated for urban development.

- "7. *Protect reserves from encroachment. Blocks of habitat that lack roads or are otherwise inaccessible to human disturbance better serve target species. . . . [The] greatest potential for encroachment is from urban edges. . . . [which provide access for] weeds, cats, dogs, children, . . . [and] wildfire.*" The reserve design as mapped creates excessive edge, human disturbance, and the need for more roads to connect the developed areas.

Lessons

A metapopulation model in conjunction with site-specific data can influence decisions on land use. Model predictions alone could not be implemented without data on the location of travel routes and would not be persuasive without data showing that the target species will use corridors.

My attempts to bring these findings to decision makers had decidedly mixed results. The main obstacle preventing the results of metapopulation analyses from being implemented is the lack of regional planning authority. Under the current mechanism for implementation, concerned citizens must detect and force mitigations on each proposed project that threatens the metapopulation. For the cougar population in the Santa Ana Mountains, this requires monitoring and being prepared to litigate decisions made by five county governments, seventeen municipal governments, two transportation authorities, and the world's largest water district. The linkages among metapopulation centers are most vulnerable. Because a corridor is only as strong as its weakest link, a single oversight on the part of conservationist volunteers is sufficient to lose a linkage and imperil the metapopulation.

A land use plan will fail to conserve a metapopulation if scientific advice for that plan is limited to general rules ("preserve large areas and connect them") and developers and politicians are trusted to draw the map from those rules. To make their advice useful, conservation biologists should develop maps that present biologically optimal designs. Although nonbiological considerations will influence the ultimate map, biologists should provide formal and independent review of the final map for its consistency with stated conservation objectives.

Biologists can be effective advocates for incorporating metapopulation concepts into land use planning, but only if they are committed to a sustained effort: writing detailed comments, preparing testimony for public

hearings, and meeting frequently with persons who may not want biological expertise. Scientific advocates must be scrupulously careful with the facts, acknowledge the limits of the data or models they use, and admit to mistakes. Biologists must resist well-meaning pressure from citizen activists to overstate the biological evidence; overstatement is a sure way to lose credibility.

Although a reserve designed for a cougar metapopulation would not suffice for habitat specialists (such as the California gnatcatcher), an area-sensitive species such as the cougar is an appropriate umbrella species (Noss 1991) for a regional conservation plan because its low density renders it most sensitive to habitat fragmentation. Cougars also are more likely than less mobile species to yield data on habitat linkages essential to metapopulation function. Using telemetered cougars to identify movement corridors is certainly a big improvement over the prevalent practice in southern California, which is to label leftover shards of habitat, and passages under bridges built for hydrologic or geologic reasons, as "wildlife corridors."

There is a lack of data on whether most species use corridors (Chapter 5 in this volume), and a few biologists have speculated that connectivity might have biological drawbacks in addition to benefits (Simberloff et al. 1992). Clearly we need more data and better data. But biologists should not let developers misrepresent this spirit of inquiry as a disagreement among the experts on the *value* of habitat connectivity. By such misrepresentation, developers have persuaded planning agencies that habitat fragmentation should proceed unhindered and, moreover, that conservationists should bear the burden of proof for preserving each remaining corridor. Without abandoning our scientific endeavors, we need to make decision makers hear our united voice on the value of connectivity, thus shifting the burden of proof to those who would destroy the last remnants of natural connectivity.

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