Determining Minimum Habitat Areas and Habitat Corridors for Cougars

PAUL BEIER*

Department of Forestry and Resource Management
University of California
Berkeley, CA 94720, U.S.A.

Abstract: *I simulated population dynamics of cougars to predict the minimum areas and levels of immigration needed to avoid population extinction caused by demographic and environmental stochasticity for a period of 100 years. Under most plausible parameter values, the model predicted very low extinction risk in areas as small as 2200 km^2, and (in the absence of immigration) increasing risk as area decreased below 2200 km^2. If as few as one to four animals per decade could immigrate into a small population, the probability of population persistence increased markedly. Thus a corridor for immigration will benefit a small population in an area where further loss of habitat will occur.*

The model was applied to the cougar population in the Santa Ana Mountain Range of southern California (2070 km^2, with about 20 adults). Field data support the model's conclusion that this population is demographically unstable. There will be a high risk of extinction if the habitat is reduced to currently protected and connected areas (1114 km^2). A movement corridor allowing immigration from the adjacent population and intra-range corridors would greatly enhance the prognosis. However, the last corridor for immigration has been degraded by recent human activity. Within the mountain range, cougars recently became extinct in a 75-km^2 habitat fragment recently isolated by development, and cougars will become extinct in another 150-km^2 of habitat if a proposed housing project occludes a critical corridor. Radio tracking has confirmed use of this and other important corridors.

Neither the model nor the field data alone would have much influence in the face of development pressure; together they have stimulated interest in restoring and protecting critical corridors in this range. Nonetheless, the long-term prognosis for this population is bleak, because 22 local governments review potential impact on a case-by-case basis.

Determinando áreas mínimas de hábitat y hábitat en corredes para pumas

Resumen: *Simulé la dinámica de la población de pumas para predecir áreas mínimas y niveles de inmigración necesarios para evitar la extinción de la población debido a estocasticidad demográfica y ambiental por un periodo de 100 años. Usando los parámetros más viables, el modelo predice riesgos de extinción muy bajos en áreas tan pequeñas como 2200 km^2, y (en ausencia de inmigración) un riesgo creciente a medida que el área decrece por debajo de 2200 km^2. Si tan solo 1–4 animales por década puediesen inmigrar a una pequeña población, la probabilidad de persistencia se incrementaría marcádamente. Por consiguiente, un corredor para la inmigración puede beneficiar una pequeña población en un área dónde ocurrirá una mayor pérdida del hábitat.*

El modelo fue aplicado a la población de pumas en la cadena Montañosa de Santa Ana, al Sur de California (2070 km^2, con unos 20 adultos aproximádamente). Datos de campo apoyan las conclusiones del modelo, que indican una población demográficamente inestable. Si el hábitat es reducido a las actuales áreas protegidas y conectadas (1114 km^2) habría un alto riesgo de extinción. La prognosis se podría mejorar ampliamente con un corredor de movimiento que permitiera la inmigración desde poblaciones en áreas adyacentes y corredores dentro del área de distribución. Sin embargo, el último corredor para la inmigración ha sido degradado por el reciente impacto humano. Dentro de la cadena montañosa, los pumas se han extinguido recientemente en un fragmento de hábitat de 75 km^2 aislado a causa del desarrollo; los pumas se extinguirán en otros 150 km^2 de hábitat si un proyecto de viviendas propuesto obstruye un corredor crítico. El uso de este y otros importantes corredores ha sido confirmado a través de telemetría.

Ni el modelo ni los datos de campo por si solos tendrían mucho impacto ante la presión por el desarrollo; juntos han estimulado el interés en restaurar y proteger corredores que son crítcos en esta cadena. A pesar de todo, la prognosis a

---

**Current address: School of Forestry, Northern Arizona University, Flagstaff, AZ 86011, U.S.A.*

Paper submitted September 3, 1991; revised manuscript accepted February 12, 1992.

Effective land-use planning must be spatially explicit and regional in scope. Because cougars need corridors and because telemetered cougars can quickly identify movement corridors, cougar research is an efficient and appropriate way to inject biological data into such planning efforts.

largo plazo para esta población es yerma ya que 22 gobiernos locales revisaron los impactos potenciales caso por caso. Una effectiva planificación del uso de la tierra debe ser explícita espacialmente y regional en extensión. La investigación sobre pumas es una vía eficiente y apropiada de introducir datos biológicos en los esfuerzos de planificación. Esto es así porque los pumas necesitan corredores y al estar marcados telemétricamente permiten identificar rápidamente los corredores de movimiento.

Introduction

As landscapes are fragmented into ever-smaller patches of habitat isolated by high-speed barriers (Harris & Gallagher 1989), it has become important to determine the minimum area needed to preserve functioning ecosystems. Because there are no methods to determine the minimum areas of reserves with reference only to ecosystem properties, biologists are forced to conduct viability analyses for a few "indicator" or "umbrella" species as an efficient way to address the viability of the whole system (Soulé 1987*a*:8; Noss 1991).

Species such as the grizzly bear (*Ursus arctos horribilis*), the wolf (*Canis lupus*), and the cougar or mountain lion (*Felis concolor*) make ideal candidates for such analysis because they exist at low density and require large areas. Of these, only the cougar plays a significant ecological role in much of the lower forty-eight states. Therefore, viability analysis for this species would have widespread utility. Shaffer (1983) presented an analysis for the grizzly bear. In this paper, I present such an analysis for the cougar.

I focus solely on the issue of identifying the minimum area and immigration rate needed to avoid extinction caused by demographic and environmental stochasticity, ignoring inbreeding effects. Previous analyses have shown that the areas needed to avoid inbreeding depression in the long term are so large "that the only recourse in most situations will be to establish the species in several sites since there won't be enough space in any given site" (Soulé 1987*b*:177). My analyses address the issue of how large each of these "several sites" must be so that management intervention can be limited to that needed to maintain genetic variability.

Simulation models are superior to analytic models when addressing a particular species, because the analytic calculations are possible only for unduly simplified models (Ewens et al. 1987:67). But there are pitfalls to the simulation approach, especially with small populations. For example, most simulation models account only for females and make no allowance for an "Allee effect" whereby animals at low density may have difficulty finding mates. This creates an inverse density-dependence in fecundity when numbers of one sex are very low (Begon & Mortimer 1981:30), which has been documented in a cougar population (Padley 1990). Another problem is that most subroutines for incorporating stochastic variation in survival rates introduce crucial errors when simulated populations become small (see Methods section). Most important, even though "habitat fragmentation ... is the primary cause of the present extinction crisis" (Wilcox & Murphy 1985: 884), few simulation models allow analysis of the effects of movement corridors; such analysis requires explicitly modeling various levels of immigration.

In this paper I describe a model that realistically simulates the population dynamics of small populations of cougars. My goal was to predict the conditions under which a cougar population can avoid extinction in the short term (100 years), ignoring inbreeding effects. My main conditions of interest were those that humans can control, namely, area of habitat (controlled by restrictions on human development) and the amount of immigration into the population (controlled via provision for wildlife movement corridors to adjacent populations). In addition, I examined how estimates of extinction risk depends on estimates of life history parameters, many of which vary geographically or are difficult to measure.

Finally, I apply the model to the cougar population in the Santa Ana Mountains of southern California, which I have studied since 1988, and I summarize some of the relevant field observations from that study. This real-world application illustrates that model results have little impact on land-use decisions unless they are supplemented by field study to identify actual or potential movement corridors. My goals in this illustration are to promote the use of data from telemetered cougars to identify and protect wildlife corridors, and to advocate that regional planning efforts based on geographic information systems (GIS) replace current piecemeal approaches.

Methods

Simulation Model

The simulation model used standard Leslie-matrix computations, with subroutines that controlled immigration and adjusted survival and fecundity rates for density-dependence, demographic and environmental stochasticity, and an Allee effect. For each combination of input conditions, the population dynamics were simulated 100 times; each simulation was 100 years in duration. In each case, the initial number of adults (animals 2 or more years of age) was set equal to the carrying capacity and evenly distributed among age classes. Initial numbers of 0-year-olds and 1-year-olds were set at a half and a quarter, respectively, of the number of adult females.

The question of what constitutes preservation is "the most crucial and least addressed" issue in conservation biology: "Does a 95% probability of persistence for 100 years make extinction sufficiently remote or all too immanent?" (Shaffer 1987:81,84). I advocate planning for an extinction risk of less than 1%, and I label "significant" any extinction risk 2% or more.

For each set of 100 runs, the program recorded the population trajectory by sex and age class, the number of runs on which the population went extinct, mean population size in year 100, and other summary statistics.

INPUT CONDITIONS

The main factors of concern were area of habitat and level of immigration. Simulations were run with habitat areas as small as 200 km^2 and in increments of 200 km^2 until extinction risk declined to less than 2%. Four levels of immigration were considered. The first level depicted no wildlife movement corridor (no immigration). The second and third levels reflected a marginal corridor, allowing immigration of one or two males per decade, respectively. The fourth level of immigration was three males plus one female per decade. These levels reflect the finding that about 80% of juvenile males, but only about 25% of juvenile females, dispersed out of their natal mountain range, often crossing inhospitable desert habitat to reach another range (Ashman et al. 1983).

For each combination of habitat area and level of immigration, simulations were run under many combinations of estimates for life history and environmental attributes (Table 1). We have poor estimates for some of these parameters (for example, male and female equilibrium densities, juvenile survival rates) and some parameters may vary geographically, so I used many combinations initially. A smaller subset was obtained by dropping values that produced unrealistic outcomes and variables that did not influence the results.

Table 1. Input states for biological parameters used in simulating population dynamics of cougars.

Parameter	*Possible States*
Mean litter size	2.4[a]
	2.8
	3.2[b]
Juvenile[c] survival	0.55 (0.50)[d]
	0.65 (0.60)
	0.75 (0.70)
Adult[e] survival	0.65[a]
	0.75
	0.85
Carrying capacity (breeding adults per 100 km^2)	Sex ratio of 2 femles per 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 females per male:
	0.8 females, 0.2 males
	1.2 females, 0.4 males
	Sex ratio near unity:
	0.4 females, 0.4 males
	0.8 females, 0.6 males
	None (constant carrying capacity)
Severity of catastrophe (loss of carrying capacity)	20% in years 25–27, 50–53, 75–77
	40% in years 25–27, 50–53, 75–77[f]

[a] *This value was dismissed because it produced unrealistically low population sizes even when used in concert with optimistic estimates for other variables. See first section of Results.*
[b] *This value was dismissed because it produced extinction probabilities that did not differ from those under a mean litter size of 2.8, and this value is best supported by field studies. See first section of Results.*
[c] *0- and 1-year olds of both sexes, and 2-year-old males.*
[d] *Survival of 1-year-old males indicated in parentheses.*
[e] *Females ≥2 years old and males ≥3 years old.*
[f] *This value was dismissed because extinction probabilities varied only trivially from the 20% case. See first section of Results.*

Litter size. Mean litter size (Table 1) was based on reports of Robinette et al. (1961), Ashman et al. (1983), and Anderson's (1983:34) compilation of data from 407 litters. In the simulations, up to 40% of the 2-year-old females bred each year and no kittens or yearling females bore young, based on minimum and mean ages of primiparous females of 25 and 32 months (Ashman et al. 1983). Because the mean interval between births (except when a litter dies) is usually about 24 months (Hornocker 1970:16, Robinette et al. 1961:215), the model excluded from breeding those females with surviving litters from the previous year. The model assumed that a female whose litter dies comes into estrus and breeds the next year (Hornocker 1970:16; Seidensticker et al. 1973:56; Eaton & Velander 1977:65).

Juvenile survival rates. There are few estimates of survival of 0-year-olds. Comparing mean litter sizes near birth and at 12 months (not the same litters followed through time) Ashman et al. (1983) suggested a value of 0.78. Similar data in Robinette et al. (1961:213, inferring age from weight) suggested a survival rate of 0.73. To the extent that entire litters died, this is a high estimate (Robinette et al. 1961:213); it is also higher than the adult survival rate reported by Lindzey et al. (1988). Survival rates of African felid cubs (lion, cheetah) are about 0.50 (Schaller 1972:191,300). Preliminary analysis of 172 cougar-months of telemetry data (0- and 1-year-olds combined) suggests an annual survival rate for cougar cubs of 0.48 (Beier, unpublished data). Hemker et al. (1986) reported a survival rate of 72% for cubs between 3 and 10 months of age in an area of extremely low cougar density (gross density of 0.5 cougars per 100 km^2); this rate may reflect density-dependent enhancement of survival rates at low density. In any event, if additional mortality during 0–3 months of age is considered, 0.75 is probably a high estimate and was used as the highest estimate in the simulations.

There are no published estimates of survival of 1-year-olds. Hemker et al. (1986) reported a survival rate of 92% for cubs from 10 months to dispersal at 16–19 months, from the same low-density population. This figure ignores higher post-dispersal mortality (Hornocker 1970:18). Lacking better evidence, I set yearling survival rates equal to 0-year-old survival rates. In the simulations kittens died when orphaned in the year of birth, but kittens orphaned in the year after birth had the same survival rate as nonorphans.

Adult survival rate. I used adult survival rates of 65% (Robinette et al. 1977:123, Ashman et al. 1983), 75% (Lindzey et al. 1988), and 85% (Anderson et al. 1989).

Longevity. A maximum longevity of 12 years was used in all simulations. The longest lifespan reported for a wild cougar is 13–15 years (Hopkins 1989:23); I found no other reports of wild cougars living past 12 years of age. Extreme longevities for captive cougars are 12, 15, and 18 years (Young 1946:59), and 12 and 19 years (Eaton & Velander 1977:56). My preliminary analyses showed that risk of extinction decreased only slightly as maximum longevity increased past 12 years, especially in the critical right tail (Figs. 3–6) of the extinction curve.

Carrying capacity. Although they are not territorial, social intolerance among adult females is thought to regulate their density, whereas territoriality among males separately regulates male density (Seidensticker et al. 1973). Apparently female density is calibrated to vegetation, topography, and prey availability, whereas males compete for access to females (Seidensticker et al. 1973:59,56). To model density-dependent survival rates, separate estimates of carrying capacity for males and females were needed.

Estimates of densities for male and female adult cougars vary widely (Hornocker 1970; Seidensticker et al. 1973; Sitton & Wallen 1976; Currier et al. 1977; Shaw 1977; Hemker et al. 1984; Logan et al. 1986; Neal et al. 1987; Hopkins 1989). Because many study sites were selected because of expected high cougar density, some reported densities are atypically high. Also, not all studies reported how many of these adults were nonbreeding transients as described by Hornocker (1970) and Seidensticker et al. (1973).

In light of these uncertainties, I ran the model under a variety of carrying capacities (Table 1). Because most studies (excluding male-biased summaries of hunting returns) report a 2:1 ratio of breeding adults (females: males) (Seidensticker et al. 1973:17, first 3 years; Currier et al. 1977; Ashman et al. 1983; Murphy 1983; Hemker et al.1984; Logan et al. 1986; Neal et al. 1987; Hopkins 1989:23), most simulations used this ratio between carrying capacities for males and females. However, other adult sex ratios have been reported, for example, 3:1 (Currier et al. 1977; Shaw 1977; Quigley et al. 1989; M. Jalkotzy and I. Ross, Calgary, Alberta, unpublished data), 1.3:1 (Hornocker 1970:15), and 1:1 (Seidensticker et al. 1973:17, last 3 years; Hopkins 1981). Therefore I also used similar ratios (Table 1).

I excluded high densities due to winter concentration. The markedly lower gross density of 0.4/100 km^2 reported by Hemker et al. (1984) and the markedly higher adult density of 3/100 km^2 reported by Neal et al. (1987) were also excluded as outliers which may deviate from the actual long-term carrying capacity.

Catastrophic reductions in carrying capacity. On each run, simulated carrying capacity decreased by either 0%, 20%, or 40% during years 26–28, years 51–53, and years 76–78. This modeled prey die-offs due to droughts or severe winters.

DENSITY-DEPENDENCE IN FECUNDITY

Because the gestation period is only 92 days and neonates weigh only 500 grams (Anderson 1983:33–34), cougar pregnancy is relatively cheap; therefore simulated litter sizes were independent of density and maternal age. When the simulated number of adult females was less than carrying capacity, all females over 2 years old (except those with a surviving litter from the previous year) and 40% of 2-year-old females (Ashman et al. 1983) bore litters. The program allowed females in excess of carrying capacity to breed with probability equal to 0.20, and assigned the youngest females to nonbreeding status, reflecting the inhibition of reproduction in young females until home range establishment (Seidensticker et al. 1973).

The probability of a female breeding was inversely density-dependent when numbers of breeding males were below the carrying capacity for adult males. When there were vacant male territories, the proportion of adult females that were bred was reduced by a factor of

$$\frac{\mathrm{KM} - \#\mathrm{AdM}}{\mathrm{KM}} * 1.15^{\mathrm{KM} - \#\mathrm{AdM}},$$

where KM = carrying capacity for breeding males and #AdM = number of adult males. Under this expression, each adult male increases his home range size by 15% for each "deficit male"; thus the effect is very mild except at very small population sizes; for example, when KM = 5 and #AdM = 4, 92% (not 80%) of the females are bred.

DENSITY DEPENDENCE IN SURVIVAL RATES

In preliminary analyses, some simulations were run without any density dependence in survival rates; resulting extinction rates were about ten times higher than those produced using density-dependent survival rates for all ages. Other simulations were run with mild density dependence in juvenile survival rates (Fig. 1, curve A) and density independent adult survival rates, producing extinction rates about five times higher than when survival rates for all ages were density-dependent. In simulations lacking density-dependent survival rates, the mean number of adults in year 100 (in surviving populations) far exceeded carrying capacity. Because density independence produced such unrealistic ending population sizes, I ran all remaining simulations with density-dependent survival rates (Fig. 1, Table 2).

In the model, density dependence operated most strongly on 0- and 1-year-olds, whose survival rates depended on the number of adult females; survival of 1-year-old males also varied with the number of adult males, reflecting density-dependent mortality of young males during dispersal. Density-dependence was relatively mild for animals less than 2 years old. There is no empirical data to support these particular functions (Table 2); they were chosen for computational simplicity. In light of the markedly changed outcomes when density dependence was added to the model (above), I tested the model using more severe density-dependent functions. Neither risk of extinction nor ending population size varied among the functions illustrated in Figure 1.

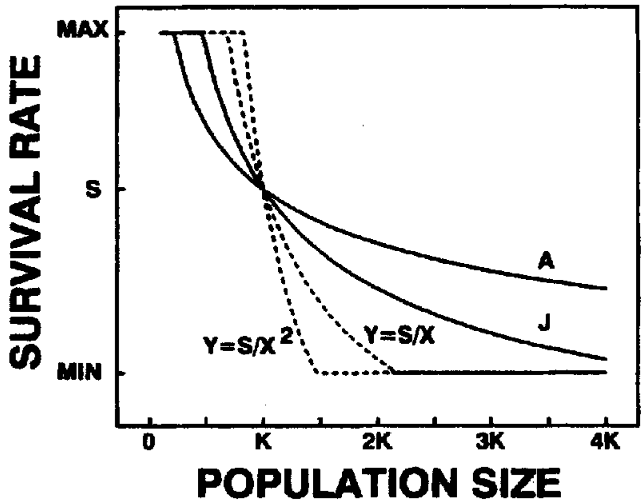

Figure 1. Density-dependent functions relating survival rates to population density. Lines A and J, respectively, illustrate the adult and juvenile survival functions (Table 2) used in all simulations illustrated in Figures 3–7. Simulations using stronger density-dependent functions (dashed lines) did not change the risk of extinction. In all simulations the juvenile survival function was one line steeper than the adult survival function. K = Carrying capacity for the appropriate sex. Max = 0.95 (adults) or 0.9 (juveniles). Min = 0.5 (adults) or 0.3 (juveniles). S = Survival rate at carrying capacity.

Table 2. Equations used to create density-dependence in cougar survival rates. S = the 12-month survival rate at carrying capacity; KF and KM = carrying capacity for breeding females and males respectively; #AdFemales and #AdMales = number of ≥2-year-old females and males, respectively.

Age	*Sex*	*Expression for Density-Dependent Survival Rate*[a]
0	both	$S * (KF/\#AdFemales)^{0.5}$
1	F	$S * (KF/\#AdFemales)^{0.5}$
	M	Minimum of: $S * (KF/\#AdFemales)^{0.5}$ or $S * (KF/\#AdFemales)^{0.5} * (KM/\#AdMales)^{0.5}$
2	F	$S * (KF/\#AdFemales)^{0.5}$
	M	$S * (KM/\#AdMales)^{0.5}$
3+	F	$S * (KF/\#AdFemales)^{0.25}$
	M	$S * (KM/\#AdMales)^{0.25}$

[a] *To avoid unrealistic results that the above expressions yield under certain conditions (such as when a divisor approaches or equals zero), the program truncated all survival rates to values between 0.3 and 0.9 for animals under 3 years of age, and between 0.5 and 0.95 for adults.*

STOCHASTIC VARIATION

Most simulation models introduce stochastic variation into survival rates by randomly selecting a rate from a normal distribution and then multiplying this rate by the number of individuals in an age-sex class. When there are only one or two animals in a sex-age class, this approach introduces rounding errors that increase the survival rate to near 100% and, ironically, eliminate stochastic variation (Beier, unpublished data). To avoid this problem, the model applied the appropriate probability to each individual animal in the population. For example, if the survival rate for yearling males was 0.60 and there were two yearling males in a given year, 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.

Similar procedures introduced stochasticity into primary sex ratio, litter sizes, and immigration rates. Each newborn had a 50% chance of being male. Each litter had two, three, or four cubs with probabilities appropriate to the specified mean value. Each year one male or one female immigrated with the appropriate probability, and the immigrant was assigned to the 1-year, 2-year, or 3-year age class with probability equal to 0.3, 0.5, and 0.2, respectively.

Field Work in the Santa Ana Mountains

The cougar population in the Santa Ana Mountain Range of southern California consists of about twenty adults on about 2070 km^2 of habitat (Fig. 2) (Beier & Barrett 1992*b*). The surrounding urban areas do not offer even marginal cougar habitat. About 1270 km^2 of this habitat (61%) is protected from urban uses, primarily within lands owned by the U.S. Forest Service and U.S. Navy (Table 3). Of the protected land, about 1114 km^2 forms a contiguous block; if all private lands were developed,

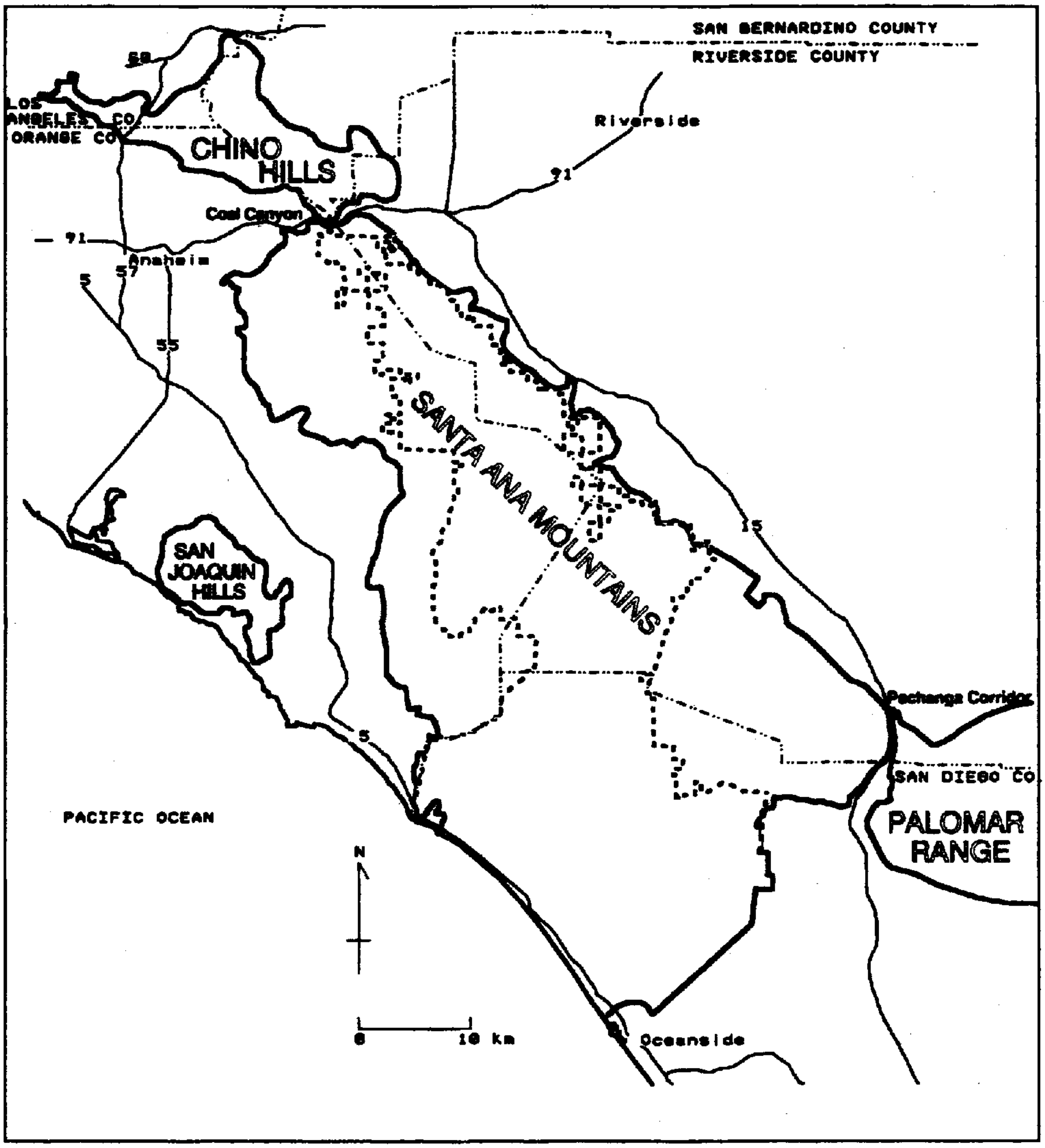

Figure 2. The heavy solid line encloses three areas: 2070 km^2 of cougar habitat in the Santa Ana Mountain Range (including the Chino Hills); 75 km^2 of suitable habitat in the San Joaquin Hills (recently extinct); and (east of Highway 15) a portion of the habitat in the adjacent Palomar Range. The heavy dashed line encloses 1114 km^2 of protected and connected parcels (Table 3). All roads shown are 6- to 10-lane freeways.

Table 3. Area in hectares of protected lands contained within cougar habitat in the Santa Ana Mountain Range, California.

Ownership and Parcel Name	*Areas Forming a Large Contiguous Block*	*Areas Surrounded by Unprotected Land*
Federal		
Cleveland National Forest	53,604[a]	
Cleveland National Forest (6 parcels)		626
Camp Pendleton	49,292[b]	
Fallbrook Naval Weapons Station	3,099	
Bureau of Land Management (7 parcels)		550
Bureau of Land Management (1 parcel)	364	
State		
Chino Hills State Park		5,059
San Diego State University Field Station		1,805[c]
Dept Fish & Game Coal Canyon Preserve	385	
Orange County Parks		
Caspers	3,085	
Limestone Canyon		2,169[d]
O'Neill		805
Whiting Ranch		632
Irvine		193
Wagon Wheel		178
Santiago Oaks		142
Private Reserves		
Santa Rosa Plateau Preserve		2,803[e]
National Audubon Society Starr Ranch	1,578	
Rancho Mission Viejo Conservancy		486
Total	111,407	15,448

[a] *Excludes private inholdings.*
[b] *Includes land leased to San Onofre Beach State Park; excludes 1700 hectares in urban use and airfield; includes some severely affected bombing ranges that may not be suitable habitat.*
[c] *Includes 510 hectares of Bureau of Land Management land administered by the field station.*
[d] *Expected to be transferred to county from private ownership.*
[e] *Administered by The Nature Conservancy (TNC); includes lands owned by TNC, State of California, and Riverside County.*

the other 154 km^2 of protected land would be isolated into fragments unusable by cougars.

The six counties of southern California contain 5% of the U.S. human population. 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 of this growth is expected to occur in tract homes built in privately-owned open spaces, including most of the best cougar habitat. In addition to outright habitat destruction, some wildlands are lost to the cougar population because they become isolated by freeways and other development. For example, after urbanization isolated a 75-km^2 fragment of cougar habitat (Fig. 2, San Joaquin Hills) in the late 1970s, cougars became extinct there by June 1990 (Beier & Barrett 1990*a*).

In early 1988, field work began in the southern half of the range, focusing on seven telemetered adult females. In January 1988, one such female had 3-month-old triplets and a second had a single yearling cub at heel. After the death of a mature male cougar in February 1988, there was no additional reproductive activity and no sign of a breeding male for over 12 months (Padley 1990:40–43). When two young males established themselves as breeders in early 1989, their tracks and vocalizations were obvious. In April 1989 we heard copulatory vocalizations involving four telemetered females, and that summer six of the seven females bore cubs (Padley 1990). The presumed sires of these litters (two adult males subsequently captured and radio-tagged) were both 2 years old at the time they became breeders. Therefore, all evidence suggests that there was no adult male and no reproduction in the southern half of the range for a full year.

In 1989 the study expanded to include the entire mountain range. We intensified our efforts to collar predispersing animals, and four times per month we selected a focal animal whose location was determined every 15 minutes from 1 hour before sunset until 1 hour after sunrise. This research has focused on (1) identification of existing or potential corridors for immigration into the population as a whole; (2) identification of lands within the mountain range that connect nearly-isolated patches of habitat; and (3) documentation of the travel paths used by cougars, especially dispersing animals, and especially paths between areas designated as permanent open space. If protected, such paths can be expected to become corridors as future human activities affect the adjacent habitat.

Results

Rejection of Unrealistic or Uninformative Parameter Values

To reduce the results to a digestible mass, I first rejected parameter values that produced unrealistic outcomes or that did not influence the results. For example, the mean number of adults in year 100 was 70–80% of carrying capacity whenever adult survivorship equalled 0.65, even with a habitat area of 3000 km^2 and the highest estimates for juvenile survival rate, mean litter size, and carrying capacity. If carrying capacity is ever to be observable in nature, it should be so under these conditions, so I excluded the adult survival rate of 0.65 from consideration.

Similarly, because a mean litter size of 2.4 tended to produce ending population sizes about 15% below carrying capacity, this litter size was excluded. Extinction rates decreased only trivially when mean litter size increased from 2.8 to 3.2. Because available data best support a mean litter size of 2.8, the mean litter size of 3.2 was also excluded from further consideration. Finally, extinction risk increased only trivially as the severity of the catastrophe (temporary loss of carrying capacity) increased from 0% to 20% to 40%. All results reported herein used the 20% reduction.

Influence of Habitat Area and Level of Immigration

The main factors of interest were those under human control, i.e., area of habitat and the presence (or absence) of a corridor allowing various levels of immigration. As expected, both factors influenced the probability of extinction (Figs. 3–5).

Despite variation in model predictions due to uncertainty in biological parameters, 98% or more of simulated populations persisted for 100 years when there was 2200 km^2 or more of habitat available, except under the most pessimistic estimates of biological parameters (carrying capacity of 0.4 or fewer adult females and 0.2 adult males per 100 km^2, in concert with adult survivorship of 0.75 or less).

As expected, the probability of extinction increased as area of habitat decreased. With only 1000 km^2 of habitat and no immigration, simulated populations had 98% persistence only under the most optimistic estimates of biological parameters (carrying capacities of 1.0 or more adult females and 0.5 adult males per 100 km^2, in concert with adult survivorship of 0.85 or more and juvenile survivorship of 0.65 or more). In the absence of an immigration corridor, therefore, the critically small habitat area lies between 1000 and 2200 km^2. Within this range, the critical size depends on demographic parameters (next section).

Immigration improved the probability of survival at surprisingly low levels—as low as one male per decade. For any given combination of biological parameter estimates, the critical habitat area was 200–600 km^2 smaller with an immigration corridor than without. Immigration had no influence on the mean size of the adult population in year 100 for populations that survived.

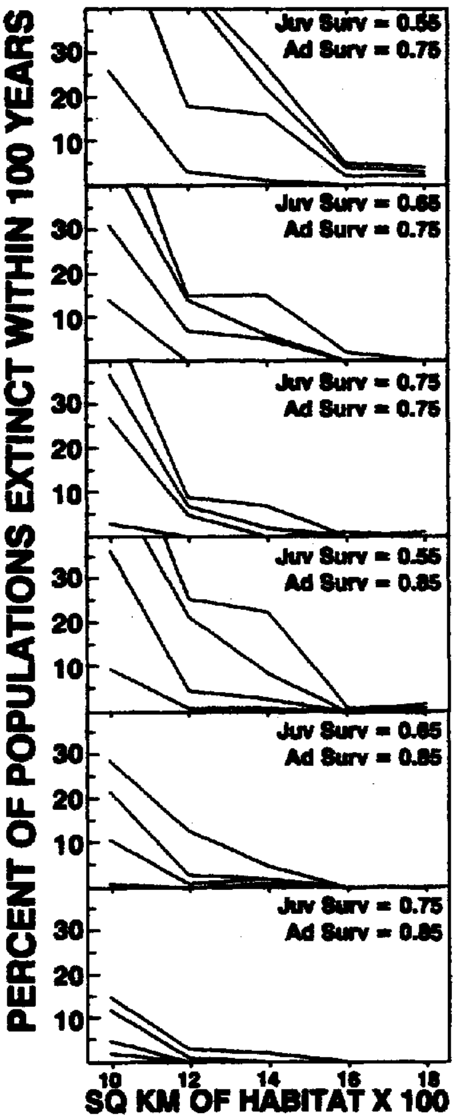

Figure 3. Effect of habitat area and immigration on cougar population persistence, given a carrying capacity of 0.6 breeding adult females and 0.3 breeding adult males per 100 km^2. In each graph the top through bottom lines give the percent of simulated populations that went extinct within 100 years when the numbers of immigrants per decade were 0, 1 male, 2 males, or 3 males and 1 female, respectively. Juv Surv (juvenile survival rate) and Ad Surv (adult survival rate) are defined in Table 1.

Influence of Biological Parameters

Predictions were sensitive to all of the biological parameters, especially the estimates of carrying capacity (Figs.

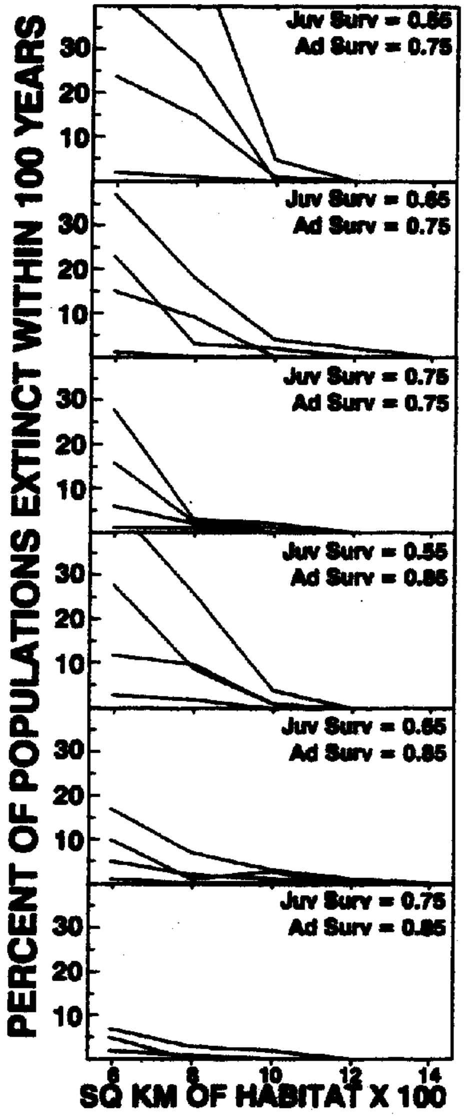

Figure 4. Effect of habitat area and immigration on cougar population persistence, given a carrying capacity of 1.2 breeding adult females and 0.4 breeding adult males per 100 km². In each graph the top through bottom lines give the percent of simulated populations that went extinct within 100 years when the numbers of immigrants per decade were 0, 1 male, 2 males, or 3 males and 1 female, respectively. Juv Surv (juvenile survival rate) and Ad Surv (adult survival rate) are defined in Table 1.

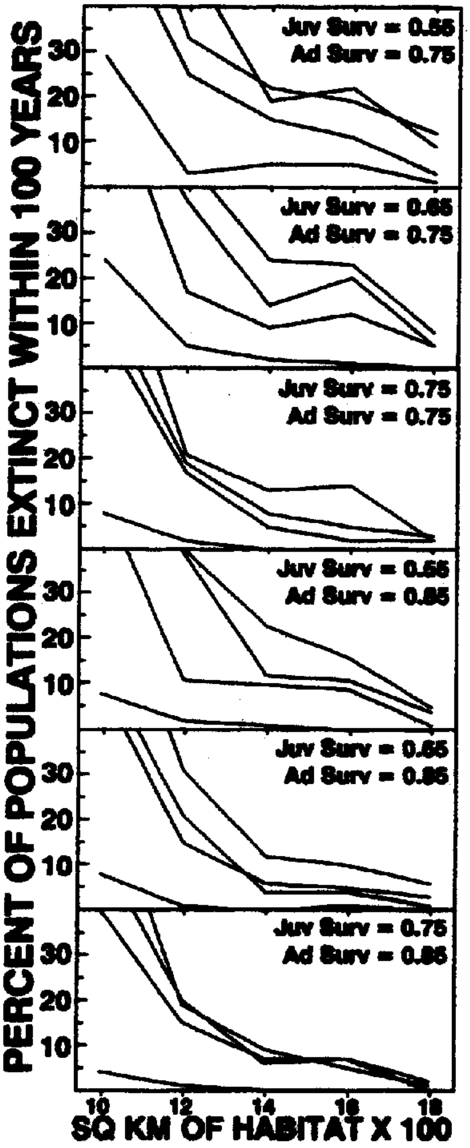

Figure 5. Effect of habitat area and immigration on cougar population persistence, given a carrying capacity of 0.4 breeding adult females and 0.4 breeding adult males per 100 km². In each graph the top through bottom lines give the percent of simulated populations that went extinct within 100 years when the numbers of immigrants per decade were 0, 1 male, 2 males, or 3 males and 1 female, respectively. Juv Surv (juvenile survival rate) and Ad Surv (adult survival rate) are defined in Table 1.

3–5; graphs for carrying capacities listed in Table 1 but not illustrated herein are available on request). Both juvenile and adult survivorship values also had important influences on model results (Figs. 3–5).

The adult sex ratio (the ratio of carrying capacity for females to that for males) was also important. When the adult sex ratio was skewed toward females (Figs. 3–4), immigration of one or two males per decade had the most pronounced rescue effects. This was most evident with a highly skewed sex ratio (Fig. 4). In contrast, immigration of one or two males had a relatively muted rescue effect on populations with equal sex ratios. These populations, however, benefited dramatically from a corridor that allowed four immigrants (including one female) per decade (Fig. 5).

Population Trajectory

For populations with low extinction risk, the population trajectory on a run of 100 years fluctuated near carrying capacity (for example, see Fig. 6A). Despite this relative stability, the age and sex composition of the simulated population showed considerable variation, even when smoothed by taking 5-year running means (Fig. 6B). Surprisingly, most trajectories showed no response to the simulated "catastrophes," despite 20–40% reductions in carrying capacity in years 26–28, 51–53, and 76–78 (see Fig. 6A).

Populations at greater risk of extinction showed even greater demographic instability (Fig. 6C). When the sex ratio was skewed toward females, the most common extinction scenario was loss of breeding males at a time when no male cubs survived.

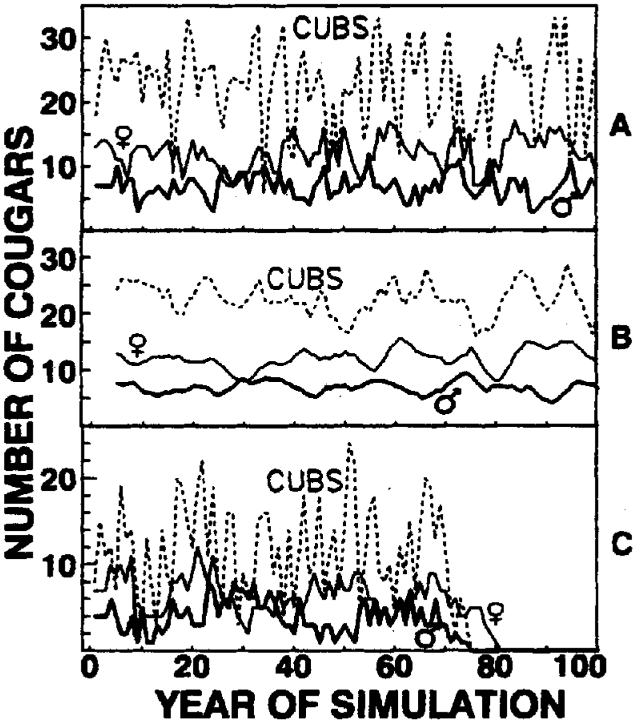

Figure 6. Trajectories of simulated cougar populations with juvenile survivorship = 0.55, adult survivorship = 0.85, carrying capacity = 0.6 female and 0.3 male adults/100 km², no immigration, and a 20% loss of carrying capacity lasting 3 years every 25 years. **A.** *With 2200 km² of habitat, all populations persisted. As in this typical trajectory, age and sex composition of the population varied markedly over time.* **B.** *Five-year running means from panel A, showing that even with five years of observation, population demographics varied considerably.* **C.** *With 1200 km² of habitat, demographic instability increased and 25% of the simulated populations went extinct. As in this typical trajectory, extinction was usually initiated by loss of adult males.*

Applying the Population Model in the Santa Ana Mountains

Given the best local estimates for survivorship rates and carrying capacity, the model predicted that the cougar population in the Santa Ana Mountains is clearly endangered. Although there is less than 3% risk of extinction in the next 100 years with the current 2070 km² of habitat and no immigration, every parcel of habitat lost increases the risk of extinction (Fig. 7). If the population is confined to the 1114-km² block of contiguous protected lands, extinction risk rises to about 33%; an immigration corridor, necessarily including some lands now in private ownership, would greatly improve the prognosis.

Inter-Range Corridor

The only population that can potentially supply immigrants to the cougar population in the Santa Ana Mountain Range is that in the Palomar Range. Interstate Highway 15 and the urban developments along it present the most formidable barrier to wildlife movements between these ranges. A bridged river provides the only safe undercrossing of Highway 15, and there is only one potential corridor between the Palomar range and this un-

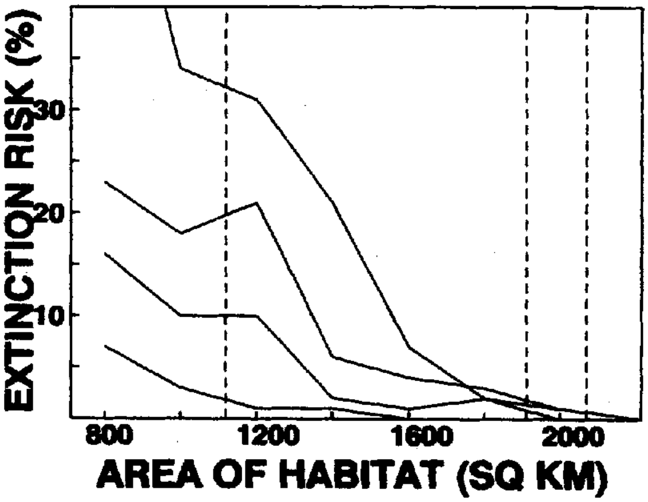

Figure 7. Extinction risk for the cougar population in the Santa Ana Mountains. The top through bottom lines give the percent of simulated populations that went extinct within 100 years when the numbers of immigrants per decade were 0, 1 male, 2 males, or 3 males and 1 female, respectively. From right to left, the vertical lines indicate total available habitat in 1992, total available habitat if the Chino Hills is lost, and total area of the protected and interconnected habitat block. Simulations were run with the following estimates: carrying capacity = 0.7 adult females and 0.35 breeding adult males/100 km², juvenile survivorship = 0.50, and adult survivorship = 0.80.

derpass (Beier & Barrett 1990*b*, 1992*b*). The potential corridor is about 4.5 km long and follows an intermitent watercourse (Pechanga Creek) and the wooded ridges south of this creek (Fig. 2: Pechanga Corridor). Although creeks tend to be natural travel corridors, the utility of lower Pechanga Creek as a corridor is compromised by night lighting from adjacent tract homes, streambed degradation by recent construction, a concrete embankment on portions of the north bank, and removal of woody vegetation for golf courses on the south bank. There are also several residences, an abandoned quarry, a two-lane paved road, and a golf course in the wooded ridges south of the creek.

Although no single one of these obstacles occludes the corridor, collectively they probably prevent immigration by mountain lions into the Santa Ana Range. Field evidence suggests that the corridor *almost* works. On 3 August 1990, a dispersing male mountain lion failed to negotiate the corridor, wandering into a rural residential area where he was captured by wardens. On 29 October 1990, another cougar was killed on I-15 just south of the bridged underpass. On 21 January 1992, a telemetered dispersing male successfully used the corridor to emigrate from the Santa Ana Mountains to the Palomar Range. However, he avoided the bridged undercrossing and the lower 4 kilometers of Pechanga Creek, and was lucky not to have been struck crossing I-15. The pattern of topography and habitat degradation makes it even less likely that a west-bound immigrant would successfully find the undercrossing (Beier & Barrett 1992*b*).

Intra-Range Corridors and Travel Paths

Our data on cougar travel paths (including detailed observations on dispersal routes) have identified specific areas that now prevent intra-range fragmentation. The most threatened link is that connecting the Chino Hills (about 150 km^2 of cougar habitat, including a 57-km^2 state park) to the rest of the mountain range (Fig. 2: Coal Canyon Corridor). State Route 91 and adjacent developments present the greatest obstacle to movement between these areas. The Coal Canyon corridor provides an excellent natural travel route to the freeway and two usable passageways under it (Beier & Barrett 1990*a*, 1991). At least two (probably three) cougars successfully used the Coal Canyon corridor and its underpasses to cross Route 91 into the Chino Hills. In addition, one telemetered cougar was struck by a vehicle attempting to cross the freeway at the mouth of Coal Canyon. One telemetered male dispersed from over 60 kilometers away to establish a home range that now straddles Route 91; he has used the Coal Canyon corridor to cross the freeway at least 16 times during May–December 1991. A pending proposal to build 1500 homes on a 150-ha parcel in Coal Canyon would sever this link, eliminating cougars from the Chino Hills.

Discussion

Population Model

In the absence of immigration, a habitat area of 1000–2200 km^2 (depending on the demographics of a particular population) is needed to support a cougar population with a 98% or more probability of persistence for 100 years; these minimum areas would hold about 15–20 adult cougars. These areas are far smaller than the area assumed necessary to support a population of large carnivores for several centuries without loss of genetic variability (Franklin 1980). It must therefore be stressed that provision of the minimum areas suggested by this model will not guarantee long-term survival of a population. In cases where no immigration corridor is provided, populations confined to such small areas will require monitoring and perhaps periodic intervention—such as introduction of new genetic material through translocation.

The attempt to eliminate some of the values for biological parameters (Table 1) yielded two biological insights. First, natural catastrophes of moderate severity (up to 40% loss of carrying capacity), frequency (every 25 years), and duration (3 years) appear unimportant to cougar population persistence. Shaffer (1983) similarly concluded that catastrophes were relatively unimportant to the population dynamics of grizzly bears. Future modeling efforts can investigate whether this surprising result also holds for disturbances of greater severity and frequency. Second, because adult survivorship of 0.65 or less prevented simulated populations from reaching carrying capacity, management of small populations should include attempts to control factors—such as depredation permits, construction of road undercrossings—that might influence adult survival rate.

These minimum areas and the number of cougars present therein are comparable to the minimum area and number suggested by Shaffer (1983) for grizzly bears. Both my model and Shaffer's incorporated density dependence and produced minimum areas and populations much smaller than predicted by analytic models (see Belovsky 1987) or simulation models lacking density dependence (Captive Breeding Specialists Group 1989; Ginzburg et al. 1990; this paper, Methods).

Ginzburg et al. (1990) advocated use of density-independent models to generate conservative estimates of extinction risk when it is highly sensitive to the shape of the density-dependent function (assuming the true function is unknown). However, to the extent that a density-independent analysis misclassifies viable populations as "hopelessly" small, it can be a *less* conservative approach. Furthermore, extinction risk in my model was not sensitive to the shape of the density-dependent function (Fig. 1). Therefore I chose a density dependent model because it is more realistic. In general, "all natural populations are ... influenced by density-dependent processes" (Begon & Mortimer 1981:162). For cougars in particular, long-term observation in Idaho (Hornocker 1970; Seidensticker et al. 1973; Quigley et al. 1989) and the Ruby Mountains of Nevada (Ashman et al. 1983) show the stability characteristic of populations with density-dependent regulation. The data of Quigley et al. (1989) also suggest that cougar numbers track major long-term changes in carrying capacity (prey abundance). Finally, simulated populations with density-independent survival rates (when they persisted) often had unrealistically high ending densities (see Methods, Density-Dependence in Survival Rates).

If a wildlife movement corridor is available to allow immigration of up to three males and one female per decade, an area as small as 600–1600 km^2 (depending on the demographics of a particular population) can support a cougar population without significant extinction risk in 100 years. Doubtless higher levels of immigration would allow even smaller areas to support cougars. Thus, in areas where isolation or fragmentation of a cougar population appears imminent, protection and enhancement of any remaining corridor is valuable.

The model predicts that south Florida, with 8800 km^2 of occupied range and an adult density of about 0.6 adults per 100 km^2 (Maehr 1990) has adequate habitat for demographic persistence. Captive Breeding Specialists Group (1989), also using a simulation approach, concluded that the Florida population faced a high risk of extinction. These predictions do not necessarily conflict, however, because the CBSG model included extinctions caused by inbreeding effects and excluded enhancement of survival rates when populations were below carrying capacity. In any event, the best panther habitat in Florida is privately owned (Maehr 1990), and rapid agricultural and urban development could soon fragment this habitat into dangerously small parcels. The aggressive protection of habitat and movement corridors is essential to ensure the persistence of Florida panthers.

Two Caveats in Applying this Model

Two caveats apply to this model. First, the model is sensitive to the estimates for carrying capacities for adult males and females. Uncritical use of estimates from a different area or habitat type should be avoided. Because cougars are K-selected, it is probably reasonable to estimate carrying capacity from locally observed densities. However, the great variation in sex and age composition in simulated populations suggests that at least five years of study are needed for reliable estimates (Fig. 6A–B). Also, the carrying capacities used in this model must be estimated by numbers of breeding adult males and females, excluding the pool of nonbreeding male and female transients that characterize most populations (Seidensticker et al. 1973). Categorizing all individuals over 1 year of age as adult breeders would lead to overly optimistic predictions.

Second, survival rates observed for a population occupying a large area will probably decrease as area decreases and degree of isolation increases, due to increased highway mortality (Beier & Barrett 1992*a*) and decreased dispersal success. A conservative approach necessitates use of lower-than-observed survival rates in making projections for a population that has not yet been fragmented or isolated.

Application to the Santa Ana Mountain Range: Site-Specific Data along with Model Conclusions Can Save Land

If survival of this population is a goal, the model yields several clear conclusions (Fig. 7). Developments that isolate or destroy large tracts of habitat should be avoided. A corridor for immigration is of paramount importance. Within the mountain range, corridors are also needed to interconnect the protected parcels (Table 3).

Unfortunately, these conclusions alone have little power to save land in the prodevelopment political climate of southern California. For example, although the admonition to "avoid destroying large tracts" can be implemented without additional data, few planning decisions involve tracts that are "large" relative to the habitat needed to support a cougar population. The other conclusions cannot be heeded without additional data, especially on the location of movement corridors.

Field data suggest that habitat degradation probably prevents any regular inflow via the last potential corridor for immigration (Fig. 2: Pechanga Corridor). Except for the 15-year-old freeway, the obstacles to the Pechanga Corridor are less than 5 years old. If a regional, spatially-explicit land-use plan had been in place in 1986, the importance of this corridor would have been obvious and the obstacles preventable. Strict protection of the remaining habitat and additional habitat modification and restoration will now be necessary if the Pechanga Corridor is to function (Beier & Barrett 1992*b*). The Nature Conservancy is actively interested in taking such steps but faces an uphill struggle.

Our work has also spotlighted a critical corridor necessary to prevent intra-range fragmentation (Fig. 2: Coal Canyon). The City of Anaheim is now considering approval of a housing project that would destroy this corridor. Our documentation of both the importance and use of this corridor should result in a scaled-back project that leaves the corridor intact. The population model convincingly predicts that loss of this corridor would guarantee the extinction of cougars from the 150 km^2 of habitat north of the freeway, reducing by 7.5% the total habitat available to our population and pushing the population leftward to the steeply rising part of the risk curve (Fig. 7). The field work shows that the corridor is in fact used. Thus the model and the field work together may provide sufficient documentation to protect this corridor; certainly neither could do so alone.

In another application, the model and complementary fieldwork are having limited success in mitigating the effects of a planned freeway; its proposed route slices through a pristine area with no human residents along its 21-kilometer length (Anonymous 1990). This freeway would affect wildlife movement between the bulk of habitat on one side of the road and five smaller areas of dedicated open space on the other side. By all-night radio-tracking of individual focal animals, we have learned the actual routes by which cougars travel among these areas. Although these routes now traverse pristine open space, they will become corridors (at best) as freeway-induced growth removes the adjacent habitat. The transportation agency has responded to this information by planning bridged undercrossings at the five most important crossing points. Previously, the agency had planned on only one of these bridges, and the location was based on geological rather than biological considerations.

Unfortunately, preserving a corridor is not as simple as building a bridge at one point along the corridor. The road-building agency has acknowledged that the freeway, by providing "critical infrastructure to large expanses of open space," will induce massive urban growth (Anonymous 1990:5.13); such growth could sever all of the wildlife corridors, rendering the underpasses pointless. The agency has refused requests to purchase easements to the three most important corridors as mitigation for this induced growth, and it currently faces a lawsuit on this issue.

Conclusions

The cougar is an ideal species for identification of movement corridors for two reasons. First, cougars are an area-sensitive species; therefore a corridor identified on the basis of cougar use will benefit at least one species. Second, a hunting cougar travels an average of 5.5 miles per night (Beier, unpublished data) and thus generates a lot of corridor data in a short time. Collection of comparable data for a less wide-ranging species may take years or generations.

I do not advocate using cougars as a proxy for all species of concern. However, management decisions will not await the conclusion of long-term studies on more sedentary species. In western North America, use of data from telemetered cougars may be the most expedient way to interject biological facts into the analysis of environmental impact and mitigation related to movement corridors. It is certainly a big step above current practices, which include (1) looking at aerial photos in an office and guessing where a corridor ought to be; or (2) labeling the leftover shards of habitat, or the bridge built according to geological constraints, as the "wildlife corridor."

Effective protection of wildlife corridors requires *putting them on the map.* Unfortunately, the current mechanism for such protection is for concerned citizens to detect and force mitigation on each proposed project that threatens the corridor. 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. Because a corridor is only as strong as its weakest link, a single oversight or failure on the part of conservationist volunteers is sufficient to lose the linkage.

Putting wildlife corridors and critical habitat on a planner's map can best be done through a geographic information system covering a *regional* landscape. Although General Plans are mandated for each county in California, such plans are rarely site-specific in any recommendations and are almost never tied to a GIS. Furthermore, as the present case illustrates, a single population or wildland may span several counties, and land-use planning is nonexistent at the regional level.

A spatially-explicit planning tool such as a GIS is essential because it provides the only efficient means of addressing cumulative impact and an accessible forum on which developers, conservationists, and other citizens express their vision of the regional landscape at build-out. Scott et al. (1990) describe a GIS-based approach that would admirably serve a regional plan, and Hollings (1978) gives practical advice that should inspire such planning.

Acknowledgments

This paper is dedicated to agency personnel and biological consultants who risk their jobs to share information that their superiors or clients want to suppress. I thank Dave Bontrager, who first nudged me toward this research in 1989. Field work was supported by California Agricultural Experiment Station Project 4326-MS, California Department of Fish and Game, the County of Orange, and the U.S. Marine Corps. Donna Krucki, Doug Padley, and Duggins Wroe were invaluable in the field. R. H. Barrett of the University of California and T. M. Mansfield of the California Department of Fish and Game provided logistic and moral support that kept the project alive. I thank Reed Noss, David Ehrenfeld, and an anonymous reviewer for constructive comments on the manuscript. I will send a diskette with the simulation program and the Pascal source code for cost of media (IBM-compatible) and postage.

Literature Cited

Anderson, A. E. 1983. A critical review of literature on the puma *Felis concolor.* Colorado Division of Wildlife Special Report 54.

Anderson, A. E., D. C. Bowden, and D. M. Kattner. 1989. Survival in an unhunted mountain lion population in southwestern Colorado. Proceedings Mountain Lion Workshop 3:57.

Anonymous. 1989. Growth Management Plan. Southern California Association of Governments, Los Angeles.

Anonymous. 1990. Draft Environmental Impact Report TCA EIR 3. Foothill-Eastern Transportation Corridor Agency, Costa Mesa, California.

Ashman, D. L., G. C. Christensen, M. L. Hess, G. K. Tsukamoto, and M. S. Wickersham. 1983. The mountain lion in Nevada. Nevada Department of Wildlife.

Begon, M., and M. Mortimer. 1981. Population ecology. Sinauer Associates, Sunderland, Massachusetts.

Beier, P., and R. H. Barrett. 1990*a*. Cougar surveys in the San Joaquin Hills and Chino Hills. Orange County Cooperative Mountain Lion Study, Department of Forestry and Resource Management, University of California, Berkeley.

Beier, P., and R. H. Barrett. 1990*b*. Quarterly report of 1 November 1990. Orange County Cooperative Mountain Lion Study, Department of Forestry and Resource Management, University of California, Berkeley.

Beier, P., and R. H. Barrett. 1991. Quarterly report of 1 July 1991. Orange County Cooperative Mountain Lion Study, Department of Forestry and Resource Management, University of California, Berkeley.

Beier, P., and R. H. Barrett. 1992*a*. Quarterly report of 1 January 1992. Orange county Cooperative Mountain Lion Study, Department of Forestry and Resource Management, University of California, Berkeley.

Beier, P., and R. H. Barrett. 1992*b*. Quarterly report of 1 April 1992. Orange County Cooperative Mountain Lion Study, Department of Forestry and Resource Management, University of California, Berkeley.

Belovsky, G. E. 1987. Extinction models and mammalian persistence. Pages 35–58 in M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, New York.

Captive Breeding Specialists Group. 1989. Florida panther viability analysis and species survival plan. Apple Valley, Minnesota.

Currier, M. J. P., S. L. Sheriff, and K. R. Russell. 1977. Mountain lion population and harvest near Cañon City, Colorado 1974–1977. Colorado Division of Wildlife Special Report 42.

Eaton, R. L., and K. A. Velander. 1977. Reproduction in the puma: biology, behavior, and ontogeny. The World's Cats 3(3):45–70.

Ewens, W. J., P. J. Brockwell, J. M. Gani, and S. I. Resnick. 1987. Minimum viable population size in the presence of catastrophes. Pages 59–68 in M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, New York.

Franklin, I. R. 1980. Evolutionary change in small populations. Pages 135–150 in M. E. Soulé and B. A. Wilcox, editors. Conservation Biology. Sinauer, Sunderland, Massachusetts.

Ginzburg, L. R., S. Ferson, and H. R. Akçakaya. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. Conservation Biology 4:63–70.

Harris, L. D., and P. B. Gallagher. 1989. New initiatives for wildlife conservation: the need for movement corridors. Pages 11–34 in G. Mackintosh, editor. Preserving communities and corridors. Defenders of Wildlife, Washington, D.C.

Hemker, T. P., F. G. Lindzey, and B. B. Ackerman. 1984. Population characteristics and movement patterns of cougars in southern Utah. Journal of Wildlife Management. 48:1275–1284.

Hemker, T. P., F. G. Lindzey, B. A. Ackerman, and A. J. Button. 1986. Survival of courage cubs in a non-hunted population. Pages 327–332 in S. D. Miller and D. D. Everett, editors. Cats of the world. National Wildlife Federation, Washington, D.C.

Hollings, C. S., editor. 1978. Adaptive environmental assessment and management. John Wiley & Sons, New York.

Hopkins, R. A. 1981. The density and home range characteristics of mountain lions in the Diablo Range of California. M.S. Thesis, California State University, San Jose.

Hopkins, R. A. 1989. The ecology of the puma in the Diablo Range, California. Ph.D. Thesis, University of California, Berkeley.

Hornocker, M. G. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildlife Monographs 21:1–39.

Lindzey, F. G., B. B. Ackerman, D. Barnhurst, and T. P. Hemker. 1988. Survival rates of mountain lions in southern Utah. Journal of Wildlife Management 52:664–667.

Logan, K. A., L. I. Irwin, and R. Skinner. 1986. Characteristics of a hunted mountain lion population in Wyoming. Journal of Wildlife Management 50:648–654.

Maehr, D. S. 1990. The Florida panther and private lands. Conservation Biology 4:167–170.

Murphy, K. M. 1983. Relationships between a mountain lion population and hunting pressure in western Montana. M.S. Thesis, University of Montana, Missoula.

Neal, D. L., G. N. Steger, and R. C. Bertram. 1987. Mountain lions: preliminary findings on home-range use and density in the central Sierra Nevada. Research note PSW-392. Pacific Southwest Forest and Range Experiment Station, Berkeley, California.

Noss, R. F. 1991. From endangered species to biodiversity. Pages 227–246 in K. A. Kohm., editor. Balancing on the brink of extinction. Island Press, Washington, D.C.

Padley, W. D. 1990. Home ranges and social interactions of mountain lions in the Santa Ana Mountains, California. M.S. Thesis. California State Polytechnic University, Pomona.

Quigley, H. B., G. M. Koehler, and M. G. Hornocker. 1989. Dynamics of a mountain lion population in central Idaho over a 20-year period. Proceedings of the Mountain Lion Workshop 3:54.

Robinette, W. L., J. S. Gashwiler, and O. W. Morris. 1961. Notes on cougar productivity and life history. Journal of Mammalogy 42:204–217.

Robinette, W. L., N. V. Hancock, and D. A. Jones. 1977. The Oak Creek mule deer herd in Utah. Utah Division of Wildlife Resources, Salt Lake City.

Schaller, G. B. 1972. The Serengeti lion. University of Chicago Press, Chicago, Illinois.

Scott, J. M., B. Csuti, K. Smith, J. E. Estes, and S. Caicco. 1990. Pages 282–297 in K. A. Kohm., editor. Balancing on the brink of extinction. Island Press, Washington, D.C.

Seidensticker, J. C., Jr., M. G. Hornocker, W. V. Wiles, and J. P. Messick. 1973. Mountain lion social organization in the Idaho primitive area. Wildlife Monographs 35:1–60.

Shaffer, M. L. 1983. Determining minimum population sizes for the grizzly bear. International Conference on Bear Research and Management 5:133–139.

Shaffer, M. L. 1987. Minimum viable populations: coping with uncertainty. Pages 69–86 in M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, New York.

Shaw, H. G. 1977. Impact of mountain lion on mule deer and cattle in northwestern Arizona. Pages 17–32 in R. L. Phillips and C. Jonkel, editors. Proceedings of the 1975 Predator Symposium, University of Montana, Missoula.

Sitton, L. W., and S. Wallen. 1976. California mountain lion study. California Department of Fish and Game, Sacramento.

Soulé, M. E. 1987*a*. Introduction. Pages 1–10 in M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, New York.

Soulé, M. E. 1987*b*. Where do we go from here? Pages 175–184 in M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, New York.

Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. American Naturalist 125:879–887.

Young, S. P. 1946. History, life habits, economic status, and control. Pages 1–173 in S. P. Young and E. A. Goldman. The puma, mysterious American cat. The American Wildlife Institute, Washington, D.C.