Evaluating Landscape Connectivity in Coastal Southern California Using Individual-Based Movement Models: A Report to The Nature Conservancy and the California Department of Fish and Game

Jeff A. Tracey^{*}

Department of Wildlife Ecology and Department of Statistics University of Wisconsin-Madison

> Kevin R. Crooks[†] Department of Fishery and Wildlife Biology Colorado State University

> > March 31, 2004

e-mail: jatracey@wisc.edu

 ^{†&}lt;br/>e-mail: kcrooks@cnr.colostate.edu

Contents

1	Bac	Background and Objectives												
	1.1													
	1.2													
	1.3	Animal Movement and Connectivity	6 7											
	1.4	Research Objectives	8											
2	Met	Methods												
-	2.1													
	2.2	Models Tested	9 10											
	2.3	Parameter Estimation	13											
	2.4	Field Telemetry Data	13											
	2.5	Final Models Selected for Mountain Lion Movement Simulation	15											
		2.5.1 Final Models Selected for Bobcat Movement Simulations	16											
	2.6	Individual-Based Movement Models	16											
	2.7	Core Habitats	18											
	2.8	GIS Landscapes	21											
	2.0	2.8.1 Existing Landscape	21											
		2.8.2 NCCP Landscape	23											
		2.8.3 Worst-Case Landscape	23											
		2.8.4 Highway Layer	23											
	2.9	Simulation of Individual Movement	23											
	2.10	Connectivity Evaluation	27											
	-	2.10.1 Quantifying Connectivity	27											
		2.10.2 Visualizing Connectivity	28											
		2.10.3 Comparing Connectivity Within and Between Landscapes	29											
3	Res	ults and Interpretation	29											
	Existing Landscape	29												
	3.2	NCCP Landscape	30											
	3.3	Worst-Case Landscape	32											
	3.4	Bobcat Simulations	34											
	3.5	Comparison of Existing and NCCP Landscapes	34											
	3.6	Recommendations for Improving Connectivity	35											
		3.6.1 Develop a Strategy for Preserving Connectivity	35											
		3.6.2 Identify Critical Linkages	36											
		3.6.3 Visualizing Behavioral Corridors	37											
		3.6.4 Threats to Connectivity	64											
4	Disc	cussion Regarding the Movement Models	68											
	4.1	Advantages of Our Movement Models	68											
	4.2	Limitations of Our Movement Models	69											
	4.3	Future Work	70											
		4.3.1 Field Telemetry data to be used in future modeling efforts	71											

5	Summary	71
A	Movement Summary Output	74
В	Path Summary Output	76

List of Figures

1	Diagram of a decision tree for a finite mixture model of movement.	11
2	Movement angles in relation to a polygon boundary.	12
3	Quantification of animal movement using GIS and telemetry data	14
4	Basic organization of the individual-based movement model	17
5	Mountain lion core areas used in the simulations.	19
6	Bobcat core areas used in the simulations.	20
7	Existing land cover scenario	22
8	Natural Communities Conservation Planning (NCCP) land cover scenario.	24
9	Worst-case land cover scenario.	25
10	TIGER 2K Highways.	26
11	Simulated mountain lion locations for successful dispersal paths in the existing	
	landscape scenario.	30
12	Simulated mountain lion locations for successful dispersal paths in he NCCP	
	landscape scenario.	31
13	Simulated mountain lion locations for successful dispersal paths in the worst-	
	case landscape scenario.	33
14	Connectivity graphs for the existing, NCCP, and worst-case landscapes	44
15	Simulated locations for successful bobcat dispersal.	47
16	A graph representation of one possible strategy for preserving connectivity for	
	mountain lions in the southern California ecoregion.	49
17	Encounters with boundaries of the southern California ecoregion for the ex-	
	isting landscape simulation.	52
18	Encounters with boundaries of the southern California ecoregion for the NCCP	
	landscape simulation.	53
19	Simulated locations for successful dispersal paths from the Palomar Mountains	
	(core 5) to the Santa Ana Mountains (core 4). \ldots \ldots \ldots \ldots \ldots	54
20	Simulated locations for lowest cost successful dispersal locations from the	
	Palomar Mountains (core 5) to the Santa Ana Mountains (core 4)	55
21	Simulated movements for lowest cost successful dispersal paths from the Palo-	
	mar Mountains (core 5) to the Santa Ana Mountains (core 4)	56
22	Movement routes (behavioral corridors) suggested by the models based on	
	simulated movements for lowest cost successful dispersal paths from the Palo-	
	mar Mountains (core 5) to the Santa Ana Mountains (core 4)	57
23	Movement routes (behavioral corridors) suggested by the models based on sim-	
	ulated movements for lowest cost successful dispersal paths from the Cleveland	
	National Forest (core 7) to Miramar (core 8)	59
24	Simulated movements for lowest cost successful dispersal paths between the	
	Cleveland National Forest (core 7) and the Palomar Mountains (core 5). \therefore	60
25	Simulated movements for lowest cost successful dispersal paths between the	
	Otay Mountain (core 9) and the Cleveland National Forest (core 7)	61
26	Simulated locations for dispersal from core 1 to 5	62
27	Corridors for dispersal from core 1 to 5	63

28	Encounters with highways for the existing landscape simulation. The yellow	
	areas show where the encounters occurred	64
29	Encounters with highways for the NCCP landscape simulation. The yellow	
	areas show where the encounters occurred	65
30	Encounters with urban areas for the existing landscape simulation. The yellow	
	areas show where the encounters occurred	66
31	Encounters with urban areas for the NCCP landscape simulation. The yellow	
	areas show where the encounters occurred	67

List of Tables

1	Mountain lion core habitat areas used in the simulations	21
2	Results for dispersal success in existing landscape	32
3	Results for mean dispersal cost and risk in existing landscape	39
4	Results for dispersal success in NCCP landscape.	40
5	Results for mean dispersal cost and risk in NCCP landscape	41
6	Results for dispersal success in worst-case landscape	42
7	Results for mean dispersal cost and risk in worst-case landscape	43
8	Results for bobcat dispersal success	45
9	Results for mean dispersal cost and risk for bobcats in the existing landscape.	46
10	Difference in numbers of successful dispersals for NCCP landscape versus the	
	existing landscape.	48
11	Summary of connectivity strategy linkages and their rankings according to	
	the simulation output.	50
12	Summary of connectivity ranks for each goal	51

1 Background and Objectives

1.1 Habitat Fragmentation in Southern California

The destruction of habitat has been targeted as one of the most serious threats to biological diversity worldwide (Wilcove et al. 1998). Habitat destruction results from both the overall loss of habitat per se, as well as the more subtle effects of the fragmentation of continuous landscapes into smaller patches (Fahrig 1997, Bender et al. 1998, Crooks 2002). The overall loss of habitat can result in increased extinction rates of wildlife populations, especially for wide-ranging species that require large, continuous habitat blocks. In addition, habitat fragmentation creates sharp boundaries, or edges, between natural and human-dominated habitats, resulting in multiple stressors that detrimentally impact wildlife populations. Edge effects associated with habitat fragmentation include light, noise, and chemical pollution, microclimatic changes in light and temperature, invasion of non-native plants and animals, and disturbance and mortality through direct encounters with humans (Murcia 1995). Edge effects can therefore impact wildlife populations by altering their demography or through behavioral avoidance of or attraction to fragment edges. The consequences of these edge effects can range from reduced effective area of suitable habitat within a reserve to increased probability of extinction (Woodroffe and Ginsberg 1998).

In areas with increasing urbanization, the loss and fragmentation of habitat is virtually inevitable (Soulé 1991). In coastal southern California, intensive development over the past century has destroyed most of the native sage scrub and chaparral habitats. This massive habitat loss, in conjunction with high levels of local endemism of native species, has helped create a "hot-spot" of endangerment and extinction in the region (Myers 1990, Dobson et al. 1997).

The severe effects of habitat fragmentation on the composition, structure, and function of ecosystems have made a compelling case for preserving connectivity within developing landscapes. Landscape-level connectivity is essential to allow for the natural movement of animals among foraging and breeding sites, the dispersal of individuals from natal ranges, genetic exchange between populations, natural range shifts in response to climate change, and the continuity of ecological processes such as hydrology, succession, and seed dispersal (Noss 1983, Soulé and Terborgh 1999). Where connectivity is not retained across developing landscapes, many plant and animal populations will eventually disappear. Although the fragmentation of natural landscape of coastal southern California is accelerating, large-scale assessments of regional connectivity are lacking.

1.2 The Role of Large Carnivores

The concept of focal species in reserve design is a central theme in large-scale conservation planning (Noss 1992, Noss and Cooperrider 1994, Noss and Soulé 1998, Miller et al. 1998, Soulé and Terborgh 1999). Focal species are chosen to symbolize ecological conditions that are critical to healthy, functioning ecosystems (Lambeck 1997). Mammalian carnivores can be effective focal species to evaluate the degree of landscape-level connectivity. Large carnivores are particularly vulnerable to extinction in fragmented habitat because of wide ranges and resource requirements, low densities, slow population growth rates, and direct persecution by humans (Noss et al. 1996, Woodroffe and Ginsberg 1998, Crooks 2000, Crooks 2002). Consequently, top predators may not be able to persist in landscapes that are not connected by functional movement corridors. Further, their disappearance may generate cascades that ripple down the food web. In fragmented habitat in San Diego, Crooks and Soulé (1999) have demonstrated that the extirpation of dominant predators such as coyotes (*Canis latrans*) can contribute to the ecological release of smaller predators and increased extinction rates of their avian prey. Thus, top predators may function as keystone species animals whose disappearance causes the increase in some species and the decline and extinction of others (Mills et al. 1993).

Large carnivores therefore are ecologically pivotal organisms whose status can be indicative of the functional connectivity of ecosystems. Using mammalian carnivores in conservation planning adds a critical layer of conservation strategy that may provide a robust method for protecting other species with less demanding needs (Lambeck 1997, Miller et al 1998, Carroll et al. 1999). In southern California, mountain lions (*Puma concolor*) and bobcats (*Felis rufus*) are excellent focal species for the evaluation of connectivity across multiple spatial scales (Crooks 2000, Crooks 2002). Mountain lions are the largest predator remaining in the region and are particularly sensitive to habitat fragmentation (Beier 1993, Maehr 1997, Crooks 2000, Crooks 2002). Mountain lions occupy ranges that encompass over 300 km^2 . travel on average 6 km per night (Beier et al. 1995), and disperse distances that average 65 km (Beier 1995). Our ongoing carnivore surveys in southern California indicate that mountain lions only occur in large, intact landscapes and are therefore excellent indicator species of connectivity across the scale of the entire ecoregion (Crooks 2000, Crooks 2002). Bobcats are less sensitive to fragmentation than mountain lions and are therefore valuable indicators of connectivity at smaller spatial scales. They have relatively large home ranges (ca. 50 km^2) and can disperse long distances (Lawhead 1984, Litvaitis 1986, Lovallo et al. 1996). Bobcats can persist in smaller habitat fragments, but only those that have adequate connections to larger natural areas. Thus, like mountain lions, connectivity appears to be the key to their persistence.

1.3 Animal Movement and Connectivity

This project is motivated by a need to better understand connectivity in landscapes. We focus specifically on functional or behavioral connectivity, which is the ability of animals to move among habitat or resource patches in a landscape (Taylor et al. 1993). In North America, habitat destruction is the leading cause of species decline and endangerment (Wilcove et al. 1998). This destruction results in habitat loss, degradation, and fragmentation. Habitat fragmentation is the division of larger habitat patches into a greater number of smaller habitat patches, a process that alters landscape connectivity. Properly designed and implemented habitat reserve networks can minimize the effects of habitat destruction on wildlife (Soulé and Terborgh 1999). For a reserve network to function as intended, sufficient connectivity among core habitat areas must be preserved by protecting movement corridors or landscape elements that are sufficiently permeable to movement of focal species. There are no general rules for evaluating connectivity; therefore, the problem must be addressed in a species and landscape specific manner (Soulé and Gilpin 1991).

Connectivity has been defined as "the degree to which the landscape facilitates or im-

pedes movement among resource patches" (Taylor et al. 1993). Any assessment of connectivity must take into account both animal movement behavior and landscape structure and composition. To assess connectivity, we therefore must be able to measure movement of animals in the landscape of interest and develop and apply models that can predict such movement. Field studies of animal movement are essential, but without a model of some kind, the results of these studies cannot be applied to other landscapes or the same landscape after changes have occurred.

Animal movement behavior and landscape structure are two essential features of functional landscape connectivity. Current methods for assessing connectivity such as mathematical graph theoretic, least cost path, and landscape metric approaches (Schumaker 1996, Urban and Keitt 2001) take into account the structure of the landscape, but they do not directly account for the movement behavior of animals. Spatially explicit models (SEMs) used for conservation purposes often include animal movement; however, the movement models used by these SEMs are rarely, if ever, data-supported. By data-supported we mean that the movement models can be parameterized from data, that alternative models can be compared and the best alternative selected, that models can be validated, and that such statistical methods have been used along with data to parameterize and select movement models that are used in conservation applications.

Animal movement in relation to landscape features is poorly understood, and there is a notable lack of models that are useful for analyzing such movements. We build on previous conceptual work on movement and some statistical approaches that can be applied to modeling movement. Jander (1975) presented a review of orientation ecology, or the study of animal movement. In this paper Jander defined object orientation, which is the movement of animals in relation to objects (i.e., landscape elements) and detection space, which is the region around an animal within which it can detect objects. Gustafson and Gardner (1996) used a simple individual-based movement model for patch boundary response in a grid landscape to predict patch colonization. Recent work by Zollner (2000) focuses on perceptual range, which is the distance from which an animal can perceive a particular landscape element. The work we describe below gives mathematical form to these concepts.

Defining the movement models is not enough. We must also have computational tools that can extract data from animal movement and geographic information system (GIS) data layers, estimate model parameters, and simulate animal movement on GIS landscape models. Development of spatial models with mobile agents and dynamic landscapes is an active area in GIS research (Westervelt and Hopkins 1999), and is an essential part of this project.

1.4 Research Objectives

Our research goal is to assess the degree of landscape-level connectivity within and between NCCP reserves by developing individually-based computer simulation models of animal movement through the fragmented landscape of southern California. We will focus on large mammalian carnivores because top predators are ecologically pivotal organisms whose status is indicative of the connectivity of ecosystems. We will apply these models to NCCP reserve design, monitoring, and management issues in southern California.

These models will be used to a) assess connectivity of present and projected future landscapes in southern California, b) predict the movement of individuals across space and time in the NCCP reserve network, c) identify potential linkages between core habitat patches and estimate the rates of movement between them, d) predict the rates and locations of encounters with landscape hazards, and possible mortality sinks, such as roadways and urban edges, e) guide the development of management and monitoring programs for NCCP reserves.

Based on the rationale above, we completed four main objectives for this research:

- 1. To develop methods for analyzing animal movement data (e.g., from telemetry) that can be used for model selection and parameterization. This includes:
 - (a) Developing alternative mathematical models of movement in relation to landscape features,
 - (b) Developing statistical procedures associated with each model, and
 - (c) Writing software that performs the statistical procedures.
- 2. To write computer programs for use in quantifying relations between animals and landscape elements,
- 3. To write computer programs for simulating animal movement on GIS models of landscapes.
- 4. To apply the statistical models and simulation programs by using them along with movement data to evaluate landscape connectivity for mammalian carnivores in southern California.

2 Methods

What makes our approach unique is that we rely on statistical theory and movement data to select and parameterize our movement models, rather than on what has been called a *standard of plausibility* that has been used in the past (Lima and Zollner 1996). Movement rules are often used in simulation models employed for conservation purposes, but they are generally based on rules of movement and parameter estimates that seem plausible, rather than those that have are based on analysis of data. On the other hand, models that are data-supported are overly simplified. We have been working on movement models that incorporate more biological realism and that can be fitted to data from animal movement in response to landscape features. Once the parameters for the models have been estimated, we can select the one that best describes the data and use it in simulations that predict movement across landscapes. Therefore, another unique feature of our models that they are both data supported and biologically realistic. This research is in the beginning phases and the results of this report are the first application of these models.

2.1 Basic Explanation of Models

From a biological perspective we might call the models we have developed *decision tree* models, but statistically they are called *finite mixture models* (Figure 1). In these models,

an animal is confronted with one or more landscape elements (or *objects*), and it makes a series of decisions that eventually lead to movement in response to one. If an animal does not respond to any of the features, then it moves according a *default model* (Figure 2). Examples of default models that we have considered in this study are (a) a simple random walk, (b) a correlated random walk, and (c) directional bias. In a simple random walk, the probability of moving in any direction is equal. In a correlated random walk, also called directional persistence, an animal has a tendency to move in a direction that is related to its previous direction of movement. In directional bias, an animal has a higher probability of moving in a fixed compass direction.

We conceptualize the process as a decision tree, or in a statistical sense a conditional probability tree. During each movement, the animal makes a movement decision by working its way through a series of decisions (visualized as branches of a tree) until it reaches a leaf that corresponds to a movement response. Each branch of the tree has a conditional probability that is a function of the distance and angles to landscape features. An example of a binary decision tree is shown in Figure 1.

Once a leaf (a terminal node) in the decision tree is reached (Figure 1), the animal has decided the probability density functions (pdfs) from which it will generate a move angle and move distance. Each pdf in the mixture corresponds to movement in response to some object (a discrete entity such as a habitat patch boundary) in the landscape or a default movement model (such as a simple random walk). Each pair of move angle-move distance distributions is related to one of the landscape elements. Therefore, there is a finite number of probability densities with fixed parameters in each model, and this is why they are called finite mixture models. The pdfs are continuous distributions of movement angles and movement distances because unlike most movement models that only permit movement on a grid, we allow the animals to move anywhere in space.

2.2 Models Tested

We proposed a total of 30 alternative models for movement in each land cover type for response to each boundary type. Each model varies the kind of default model (simple random walk, correlated random walk, and directional bias), whether there is no response, a unimodal (one pdf) response, a symmetric bimodal (two pdf) response, or an asymmetric bimodal (two pdf) response to the boundary, and whether the probability of response was a constant, exponential or logistic function of the distance to the boundary. In a unimodal response, the animal has a tendency to move in one mean angle in relation to the boundary (e.g., toward or away). In the bimodal models the animal can move in two mean directions, with each mean direction selected with some probability; for example, a rule might be to move parallel to the boundary to the left with probability p(left) and to the right with probability p(right). In the symmetric case, the two mean angles are equal in magnitude but of opposite signs and they have the same variance. In the asymmetric models the two mean angles and their variances are free to be whatever values yield the maximum likelihood. The symmetric models were presented as a possibility because it allows a bimodal response with 2 fewer parameters than the asymmetric models.

We considered four land cover types in the alternative landscapes: habitat, disturbed, urban, and water. Water is a relatively rare type, and we had no data on encounters with

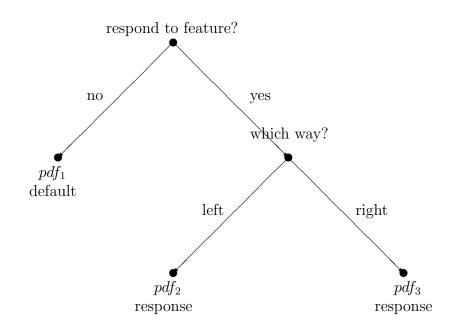


Figure 1: A decision tree model for mixture proportions. Nodes are represented as filled circles. Inner nodes correspond to decisions, while terminal (leaf) nodes correspond to an action modeled by a probability density function (pdf) from which a move angle or distance is drawn. The nodes are connected by edges represented by lines, representing alternative choices. Associated with each edge is a conditional probability. This tree corresponds to a model for response to a patch boundary. The first decision is whether to respond to the boundary at all (the feature), which may depend on how far away the boundary is. If the animal does not respond to the boundary, then it makes a movement using its default model for the patch type it occupies. If the animal does respond, then it chooses to respond by moving either left or right in relation to the patch boundary. Once this decision is made the animal makes a move using the corresponding pdf.

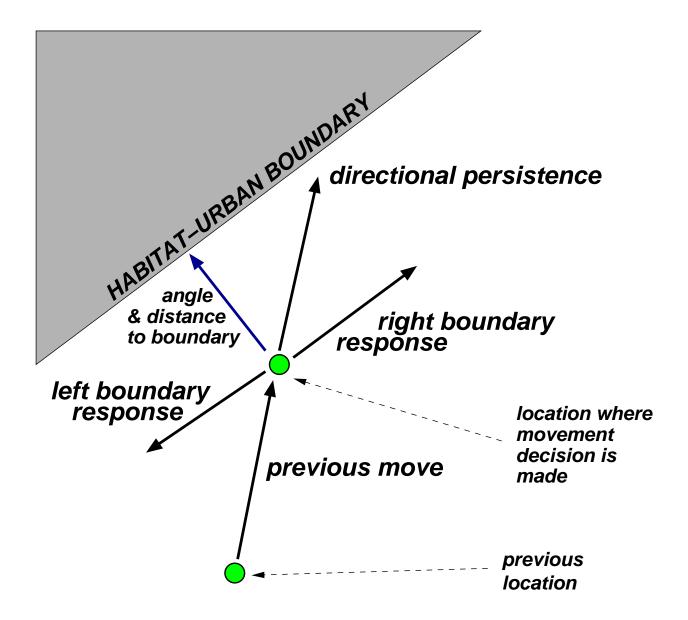


Figure 2: Here we illustrate possible ways in which an animal might chose to move according to one alternative model for movement angles in response to a habitat-urban boundary where the animal is in habitat and the nearest boundary is with an urban landscape feature. Directional persistence, the tendency to move in a direction similar to the previous move, is the default model in this case. The angle and distance to the urban boundary is shown as the blue arrow. The probability of responding to the boundary depends on the distance to the boundary. There are two response models, one for movement to the left in relation to the urban boundary, and one for movement to the right in relation to the urban boundary. If the decision is made to respond to the boundary, the angle from the animal's location to the boundary is needed to calculate the final angle of movement. The decision tree for this model is shown in Figure 1.

water, so we only considered habitat, disturbed, and urban land cover types in the analysis. Therefore, we had to test models for six boundary types: habitat-disturbed (H-D), habitaturban (H-U), disturbed-habitat (D-H), disturbed-urban (D-U), urban-habitat (U-H) and urban-disturbed (U-D). Note that the first letter in this notation indicates the type of land cover the animal currently occupies, and the second letter indicates the land cover type across the patch boundary. We assumed that the animal responds to the nearest boundary type.

2.3 Parameter Estimation

Data used in model parameterization and selection include both radio (or GPS) telemetry data and geographic information system (GIS) data layers corresponding to the site where the telemetry data were collected (Figure 3). Move angles and distances are calculated between consecutive telemetry locations. In addition, we use computer programs that we have written to calculate the angles and distances to landscape features such as land cover polygon boundaries (Figure 3). Once these calculations have been made, we can estimate model parameters using parameter estimation programs that we have written, and then compare the alternative models using Akaike's Information Criterion (AIC) or likelihood ratio tests (LRT).

In summary, our basic statistical approach is to:

- Formulate alternative models for movement to a particular type of landscape feature.
- Using a maximum likelihood approach, estimate parameters for each model from individual movement data, collected from radio-collared animals in the field.
- Compare the alternative models using Akaike's Information Criterion (AIC) to select the alternative models that best describe the field-collected movement data.
- Use the selected, parameterized models to simulate movement on each alternative landscape.

2.4 Field Telemetry Data

For the mountain lion simulations we estimated model parameters using radio telemetry data from two sub-adult dispersing males and land cover data (see Section 2.8.1). The movement data were collected by Paul Beier and his colleagues in the Santa Ana Mountains of coastal southern California (Beier 1995) between October 1990 and September 1922 (animals M8 and M10). In the analysis we used data from 143 movements made by M8 and 260 movements made by M10. These data were collected during "diel" sessions during which animals were located every 15 minutes.

We are also involved in efforts in collaboration with USGS (Lisa Lyren and Robert Fisher) in Orange County, in the Santa Ana foothills. We used data from one male resident bobcat and land cover data (see Section 2.8.1) to estimate bobcat model parameters. This male bobcat made many exploratory movements resulting in encounters with the urban boundary. We used data from a total of 287 movements collected via Global Positioning System (GPS) tracking collars at 15 minute intervals.

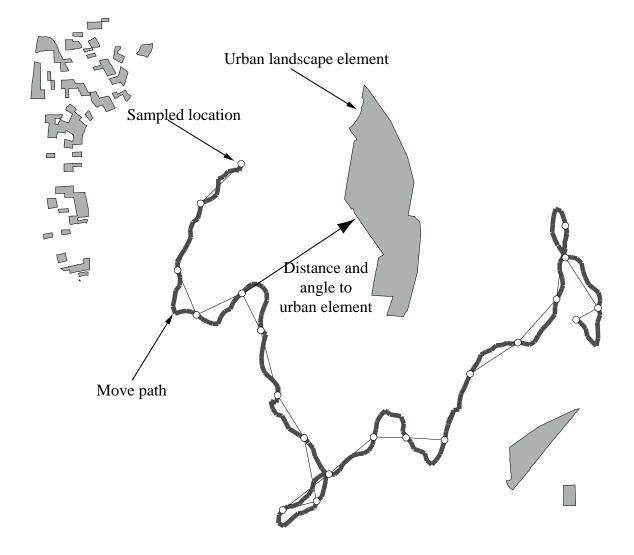


Figure 3: Using radio or GPS telemetry data and geographic information system layers we can quantify animal movement in relation to landscape features (or objects). This example was produced by simulation.

2.5 Final Models Selected for Mountain Lion Movement Simulation

After computing distances and angles to the nearest patch boundaries and the type of the nearest boundary, we observed no encounters with the U-D or D-U boundaries, so to construct models at the urban-disturbed interface we had to make educated guesses based on responses to other boundary types. For the D-H and U-H boundaries all observed distances to the boundaries were less than 400 meters and the number of observations for these boundary types were relatively small, only permitting parameterization and selection for simple response models). For the H-U and H-D boundary types, however, all 30 alternative models were tested.

H-U Boundary For the habitat-urban boundary we had 95 and 161 observations (for M8 and M10, respectively); therefore, we were able to test all 30 alternative models. The model selected was one in which the animals moved according to a correlated random walk, and then at approximately ≤ 480 meters to the urban edge had an approximately 25 percent chance of moving parallel to the H-U boundary in either the left or right direction.

H-D Boundary For the habitat-disturbed boundary, we had 36 and 68 observations (for M8 and M10, respectively); therefore, we were able to again test all 30 alternative models. However, the model selected was a correlated random walk with no boundary response (but see the D-H Boundary below).

D-U Boundary We had no observations for the urban-disturbed boundary, so we assumed that the animal moved away from the urban edge if it was near this boundary type.

D-H Boundary We had few observations for response to the disturbed-habitat boundary (3 for M8 and 4 for M10), but the observations suggested a tendency to move directly toward the habitat, and therefore we fit parameters for this simple boundary response model.

U-H Boundary For the urban-habitat boundary we had 9 and 27 observations (for M8 and M10, respectively). Due to the lower number of observations we examined only a subset of the simpler alternative models. We concluded that the animals moved parallel to the urban-habitat boundary in either the left or right direction. However, we also observed distances to this boundary greater than 185 meters, so if the animal was at a greater distance to the U-H boundary, we assumed it would have a strong tendency to move out of urban areas directly toward the habitat.

U-D Boundary We had no observations for the disturbed-urban boundary, so we assumed that the animal moved toward the disturbed edge if it was in urban areas near this boundary type.

Water Response If an animal moved into water, we assumed it moved with strong bias toward the nearest land.

In summary, the models indicated that these animals generally moved according to a correlated random walk when it was in habitat, and that they tended to move away from the urban edge. When it was in habitat near the urban edge, it tended to move parallel to it, probably in an attempt to circumvent an urban area. They did not seem to avoid the habitat-disturbed boundary, but if they entered a disturbed area they tended to move back toward the habitat. Parameters were estimated and models were selected for two mountain lions, but since the results were very similar, we only used one set of models in the simulations.

2.5.1 Final Models Selected for Bobcat Movement Simulations

H-U Boundary For the habitat urban boundary we had 287 observations, so we tested all 30 models. The model selected was one in which the animal moved according to a correlated random walk when > approximately 420 meters from the urban boundary, and when it was closer than this distance it tended to have fairly weak tendency to move away from the urban edge.

H-D Boundary We had no observations for this case so we used the same directional parameters as we did for the mountain lion simulations.

D-U Boundary We had no observations for this case so we used the same directional parameters as we did for the mountain lion simulations.

D-H Boundary We had no observations for this case so we used the same directional parameters as we did for the mountain lion simulations.

U-H Boundary For this boundary type we had 13 observations, and selected a model for a strong tendency to move out of the urban area and back toward the habitat.

U-D Boundary We had no observations for this case so we used the same directional parameters as we did for the mountain lion simulations.

Water Response If an animal moved into water, we assumed it moved with strong bias toward the nearest land.

For the bobcat we used in the analysis, there was apparently less avoidance of urban areas than we observed for the mountain lions used in the analysis.

2.6 Individual-Based Movement Models

The structure of the individual-based movement model is illustrated in Figure 4. It has six main parts: (a) a *main* function that can be thought of as the final executable program, (b) a *landscape component*, (c) an *animal component*, (d) a *simulation control component*, and (e) *GIS data files*.

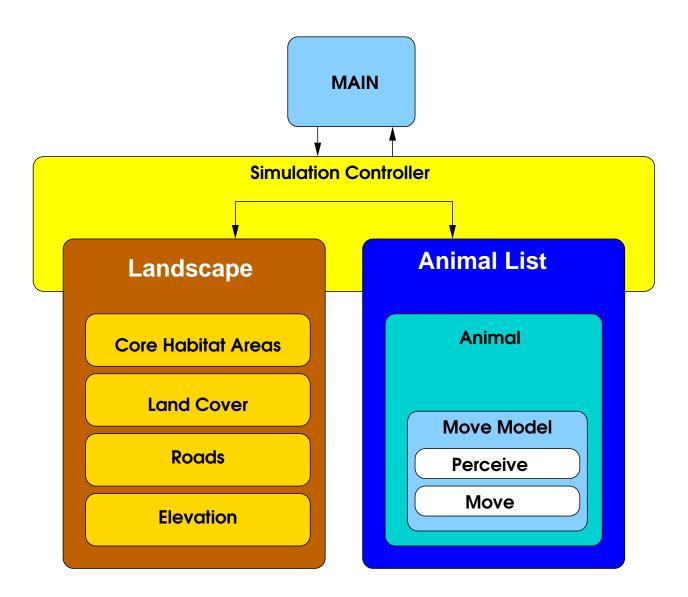


Figure 4: Basic organization of the individual-based movement model. The landscape component, by far the most complex part of the simulation, reads data from GIS layers into spatial data structures that can be rapidly queried. The animal component contains the movement rules and interacts with the landscape component through the simulation controller. The simulation controller also controls the numbers of paths and number of moves per path in each simulation, as well as writing output files.

The landscape component of the IBMM is responsible for reading, writing, organizing, and performing queries on landscape data. These data are read from and written to GIS data files. It has the potential to use both vector-based data for core areas, land cover, roads, and bridges, and grid-based data for elevation. For vector-based data (points, lines, polygons) these data are in the form of ESRI ArcView shapefiles, with the dBase file exported as a tabdelimited text file. For raster data, these data are in the form of binary raster files (a header and a raster file) exported from ESRI Spatial Analyst. The animal component of the IBMM consists of a list of programming constructs (*objects*) representing the history, current state, and behavior of each individual in the simulation. Each animal has its own movement model with its own parameters. Particular to each movement model is (a) a function to *perceive* the landscape using landscape query functions, and (b) a function to *move* according to the individual's particular movement model, movement model parameters, and the landscape data collected by the perceive function. Interactions between individuals and the landscape are coordinated by the simulation control component. The simulation control component also controls the number of realizations of the simulation to be run, the number of maximum movements for each realization, and when output files are written.

2.7 Core Habitats

In the simulations, the core area layers serve two purposes. First, all simulated animals start out in a core area. Second, if an animal reaches a core area other than the one it begins in, it is considered a "successful" disperser. The core area layers *do not* play a role in how the animal moves across the landscape. For the sake of consistent comparison among the alternative landscapes, we felt that it was important to use the same layer of core areas in all simulations.

A core habitat layer for mountain lions was constructed from protected lands and mountain lion wildlife habitat relation data layers. Protected lands layers were obtained from CASIL (California Spatial Information Library; gis.ca.gov), an updated layer for San Diego County provided by Christen Powell-Essinger (formerly with TNC), and a layer of TNC lands. We assumed all government land was adequately protected, although this is probably overly inclusive. Modified layers for mountain lion wildlife habitat relations were obtained from Rich Hunter (Talon Associates). We used categories 1 and 2 corresponding to > 50 % medium or high suitability as suitable core habitat (Hunter et al. 2003). The protected lands and suitable habitat layers were intersected to produce a layer of potential mountain lion core areas. From these, we selected polygons larger than 90 km². An area of 300 km² is more biologically realistic minimum to support a single mountain lion (*not* a minimum viable population) based on mountain lion home range estimates, but we lowered this value so that particular areas of interest were included as core areas (such as Otay Mountain and the Santa Monica Mountains). The result was a layer of 12 core habitat polygons (Figure 5; Table 1).

Table of core areas:

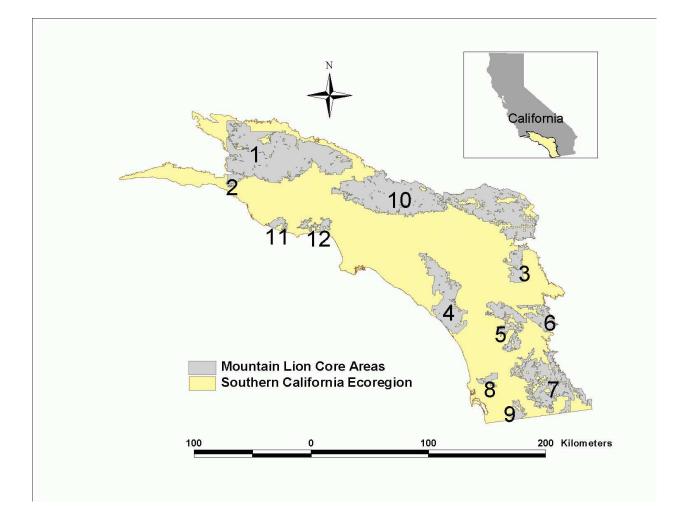


Figure 5: Mountain lion core areas used in the simulations.

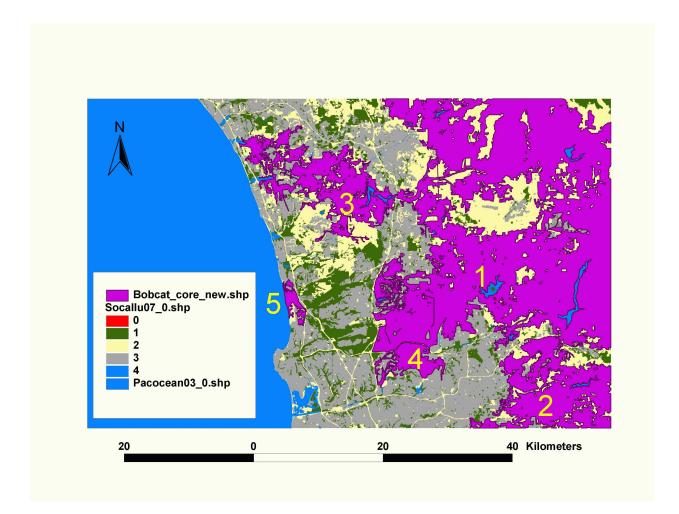


Figure 6: Bobcat core areas in the vicinity of Los Peñasquitos Canyon, Mission Trails Regional Park, and Torrey Pines State Park used in the simulations. The purple areas are the selected core areas (large non-linear undeveloped areas) and are numbered 1-5 for reference. In the underlying land cover layer, habitat is in green, disturbed areas are in yellow, urban areas are in gray, and water is in blue.

Number	Name	Area (km^2)	Perimeter (km)
1	Los Padres NF 1	3223	1115
2	Los Padres NF 2	104	102
3	San Bernadino NF	307	213
4	Santa Ana Mountains	1049	508
5	Palomar Mountains	514	583
6	Los Coyotes	305	301
7	Cleveland NF	1330	1343
8	Miramar	94	98
9	Otay Mountain	117	122
10	Angeles NF	3782	1791
11	Santa Monica Mountains 1	93	116
12	Santa Monica Mountains 2	141	273

Table 1: Mountain lion core habitat areas used in the simulations.

2.8 GIS Landscapes

We simulate movement on Geographic Information Systems (GIS) landscape models. In this application of the model we use layers for land cover. Road data is used in post-simulation analysis.

2.8.1 Existing Landscape

The existing landscape layer serves as a baseline for comparison (Figure 7). This layer was constructed from Southern California Association of Governments (SCAG) and San Diego Association of Governments (SanDAG) land use layers, which were created in approximately 1995; these layers were obtained from Rich Hunter (Talon Associates). Land cover in the existing landscape layer (and all other alternative landscape layers) was categorized into four types: habitat, disturbed, urban, and water using land cover codes (listed in parentheses below) contained in the GIS layer attribute tables. So-called "vacant" areas and undeveloped (or passive) local and regional parks, and open space preserves were classified as habitat land cover (SCAG 1272, 1822, 1832, 1900, 3100, and 3300; SanDAG 7602, 7603, and 9100). Housing, commercial, industrial, developed military, and other such areas were classified as urban land cover (SCAG 1110, 1120, 1130, 1140, 1210, 1220, 1230, 1240, 1250, 1260, 1271. 1273. 1300, 1411, 1412, 1414, 1415, 1416, 1417, 1418, 1420, 1430, 1440, 1450, 1460, 1500,1600, and 1700; SanDAG 1100, 1200, 1300, 1400, 1500, 2000, 100, 2200, 2300, 4100, 4111, 4113, 4114, 4115, 4116, 4117, 4118, 4119, 4120, 5000, 6000, 6100, 6500, 6700, 6800, 7202, 7205, 7206, 7207, 7607, and 9500). Water consists of lakes and reservoirs (SCAG 4000; SanDAG 9200). All other land use types were classified as disturbed land cover, and include such areas as roads, rural residential areas, local developed parks, and agricultural lands. Finally, we added a large polygon for the Pacific Ocean to ensure that the California coast is a reflective boundary.

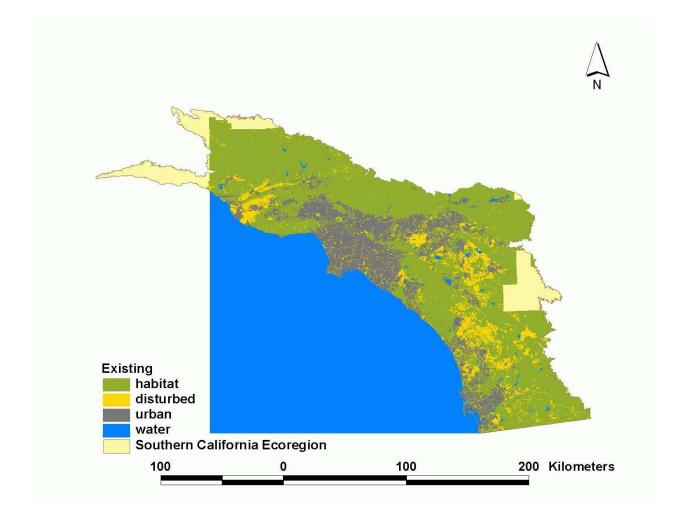


Figure 7: Existing land cover scenario used in the simulations. Green areas indicate habitat, yellow indicates disturbed, gray indicates urban, and blue indicates water. The tan background shows the boundary of the southern California ecoregion.

2.8.2 NCCP Landscape

The Natural Communities Conservation Planning (NCCP) landscape was constructed by replacing land cover in the existing landscape layer with land cover expected from available southern California NCCP reserve designs (obtained from Colleen Miller, California Department of Fish and Game; Figure 8). These NCCPs were the MSCP Multiple Habitat Planning Area/Preapproved Mitigation Area, the MHCP Focused Planning Area, MSCP North County Subarea Plan draft Preapproved Mitigation Area, and the Orange County Central/Coastal NCCP. For the MSCP Multiple Habitat Planning Area/Preapproved Mitigation Area, and the MHCP Focused Planning Area, we categorized the habitat within the plans based on the percent conserved (PC) attribute in the GIS layer attribute tables. Polygons with 0 < PC < 30 were assigned to the urban land cover type. Polygons with 30 < PC < 50 were assigned to the disturbed land cover type. Polygons with 50 < PC < 100100 were assigned to the habitat land cover type. For the Orange County Central/Coastal NCCP areas were assigned to land cover type based on the "designation" field in the GIS layer attribute table. All areas were considered habitat except those with a designation of "urban." In the MSCP North County Subarea Plan draft Preapproved Mitigation Area, no indication of percent conserved was given because this plan is in draft stages, so we assumed all areas within the preserve boundary are of the habitat land cover type. We added Miramar MCAS back into the landscape as habitat since it is included in the core habitat layer. Again, we added a large polygon for the Pacific Ocean to ensure that the California coast is a reflective boundary.

2.8.3 Worst-Case Landscape

The worst case landscape layer was constructed by regarding all government land as "protected" and assigning it to the habitat land cover type (Figure 9). Water land cover type polygons were obtained from the existing land cover layer, and all other areas within the southern California ecoregion were assumed to be completely converted to the urban land cover type. As with previous landscapes, we added a large polygon for the Pacific Ocean to ensure that the California coast is a reflective boundary.

2.8.4 Highway Layer

We used TIGER 2K line layers for State and US highways (obtained from CASIL; gis.ca.gov) to evaluate risks associated with movement among core areas (Figure 10).

2.9 Simulation of Individual Movement

In a single run of the simulation, an individual is started in a core area at a location selected from a uniform distribution within the core, and is allowed to move until it satisfies one of three stopping conditions. The first stopping condition is a limitation of 7200 moves. Since each move corresponds to a 15 minute time interval, this means each animal was allowed a total of 75 movement days. The second stopping condition is satisfied if a simulated animal moves off the edge of the boundary of the landscape region being modeled. Finally, if the simulated animal successfully reaches a core area other than the one in which it began, its

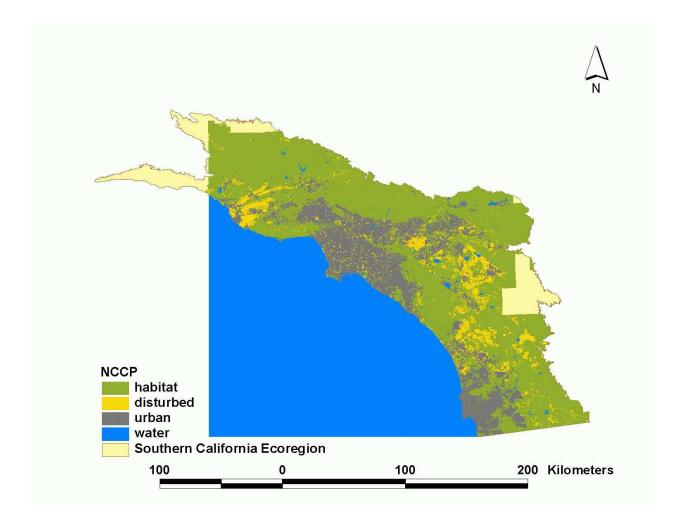


Figure 8: Natural Communities Conservation Planning (NCCP) land cover scenario used in the simulations. Green areas indicate habitat, yellow indicates disturbed, gray indicates urban, and blue indicates water. The tan background shows the boundary of the southern California ecoregion.

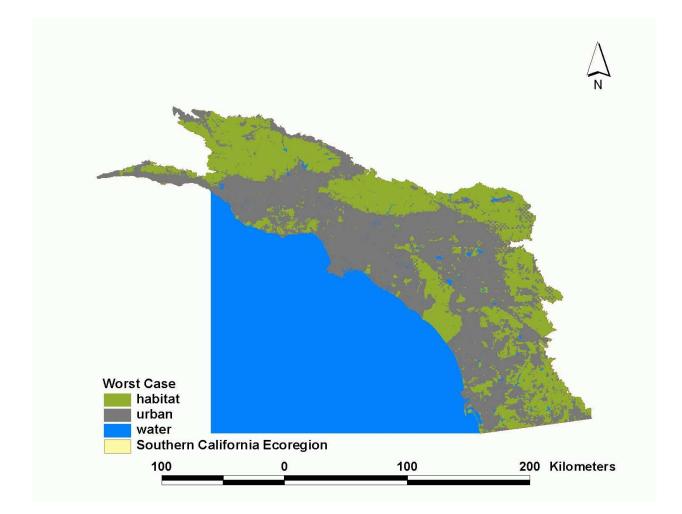


Figure 9: Worst-case land cover scenario used in the simulations. Green areas indicate habitat, yellow indicates disturbed, gray indicates urban, and blue indicates water. The tan background shows the boundary of the southern California ecoregion.

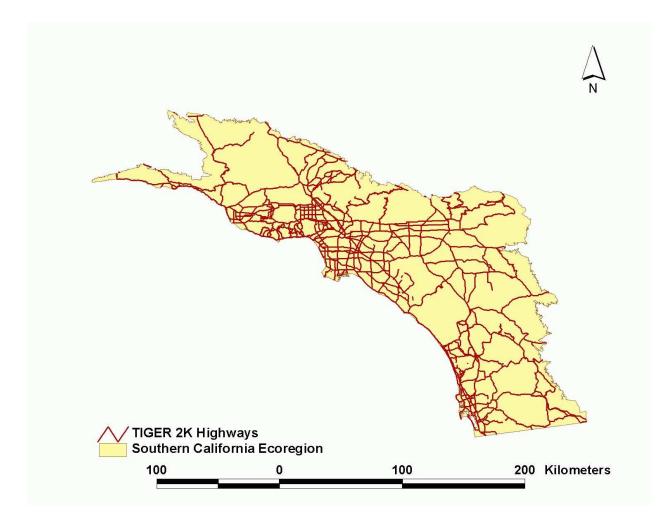


Figure 10: TIGER 2K Highways.

dispersal is considered successful and it makes no more moves. We call the sequence of moves from the starting location until the stopping condition is met a *path*.

For each landscape layer we started 250 simulated animals in each of the 12 core areas (for a total of 3000 simulated animals), and allowed each simulated animal to move through the land cover layer until it met one of three stopping conditions. During the course of the simulations, output is written to two types of files. In the move summary files, a record is written for each move. Each record has fields SIM (simulation ID number), CORE (starting core number), PATH (path ID number), MOVE (move number), X (x-coordinate), Y (ycoordinate), TYPE1 (land cover type occupied when the move is made), TYPE2 (land cover type across the nearest boundary when the move is made), EDGEANG (angle in radians to the nearest point on the occupied land cover polygon boundary), EDGEDIST (distance in meters to the nearest point on the occupied land cover polygon boundary), INCORE (ID number of the core occupied at the time the move was made), MOVE_ANG, (angle of movement in radians) and MOVE_DIST (distance of movement in meters). During post-simulation processing fields SUCCESS (T/TRUE if dispersal was successful, F/FALSE otherwise), ENDCORE (the core the animal was in at its last location), DPATHLEN (length of the path in meters since last leaving the starting core), SPATHLEN (the standardized path "length", which is actually a dimensionless quantity, calculated as DPATHLEN/DMINLEN), and PURBAN (the proportion of path locations in urban land cover polygons, calculated as UCOUNT/DISPMOVES). These fields were added to each move summary file record by matching corresponding values (or quantities derived from) from the path summary files by matching records in both files according to the SIM, CORE, and PATH fields (see Appendix A).

In the *path summary* files, a record is written for each move path. Each record contains fields SIM (simulation ID number), CORE (starting core number), PATH (path ID number), TOTALMOVES (number of moves made in the path), TPATHLEN (total length of the path in meters), DISPMOVES (number of moves made since last leaving the starting core), DPATHLEN (length of the path in meters since last leaving the starting core), DMINLEN (straight-line distance between location when the starting core was left until the new core was reached; this is only relevant for successful dispersal paths), HCOUNT (number of locations in habitat land cover since last leaving the starting core), DCOUNT (number of locations in disturbed land cover since last leaving the starting core), UCOUNT (number of locations in urban land cover since last leaving the starting core), SUCCESS (T/TRUE if dispersal was successful, F/FALSE otherwise), and ENDCORE(the core the animal was in at its last location). See Appendix B for details. These results are the basis for the connectivity evaluation.

2.10 Connectivity Evaluation

2.10.1 Quantifying Connectivity

We quantified connectivity in terms of success, risk and cost.

Success If an simulated animal reached a core other than the one from which it began, it was considered a *successful* disperser (such paths and moves can be identified from the

SUCCESS field in the output). Otherwise, it was considered unsuccessful. Unsuccessful paths occurred when (a) the simulated animal reached the maximum number of moves (identified if the value in the TOTALMOVES field is 7200), or if the animal moved off the edge of the land cover layer (SUCCESS is F/FALSE and TOTALMOVES < 7200). The successful paths were used to quantify risk and cost, as well as to visualize connectivity.

Cost We quantified energetic cost of dispersal in terms of the total length of the dispersal path (DPATHLEN). As this cost increases, the chances that an animal would survive the journey decreases. This path length can be standardized by the straight-line distance from the exit point of the starting core to the entry point of the ending core:

Standardized path length =
$$\frac{DPATHLEN}{DMINLEN}$$
,

which is the ratio of the dispersal path length and the straight-line path length, and an indication of how straight the dispersal path was. If the normalized path length is 1, then the animal moved in a perfectly straight line from the starting core to the final core (a highly unlikely event).

Risk Risk due to anthropogenic sources of mortality were quantified in terms of (a) the proportion of simulated locations in a path that were in urban land cover, and (b) the proportion of locations of all successful paths between a given pair of core areas what were within 150 meters of a highway (in the TIGER highway layer). As these proportions increase, mortality due to anthropogenic sources can be expected to increase.

Overall score and rank We constructed a composite score for connectivity that combines the success, risk, and cost quantities:

$$score = success \times (1 - risk_{urban}) \times (1 - risk_{road}) \times exp(-0.00001 \times cost).$$
(1)

This equation is the result of three assumptions: (1) that probability of surviving dispersal is linearly related to the number of locations not in urban landscape elements, (2) that probability of surviving dispersal is linearly related to the number of locations that are away from roads, and that (3) the probability of survival due to energy constraints is related to the path length in a negative-exponential fashion. The cost is scaled by a small number so that the resulting score is not small and easier to understand in a table. Since we are using the score as an indicator to rank linkages, we are not concerned with any constants in the equation. The overall connectivity score increases as connectivity increases; that is, as success increases, risk decreases, or cost decreases. If success is 0, we define the score to be 0 as well. Using this score, we rank corridors within or among landscape scenarios.

2.10.2 Visualizing Connectivity

For the entire ecoregion, we plotted the simulated animal locations for successful paths against the ecoregion and core area layers to illustrate where successful dispersers moved in the landscape. We illustrated the quantities described above using a connectivity graph. In a connectivity graph, core areas (called nodes) are illustrated as filled circles with an ID number indicating the core to which it corresponds. Arrows (called edges) indicate the directions between each pair of core areas for which successful dispersal occurred. The width of the arrow indicates the number (of percent) of successful dispersers. Thin arrows indicate 1–2 successful paths (0 to 1 percent success), medium width arrows indicate 3–24 successful paths (1 to 10 percent success), and thick arrows indicate ≥ 25 successful paths (over 10 percent success).

For particular pairs of core areas, we provide examples of plots of movement paths between the core areas. In these plots we focus on the lowest cost paths, unless the number of successes is few (less than 5), in which case we show all of the paths. In section 3.6.3 we provide a step-by-step example of how we created these plots. Such visualizations can be useful for identifying potential routes that are important to maintaining connectivity.

We also provide plots of locations within 2000 meters of the boundary of the southern California ecoregion, along with 3000 meter buffers around the points, which may be useful for identifying areas that are important for maintaining connectivity with adjacent ecoregions. Locations within 150 meters of highways, along with 150 meter buffers, are also plotted to indicate locations were encounters with highways may be frequent. Likewise, we plot locations that fall within urban areas to indicate locations were encounters the urban matrix may be frequent.

2.10.3 Comparing Connectivity Within and Between Landscapes

Landscapes can be compared qualitatively from the visual output, and quantitatively using the success, risk, and cost quantities. We provide quantitative comparisons in the form of tables showing the difference or percent change in the success, risk, and cost quantities. Other comparisons are discussed in section 3.

3 Results and Interpretation

For the discussion below we define a *linkage* in conceptual terms as a connection between a pair of core areas in one direction, and use the term *behavioral corridor* to identify a route of animal movement between a pair of core areas. We therefore distinguish a behavioral corridor from a traditional corridor, which is usually defined as a narrow landscape element that is dissimilar from the adjacent matrix and serves to connect a pair of core areas. Traditional corridors are usually defined in terms of land cover polygons in a GIS layer; that is, they refer to landscape structure rather than the response of animals to the landscape.

3.1 Existing Landscape

The simulated locations that contributed to successful dispersal between core areas on the existing landscape are shown in Figure 11. Of the 132 possible linkages ((number of cores)² – number of cores), 35 were realized in the simulations on the existing landscape. Of these, 9 of the linkages had ≤ 2 successful paths, 17 had from 3 to 24 successful paths, and 9 of the linkages had ≥ 25 successful paths. The exact number of successes are shown in Table

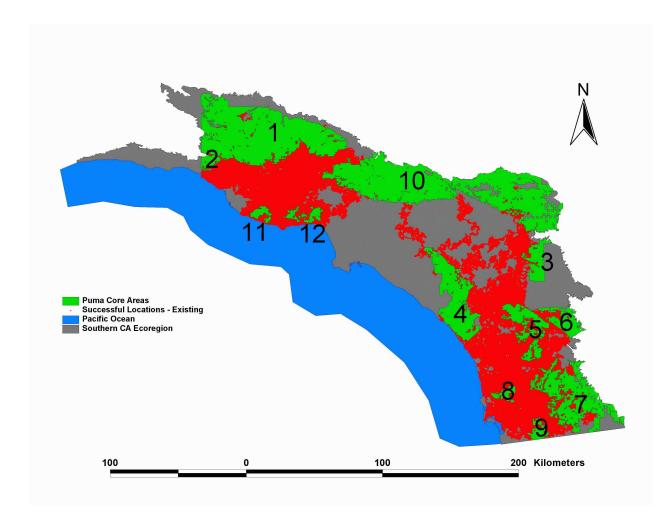


Figure 11: Simulated mountain lion locations for successful dispersal paths in the existing landscape scenario. The core areas are shown in green, the pacific ocean in blue, the southern California ecoregion in gray, and the simulated animal locations in red.

2 and are illustrated as a mathematical graph in Figure 14. In Table 3, we provide results of success, cost, and risk for each successful linkage. We also rank the linkages according to their "score" calculated using equation (1).

3.2 NCCP Landscape

The simulated locations that contributed to successful dispersal between core areas in the NCCP landscape is shown in Figure 12. Of the 132 possible linkages, 33 were realized in the simulations on the NCCP landscape. Of these, 6 of the linkages had ≤ 2 successful paths, 19 had from 3 to 24 successful paths, and 8 of the linkages had ≥ 25 successful paths. The exact number of successes are shown in Table 4 and illustrated as a mathematical graph in Figure 14. In Table 5, we provide results of success, cost, and risk for each successful linkage. We also rank the linkages according to their "score" calculated using equation (1).

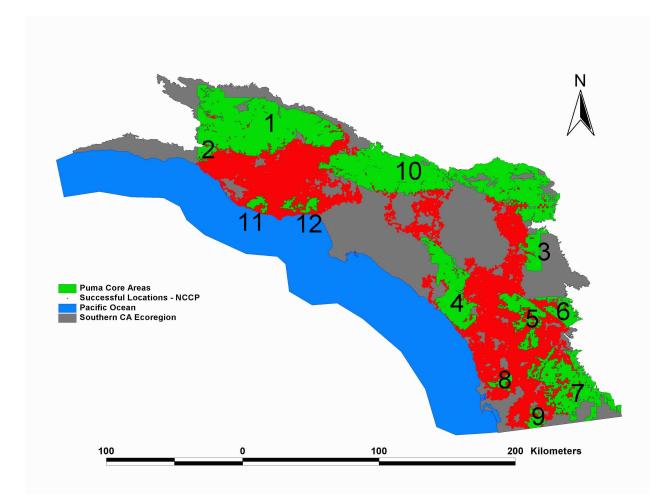


Figure 12: Simulated mountain lion locations for successful dispersal paths in he NCCP landscape scenario. The core areas are shown in green, the pacific ocean in blue, the southern California ecoregion in gray, and the simulated animal locations in red.

Table 2: Results for dispersal success in existing landscape. Dispersal success quantifies the ability of dispersers to find their way from one core area to another. The first column (*start core*) indicates the core area from which the simulated disperser began by the core ID number. There were a total of 250 simulated dispersal paths for each core. The column *left region* is the number of paths that went out-of-bounds. The *failed* column indicates the number of paths leaving the start core that reached the maximum number of moves (7200). The *success out* column gives the number of successful paths leaving the start core. This is an indicator of dispersal success for dispersers *leaving* the core. The remaining columns break down the number of successful paths leaving the start core by core reached (indicated by core ID number). The *success in* column sums indicate the number of successful paths *coming into* the core indicated by the core ID number in the column header.

start	left	failed	success	number of successes by core reached											
core	region		out	1	2	3	4	5	6	7	8	9	10	11	12
1	153	59	38	-	20	0	0	0	0	0	0	0	15	1	2
2	161	3	86	86	-	0	0	0	0	0	0	0	0	0	0
3	230	14	6	0	0	-	1	0	0	0	0	0	5	0	0
4	56	177	17	0	0	1	-	13	0	0	1	0	2	0	0
5	97	56	97	0	0	4	13	-	56	21	3	0	0	0	0
6	215	0	35	0	0	0	0	35	-	0	0	0	0	0	0
7	181	23	46	0	0	0	0	13	0	-	7	26	0	0	0
8	17	134	99	0	0	0	2	7	0	69	-	21	0	0	0
9	179	6	65	0	0	0	0	0	0	58	7	-	0	0	0
10	181	55	14	12	0	2	0	0	0	0	0	0	-	0	0
11	1	111	138	31	2	0	0	0	0	0	0	0	3	-	102
12	0	154	96	11	0	0	0	0	0	0	0	0	7	78	-
	succes	s in \rightarrow	737	140	22	7	16	68	56	148	18	47	32	79	104

3.3 Worst-Case Landscape

The simulated locations that contributed to successful dispersal between core areas on the worst-case landscape is shown in Figure 13. Of the 132 possible linkages, 33 were realized in the simulations on the worst-case landscape. Of these, 6 of the linkages had ≤ 2 successful paths, 19 had from 3 to 24 successful paths, and 8 of the linkages had ≥ 25 successful paths. The exact number of successes are shown in Table 6 and illustrated as a mathematical graph in Figure 14. In Table 7, we provide results of success, cost, and risk for each successful linkage. We also rank the linkages according to their "score" calculated using equation (1).

Clearly, we do not expect this scenario to actually occur. This landscape represents an ecological disaster and a complete break-down in landscape connectivity. However, it sets a lower bound on what we expect to occur.

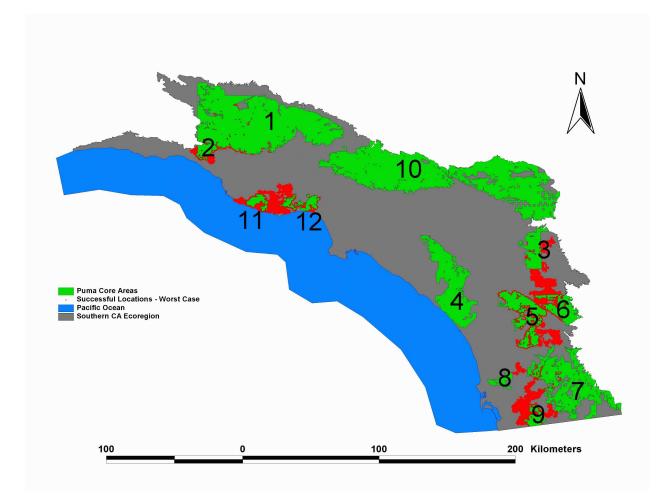


Figure 13: Simulated mountain lion locations for successful dispersal paths in the worst-case landscape scenario. The core areas are shown in green, the pacific ocean in blue, the southern California ecoregion in gray, and the simulated animal locations in red.

3.4 Bobcat Simulations

The bobcat simulations are more limited in scope than the mountain lion simulations. Simulated locations that contributed to successful dispersal between core areas on the existing landscape in coastal central San Diego County are shown in Figure 15. Of the 20 possible linkages, 14 were realized in the simulations on the existing landscape. Of these, 2 of the linkages had ≤ 2 successful paths, 5 had from 3 to 24 successful paths, and 7 of the linkages had ≥ 25 successful paths. The exact number of successes are shown in Table 8. In Table 9, we provide results of success, cost, and risk for each successful linkage.

3.5 Comparison of Existing and NCCP Landscapes

In the GIS layers, most of the changes from the existing landscape to the NCCP landscape occurred in San Diego and Orange Counties, which are in the vicinity of puma core habitats 4 (Santa Ana Mountains), 5 (Palomar Mountains), 7 (Cleveland NF), 8 (Miramar), and 9 (Otay Mountain). Visually, the change in landscape connectivity can be compared by the contrast in Figures 11 and 12, and studying the connectivity graphs in Figure 14. Numerically, we have calculated the difference between the number of successes in the NCCP landscape minus number of successes in the existing landscape (Table 10).

When looking at Table 10, keep in mind that there are two factors that can lead to a difference in numbers of success between the landscapes: (1) landscape differences, and (2) random variation in the simulation results for the number of successes. Statistically, the probability of successful dispersal from one core to another is marginally distributed as a binomial random variable. With binomial random variables, the variance increases as the probability of success gets closer to 0.5. Therefore, since connections between cores 2 and 1, 11 and 12, 12, and 11, and 8 and 7 have a high probability of success, they will also have a higher variance in simulation predictions for numbers of successful dispersal. However, part of the difference is also due to changes in the landscape, which we can expect to occur in the connections between the core areas listed above. In the future we plan to work out statistical procedures for evaluating these effects.

In Table 10 and Figure 14, we can see that there is a decline in successes both into and out of cores 7 (Cleveland NF), 8 (Miramar), and 9 (Otay Mountain). As development continues around the city of San Diego, we will expect such a decline to occur, and this decline would likely be worse without the NCCP plans in place. The primary effects appear to be a decrease in the connectivity in both directions between core 9 (Otay Mountain) and cores 7 and 8 (Cleveland NF and Miramar, respectively).

Successes into and out of core 4 (Santa Ana Mountains) seems to be little affected by the landscape change from the existing landscape to the NCCP. However, two cautions should be observed. First, some areas leading out of the Santa Ana Mountains in the vicinity of the Pechanga Corridor that were disturbed in the existing landscape were classified as habitat in the NCCP landscape. While this was the result of a clear consideration for movement corridors from the Santa Anas to Palomar Mountain, in the absence of a major ecological restoration project this change will not be realized on the ground. Second, because the persistence of the Santa Ana puma population will rely heavily on immigration from the outside (Beier 1993), and our models predict that the major supplier of immigrants will be from the Palomar Mountains (core 5), this linkage should be protected if we want to sustain the puma population in the Santa Ana Mountains.

Connectivity among other cores cannot be evaluated at this time because the GIS layers for NCCP plans provided to not include areas in the northern and eastern portion of the ecoregion.

3.6 Recommendations for Improving Connectivity

3.6.1 Develop a Strategy for Preserving Connectivity

In order to make good use of the model output, we must have a strategy for preserving connectivity. Below we suggest a connectivity strategy and then use the model output to provide guidance for improving and conserving connectivity. The strategy is outlined as a list of goals, and is illustrated in Figure 16.

Goal 1: Conserve connectivity among large core areas If we are to ensure that mountain lions have a continued presence in coastal southern California, then it will be essential to maintain connectivity among the larger core areas in the eastern parts of the southern California ecoregion. Primarily, this requires connectivity conservation from Los Padres NF 1 (core 1) to Angeles NF (core 10), from Angeles NF to San Bernadino NF (core 3), from San Bernadino NF to Palomar Mountains (core 5), from Palomar Mountains to Cleveland National Forest (core 7). Of course, this includes connectivity in both directions.

Goal 2: Connectivity throughout California By maintaining connectivity between large core areas in the southern California ecoregion and large core regions in adjacent ecoregions, we can help conserve connectivity at larger spatial scales. Important benefits of this connectivity is demographic and genetic exchange among mountain lion populations in neighboring ecoregions, and preserving opportunities for range shifts for mountain lions and other species in the face of regional or global climate change. Connectivity to the north should be maintained from the Los Padres NF 1 and 2 (cores 1 and 2). Connectivity to the south should be maintained through the Cleveland NF (core 7) and Otay Mountain (core 9). Additional connectivity to the east should be considered, perhaps through Angeles NF (core 10) and Los Coyotes (core 6). Clearly, achieving this goal is largely dependent upon successfully conserving connectivity among large core areas.

Goal 3: Connectivity for important coastal core areas Several coastal core areas, most notably the Santa Ana Mountains (core 4) and the Santa Monica Mountains (core 11 and 12), can still support mountain lions. However, for these populations to persist, connectivity from larger eastern cores *into* the coastal cores must be maintained. On the other hand, these core probably will make little contribution to the long term viability of the larger core areas (but see Goal 5), so successful dispersal from these areas to the larger easter cores is less essential.

Goal 4: Connectivity for nearby small cores By linking small nearby core areas to other core areas (large or small) we can increase the effective area of both core areas. Some

smaller cores, such as the two protected regions of the Santa Monica Mountains (core 11 and 12), will require strong connectivity with each other in order to form a single larger viable core area. Other small core areas, such as Los Padres NF2 (core 2) and Los Padres NF1 (core 1) or the Chino Hills and the Santa Ana Mountains (core 4). The Chino Hills were not included as a core in our analysis, but could be considered a small core that can add to the total area of the larger Santa Ana Mountains if strong connectivity between them is maintained (Beier 1993). Other small areas, such as San Bernadino NF (core 3) and Otay Mountain (core 9) are important strategically because they make major contributions to achieving Goal 1 and Goal 2.

Goal 5: Create redundant connections where possible In some cases, core areas are too small to support a single individual for a long period of time, but they may be useful for maintaining redundancy in linkages among more important core areas. The coastal core areas such as Santa Ana Mountains (core 4), Santa Monica Mountains 1 and 2 (cores 11 and 12), Mira Mar (core 8), and Otay Mountain (core 9) can play a role in maintaining alternate, albeit less viable, connections among the large cores.

It is clear than a single core area can contribute to achieving more than one goal.

Other Considerations In some cases, we may want to reduce connectivity to a core area that cannot support a single individual for some part of its life history and if movement to that area decreases the likelihood that the animal will find a suitable stable home range. One prediction of the model is the if landscape structure diverts movement in one direction, connectivity in other directions may increase. On the other hand, if connectivity in one direction is decreased due to increased risk or cost (which translates into higher dispersal mortality), then connectivity in the other directions may not be increased.

3.6.2 Identify Critical Linkages

The connectivity conservation strategy outlined above and the results of the simulations on the existing and NCCP landscapes can be used to identify linkages that deserve consideration in future conservation planning. In Table 11, we list linkages in the strategy, identify the role they play, and give their rankings. Goal 2 of the strategy is omitted from the table because it related to connections to areas outside of the southern California ecoregion, which have not been directly evaluated in this project. This Table is further summarized in Table 12, which provides a general overview.

With respect to Goal 1, which is to preserve connectivity among large core areas, linkages among the larger core areas have the second highest ranks, according to Table 12. The most vulnerable linkages, from a strategic perspective, are between core 3 (San Bernadino NF) and core 10 (Angeles NF) because these connections are predicted to be fairly weak. If severed, then the only way to maintain connectivity for pumas between the northern and southern parts of the ecoregion is via movement through desert areas to the east. Connections between core 1 (Los Padres NF 1) and core 10 (Angeles NF) are not predicted to be as weak, but are no less critical. In the southern areas, the connection between core 3 (San Bernadino NF) and core 6 (Los Coyotes) are probably not as weak as the simulation results imply because the land cover data that we had did not cover part of the ecoregion between these cores. There was no way to move between them without encountering the edge of the land cover layer, which satisfies one of the stopping conditions of a movement path in the simulations. This is an important point because the connection between core 3 (San Bernadino) and core 5 (Palomar Mountain) is predicted to be weak, and not present at all in the core 3-to-5 direction in both the existing and NCCP landscape simulations. Connections between core 5 (Palomar Mountains) and core 7 (Cleveland NF) are similar in predicted strength to the connection between cores 1 and 10 (described above), and are no less critical.

Using the simulation results, we cannot directly evaluate Goal 2, which is to maintain connections to adjacent ecoregions, since these regions were not included in the landscape. However, we can use the simulations to visualize where the simulated animals encountered the boundary of the landscape on which movement was simulated (Figure 17 and 18). These results serve as a guide for areas that may be important for maintaining connections to adjacent ecoregions.

With respect to Goal 3, which is to provide connectivity to important coastal areas, linkages among the core areas for this goal are predicted to be among the weakest. In particular, puma populations in the Santa Ana Mountains (core 4) and the Santa Monica Mountains (core 11 and 12) will rely on immigration from larger core areas to the east for their persistence. Smaller cores are at a disadvantage in terms of immigration because they present a smaller "target" for dispersers to find. Furthermore, these cores (and a few others) are in the most fragmented parts of the ecoregion. Given the importance of this goal, the tenuous connections that remain, and the threats these connections presently face, this goal will require the most immediate attention. Failure to preserve connectivity for coastal core areas will likely result in extirpation of puma from coastal southern California.

Goal 4 is to maintain connectivity for nearby small core areas. This core, according to Table 12, has the strongest connections.

Goal 5 is to maintain redundancy among connections. For the most part, this involves movement through coastal core areas (except for the connections among cores 3, 5, and 6), and therefore are also predicted to be very weak.

Although some of these goals (such as Goal 3 and 5) require immediate response, goals that appear to be more secure (such as Gaol 2 and 4) should not be neglected. They are likely to face increased threats in the future, and it will be easier to plan for how to deal with such threats now while we have more options for preserving connectivity related to these goals.

3.6.3 Visualizing Behavioral Corridors

Fine-Scale Visualization of Movement Through the Pechanga Corridor In this example, we show the step-by-step process we followed to visualize movement from the Palomar Mountains (core 5) to the Santa Ana Mountains (core 4). This example illustrates how one might use the data CDs included in this report to examine predicted movement routes through an area.

The steps we followed are:

1. In ArcView, select the locations for the linkage of interest in the simulated location file. The starting core is identified in the CORE field, and the ending core is identified in the ENDCORE field. Results for this example are shown in Figure 19.

- 2. For the linkage of interest, find the mean standardized path length (called standard length in Table 3 for the existing landscape) and select ("from set") the locations with standardized path length (given in the SPATHLEN) field less than or equal to the mean standardized path length. In this example, the mean standardized path length is 21.97. This will give the locations for the low cost successful paths. Cut-off values other than the mean standardized path length can be used if desired. Results for this example are shown in Figure 20. The results from the selection should be saved as a new shapefile.
- 3. Next, polylines from the selected low-cost paths should be created (e.g., using the Animal Movement Analysis ArcView extension, www.absc.usgs.gov/glba/gistools/an-imal_mvmt.htm). The resulting simulated movement paths for this example are shown in Figure 21.
- 4. Finally, buffer the movement paths to create polygons for behavioral corridors. We buffered the paths by 250 meters, which is approximately the estimated mean move distance over a 15 minute time interval of the mountain lions we used for our data analysis. As an optional step, since we may want to focus on habitat land cover that should be considered important for preserving connectivity (although some disturbed areas may also be important), we clipped the resulting movement path buffers by the habitat land cover polygons using the ArcView GeoProcessing Wizard. The final predicted behavioral corridors for this linkage are shown in Figure 22.

Table 3: Results for mean dispersal cost and risk in existing landscape. Cost is quantified by mean path length, which is related to the energetic cost of dispersal. The *standard length* is the ratio of the total dispersal path length to the straight-line path length and is therefore an indicator of the straightness of the dispersal path. Risk is quantified by (a) the proportion of locations in urban land cover, and (b) the proportion of locations within 150 m of a highway. The risk quantities are related to the probability of mortality due to anthropogenic causes. The score was calculated using equation 1, which were then ranked in the final column. Keep in mind that a low rank indicates stronger predicted connectivity.

initial	final	number of	mean path	standard	proportion	n of locations	score	rank
core	core	paths	length (m)	length	in urban	near hwy		
1	2	20	51515.41	5.49465	0.18078	0.03312	9.46404	5
1	10	15	240156.5	11.6095	0.22101	0.05755	0.99746	13
1	11	1	1053380	32.51514	0.08284	0.03566	0.00002	29
1	12	2	1241205	28.18395	0.13299	0.03839	0.00001	30
2	1	86	94746.07	7.13628	0.09916	0.04290	28.74920	2
3	4	1	1933090	39.34555	0.04868	0.04277	0.00000	35
3	10	5	463301.2	26.23427	0.08838	0.03441	0.04280	17
4	3	1	1179880	26.17918	0.07907	0.04782	0.00001	31
4	5	13	838119.77	26.39745	0.15603	0.05093	0.00239	22
4	8	1	602737	13.2015	0.43958	0.04926	0.00129	24
4	10	2	1294770	31.92204	0.43918	0.05129	0.00000	34
5	3	4	713046.75	21.96823	0.02464	0.02397	0.00305	19
5	4	13	552161.46	21.97292	0.09732	0.04220	0.04495	16
5	6	56	49912.71	5.19756	0.00387	0.03827	32.56770	1
5	7	21	157837.04	12.3187	0.05339	0.03100	3.97406	8
5	8	3	845281.67	24.93949	0.22854	0.04775	0.00047	27
6	5	35	32433.05	5.83882	0.00403	0.02681	24.52779	3
7	5	13	98404.56	10.0581	0.006	0.01775	4.474447	7
7	8	7	292331.11	18.78091	0.25206	0.02757	0.27368	14
7	9	26	128855.03	11.79326	0.04297	0.02356	6.69784	6
8	4	2	1259790	27.11646	0.33066	0.10537	0.00000	32
8	5	7	795374.86	30.98774	0.26428	0.07630	0.00167	23
8	7	69	319305.84	19.8006	0.2886	0.06874	1.87631	11
8	9	21	637899.24	23.74527	0.50388	0.09923	0.01592	18
9	7	58	132626.85	10.29857	0.07616	0.03410	13.73940	4
9	8	7	714650.57	27.22668	0.44885	0.08281	0.00279	20
10	1	12	178678.4	13.47678	0.12268	0.07127	1.63771	12
10	3	2	275856.5	20.3893	0.08992	0.03982	0.11077	15
11	1	31	986717.35	28.62671	0.14094	0.07999	0.00127	25
11	2	2	1039095	22.69417	0.09368	0.05544	0.00005	28
11	10	3	1355952	28.0972	0.24058	0.09910	0.00000	33
11	12	102	322301.94	21.8705	0.22914	0.11335	2.77709	9
12	1	11	953611	24.06464	0.2057	0.08323	0.00058	26
12	10	7	714155	23.01234	0.43308	0.13517	0.00272	21
12	11	78	288118.07	18.43477	0.28645	0.13864	2.68797	10
		,			•	,		

Table 4: Results for dispersal success in NCCP landscape. Dispersal success quantifies the ability of dispersers to find their way from one core area to another. The first column (*start core*) indicates the core area from which the simulated disperser began by the core ID number. There were a total of 250 simulated dispersal paths for each core. The column *left region* is the number of paths that went out-of-bounds. The *failed* column indicates the number of paths leaving the start core that reached the maximum number of moves (7200). The *success out* column gives the number of successful paths leaving the start core. This is an indicator of dispersal success for dispersers *leaving* the core. The remaining columns break down the number of successful paths leaving the start core by core reached (indicated by core ID number). The *success in* column sums indicate the number of successful paths *coming into* the core indicated by the core ID number.

init.	left	failed	success		n	uml	əer o	f suc	cesse	es by o	core	rea	ched		
core	region		out	1	2	3	4	5	6	7	8	9	10	11	12
1	151	64	35	-	19	0	0	0	0	0	0	0	14	1	1
2	164	6	80	80	-	0	0	0	0	0	0	0	0	0	0
3	234	12	4	0	0	-	0	0	0	0	0	0	4	0	0
4	64	171	15	0	0	1	-	13	0	0	0	0	1	0	0
5	87	65	98	0	0	3	12	-	51	29	3	0	0	0	0
6	208	0	42	0	0	0	0	42	-	0	0	0	0	0	0
7	174	44	32	0	0	0	0	20	0	-	5	7	0	0	0
8	0	172	78	0	0	0	3	20	0	55	-	0	0	0	0
9	195	10	45	0	0	0	0	0	0	45	0	-	0	0	0
10	149	84	17	10	0	3	3	0	0	0	0	0	-	0	1
11	0	137	113	22	5	0	0	0	0	0	0	0	1	-	85
12	1	141	108	10	0	0	0	0	0	0	0	0	7	91	-
success in \rightarrow		667	122	24	7	18	95	51	129	8	7	27	92	87	

Table 5: Results for mean dispersal cost and risk in NCCP landscape. Cost is quantified by mean path length, which is related to the energetic cost of dispersal. The *standard length* is the ratio of the total dispersal path length to the straight-line path length and is therefore an indicator of the straightness of the dispersal path. Risk is quantified by (a) the proportion of locations in urban land cover, and (b) the proportion of locations within 150 m of a highway. The risk quantities are related to the probability of mortality due to anthropogenic causes. The score was calculated using equation 1, which were then ranked in the final column. Keep in mind that a low rank indicates stronger predicted connectivity.

initial	final	number of	mean path	standard	proportion	n of locations	score	rank
core	core	paths	length (m)	length	in urban	near hwy		
1	2	19	173912.47	11.3411	0.07374	0.02728	3.00733	6
1	10	14	323286.15	18.16468	0.30402	0.08277	0.35253	13
1	11	1	684882	20.62096	0.20948	0.05479	0.00079	23
1	12	1	1244590	28.85598	0.13152	0.05117	0.00000	29
2	1	80	50318.14	5.61254	0.09943	0.04235	41.71435	1
3	10	4	484632	21.71998	0.08086	0.04276	0.02765	15
4	3	1	1286350	29.11157	0.06747	0.00917	0.00000	30
4	5	13	767478.31	26.82986	0.12821	0.05477	0.00497	19
4	10	1	1230640	29.67486	0.53749	0.08733	0.00000	32
5	3	3	809117.67	24.83835	0.09176	0.04682	0.00080	22
5	4	12	689569.92	26.92015	0.07717	0.04997	0.01065	17
5	6	51	65086.53	6.07796	0.00078	0.04239	25.45393	3
5	7	29	154298.97	12.18876	0.03257	0.03372	5.79440	4
5	8	3	543887	22.14785	0.33012	0.05590	0.00824	18
6	5	42	21420.05	4.61577	0.00613	0.02616	32.81257	2
7	5	20	128486.71	11.26502	0.07883	0.02704	4.95969	5
7	8	5	199245.8	16.41279	0.39511	0.02042	0.40399	12
7	9	7	281876.69	15.83297	0.40382	0.02422	0.24302	14
8	4	3	1359200	28.84634	0.3403	0.09149	0.00000	31
8	5	20	668110.8	25.15266	0.25749	0.06674	0.01738	16
8	7	55	300548.04	20.16194	0.33185	0.06405	1.70304	9
9	7	45	323378.4	19.24933	0.36991	0.04752	1.06428	10
10	1	10	210986.14	12.45845	0.17128	0.07936	0.92512	11
10	3	3	693483.33	28.56637	0.07425	0.03152	0.00262	20
10	4	3	1461173.33	38.63205	0.45188	0.06618	0.00000	33
10	12	1	867767	38.07933	0.56507	0.05978	0.00007	26
11	1	22	897797.59	24.4327	0.1651	0.08342	0.00212	21
11	2	5	1239573.6	27.45771	0.14392	0.06981	0.00002	28
11	10	1	714799	14.27885	0.19383	0.14097	0.00054	25
11	12	85	346423.55	22.39703	0.26969	0.11705	1.71539	8
12	1	10	939918.1	22.22724	0.19612	0.08842	0.00061	24
12	10	7	1065525.71	36.00131	0.51337	0.15317	0.00007	27
12	11	91	343557.77	21.4216	0.29076	0.13824	1.79130	7

Table 6: Results for dispersal success in worst-case landscape. Dispersal success quantifies the ability of dispersers to find their way from one core area to another. The first column (*start core*) indicates the core area from which the simulated disperser began by the core ID number. There were a total of 250 simulated dispersal paths for each core. The column *left region* is the number of paths that went out-of-bounds. The *failed* column indicates the number of paths leaving the start core that reached the maximum number of moves (7200). The *success out* column gives the number of successful paths leaving the start core. This is an indicator of dispersal success for dispersers *leaving* the core. The remaining columns break down the number of successful paths leaving the start core by core reached (indicated by core ID number). The *success in* column sums indicate the number of successful paths *coming into* the core indicated by the core ID number.

init.	left	failed	success		nı	ımb	er o	of sue	ccess	es by	CO	re r	eache	ьe	
core	region	lanoa	out	1	2	3	4	5	6	7	8	9	10	11	12
1	109	124	17	-	17	0	0	0	0	0	0	0	0	0	0
2	161	2	87	87	-	0	0	0	0	0	0	0	0	0	0
3	178	69	3	0	0	-	0	0	3	0	0	0	0	0	0
4	0	250	0	0	0	0	-	0	0	0	0	0	0	0	0
5	0	221	29	0	0	0	0	-	24	5	0	0	0	0	0
6	217	15	18	0	0	4	0	14	-	0	0	0	0	0	0
7	167	81	2	0	0	0	0	0	0	-	1	1	0	0	0
8	0	250	0	0	0	0	0	0	0	0	-	0	0	0	0
9	215	21	14	0	0	0	0	0	0	14	0	-	0	0	0
10	191	59	0	0	0	0	0	0	0	0	0	0	-	0	0
11	0	193	57	0	0	0	0	0	0	0	0	0	0	-	57
12	0	233	17	0	0	0	0	0	0	0	0	0	0	17	-
	succes	s in \rightarrow	244	87	17	4	0	14	27	19	1	1	0	17	57

Table 7: Results for mean dispersal cost and risk in worst-case landscape. Cost is quantified by mean path length, which is related to the energetic cost of dispersal. The *standard length* is the ratio of the total dispersal path length to the straight-line path length and is therefore an indicator of the straightness of the dispersal path. Risk is quantified by the proportion of locations in urban land cover. The risk quantity is related to the probability of mortality due to anthropogenic causes.

i	nitial	final	number of	mean path	standard	proportion
	core	core	paths	length(m)	length	in urban
	1	2	17	890.35	2.05145	0.0000
	2	1	87	725.38	2.0842	0.0000
	3	6	3	766678.33	34.07123	0.00088
	5	6	24	26067.4	6.21404	0.00092
	5	7	5	676773.6	47.94304	0.04755
	6	3	4	475725	21.41228	0.00873
	6	5	14	22571.67	4.12766	0.00562
	7	8	1	389706	34.09501	0.0000
	7	9	1	1600770	96.78233	0.00126
	9	7	14	446546.29	33.23321	0.0023
	11	12	57	291332.68	29.70936	0.02386
	12	11	17	241955.66	25.9586	0.04222

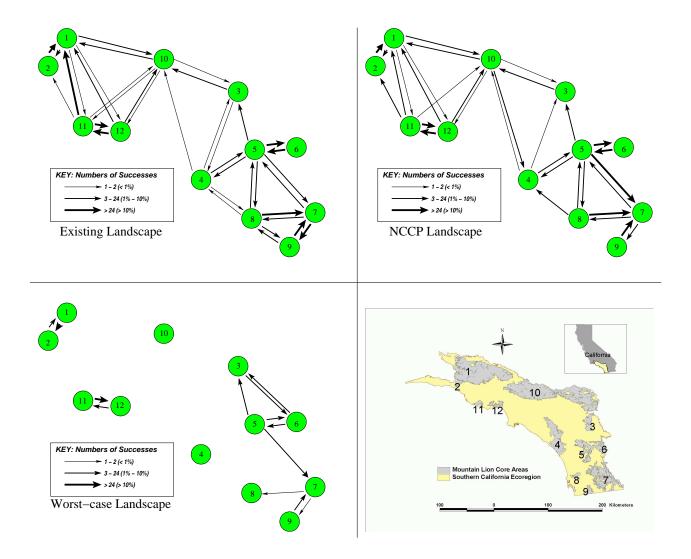


Figure 14: In Figures (a) - (c) above, the green circles (nodes) represent mountain lion core areas. The arrows (directed edges) indicate successful dispersal between each direct pair of core areas. Note, however, that the arrows represent a linkage, NOT a movement route. No arrow indicates that no successful dispersal occurred in the simulation. The width of the line/arrow indicates the number of successful paths. In order of increasing thickness: 0 < successful paths < 2 (0 % < successful paths < 1 %); $3 \leq \text{successful paths} \leq 24$ (1 % < successful paths < 10 %); and $25 \leq \text{successful paths}(10 \% \leq \text{successful paths})$. The top left figure corresponds to the existing landscape, the top right figure corresponds to the MCCP landscape, and bottom left figure corresponds to the worst-case landscape. The map of mountain lion core areas is included at the bottom right for reference.

Table 8: Results for bobcat dispersal success in the existing landscape in the vicinity of Los Peñasquitos Canyon, Torrey Pines State Park, and Mission Trails Regional Park. Dispersal success quantifies the ability of dispersers to find their way from one core area to another. The first column (*start core*) indicates the core area from which the simulated disperser began by the core ID number. There were a total of 250 simulated dispersal paths for each core. The column *left region* is the number of paths that went out-of-bounds. The *failed* column indicates the number of paths leaving the start core that reached the maximum number of moves (7200). The *success out* column gives the number of successful paths leaving the start core. The remaining columns break down the number of successful paths leaving the start core by core reached (indicated by core ID number). The *success in* column sums indicate the number of successful paths coming into the core indicated by the core ID number in the column header.

init.	left	failed	success	succe	esses	by core reached					
core	region		out	1	2	3	4	5			
1	159	17	74	0	22	13	35	4			
2	187	0	63	60	0	0	2	1			
3	81	33	136	105	0	0	0	31			
4	38	1	211	192	19	0	0	0			
5	14	25	211	137	0	64	10	0			
	succes	$\sin \rightarrow$	695	494	41	77	47	36			

Table 9: Results for mean dispersal cost and risk for bobcats in the existing landscape in coastal central San Diego County. Cost is quantified by mean path length, which is related to the energetic cost of dispersal. Risk is quantified by (a) the proportion of locations in urban land cover, and (b) the proportion of locations within 150 m of a highway. The risk quantities are related to the probability of mortality due to anthropogenic causes.

initial	final	number of	mean path	standard	proportion
core	core	paths	length (m)	$\cos t$	in urban
1	2	22	7005.54	3.06677	0.5059
1	3	13	43334.15	7.33015	0.47233
1	4	35	21280	5.92111	0.51816
1	5	4	185476	14.83217	0.41431
2	1	60	11259.17	5.09666	0.42687
2	4	2	214694	21.2663	0.79498
2	5	1	460305	13.92496	0.67063
3	1	105	74787.02	9.0584	0.38223
3	5	31	224618.92	19.68646	0.30936
4	1	192	17089.48	5.62878	0.57061
4	2	19	142742.01	14.65109	0.75513
5	1	137	246432.72	18.79511	0.38411
5	3	64	187013.69	17.40357	0.30857
5	4	10	353611.66	21.27139	0.5449

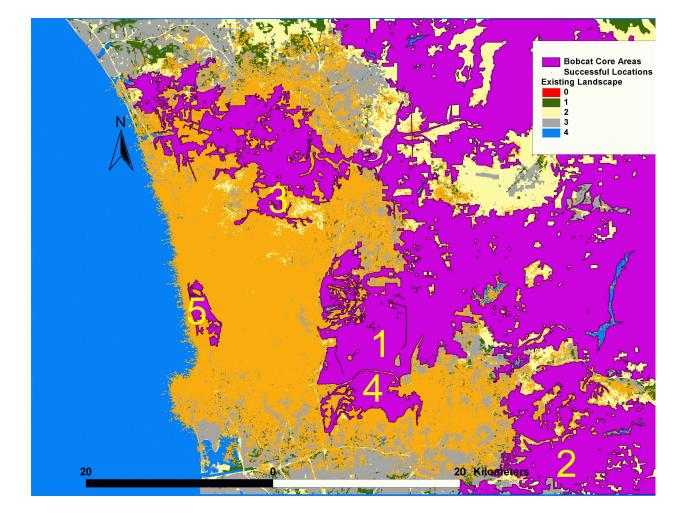


Figure 15: Simulated locations for successful bobcat dispersal. The core areas are in purple and the simulated locations are in orange.

Table 10: Difference in numbers of successful dispersals for NCCP landscape versus the existing landscape. This table was calculated by subtracting values in Table 2 from those in Table 4. Negative values indicate fewer successful dispersal paths in the NCCP landscape versus those in the Existing landscape, while positive values indicate more successful dispersal paths.

start	diff out		difference in success by core reached										
core		1	2	3	4	5	6	7	8	9	10	11	12
1	-3	-	-1	0	0	0	0	0	0	0	-1	0	-1
2	-6	-6	-	0	0	0	0	0	0	0	0	0	0
3	-2	0	0	-	-1	0	0	0	0	0	-1	0	0
4	-2	0	0	0	-	0	0	0	-1	0	-1	0	0
5	+1	0	0	-1	-1	-	-5	8	0	0	0	0	0
6	+7	0	0	0	0	7	-	0	0	0	0	0	0
7	-14	0	0	0	0	7	0	-	-2	-19	0	0	0
8	-21	0	0	0	1	13	0	-14	-	-21	0	0	0
9	-20	0	0	0	0	0	0	-13	-7	-	0	0	0
10	+3	-2	0	1	3	0	0	0	0	0	-	0	1
11	-25	-9	3	0	0	0	0	0	0	0	-2	-	-17
12	+12	-1	0	0	0	0	0	0	0	0	0	13	-
diff in \rightarrow	-70	-18	+2	0	+2	+27	-5	-19	-10	-40	-5	+13	-17

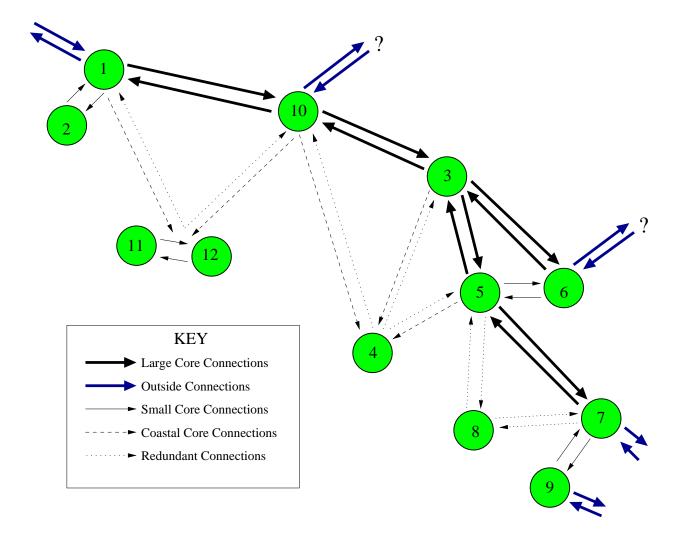


Figure 16: A graph representation of one possible strategy for preserving connectivity for mountain lions in the southern California ecoregion.

Table 11: Summary of connectivity strategy linkages and their rankings according to the simulation output. Each linkage is identified by the *from* and *to* columns. The primary connectivity conservation strategy goal to which the linkage related is indicated by an "X" in the appropriate *Strategy Goal* column. The ranks of each linkage are listed in the *existing* and *NCCP* columns for the existing and NCCP landscape, respectively. The *change* column gives the difference of the NCCP rank and the existing rank. A positive value for change indicates a reduction in connectivity. An "*" indicates a missing value due to no successes for that linkage.

Linka	age	Str	ateg	gy G	oal		Ranks	
from	to	1	3	4	5	Existing	NCCP	Change
1	2			Х		5	6	1
1	10	Х				13	13	0
1	11		Х			29	23	-6
1	12		Х			30	29	-1
2	1			Х		2	1	-1
3	4		Х			35	*	*
3	5	X				*	*	*
3	6	X				*	*	*
3	10	X				17	15	-2
4	3				Х	31	30	-1
4	5				Х	22	19	-3
4	10				Х	34	32	-2
5	3	X				19	22	+3
5	4		Х			16	17	+1
5	6			Х		1	3	+2
5	7	Х				8	4	-4
5	8				Х	27	18	-9
6	3	Х				*	*	*
6	5			Х		3	2	-1
7	5	Х				7	5	-2
7	8				Х	14	12	-2
7	9			Х		6	14	+8
8	5				Х	23	16	-7
8	7				Х	11	9	-2
9	7			Х		4	10	+6
10	1	Х				12	11	-1
10	3	X				15	20	+5
10	11		Х			*	*	*
10	12		Х			*	26	*
11	1				Х	25	21	-4
11	10				Х	28	25	-3
11	12			Х		9	8	-1
12	1				Х	26	24	-2
12	10				Х	21	27	+6
12	11			Х		10	7	-3

Table 12: Summary of connectivity ranks from Table 11 for each goal. This table provides a very general overview of the simulation results. For the existing landscape, NCCP landscape, and the change in ranks, the minimum (min) rank, maximum (max) rank, median (med) rank, and the range (the maximum minus the minimum ranges) are given. The median rank is a measure of central tendency, and a shift in this value under the *NCCP - Existing* column would indicate a general shift in the ranks of the linkages for this goal for the NCCP versus existing landscape. There was, however, little change in the medians of the ranks. The range is a measure of the variability in the ranks.

Goal		Exi	sting			NO	CCP		N	ICCP -	Exist	ing
	min	max	med	range	min	max	med	range	min	max	med	range
1	7	19	13	12	4	22	13	18	-4	+5	-1	+9
3	16	30	29	14	17	29	23	12	-6	+1	-1	+7
4	1	10	5	9	1	14	6	13	-3	+8	-1	+11
5	11	34	25	23	9	32	21	23	-9	+6	-2	+15

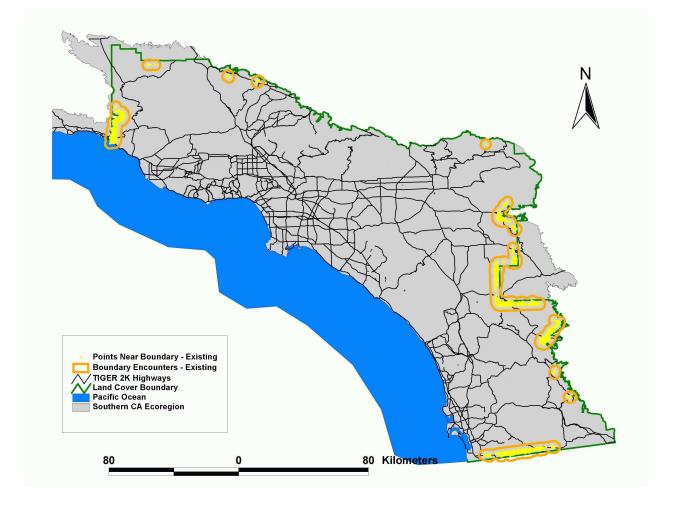


Figure 17: Encounters with boundaries of the southern California ecoregion for the existing landscape simulation. Simulated locations that were within 3 km of the landscape boundary are shown in yellow. These points were buffered by circles with a 3 km radius which are shown as orange polygons. The boundary of the landscape is shown as a green line. Highways (as black lines) are shown for reference.

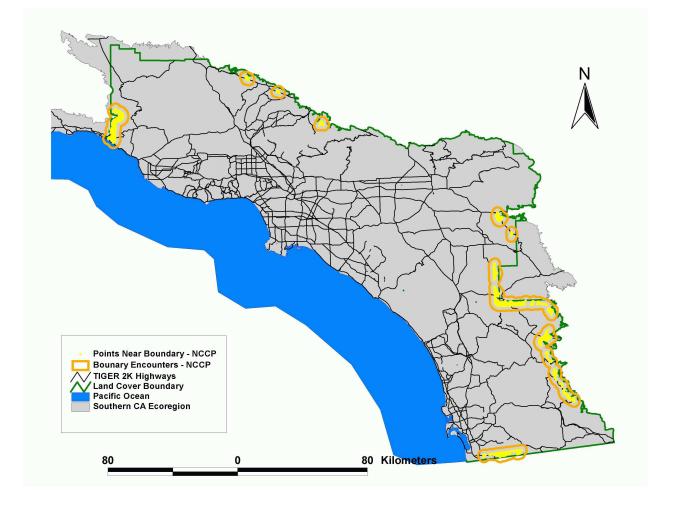


Figure 18: Encounters with boundaries of the southern California ecoregion for the NCCP landscape simulation. Simulated locations that were within 3 km of the landscape boundary are shown in yellow. These points were buffered by circles with a 3 km radius which are shown as orange polygons. The boundary of the landscape is shown as a green line. Highways (as black lines) are shown for reference.

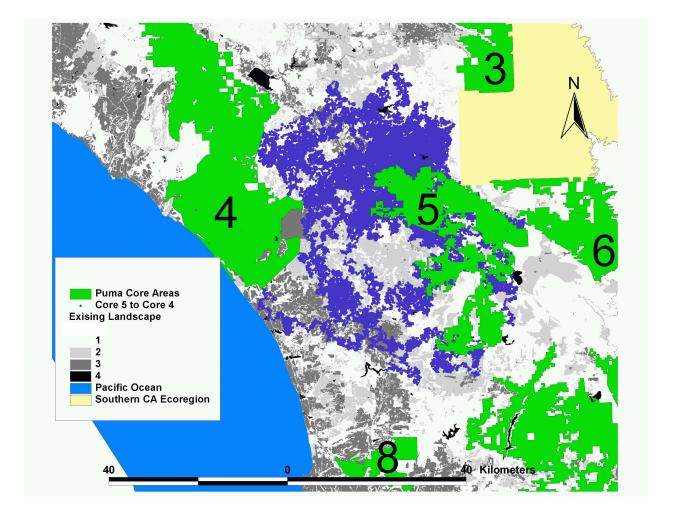


Figure 19: Simulated locations for successful dispersal paths from the Palomar Mountains (core 5) to the Santa Ana Mountains (core 4). The core areas are shown in green, and simulated locations for the successful dispersal paths from core 5 (Palomar Mountains) to core 4 (Santa Ana Mountains) are shown in dark blue.

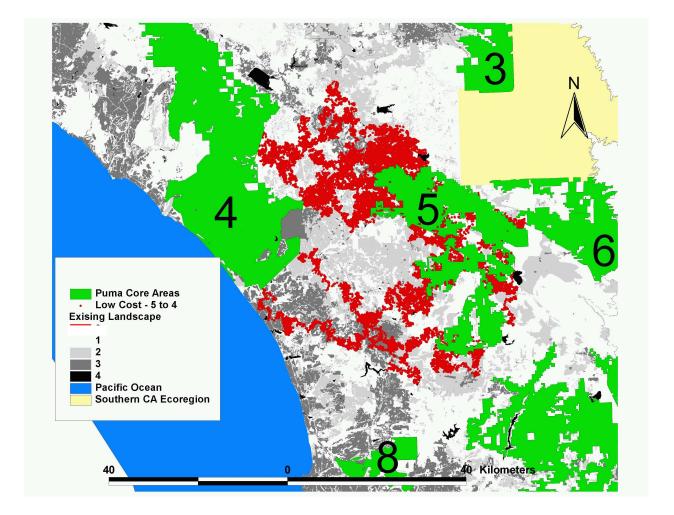


Figure 20: Simulated locations for lowest cost successful dispersal locations from the Palomar Mountains (core 5) to the Santa Ana Mountains (core 4). The core areas are shown in green, and simulated locations for the lowest-cost successful dispersal paths from core 5 (Palomar Mountains) to core 4 (Santa Ana Mountains) are shown in red.

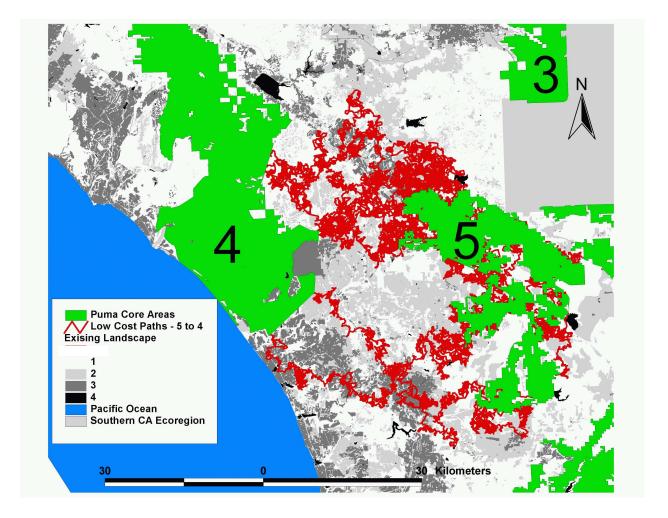


Figure 21: Simulated movements for lowest cost successful dispersal paths from the Palomar Mountains (core 5) to the Santa Ana Mountains (core 4). The core areas are shown in green, and simulated movement paths for the lowest-cost successful dispersal paths from core 5 to core 4 are shown in red.

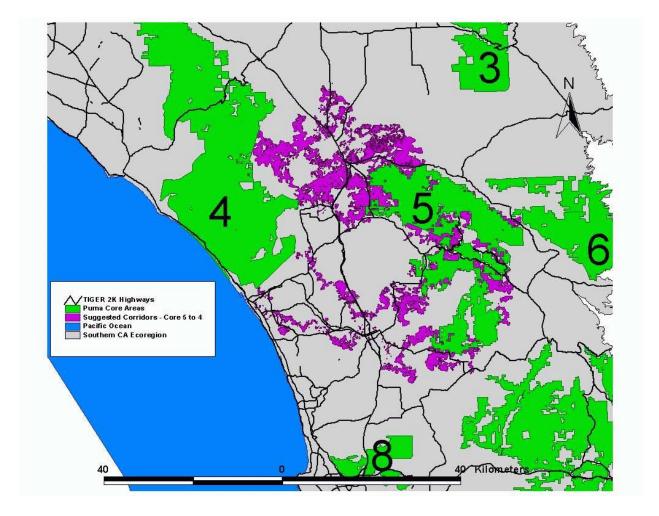


Figure 22: Movement routes (behavioral corridors) suggested by the models based on simulated movements for lowest cost successful dispersal paths from the Palomar Mountains (core 5) to the Santa Ana Mountains (core 4). The core areas are shown in green, and the predicted behavioral corridors are shown in purple. Highways are included as black lines for reference.

Fine-Scale Visualization of Movement Through Other Selected Areas The final result of the application of this method for behavioral corridors for the Cleveland National Forest (core 7) to Miramar (core 8) linkage is shown in Figure 23. We applied a "short-cut" procedure to look at predicted movement routes between other pairs of core areas. This short cut consists of completing steps 1-2 above. Next, instead of creating polylines and buffering the lines by a fixed distance, we buffered the selected points by the move distance (in the MOVE_DIST field), and then clipped out the habitat areas. Results of this procedure are shown in Figure 24 and 25. These figures show predicted behavioral corridors in both directions. In Figure 24 the behavioral corridor from the Cleveland National Forest (core 7) to the Palomar Mountains (core 5) and from the Palomar Mountains (core 5) to the Cleveland National Forest (core 7) is shown. In Figure 25 the behavioral corridor from Otay Mountain (core 9) to the Cleveland National Forest (core 7) and from the Cleveland National Forest (core 7) to Otay Mountain (core 9) are shown. Such visualizations may be helpful in planning reserve designs.

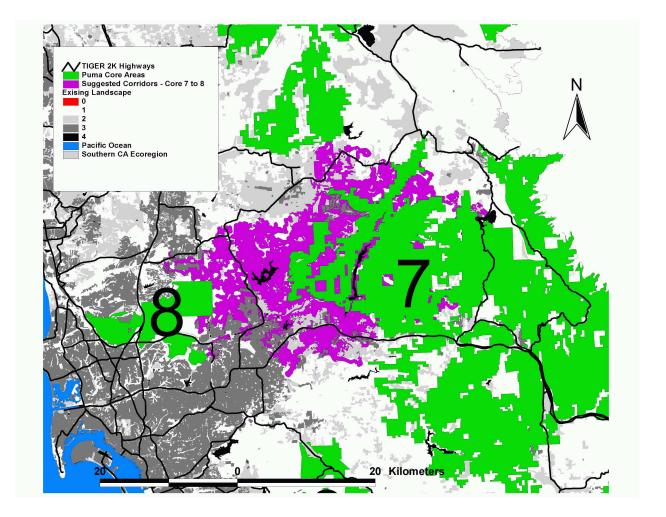


Figure 23: Movement routes (behavioral corridors) suggested by the models based on simulated movements for lowest cost successful dispersal paths from the Cleveland National Forest (core 7) to Miramar (core 8). The core areas are shown in green, and the predicted behavioral corridors are shown in purple. Highways are included as black lines for reference.

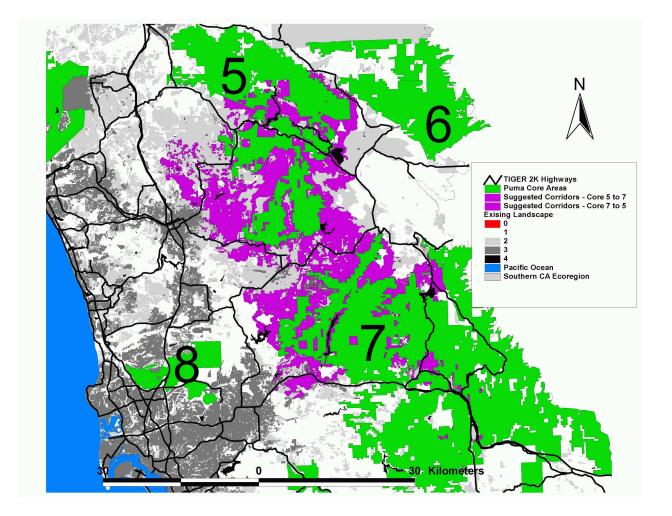


Figure 24: Simulated movements for lowest cost successful dispersal paths between the Cleveland National Forest (core 7) and the Palomar Mountains (core 5). The core areas are shown in green, and the predicted behavioral corridors are shown in purple. Highways are included as black lines for reference.

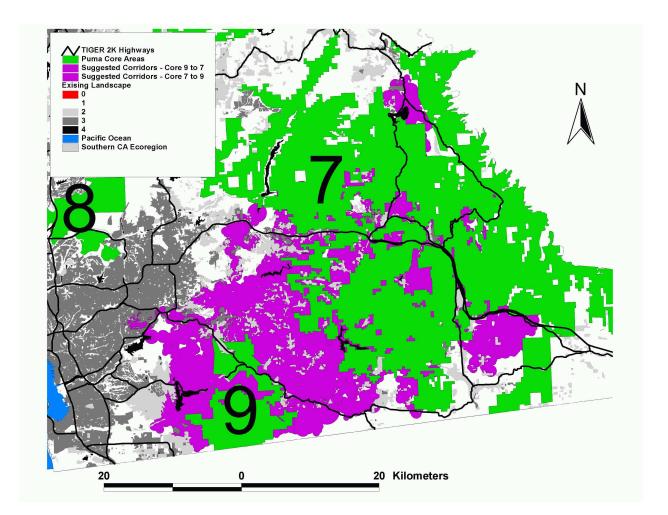


Figure 25: Simulated movements for lowest cost successful dispersal paths between the Otay Mountain (core 9) and the Cleveland National Forest (core 7). The core areas are shown in green, and the predicted behavioral corridors are shown in purple. Highways are included as black lines for reference.

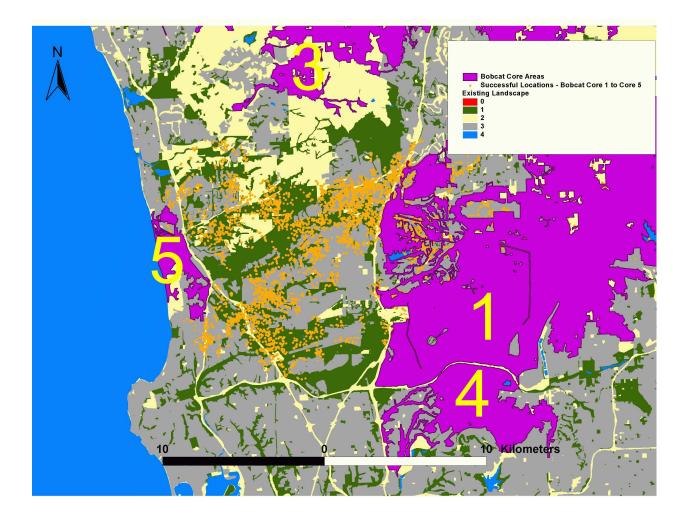


Figure 26: Simulated locations for successful bobcat dispersal from core 1 (Miramar/Mission Trails) to core 5 (Torrey Pines State Park).

Finally, we provide an example of a predicted behavioral corridor for bobcats moving from core 1 (Miramar/Mission Trails) to core 5 (Torrey Pines). The successful simulated locations are shown in Figure 26, and the predicted behavioral corridor is shown in Figure 27.

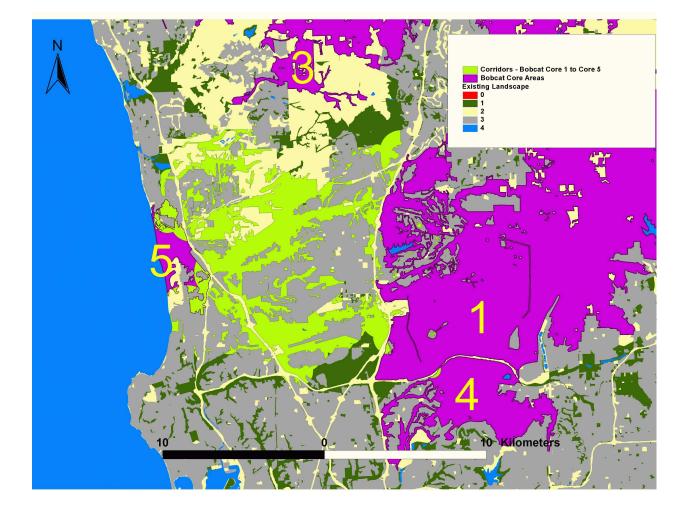


Figure 27: Predicted corridors for bobcat dispersal from core 1 (Miramar/Mission Trails) to core 5 (Torrey Pines State Park).

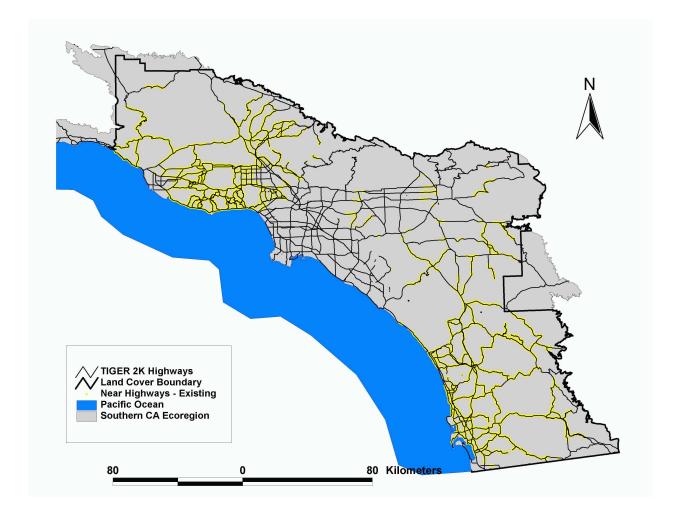


Figure 28: Encounters with highways for the existing landscape simulation. The yellow areas show where the encounters occurred.

3.6.4 Threats to Connectivity

We can use the simulation results to visualize locations where threats to dispersing mountain lions may be highest, as predicted by the simulation models. We can expect human-caused mortality to be highest where individuals encounter roads or urban areas. Locations where encounters with highways occurred in the simulations are shown for the existing landscape (Figure 28) and the NCCP landscape (Figure 29). Similarly, locations where encounters with urban areas occurred in the simulations are shown for the existing landscape (Figure 30) and the NCCP landscape (Figure 31). Numerical results related to risk are given in Tables 3 and 5 for the existing and NCCP landscapes, respectively.

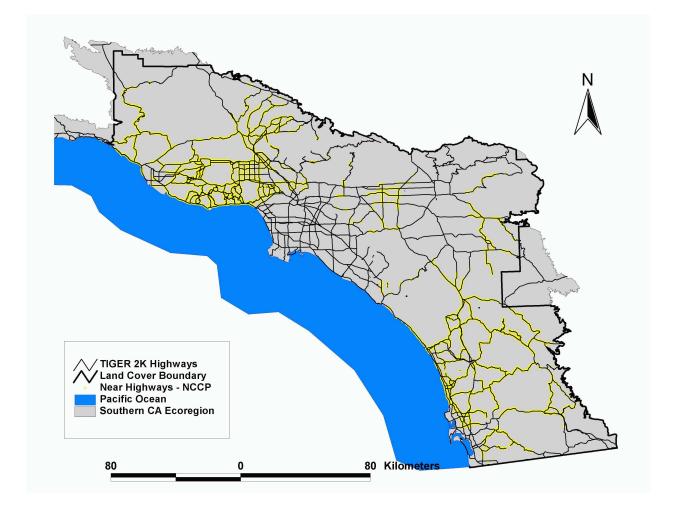


Figure 29: Encounters with highways for the NCCP landscape simulation. The yellow areas show where the encounters occurred.

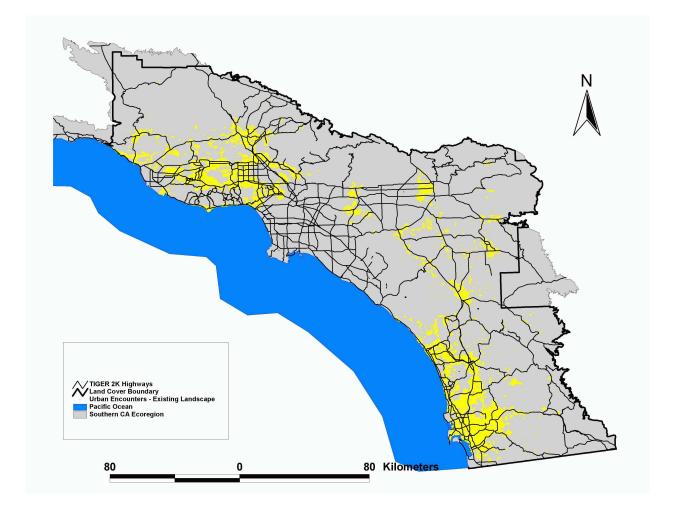


Figure 30: Encounters with urban areas for the existing landscape simulation. The yellow areas show where the encounters occurred.

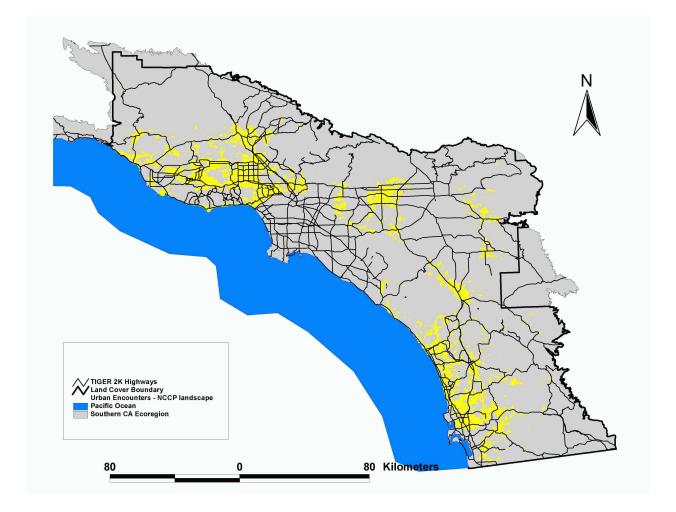


Figure 31: Encounters with urban areas for the NCCP landscape simulation. The yellow areas show where the encounters occurred.

4 Discussion Regarding the Movement Models

4.1 Advantages of Our Movement Models

- **Our models are supported by data** The models we develop are more complex and biologically realistic than previously proposed data-supported models of movement. This is very important for several reasons. First, it provides a basis for parameterizing and selecting models using data. Second, because the models are data based, we have a basis for evaluating our ideas about movement and for improving upon the models in a rigorous way. Third, data supported models are more defensible.
- **Our models combine both landscapes and movement** Our movement models incorporate landscape structure and animal movement behavior, which are the essential features of connectivity.
- Our models provide a behavior-oriented perspective on connectivity It is easy for an expert to look at a GIS layer and see what they believe is a clear path through the landscape mosaic between core habitat areas; however, animals dispersing through a landscape for the first time do not have this global view and must make decisions based on their past and present situation. In fact, they may never have such a global, map-like view of the landscape.
- Our models can simulate many more movement paths Using computers, we can simulate many movement paths many more than can be observed in nature under a wide range of conditions. This allows us to obtain a clear prediction for target quantities such as success, risk, and cost, and of movement paths through the landscape mosaic.
- **Our models can simulate movement on many landscapes** Using our simulation models and GIS landscape data for a region of interest, we can predict movement in places for which we have no empirical movement data. The GIS data must be similar in resolution and identical in classification of land cover types and other features as that used in the analysis of existing data. Such predictions can be used to guide empirical studies, monitoring efforts, and reserve designs. Using the simulations we can make predictions for connectivity in landscapes that do not yet exist. This will provide a valuable tool for reserve design planning.
- **Our simulation framework is more flexible** Most simulations that incorporate movement use grid landscapes that are better suited to continuously distributed quantities such as elevation. Our simulations can use grid, point, and line data. Modeling landscape features as vector objects makes simulation on larger landscape scales more feasible. Furthermore, the landscape component of the individual-based movement models employs efficient spatial algorithms that make simulation on complex landscapes more practical.
- **Our models produce quantitative results** We can use our models to quantify connectivity (e.g., in terms of success, risk, and cost) making comparisons within and among alternative landscapes more rigorous.

Our models are useful for learning about movement The statistical models of movement we have developed, and will continue to develop, allow us to test hypotheses about movement, which is important in research and for developing better models of movement.

4.2 Limitations of Our Movement Models

- Limitations of available data Because we use data-supported models, the complexity of the movement model selected through the statistical methodology is limited by the amount of available data, the numbers of encounters with each type of landscape feature, and the ranges of the predictor variables in the data.
- Quality of GIS data It is beyond our capability to ground truth the GIS data used in the simulations. Furthermore, software products such as ESRI ArcView and its Geoprocessing Wizard do not always produce clean, correct results when processing polygon layers. Therefore, we make the assumption that such data is reasonably correct and accurate.
- Models are a simplification of reality Real animals collect large amounts of information from their environment and internal state almost continually, process it through a large neural system, and arrive at a decision on how to act. As such, they are capable of producing very specific responses to a very large number of possible situations. We can view the intelligence of an animal as a computational system, but it is not one that we can presently match with a computer program (or hardware), much less to construct such a complex model and estimate parameters for it from data. Our approach (any theoretical approach), is to propose a simplified model of reality that we believe is generally correct. What we cannot account for we attribute to random error in the model. Therefore, the patterns of movement we generate may be similar to those of real animals in important ways, but will respond in specific instances in ways that may seem unreasonable, although they are on average reasonable given the data we have and the model. As the saying (attributed to G. E. Box) goes: "All models are wrong, some are useful." As we progress we would like to construct models that behave increasing like real animals, but this goal will never be fully realized. However, the models may generate movement patterns that are similar enough to those of real animals to be useful for evaluating connectivity.
- **Predictions depend on the model** If we performed the same connectivity evaluation using different models, we may get different predictions. We cannot guarantee that future evaluations using new models will not suggest different ways of conserving connectivity. What we can expect is that with more and better data, we will develop models that will improve predictions. If the quantity of data increases, then we can also expect the specificity of the predictions to increase. Furthermore, the predictions apply only to the species of the individuals for whom parameters were estimated. In addition, the inference of our statistical models apply only to the individual-level. In order to obtain a population-level evaluation of connectivity, we require movement data from a sumple of individuals in the population.

4.3 Future Work

Our approach to evaluating landscape connectivity is only in its beginning stages of development. We plan much more work on these methods in the near future, including development of new movement models, analysis of more movement data, improvement our movement simulation capabilities, and refinement of our approaches for using simulation output to evaluate connectivity. As more and better data is obtained and analyzed with respect to more detailed landscape models, we expect the specificity of model predictions to increase. In other words, as we obtain data that can support analysis of movement in response to land cover, roads, elevation, and other features simultaneously, the models should make more specific predictions about routes of movement across landscapes. As this work proceeds, we would like to continue collaboration with the California Department of Fish and Game and The Nature Conservancy; however, this is not an agreement for additional work and we retain the academic freedom to alter our research plan as we learn more about how to develop and apply this approach. Below, we summarize work we plan to do in the future and how we might apply the models to conservation questions of interest to CDFG and TNC.

- 1. Further development of strategies for preserving connectivity in the southern California ecoregion and other areas.
- 2. Later, incorporate energetic cost and mortality risk due to roads and urban areas directly into the simulations.
- 3. Identify and refine techniques for statistically comparing dispersal success matrices from alternative landscapes (e.g., perhaps based on multinomial distributions). For example, we want to develop (or identify existing) statistical tests of significance to separate changes in success due to random variation in simulation results versus those due to changes in the landscapes being compared.
- 4. Develop other classes of models (and associated data analysis programs) for analyzing and simulating animal movement.
- 5. Add new movement models to the IBMM (based on the new classes of models above) and a more flexible framework for modifying movement models within the IBMM.
- 6. Increase the functionality of the landscape component of the IBMM; that is, incorporate more kinds of landscape queries (such as the calculation of viewsheds and parts of vector-based objects that fall within veiwsheds) and to directly write output in the form of ESRI shapfiles.
- 7. Test, revise and optimize the IBMM and the data extraction program to take advantage of the increased functionality of the landscape component of the IBMM.
- 8. Develop additional methods for visualizing and quantifying landscape connectivity from model output (particularly given the large volumes of output produced by the simulations). Specifically, develop better techniques for extracting behavioral corridors from simulated movement paths.

- 9. Automate, as much as possible, the calculations of connectivity measures and the production of results tables and figures.
- 10. Run the IBMMs on more alternative landscapes (particularly if CDFG or TNC has particular alternative landscapes in mind and can create *clean, correct* GIS layers for them). Of particular immediate interest is to simulate movement on SanDAGs 2030 land use projection and future road layers.
- 11. As a long-term goal, develop the IBMM to the point that it can be released as an executable program with supporting documentation.
- 12. As another long-term goal, incorporate the cellular automata urban growth model developed by Clark into the IBMM.

4.3.1 Field Telemetry data to be used in future modeling efforts

Much of the future success of this approach relies on movement data. For more complex models, more and better data is needed. In particular, data collected using new GPS tracking collars will be essential. In the near future, we would like to work with Ray Sauvajot and Seth Riley of the National Park Service, Walter Boyce of University of California Davis, and Steve Torres of CDFG to analyze the data they have collected, use it in simulations to predict connectivity in their study areas and else where, and perhaps work with them in designing and obtaining funding for future studies. We will also be applying our models to bobcat and puma data we have collected in collaboration with Lisa Lyren and Robert Fisher (USGS). Finally, we forsee using these models to study and predict movement for other species that can be tracked with GPS tracking equipment.

5 Summary

In this project, we have developed novel models for analyzing and simulating animal movement on landscapes. We have applied these simulations to an existing, NCCP, and worst-case land cover layer for the southern California ecoregion. We have also conducted a limited simulation for bobcats in central coastal San Diego County. Using the simulation results, we compared connectivity in the existing and NCCP landscapes. We suggested a strategy for preserving connectivity in the ecoregion that consists of five goals, and used the simulation results to address each goal. We used the simulation results to quantify and visualize risks to dispersing pumas. Finally, we discussed advantages and limitations of our approach, and future directions in this research.

Acknowledgments

We would like to thank Paul Beier for allowing us to use his mountain lion data. We thank Lisa Lyren and Robert Fisher for their collaboration in studying bobcat movement, and Robert Fisher and the US Geological Survey for funding part of this research. Rich Hunter did some very useful GIS analysis that we used in this project. We thank Ray Sauvajot and Seth Riley for many useful comments and interest in our project. Jim Bauer gave many insights into puma movement and habitat use in the Cuyamaca Mountains.

References

- [Beier 1993] Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7:94-108.
- [Beier 1995] Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitats. Journal of Wildlife Management 5:228-237.
- [Beier et al. 1995] Beier, P., D. Choate, and R. H. Barrett. 1995. Movement patterns of mountain lions during different behaviors. Journal of Mammalogy 76:1056-1070.
- [Bender et al. 1998] Bender, D. J., T. A. Contreras, and L. Fahrig. 1998. Habitat loss and population decline: a meta- analysis of the patch size effect. Ecology 79:517-533.
- [Carroll et al. 1999] Carroll, C., W.J. Zielinski, R.F. Noss. 1999. Using presence-absence data to build and test spatially-explicit habitat models for the fisher in the Klamath Region, U.S.A. Conservation Biology 13:1344-1359.
- [Crooks 2000] Crooks, K. R. 2000. Mammalian carnivores as target species for conservation in southern California. Pages 105-112 In Second interface between ecology and land development in California. Eds. J. E. Keeley, M. Baer-Keeley, and C. J. Fotheringham, editors. U. S. Geological Survey. Open-File Report 00-62.
- [Crooks 2002] Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology.
- [Crooks et al. 1998] Crooks, K. R., M. A. Sanjayan, and D. F. Doak. 1998. New insights on cheetah conservation through demographic modeling. Conservation Biology 12:889-895.
- [Crooks and Soulé 1999] Crooks, K. and M. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563-566.
- [Dobson et al. 1997] Dobson, A.P., J.P. Rodriguez, W.M. Roberts, and D.S. Wilcove. 1997. Geographic distribution of endangered species in the United States. Science 275:550-553
- [Fahrig 1997] Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. Journal of Wildlife Management 61:603-610.
- [Gustafson and Gardner 1996] Gustafson, E. J. and R. H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77: 94-107.
- [Hunter et al. 2003] Hunter, R., R. Fisher, and K. Crooks 2003. Landscape-level connectivity in coastal southern California as assessed by carnivore habitat suitability. Natural Areas Journal 23:302-314.

- [Jander 1975] Jander, R. 1975. Ecological aspects of spatial orientation. Annual review of Ecology and Systematics 6: 171-188.
- [Lambeck 1997] Lambeck, R.J. 1997. Focal species: A multi-species umbrella for nature conservation. Conservation Biology 11: 849-856.
- [Lawhead 1984] Lawhead, D. N. 1984. Bobcat (Lynx rufus) home range, density, and habitat preference in south-central Arizona. The Southwestern Naturalist 29:105-113.
- [Litvaitis 1986] Litvaitis, J. A., J. A. Sherburne, and J. A. Bissonette. 1986. Bobcat habitat use and home range size in relation to prey density. Journal of Wildlife Management 50:110-117.
- [Lovallo et al. 1996] Lovallo, M. J., and E. M. Anderson. 1996. Bobcat (Lynx rufus) home range size and habitat use in northwest Wisconsin. American Midland Naturalist 135:241-252.
- [Maehr 1997] Maehr, D. S. 1997. The Florida Panther: Life and Death of a Vanishing Carnivore. Island Press. Washington D. C.
- [Miller et al. 1998] Miller, B., R. Reading, J. Strittholt, C. Carroll, R. Noss, M. Soulè, O. Sanchez, J. Terborgh, D. Brightsmith, T. Cheeseman, D. Foreman. 1998. Using Focal Species in the Design of Nature Reserve Networks. Wild Earth 8: 81-92.
- [Mills et al. 1993] Mills, L. S., M. E. Soulé, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. Bioscience 43:219-224.
- [Murcia 1995] Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution 10:58-62.
- [Myers 1990] Myers, N. 1990. The biodiversity challenge: expanded hot-spots analysis. The Environmentalist 10:243-256.
- [Noss 1983] Noss, R. F. 1983. A regional landscape approach to maintain diversity. Bioscience 33:700-706.
- [Noss 1992] Noss, R.F. 1992. The Wildlands Project: Land conservation strategy. Wild Earth Special Issue.
- [Noss and Cooperrider 1994] Noss, R.F., A.Y. Cooperrider. 1994. Saving Nature's Legacy: Protecting and Restoring Biodiversity. Island Press. Covelo, CA.
- [Noss et al. 1996] Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology 10:949-963.
- [Noss and Soulé 1998] Noss, R.F. and M. E. Soulé. 1998. Rewilding and biodiversity: Complementary goals for continental conservation. Wild Earth 8: 18-28.

- [Schumaker 1996] Schumaker, N. H. 1996. Using landscape indices to predict habitat connectivity. Ecology 77: 1210-1225.
- [Soulé 1991] Soulé, M. E. 1991. Land use planning and wildlife maintenance: guidelines for conserving wildlife in an urban landscape. Journal of the American Planning Association 57:313-323.

[Soulé and Gilpin 1991] Soulé and Gilpin, 1991

- [Soulé and Terborgh 1999] Soulé, M.E and J. Terborgh. 1999. Continental conservation: scientific foundations for regional reserve networks. Island Press, Washington D.C.
- [Taylor et al. 1993] Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos: 68: 571-573.
- [Urban and Keitt 2001] Urban and Keitt, 2001. Landscape connectivity: A graph-theoretic perspective. Ecology 82: 1205-1218.
- [Westervelt and Hopkins 1999] Westervelt and Hopkins, 1999
- [Wilcove et al. 1998] Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48: 607-615.
- [Woodroffe and Ginsberg 1998] Woodroffe, R., and J.R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science 280:2126-2128.
- [Zollner 2000] Zollner, P. A. 2000. Comparing landscape-level perceptual abilities of forest sciurids in fragmented agricultural landscapes. Landscape Ecology 15: 523-533.
- [Lima and Zollner 1996] Lima S. L. and P. A. Zollner. 1996. Toward a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution 11: 131-135.

A Movement Summary Output

Here we describe the fields in the movement summary output files included on data CD.

- **SIM** Simulation ID number. This number is used to identify the simulation that produced the output data. Together with the CORE and PATH variables, they uniquely identify a movement path.
- **CORE** Starting core number as given in the tables and figures.
- **PATH** Path ID number. This number is assigned sequentially (starting at 0) for each path within a simulation and core.
- **MOVE** Move number. This number is sequentially assigned to the movements within each simulation, core, and path. It can be used to temporally order the simulated locations.

- **X** The x-coordinate in Albers projection.
- **Y** The y-coordinate in Albers projection.
- **TYPE1** Land cover type occupied when the move is made (1=habitat, 2=disturbed, 3=urban, and 4=water).
- **TYPE2** Land cover type across the nearest boundary when the move is made (1=habitat, 2=disturbed, 3=urban, and 4=water).
- **EDGEANG** Angle in radians to the nearest point on the occupied land cover polygon boundary. A negative value indicates a clockwise direction, and a positive value indicates a counter-clockwise direction. Radians are measured from the positive x-axis and are on the interval from $-\pi$ to π .
- **EDGEDIST** Distance in meters to the nearest point on the occupied land cover polygon boundary.
- **INCORE** ID number of the core occupied at the time the move was made (the same number used to identify the core areas in the figures and tables). It has a value of -1 if the location was outside of a core area.
- **MOVE_ANG** Angle of movement in radians. A negative value indicates a clockwise direction, and a positive value indicates a counter-clockwise direction. Radians are measured from the positive x-axis and are on the interval from $-\pi$ to π . This field is named MOVE.ANG in the shapefile attribute tables.
- **MOVE_DIST** Distance of movement in meters. This field is named MOVE.DIST in the shapefile attribute tables.
- SUCCESS T/TRUE if dispersal was successful, F/FALSE otherwise.
- **ENDCORE** The core the animal was in at its last location. This field identifies the core (by the number used in the figures and tables) that the animal successfully dispersed into. It have a value of -1 for unsuccessful paths.
- **DPATHLEN** Length of the path in meters since last leaving the starting core.
- **SPATHLEN** The standardized path length (=DPATHLEN/DMINLEN). It is actually a dimensionless quantity that serves as an indicator of the straightness or efficiency of the movement path.
- **PURBAN** The proportion of locations in the path that were in urban land cover (=UCOUNT /DISPMOVES; see below).

B Path Summary Output

In the *path summary* files, a record is written for each move path. Here we describe the fields in the path summary output files included on data CD.

SIM Simulation ID number (as described above).

CORE Starting core number (as described above).

PATH Path ID number (as described above).

TOTALMOVES Number of moves made in the entire path.

TPATHLEN Total length of the entire path in meters.

DISPMOVES Number of moves made since last leaving the starting core.

DPATHLEN Length of the path in meters since last leaving the starting core.

DMINLEN Straight-line distance between location when the starting core was left until the new core was reached; this is only relevant for successful dispersal paths.

HCOUNT Number of locations in habitat land cover since last leaving the starting core.

DCOUNT Number of locations in disturbed land cover since last leaving the starting core.

UCOUNT Number of locations in urban land cover since last leaving the starting core.

SUCCESS T/TRUE if dispersal was successful, F/FALSE otherwise.

ENDCORE The core the animal was in at its last location (as described above).