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Uncertainty analysis of least-cost modeling for designing wildlife linkages

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Abstract. Least-cost models for focal species are widely used to design wildlife corridors. To evaluate the least-cost modeling approach used to develop 15 linkage designs in southern California, USA, we assessed robustness of the largest and least constrained linkage. Species experts parameterized models for eight species with weights for four habitat factors (land cover, topographic position, elevation, road density) and resistance values for each class within a factor (e.g., each class of land cover). Each model produced a proposed corridor for that species. We examined the extent to which uncertainty in factor weights and class resistance values affected two key conservation-relevant outputs, namely, the location and modeled resistance to movement of each proposed corridor. To do so, we compared the proposed corridor to 13 alternative corridors created with parameter sets that spanned the plausible ranges of biological uncertainty in these parameters. Models for five species were highly robust (mean overlap 88%, little or no increase in resistance). Although the proposed corridors for the other three focal species overlapped as little as 0% (mean 58%) of the alternative corridors, resistance in the proposed corridors for these three species was rarely higher than resistance in the alternative corridors (mean difference was 0.025 on a scale of 1–10; worst difference was 0.39). As long as the model had the correct rank order of resistance values and factor weights, our results suggest that the predicted corridor is robust to uncertainty. The three carnivore focal species, alone or in combination, were not effective umbrellas for the other focal species. The carnivore corridors failed to overlap the predicted corridors of most other focal species and provided relatively high resistance for the other focal species (mean increase of 2.7 resistance units). Least-cost modelers should conduct uncertainty analysis so that decision-makers can appreciate the potential impact of model uncertainty on conservation decisions. Our approach to uncertainty analysis (which can be called a worst-case scenario approach) is appropriate for complex models in which distribution of the input parameters cannot be specified.

Key words: connectivity; conservation planning; focal species; least-cost modeling; permeability; umbrella species; uncertainty analysis; wildland linkage; wildlife corridor.

Introduction

Wildlife corridors are designed to maintain or restore connectivity through landscapes threatened by habitat loss and fragmentation (Crooks and Sanjayan 2006). The most widely used approach for designing corridors is least-cost modeling. Least-cost corridor models are developed by creating a GIS raster of potential resistance a species will face when moving through the landscape (Adriaensen et al. 2003, Beier et al. 2008). This GIS raster has two key sources of uncertainty, namely the *weights* assigned to *factors* such as land cover or road density and *resistance values* assigned to each *class* within a factor, such as each land cover class or road density class (Eq. 1). Weights and resistance values are typically estimated by interpretation of literature or data on habitat use. Unfortunately, studies of habitat use do not produce estimates of resistance, but instead produce a ranked list of land cover classes (or road density classes, topographic positions, etc.), a ratio or difference between use and availability of each class, number of animal occurrences in each class, or the mean distance from animal locations to the nearest occurrence of each class. For instance, data showing that an animal most prefers class a, followed by classes b, c, and d, are consistent with any of the following ordered sets ({a, b, c, d}) on a 1–10 resistance scale: {1, 4, 6, 10}, {3.8, 3.9, 4, 4.01}, or {1, 1.01, 9.99, 10}. As this example illustrates, it is reasonable to assume that the resistance values derived from habitat use data have the correct rank order, but there is still enormous uncertainty in the estimates. In this paper, we address the impact of this uncertainty on linkage design.

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We also address the impact of another source of uncertainty: namely uncertainty about which focal species should inform linkage design. About half of published corridor analyses involve a single focal species, typically a large carnivore (summary in Beier et al. 2008). Although area-sensitive species like large carnivores will be among the first to become extinct if corridors are lost (Noss 1991, Soulé and Terborgh 1999), many large carnivores are habitat generalists, and a corridor designed for large carnivores may not meet the movement needs of all species. The extent to which carnivores can be effective umbrellas for multiple-species connectivity has not been investigated.

Least-cost models were used to produce 15 linkage designs that are being implemented by conservation investors and land-use planners in southern California (*available online*).[5] Each of these designs was based on models for >10 focal species, always including non-carnivores, and each model used factor weights and class resistance values based on literature review. Linkage designers and conservation decision-makers need to know whether these linkage designs are robust to uncertainty in factor weights and class resistance values, and whether a carnivore-based linkage design would have been adequate for other focal species. We used uncertainty analysis (Leamer 1985, Saltelli et al. 1998, Crosetto et al. 2000, Burgman et al. 2005) to address these issues. In contrast to sensitivity analysis (which asks which input parameters have the greatest influence on model output), uncertainty analysis asks how much model output changes in response to uncertainty in the input parameters. The model is judged robust "only if the neighborhood of assumptions is wide enough to be credible and the corresponding interval of inferences is narrow enough to be useful" (Leamer 1985).

In this paper we evaluate how poorly the predicted linkage design (the design being implemented by decision-makers) might perform if parameter values are pushed to the extremes of the "credible neighborhood" of potential parameter values. Our approach can be called a worst-case scenario approach to distinguish it from traditional approaches such as differential calculus and repeated sampling. Differential calculus can only evaluate small amounts of uncertainty in a single input parameter, and the repeated-sampling approach requires that the distributions of the input parameters are known. In contrast, least-cost models involve many parameters whose unknown distributions encompass a large range of uncertainty (example in the first paragraph and Table 1). The worst-case scenario approach to uncertainty analysis has long been used in economics and other disciplines, at least informally (Leamer 1985). Here we illustrate the approach in a GIS context and advocate its wider use in applied ecology.

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Because the output of a least-cost model depends on the focal species and the landscape, the impact of uncertainty can be evaluated only by case studies. We illustrate our approach to uncertainty analysis with a case study of the linkage design for the Tehachapi Linkage Area (Fig. 1). We selected this one of the 15 linkage designs because it was the longest (65 km between protected wildland blocks, compared to lengths of 2–21 km for the other 14 linkages), was least constrained by existing urban barriers, and had the highest diversity and interspersion of vegetation types and topography. In shorter, more homogeneous linkages hemmed in by existing urban areas, predicted corridors would show much less sensitivity to uncertainty.

To describe our objectives, we must define a few key concepts. A *proposed corridor* is a mapped area predicted to best facilitate movement of one focal species between wildland blocks, whether in a single movement event or over multiple generations. As described in the first paragraph, the proposed corridor is a function of weights assigned to factors and resistance values assigned to each class within a factor. The proposed corridors of all focal species are combined into a *preliminary linkage design*. This becomes the *final linkage design* after it is modified to accommodate ecological processes, buffer against edge effects, or achieve other conservation objectives. These modifications may involve adding areas of conservation interest or eliminating redundant habitat.

Our first goal in this case study was to address four questions about the least-cost modeling approach used in these 15 linkages: Given reasonable uncertainty in factor weights and resistance values, what is the risk that the proposed corridor and the preliminary linkage design could fail to overlap the true least-cost corridor? Given this same uncertainty, how much increased resistance to movement might the focal species experience in the proposed corridor? Is robustness of the model related to habitat breadth of the focal species? How well do carnivores serve as an umbrella species to design linkages that will serve other species? Our second goal was to illustrate an approach to uncertainty analysis that can be used to evaluate the utility of complex models in ecology and conservation biology.

Methods

We evaluated a slightly modified version of the least-cost modeling approach used to design 15 linkages in Southern California (Beier et al. 2006). We selected this modeling approach and these linkage designs because (1) each report listed weights, resistance values, and biologically plausible maximum and minimum weights and resistance values for each modeled species; (2) the design involved many focal species, allowing us to evaluate how well carnivores serve as umbrella species; and (3) the designs are being actively implemented, with real resources allocated to designs of unknown reliability.

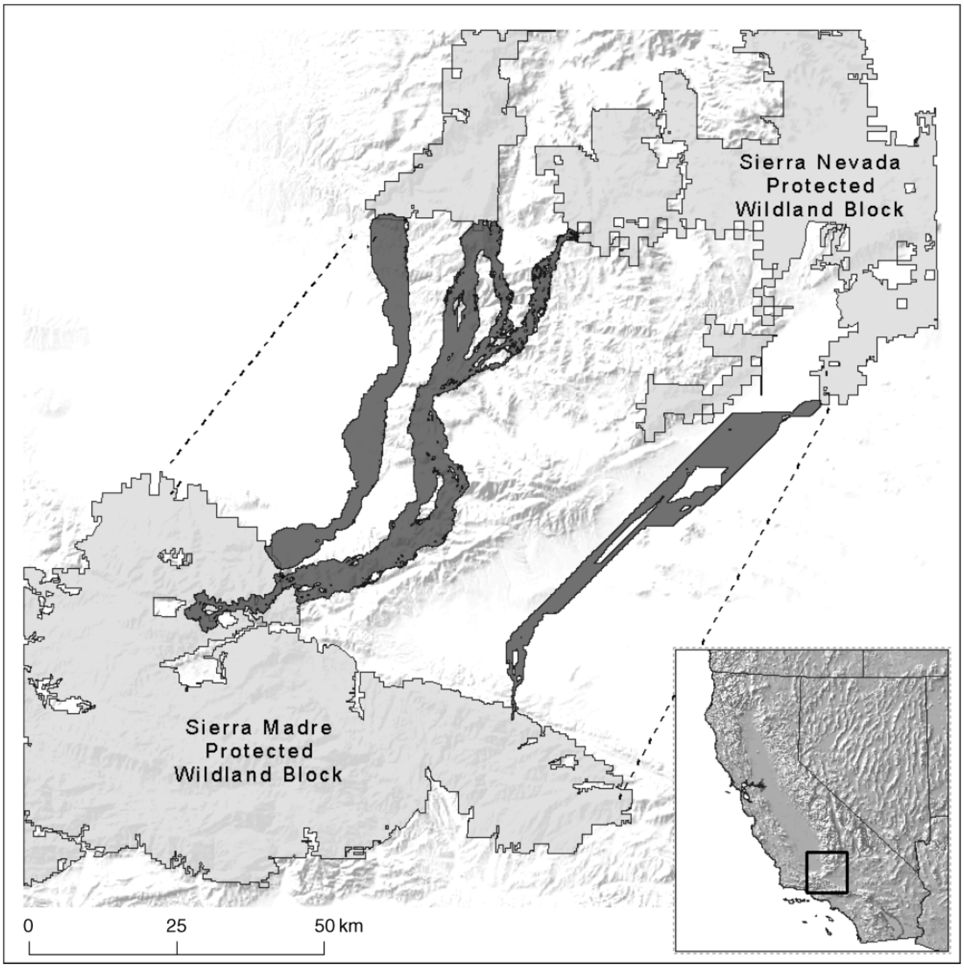

FIG. 1. The analysis area (2.3 million ha) in southern California, USA, included ~665 000 ha of matrix between the two wildland blocks, of which the preliminary linkage design (dark gray) occupied ~108 500 ha, which is 4.7% of the analysis area and 16% of the area between wildland blocks (dashed lines). The preliminary linkage design is the union of eight single-species corridors; the source areas for each single-species corridor were large blocks of species-specific suitable habitat in protected lands in the Sierra Madre or Sierra Nevada. The Tehachapi Mountains are the main mountain range in the matrix.

For this case study, we selected the Tehachapi Linkage (118.5° W, 35° N; Fig. 1), which was designed to conserve and restore connectivity between large publicly owned wildlands in the Sierra Nevada and southern coastal ranges (Sierra Madre) of California, USA (Penrod et al. 2003). These conserved lands are separated by a 65-km swath of unprotected land in the Tehachapi Mountains and adjoining valleys. The Tehachapi Linkage has enormous biological importance as the only potential montane connection between the 3200-km Sierra Nevada–Cascade cordillera and the 1300-km cordillera of the Sierra Madre, Transverse, and Peninsular Ranges of southern California (Fig. 1 inset). The region's diversity stems from its location at the juncture of four major ecoregions (Sierra Nevada, Sierra Madre, Great Central Valley, Mojave Desert; Penrod et al. 2003). Since the linkage design was released, over half of the area in the linkage design has been acquired for conservation.

We used the least-cost models for eight focal species developed by Penrod et al. (2003): puma (*Puma concolor*), mule deer (*Odocoileus hemionus*), American badger (*Taxidea taxus*), San Joaquin kit fox (*Vulpes macrotis mutica*), western gray squirrel (*Sciurus griseus*), Tipton kangaroo rat (*Dipodomys nitratoides nitratoides*), Tehachapi pocket mouse (*Perognathus alticola inexpectatus*), and California Spotted Owl (*Strix occidentalis occidentalis*). The focal species were selected for their high area sensitivity or barrier sensitivity, low vagility, or close association with particular habitat conditions.

Least-cost modeling is only part of developing a linkage plan. Indeed, Penrod et al. (2003) did not build least-cost models for 22 other focal species in this linkage because it was not feasible to develop least-cost models for species, such as trees, that can take a century to move their genes across a landscape, or species, such as insects, whose movements are weakly related to the available GIS layers (Beier et al. 2006). After the

TABLE 1. Levels of uncertainty in factor weights and resistance scores in models for eight focal species used to design wildlife corridors in the Tehachapi Linkage Area, California, USA.

Factor	Mean factor weight (%)	Mean uncertainty in weight (%)†	Uncertainty in resistance (maximum minus minimum) for classes within factor (%)‡							Mean uncertainty in resistance§
			0	1	2	3	4	5–6	7–8	
Land cover	68	26	32¶	19	18	18	8	3	2	1.8
Elevation	4	5	37	16	16	5	15	10	0	1.9
Topographic position	13	8	21	0	29	12	4	12	21	3.2
Road density	15	17	13	7	21	5	19	19	14	3.6

† Mean difference between maximum and minimum weights, across eight species. In each species model, the weights summed to 100%.

‡ Percentage of resistance scores for which the difference between the maximum and minimum possible score was 0, 1, 2, and so on. Resistance scores were integers that ranged from 1 to 10.

§ Mean difference between maximum and minimum resistance scores for species–class combinations. There were 48 land cover classes, four topographic position classes, eight road density classes, and five elevation classes.

¶ Eight-four percent of the land cover classes with an estimated uncertainty of zero were considered completely unsuitable (resistance score = 10); the other 16% were classes considered the best possible habitat (resistance score = 1).

preliminary linkage design was derived for the eight focal species, Penrod et al. (2003) expanded it (by ~10%) to encompass known or modeled occurrences of the other focal species, buffer against edge effects, and achieve other conservation objectives.

Model structure

For each focal species, an expert with experience with that species in southern California assigned a weight (W) from 0% to 100% to each of four habitat factors: land cover (denoted by the subscript L), elevation (E), topographic position (T), and paved road density (P), such that the weights sum to 100%. The species expert also assigned a resistance value (R) to each of the *classes* within each factor (e.g., land cover classes included desert scrub, marsh, and urban). Resistance values range from 1 (least) to 10 (most). Because the species expert rarely had data on animal movement to directly parameterize resistance, resistance was conceptualized as habitat quality. Values of 1–3 indicated the most preferred breeding habitat (or habitat with highest breeding success), 4–5 indicated classes of marginal utility for breeding, 6–7 indicated habitat usable as nonbreeding habitat, and 8–10 indicated increasing degrees of avoidance. For each factor weight and resistance value, the species expert provided a point estimate (used to develop the proposed corridor) and a minimum and maximum value, which we use to bracket the range of biological uncertainty (Table 1). As recommended by Clevenger et al. (2002), the species experts documented their ratings by reference to scientific literature.

Resistance of a pixel (100 × 100 m) for a particular focal species was calculated as

$$R_L W_L + R_E W_E + R_T W_T + R_P W_P. \tag{1}$$

All GIS data layers were transformed to matching projections and resolution (100 m). For each pixel, we used the ArcGIS 9.1 Cost Distance function to calculate the lowest cumulative resistance incurred on a path running from the pixel to suitable habitat in each wildland block, and the ArcGIS Corridor function to add these two costs for each pixel (ESRI 2002). The resulting cumulative cost layer produces a series of increasingly wide corridors displayed as nested polygons, each defined by the maximum cost allowed in the polygon.

Unlike a least-cost path, which is only one pixel wide, a least-cost corridor has a width that varies, becoming wide in areas of high-quality habitat and narrow where unsuitable habitat creates pinch-points. We defined the proposed corridor as the swath of lowest cost pixels totaling 25 000 ha, equivalent to an average width of ~3 km. In contrast, Penrod et al. (2003) selected the swath such that any bottleneck in the corridor exceeded a species-specific minimum width. Although our procedure was less grounded in ecological understanding of each species, it was objective and repeatable, which let us compare dozens of alternative models. For each species, our procedure produced a corridor less than half as large as the corridor produced by Penrod et al. (2003), ensuring that we overestimated, rather than underestimated, the impact of uncertainty. If we had used broader corridors, alternative corridor maps would have overlapped more, suggesting the model is robust to all parameter estimates: a self-serving result with little biological insight. In a corridor over 65 km long, an average width narrower than 3 km would be unreasonable both for small animals (which need a corridor wide enough to support metapopulations for many generations to move their genes that far) and larger animals (which may be sensitive to human-caused mortality and edge effects).

Finally, the preliminary linkage design was defined as the simple union of the proposed corridors for each focal species. Thus, any pixel that was a part of the proposed corridor for one focal species was included in the preliminary linkage design.

Alternative scenarios for resistance values and weights

Our objective was not to test all possible values of model parameters, but to test across the plausible range

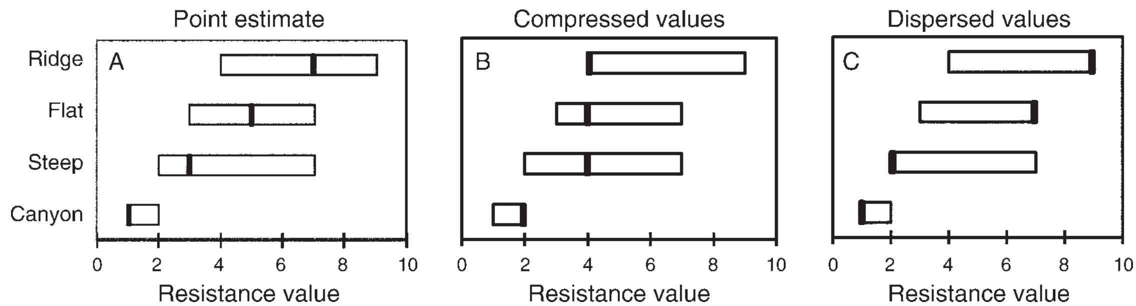

FIG. 2. Illustration of compressed- and dispersed-resistance scenarios for a hypothetical species. A species expert estimated resistance to movement (on a scale of 1 to 10) and the range of uncertainty around that estimate (indicated by the rectangle in each panel). The thick bars represent (A) the point estimate provided by the species expert, (B) the compressed-resistance scenario in which each value is moved toward the mean without changing rank order, and (C) the dispersed-resistance scenario, in which each value is moved toward the extreme without changing rank order. For details, see *Methods: Alternative scenarios for resistance values and weights*.

of biological uncertainty. As described in the *Introduction*, we assumed this range was bracketed by the expert's estimates of minimum and maximum values. We varied factor weights and class resistance values to create 13 worst-case scenarios, (i.e., five compressed resistance scenarios, five dispersed-resistance scenarios, one compressed-weight scenario, one dispersed-weight scenario, and one worst-combination scenario).

In the five compressed-resistance scenarios, the highest and lowest point estimates in each set of resistance values were replaced by values closer to the mean of the point estimates (Fig. 2). These scenarios reflect the possibility that differences among classes were much smaller than reflected in the point estimates provided by the expert. For example, given literature showing that an animal most prefers canyon bottoms, followed by steep slopes, flat terrain, and ridges, the expert might assign resistance values as the vector {1, 3, 5, 7} (Fig. 2A, which also depicts the expert's estimate of uncertainty in each value). The most compressed scenario that fits within the expert's uncertainty is the vector {2, 3.99, 4, 4.01}, which can be rounded to {2, 4, 4, 4}. There were five compressed-resistance scenarios (compressing resistance scores for each of the four factors singly, plus all four in concert).

Similarly, we created five dispersed-resistance scenarios in which point estimates were replaced by values further from the mean, reflecting the possibility that the expert's point estimates grossly underestimated differences among classes or factors (Fig. 2). There was one compressed-weight scenario and one dispersed-weight scenario, again reflecting the possibility that the expert grossly exaggerated or underestimated the true differences in weights, subject to the constraint that the weights must sum to 100% (Table 2). After we ran the first 12 scenarios, we created the worst combination scenario by combining the sets of resistance values and weights (compressed or dispersed) that produced the least overlap with the proposed corridor.

Impact of model uncertainty

We assessed how uncertainty in factor weights and class resistance values affected two important model outputs, namely corridor location and resistance in the predicted corridor. We assessed stability of corridor location by percent overlap, calculated as the percentage

TABLE 2. Illustration of compressed- and dispersed-weight scenarios for a hypothetical species.

Factor	Point estimate (minimum–maximum)†	Compressed weights‡	Dispersed weights§
Land cover	60 (40–90)	40	90
Elevation	20 (0–35)	20	6
Topographic position	15 (0–25)	20	4
Road density	5 (0–25)	20	0

† Specified by species experts, based on literature review and experience.

‡ To develop this scenario, we set the largest weight to the greater of its minimum or (100 − sum of other three maxima), then moved the smallest weight to the lesser of its maximum or one-third of the remaining weight. We kept the remaining two weights in the same ratio to each other, or set them equal to the smallest weight if needed to avoid reversals of rank order. If two or more factors were tied for highest or lowest, we considered the weight for land cover larger than any tied weight, followed by elevation, topographic position, and road density.

§ We set the largest weight at the lesser of its maximum or (100 − sum of other three minima). We then moved the smallest weight as close as possible to its minimum without moving the other two weights below their minimums. We kept the remaining two weights in the same ratio to each other.

TABLE 3. For each of eight focal species, we assessed the impact of uncertainty in class resistance values and factor weights by calculating the extent to which the proposed corridor and preliminary linkage design overlapped corridors produced by 13 plausible alternative corridors; we also calculated how much resistance in the proposed corridor increased compared to resistance in the 13 alternatives.

Species	Overlap, mean (%) and range		Mean increase in resistance§	Four largest increases in resistance§
	Proposed corridor†	Preliminary linkage design‡		
Puma	49 (3–99)	58 (8–99)	0.11	0.36, 0.35, 0.32, 0.34
American badger	66 (0–100)	72 (23–100)	0.00	0.27, 0.11, 0.06, 0.04
San Joaquin kit fox	94 (89–100)	97 (92–100)	0.01	0.09, 0.07, 0.06, 0.01
Mule deer	82 (59–97)	94 (78–100)	−0.01	0.20, 0.08, 0.05, 0.02
Western gray squirrel	91 (77–100)	97 (90–100)	0.01	0.08, 0.08, 0.06, 0.02
Tipton kangaroo rat	94 (75–99)	95 (75–100)	0.03	0.31, 0.02, 0.02, 0.02
Tehachapi pocket mouse	58 (0–100)	63 (0–100)	0.06	0.39, 0.30, 0.23, 0.05
California Spotted Owl	82 (48–100)	92 (76–100)	0.00	0.15, 0.04, 0.01, 0.01

† Percentage of the alternative corridor overlapped by the proposed corridor.
‡ Percentage of the alternative corridor overlapped by the union of the eight single-species proposed corridors.
§ Mean resistance (scale 1 to 10) of all pixels in proposed corridor minus mean resistance in the alternative corridor, with both values calculated using parameter estimates of the alternative corridor. Resistance was measured on a scale of 1–10.

of the alternative corridor overlapped by the proposed corridor or preliminary linkage design. We deliberately chose this over the alternative measure of overlap (namely the percentage of the proposed corridor or linkage design overlapped by each alternative corridor). Our rationale was that the proposed corridors and linkage design are being implemented as a conservation intervention, and conservation investors need estimates of the errors associated with implementing the proposed plan if an alternative scenario is in fact correct.

Percentage of overlap tells only part of the story. For instance, a proposed corridor that totally fails to overlap an alternative corridor might still have resistance similar to the alternative. Therefore, for each alternative corridor, we calculated the potential increase in resistance by subtracting the mean resistance of all pixels in the proposed corridor from the mean resistance of pixels in the alternative corridor, using parameter estimates of the alternative scenario to calculate the resistance raster for both corridors. As with overlap, this calculation reflects the ecological consequence of implementing the proposed corridor when the alternative scenario is correct.

We examined whether model robustness was associated with the degree of habitat specialization of the focal species. To characterize habitat breadth of each species, for the 34 land cover classes that occupied at least 200 ha in the linkage area, we calculated the proportion of resistance scores ≤ 5. This produced the following array from relative habitat specialists to relative habitat generalists: Tipton kangaroo rat (0.09), San Joaquin kit fox (0.12), California Spotted Owl (0.38), western gray squirrel (0.41), Tehachapi pocket mouse (0.53), mule deer (0.59), American badger (0.65), and puma (0.68).

Carnivores as umbrella species

To estimate the effectiveness of the focal carnivores (puma, badger and San Joaquin kit fox) as umbrella species, we calculated how well predicted corridors for each carnivore, and preliminary linkage designs for all three carnivores, overlapped the proposed corridors of the other five focal species. We also calculated resistance for each of the non-carnivores in each of the carnivore corridors.

TABLE 3. Extended.

Three scenarios least overlapped by proposed corridor		
Overlap (%)		
Proposed corridor†	Preliminary linkage design‡	Increase in resistance§
3	8	0.19
14	30	0.24
26	39	0.36
0	23	0.27
0	27	0.06
0	26	−0.36
89	92	−0.06
89	94	−0.04
90	94	0.06
59	78	−0.12
72	87	0.05
73	88	0.08
77	90	−0.02
83	94	0.06
83	95	0.08
75	75	0.31
91	93	0.02
91	97	0.02
0	17	0.39
0	21	0.30
0	12	0.23
48	76	0.01
55	81	−0.07
56	82	−0.07

RESULTS

On average, 78% of each alternative corridor was overlapped by the species' proposed corridor, but overlaps ranged from 0% to 100% (Table 3, Fig. 3). The locations of corridors for five species (San Joaquin kit fox, mule deer, western gray squirrel, Tipton kangaroo rat, and California Spotted Owl) were relatively stable as factor weights, and class resistances were varied across their biologically plausible ranges (Table 3). For instance, the proposed corridor for San Joaquin kit fox overlapped 89% of the most divergent alternative corridor for kit fox, and a mean of 94% of each of the 13 alternative corridors. The proposed corridors for mule deer, western gray squirrel, Tipton kangaroo rat, and California Spotted Owl each overlapped at least 48% of each alternative (Table 3).

The locations of proposed corridors for puma, American badger, and Tehachapi pocket mouse were less robust to biological uncertainty. For each of these three species, the proposed corridor overlapped <3% of at least one alternative corridor (Table 3). The proposed corridor for puma overlapped <60% of most alternative puma corridors and on average overlapped only 49% of the area in alternative puma corridors. The proposed corridor for Tehachapi pocket mouse overlapped >85% of 8 of the 13 alternative corridors, but overlapped 0% of the other five alternative corridors. The proposed corridor for American badger overlapped at least 68% of 10 alternative corridors, but overlapped 0% of the other three alternatives. In general, spatial robustness of the modeled corridor to uncertainty in parameters was highest for habitat specialists, and decreased with habitat breadth (Fig. 4).

Even when the proposed corridor overlapped little or none of a biologically plausible alternative corridor, resistance in the proposed corridor was typically about the same as that in the alternative corridor, using the alternative scenario's estimates for weights and resistance values (Table 3, Fig. 5). On a resistance scale of 1–10, resistance in the proposed corridor was never more than 0.39 resistance units worse than resistance in the alternative. Across all alternative corridors for all species, resistance in the proposed corridor was, on average, 0.025 resistance units greater than in the alternative. Thus, in almost every case the proposed corridor had roughly equal resistance to the alternative (Fig. 5), even when the two routes did not overlap.

The multiple-species preliminary linkage design was marginally more robust than the individual species models in its spatial response to uncertainty (Table 3). The preliminary linkage design overlapped an average of 84% of the area in alternative corridors, and overlapped <50% of 12 of the 104 alternative corridors (Fig. 3).

The proposed corridors for each of the three carnivore species performed poorly as corridors for other focal species, completely failing to overlap the proposed corridors of most other focal species (Table 4). Even more importantly, the carnivore corridor provided markedly higher resistance to movement than the predicted corridor for the other focal species (Table 5). On average, resistance increased by 2.7 points (on a resistance scale of 1–10) in the carnivore corridor compared to the predicted corridor for each focal

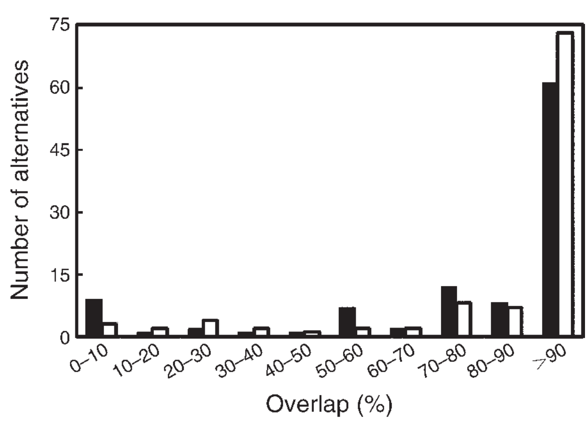

FIG. 3. Frequency distribution of percentage of the area within 104 alternative corridors (13 alternatives for each of eight species) overlapped by the species' proposed corridor (solid bars) or the multiple-species preliminary linkage design (open bars).

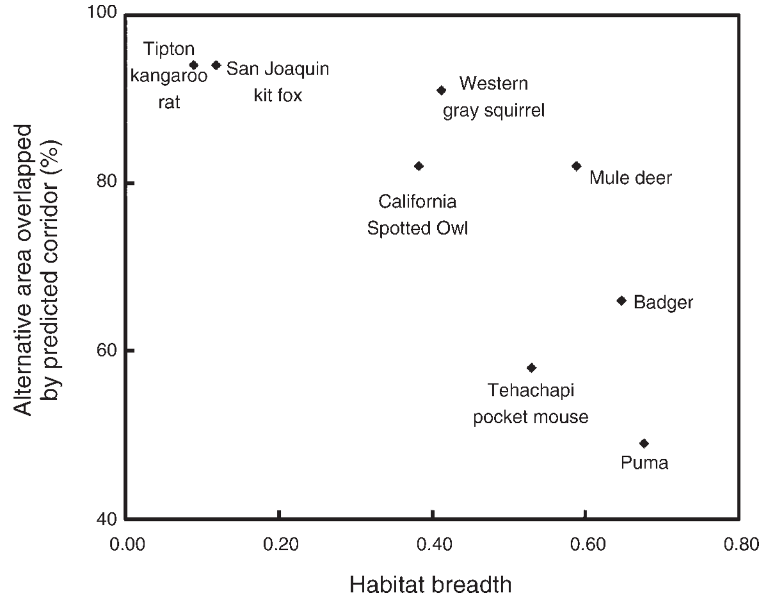

FIG. 4. Model robustness (as measured by mean percentage of 13 alternative corridors overlapped by the species predicted corridor) decreased with habitat breadth (proportion of 34 land cover classes used as breeding habitat); $R^2 = 0.64$.

species. In 9 of 27 cases, the focal species would face resistance ~4–6 points greater in the carnivore corridor than in the predicted corridor for that focal species (Table 5). The increase was <1 point in only 6 of 27 cases.

DISCUSSION

Impact of uncertainty on the Tehachapi Linkage Design

For five of eight focal species, the proposed corridor usually overlapped most of the area in each biologically plausible alternative corridor, and resistance in the proposed corridor did not increase markedly under other biologically plausible estimates of factor weights and resistance scores. Although models for American badger, puma, and Tehachapi pocket mouse were somewhat less robust in spatial location (the predicted corridor overlapped less than half of some biologically plausible alternative corridors), the resistance of the proposed corridor was never more than 0.39 resistance units (mean 0.06 units on a 9-point scale) worse than any alternative corridor. Such remarkable robustness in resistance could occur if the matrix offered homogeneous resistance to each species. But this was not the case, as evidenced by the fact that carnivore corridors in the same matrix offered high resistance to the other focal

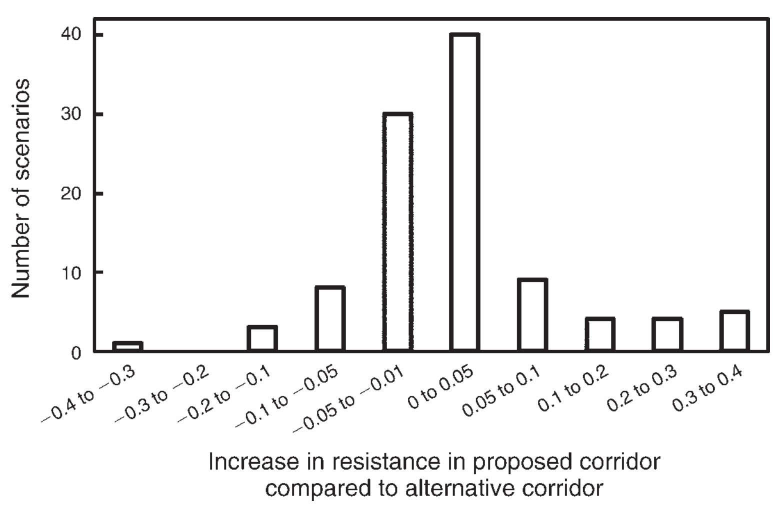

FIG. 5. If conservation investors implemented the predicted corridor when another plausible corridor was correct, how much would resistance to movement increase? Typically, resistance (scaled 1–10) did not increase at all, and it rarely increased more than 0.1 point (on a nine-point scale) across 104 alternative scenarios (13 scenarios for each of eight focal species).

Table 4. Percentage of predicted corridors of each focal species overlapped by a "carnivore corridor" for a single carnivore, or for all three carnivore species.

Focal species	Species used to design the "carnivore corridor" (%) Puma	American badger	San Joaquin kit fox	All three carnivores
Puma		0	0	
American badger	0		0	
San Joaquin kit fox	0	0		
Mule deer	48	0	0	48
Western gray squirrel	33	0	0	33
Tipton kangaroo rat	0	0	94	94
Tehachapi pocket mouse	0	0	91	91
California Spotted Owl	43	0	0	43
Mean	18	0	26	62

species. We conclude that both locations and permeability of the predicted corridors for all eight species are robust to uncertainty in factor weights and class resistance values. Quinby et al. (1999), Schadt et al. (2002), Larkin et al. (2004), Kautz et al. (2006), and Adriaensen et al. (2007) similarly found that locations of modeled corridors or least-cost paths were robust to uncertainty in resistances or weights.

Our minimum and maximum values were subjectively estimated by a single species expert relying on scientific literature and experience. Except when assigning values to the most strongly avoided and most preferred classes, the ecologists who parameterized our models readily admitted uncertainty in their estimates (Table 1), such that the alternatives we evaluated typically seemed constrained mostly by the rank order of the estimates (e.g., Fig. 2). Nonetheless, experts and nonexperts tend to underestimate their uncertainty (Behn and Vaupel 1982), and this problem doubtless affected our analyses. We recommend improving on our approach by recruiting more than one ecologist to parameterize each model, and using the highest and lowest point estimates to bracket the reasonable range of uncertainty.

Our case study invoked worst-case scenarios at two levels. First, we analyzed uncertainty for the linkage design that had the largest costs (largest areas of private land) and was least constrained by existing urbanization (providing maximum opportunity for divergent model results) of the 15 linkage designs produced using the same least-cost modeling effort in southern California. Furthermore, we analyzed how much the predicted corridor diverged from the most extreme combinations of alternative factor weights and resistance values. Even the most risk-averse conservation investors should be reassured by our finding that least-cost corridor designs are not highly sensitive to uncertainty as long as the resistance values and factor weights are arrayed in the correct rank order.

Almost all least-cost models estimate resistance by subjective inferences from studies of habitat use by the focal species (Beier et al. 2008). Because animal movement is not the same as habitat use, this is a fundamental weakness of these models. We recommend using empirical data on animal movement patterns, rates of interpatch movement, or landscape patterns of genetic similarity to derive more rigorous estimates of resistance (Beier et al. 2008).

Uncertainty analysis in conservation ecology

In the long term, retrospective monitoring in an adaptive management framework or via systematic reviews will yield the most reliable inferences about the effectiveness of interventions (Sutherland et al. 2004). In the short term, uncertainty analysis is a useful tool that should be a routine part of linkage designs and other model outputs offered as blueprints for conservation. Although uncertainty analysis is occasionally used to evaluate the robustness of predictions from models of population viability (e.g., Minor et al. 2008), we found few examples in which it has been used to evaluate maps offered as blueprints for conservation. In addition to five examples relevant to linkage design (see previous section), Lee et al. (2006) used Monte Carlo simulations to evaluate the impact of uncertainty on maps of habitat suitability, and Moilanen et al. (2006) modified the objective function of a reserve selection algorithm to

Table 5. Increase in mean species-specific resistance for each focal species in a linkage designed for a single carnivore.

Species	Species used to design "carnivore corridor" Puma	American badger	San Joaquin kit fox
Puma		0.84	1.02
American badger	1.93		0.45
San Joaquin kit fox	3.40	4.65	
Mule deer	0.88	4.90	4.07
Western gray squirrel	1.80	5.63	5.59
Tipton kangaroo rat	3.98	4.68	0.04
Tehachapi pocket mouse	2.14	0.25	0.04
California Spotted Owl	1.30	4.69	4.60
Mean	2.20	3.70	2.30

Notes: The increase was calculated as the mean resistance in the predicted corridor for that species minus the resistance the focal species would experience in the carnivore corridor. Resistance is scaled from 1 to 10.

discount species occurrence records based on their uncertainty.

We suggest that our worst-case scenario approach to uncertainty analysis is appropriate for least-cost models and could be adapted to other complex models in conservation ecology. From the perspective of a decision-maker investing scarce resources in a conservation plan or a conservation biologist concerned about extirpation of focal populations, an estimate of the worst possible loss may be more meaningful than the mean or typical performance of a modeling approach (Cooney and Dickson 2006). The worst-case scenario describes the impact of uncertainty in a more meaningful way than the first derivative of a function, the effect of a 1 SD change in an input variable, or other statistical approaches to uncertainty analysis. Our approach also does not require that the distribution of input parameters be known.

Previous uncertainty analyses of proposed corridors considered only how uncertainty affected the *location* of the modeled corridor. We used corridor location (percentage of each biologically plausible alternative overlapped by a proposed design) in concert with a second response variable, namely, potential *increased resistance* to movement, to provide a more complete picture of how uncertainty affects corridor design. We (P. Beier and J. Jenness) are currently developing GIS tools that will provide an even better measure, namely, the longest gaps between patches of potential breeding habitat within a corridor. In the future, we hope analysts will use even more meaningful response variables, such as estimates of population viability or rates of gene flow.

Beier et al. (2008) list over a dozen decisions and assumptions in corridor modeling that can impact a corridor design. The two sources of uncertainty we studied (uncertainty in estimating factor weights and class resistance values) are among the most important because they provide the link between species ecology and GIS (Adriaensen et al. 2003) and because there is so much uncertainty in these estimates. We call attention to two other important sources of uncertainty in linkage design. First, there are errors in the GIS layers for land cover, topographic position, road density, and elevation. Unfortunately, the most important of these four factors, land cover (mean weight of 68% in our models), is mapped with the least reliability, with typical classification errors of 20% to 40% (Yang et al. 2001). Land cover had the least uncertainty in weight (range of uncertainty was 38% of the mean, compared to 62–120% of the mean for the other three factors) and the least uncertainty in resistance values (Table 1). Thus, improving the reliability of the land cover map is probably the most effective single step to improve the reliability of any least-cost model in which land cover has a large weight and low uncertainty.

Second, model insufficiency can affect reliability of a linkage design. A model is *insufficient* (Malczewski 2000) to the extent it does not encompass all the factors that contribute to resistance. In 24 published corridor designs, there were one to five (mean 2.3, mode 2) factors per model, and the most common factors were land cover (23 of 24 models) and roads (16 of 24 models) (Beier et al. 2008). With four factors, our models were more comprehensive than most corridor models. Nonetheless, our models did not include soil type, distance to water, and other factors for which we lacked reliable maps. To the extent that an important factor was omitted, the predicted corridors could be wrong. Creation of high-resolution, reliable maps of soils, rock outcrops, and permanent water sources are critical to developing better models (Beier et al. 2008).

Carnivores and focal species

The three carnivore species were not suitable umbrellas for movement of other species in the Tehachapi Linkage Area. Each carnivore corridor offered much higher resistance to movement of most focal species compared to resistance in the predicted corridors of those focal species. Although our results are specific to this landscape and set of focal species, we believe carnivores are poor umbrellas for linkage design in most landscapes. First, many carnivores are habitat generalists, and we found that models for habitat generalists were least robust to uncertainty (Fig. 4). More important, promoting a carnivore corridor could have a "negative umbrella effect" if conservation stakeholders become less receptive to subsequent proposals for less charismatic species. Nonetheless, we advocate including carnivores as focal species because they can be flagships for a multiple-species linkage design and because many carnivores are area-sensitive and thus need connectivity. In short, carnivores are appropriate focal species for linkage designs, but are not appropriate as the *only* focal species.

We recommend using multiple and diverse focal species to design wildlife linkages. Because multiple-species designs include greater total area, they are somewhat more likely to encompass the true least-cost corridor of each focal species despite uncertainty (Fig. 3). More important, multiple-species linkage designs are more likely to serve other species sharing traits with the suite of focal species. Lambeck (1997) and Coppolillo et al. (2004) describe procedures for choosing multiple focal species to represent the needs of the entire biota. Beier et al. (2006) provide specific criteria for selecting focal species in the context of corridor design.

Ecological applications

The people and funders who conserve linkages deserve high-quality, transparent science. In particular, they deserve honest answers to questions such as: If we invest in a linkage design that turns out to be wrong, how badly could that linkage serve the focal species and the biotic community? In this paper, we have tried our best to answer this question for the least-cost modeling approach used to design 15 linkages in one hotspot of biodiversity. Given the massive investments and other conservation actions in these 15 linkage areas, we are pleased that this approach appears robust to uncertainty in two important parameters.

Uncertainty analysis should routinely be used to evaluate maps proposed to guide conservation decisions. The response variables for uncertainty analysis of corridors should, at a minimum, include location and potential increase in resistance of the corridor. A worst-case scenario approach to uncertainty analysis is relatively easy to implement and is consistent with a precautionary approach. Linkage designs should be based on the needs of multiple focal species, including but not limited to top carnivores.

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