Review

Forks in the Road: Choices in Procedures for Designing Wildland Linkages

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Abstract: *Models are commonly used to identify lands that will best maintain the ability of wildlife to move between wildland blocks through matrix lands after the remaining matrix has become incompatible with wildlife movement. We offer a roadmap of 16 choices and assumptions that arise in designing linkages to facilitate movement or gene flow of focal species between 2 or more predefined wildland blocks. We recommend designing linkages to serve multiple (rather than one) focal species likely to serve as a collective umbrella for all native species and ecological processes, explicitly acknowledging untested assumptions, and using uncertainty analysis to illustrate potential effects of model uncertainty. Such uncertainty is best displayed to stakeholders as maps of modeled linkages under different assumptions. We also recommend modeling corridor dwellers (species that require more than one generation to move their genes between wildland blocks) differently from passage species (for which an individual can move between wildland blocks within a few weeks). We identify a problem, which we call the subjective translation problem, that arises because the analyst must subjectively decide how to translate measurements of resource selection into resistance. This problem can be overcome by estimating resistance from observations of animal movement, genetic distances, or interpatch movements. There is room for substantial improvement in the procedures used to design linkages robust to climate change and in tools that allow stakeholders to compare an optimal linkage design to alternative designs that minimize costs or achieve other conservation goals.*

Keywords: connectivity, linkage, reserve design, uncertainty analysis, wildlife corridor

Bifurcaciones en el Camino: Opciones de Procedimientos para el Diseño de Enlaces de Tierras Silvestres

Resumen: *Los modelos son utilizados comúnmente para identificar tierras que mantengan la habilidad de la vida silvestre para moverse entre bloques de tierras silvestres a través de una matriz de tierras que habían sido incompatibles con el movimiento de vida silvestre. Ofrecemos 16 opciones y supuestos que se originan en el diseño de enlaces para facilitar el movimiento o el flujo de genes de especies focales entre 2 o más bloques de tierras silvestres predefinidos. Recomendamos el diseño de enlaces que sirvan a múltiples (y solo a una) especies focales que funjan como una sombrilla colectiva para todas las especies nativas y los procesos ecológicos, que explícitamente admitan supuestos no comprobados y que utilicen análisis de incertidumbre para ilustrar efectos potenciales de la incertidumbre del modelo. La mejor forma de mostrar tal incertidumbre a los interesados es mediante mapas de los enlaces modelados bajo diferentes suposiciones. También recomendamos modelar a habitantes de corredores (especies que requieren más de una generación para mover sus genes entre bloques de tierra silvestre) de manera diferente que las especies pasajeras (un individuo se puede mover entre bloques de tierras silvestres en unas cuantas semanas). Identificamos un problema, que denominamos el problema de traducción subjetiva, que surge porque un analista debe decidir subjetivamente cómo traducir medidas de selección de recursos a resistencia. Este problema puede ser*

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sobrepuesto mediante la estimación de la resistencia a partir de observaciones de movimientos de animales, distancias genéticas o movimientos entre fragmentos. Hay espacio para la mejora sustancial de los procedimientos utilizados para diseñar enlaces robustos ante el cambio climático y en herramientas que permiten que los interesados comparen un diseño óptimo con diseños alternativos que minimicen costos o alcancen otras metas de conservación.

Palabras Clave: análisis de sensibilidad, conectividad, corredor de vida silvestre, enlace, diseño de reservas

Introduction

Wildlife linkages can mitigate the impacts of habitat fragmentation on wildlife populations and biodiversity (Beier & Noss 1998; Haddad et al. 2003). Designing a linkage involves identifying specific lands that will best maintain the ability of wildlife to move between wildland blocks even if the remaining land (matrix) becomes inhospitable to wildlife movement. Modeling, such as least-cost analysis, is at the heart of most approaches to linkage design (but see Noss and Daly [2006] for seat-of-the-pants approaches and Fleury and Brown [1997] for an approach derived from first principles of conservation biology). Modeling approaches are especially important when the potential linkage is not fully constrained by urbanization or other irreversible barriers, when the linkage is designed for multiple focal species, or when planners need to provide a transparent, rigorous rationale for a linkage design.

Ironically, many linkage designs lack the transparency that should be a key advantage of a modeling approach. Key assumptions are often unstated and alternative approaches are rarely mentioned. For example, in each of 24 recent studies in which researchers used GIS procedures to identify connective habitats (Table 1), the approach seemed reasonable, but each approach was different. Some of these differences reflect the different goals of each effort, but some differences may reflect ignorance of alternatives. Few of these studies explored sensitivity of the linkage design to alternatives.

We have helped produce 31 linkage designs for landscapes in Arizona and southern California (South Coast Wildlands 2003–2006; Beier et al. 2006, 2007). In our experience, stakeholder discomfort with a poorly defined or justified model can result in objections to the entire approach (Table 2). Conservation biologists should therefore structure and explain their models in a way that addresses, or at least acknowledges, key assumptions and alternatives. Explicitly recognizing choices along the road to linkage design is essential to creating more rigorous conservation prescriptions.

Here we offer a roadmap of the assumptions and choices involved in designing linkages for focal species between 2 or more wildlands. Thus we did not consider simulated annealing approaches (Andelman et al. 1999; Possingham et al. 2000) or spatially explicit population models (Carroll et al. 2003) that take a broader approach to reserve design, simultaneously prioritizing land both for core-habitat blocks and linkages between them. Because conservation biologists often are faced with designing a linkage to connect 2 fixed reserve areas, we addressed a family of approaches appropriate in many landscapes. We concentrated on focal-species approaches, rather than approaches intended to promote general ecological connectivity (Hoctor et al. 2000; Carr et al. 2002; Marulli & Mallarach 2005) or to encompass environmental gradients or processes (Rouget et al. 2006). These latter approaches emphasize naturalness of land cover and may be more appropriate for depicting a coarse regional network than for designing a specific linkage.

Developing our procedures (South Coast Wildlands 2003–2006; Beier et al. 2006, 2007) has been a tortuous journey, with many decision points, or forks, encountered along the road to linkage design. In some cases we explored several paths before settling on one. At other forks lack of time or data propelled us along a particular path, leaving us wondering how different the resultant linkage design would be at the end of a path not taken. A framework for linkage design can facilitate sharing of lessons and reduce the risk that a practitioner will take a particular fork without noticing alternative, and potentially better, options. We outline the questions facing the analyst, describe and evaluate the ways analysts have answered these questions, and suggest better answers. Ultimately, we hope this framework will make linkage designs more defensible and successful.

The Basic Elements of Linkage Design

We define a *corridor* as a swath of land intended to allow passage by a particular wildlife species between 2 or more wildland areas. We use the term *linkage* to denote connective land intended to promote movement of multiple focal species or propagation of ecosystem processes. We also use *linkage* as a generic term when the distinction is unnecessary.

All published linkage designs for focal species (Table 1) follow the same basic steps (Fig. 1). First stakeholders define their biological goals by identifying the landscape and focal species. Then the analyst develops an

Table 1. Studies that produced maps of corridors, linkages, or cost surfaces to guide conservation decisions in the mapped landscape.

Author & year(s) of publication	*Focal species or focal ecological condition*	*Habitat factors*[a]	*Map product*[b]	*How resistance values were estimated*	*Decisions subject to uncertainty analysis*
Adriaensen et al. 2007	8 birds, forest butterflies	L, R, E	corridor	expert opinion, research on target species in linkage area	resistance values
Bani et al. 2002	9 birds, 3 carnivores	L	path	empirical data on relative abundance of focal species in linkage area	none
Beier et al. 2007	10 or more mammals, reptiles, & amphibians per linkage	L, R, E, T	corridor	expert opinion and literature review	none
Carr et al. 2002	naturalness	L, R	cost map	expert opinion and literature review	none
Epps et al. 2007	*Ovis canadensis nelsoni*	T, R	path	genetic data	defining terminuses[c]
Graham 2001	*Ramphastos sulfuratus*	L	path	empirical data on habitat use and movement in linkage area	resistance values
Hoctor et al. 2000	naturalness	L, R, edge	corridor	expert opinion and literature review	none
Hunter et al. 2003	*Lynx rufus, Puma concolor*	L, R	cost map	expert opinion and literature review	none
Joly et al. 2003	*Bufo bufo*	L, R	cost map	expert opinion and literature review	none
Kautz et al. 2006	*P. concolor*	L	path	empirical data on habitat use in linkage areas	resistance values
Kindall & van Manen 2007	*Ursus americanus*	L, edge, F	cost map	empirical data on habitat use in linkage area	none
Kobler & Adamic 1999	*U. arctos*	L	path	empirical data on animal occurrences in linkage area	none
Larkin et al. 2004	*U. arctos*	L, R	path	expert opinion and literature review	resistance values
Marulli & Mallarach 2005	naturalness	L, R	corridor	expert opinion and literature review	none
Quinby et al. 1999	*Canis lupus*	L, R, N, W	corridor	expert opinion and literature review	resistance values, factor weights
Rubert 2007	*Sylvilagus aquaticus*	L, R, W, canopy	path	expert opinion	none
Schadt et al. 2002	*L. lynx*	L, R	path	empirical data on habitat use in linkage areas	resistance values
Servheen et al. 2001	*U. arctos*	L, R	cost map	expert opinion and literature review	none
Singleton et al. 2002	*C. lupus, Gulo gulo, L. canadensis, U. arctos,* "general carnivore"	L, R, N, E, S	corridor	expert opinion and literature review	none
South Coast Wildlands 2003–2006; Beier et al. 2006; Newell 2006; www.scwildlands.org	10 or more mammals, reptiles, amphibians, fish, birds, invertebrates, or plants per linkage	L, R, E, T	corridor	expert opinion and literature review	resistance values, factor weights, number of focal species
Sutcliffe et al. 2003	2 butterfly species	L	path	empirical data on interpatch movement (best fit of 5 vectors)	none[c]
Walker & Craighead 1997	*U. arctos, P. concolor, Cervus elaphus*	L, R, edge	cost map	expert opinion and literature review	none
Wikramanayake et al. 2004	*Panthera tigris*	L, E	cost map	expert opinion	none
Williams et al. 2005	plant family Protaceae	L, C	path	not applicable[d]	none

[a] *Abbreviations: C, climate envelope model; canopy, % canopy closure of forest; E, elevation; edge, edge between land cover types; F, forest cohesion and diversity; L, land cover and land use; N, human population size; R, road density or proximity to roads or road presence mapped as a land cover type; S, slope; T, topographic feature; W, proximity to water.*

[b] *Definitions: path, a swath that is one pixel wide (pixels were 2.9-km^2 cells for Williams et al. 2005); corridor, slice encompassing the most permeable percentiles of the cost map; cost map, cumulative resistance displayed as a gradient without explicitly stating a threshold percentile constituting the recommended corridor.*

[c] *Some uncertainty analysis of resistance values occurred in fitting resistance values to data.*

[d] *Resistance was not explicitly calculated. Each species was assumed to disperse to all cells with predicted suitable climate within its dispersal distance.*

Table 2. Objections that may arise to focal-species approaches to linkage design when assumptions and choices are not clearly explained.*

Objection	*Relevant questions (Table 3)*
A linkage designed to conserve focal species may fail to conserve ecological processes.	2, 11, 15
A corridor designed for 1 or 2 large carnivores (often highly mobile habitat generalists) probably will not serve other species.	2
The model uncritically assumes that animals use the same rules to make movement decisions as they use to select habitat.	5, 9
Animals choose habitat and make movement decisions on the basis of availability of food and mates and safety from predators and hazards, but the model is derived from a few factors widely available in GIS format.	3
Because climate change will change the land-cover map used in the model, the linkage design will fail.	15
The least-cost model always produces a “best” route, but the best may not be good enough to allow movement and gene flow.	14
Basing GIS models on movement is not appropriate for species that need several generations to move their genes through a linkage.	9
A linkage may facilitate movement of invasive species.	2, 11, 16
The expense of implementing the linkage design outweighs its benefits.	14
Least-cost modeling ignores some plants, insects, and birds whose movement cannot be modeled in this framework.	14

**Linkage designers can address most issues by addressing relevant questions (second column).*

algorithm to estimate the resistance of each pixel for each species as a function of pixel attributes, such as land cover, topography, and level of human disturbance. Following Adriaensen et al. (2003), *resistance* refers to the difficulty of moving through a pixel and *cost* (or *effective distance*) is the cumulative resistance incurred in moving from a pixel to both corridor terminuses. Next the analyst selects a swath of pixels with the lowest cost between wildlands; this swath is the *corridor design* or *modeled corridor* for one focal species. Corridor designs for multiple focal species are combined into a *preliminary linkage design* (Fig. 2), which becomes the *final linkage design* after it is modified to accommodate ecological processes, incorporate other pixels of conservation interest, buffer against edge effects, or achieve other objectives.

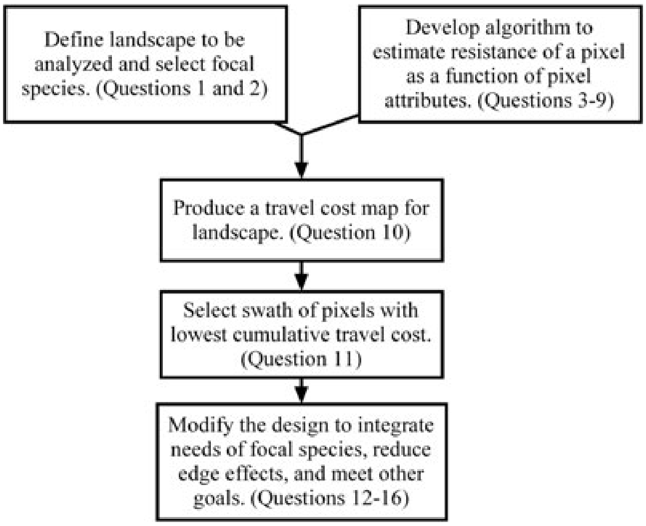

Figure 1. General flowchart for a GIS-based linkage design. The process in each box involves questions listed in Table 3 and discussed in the text.

Forks in the Road

Behind the straightforward facade of Fig. 1 lie many choices that we present in an order corresponding to sequential analytic steps (Table 3).

1. HOW SHOULD THE ANALYSIS AREA BE DEFINED?

The analysis area for a linkage design typically includes the wildland blocks to be linked, the matrix between

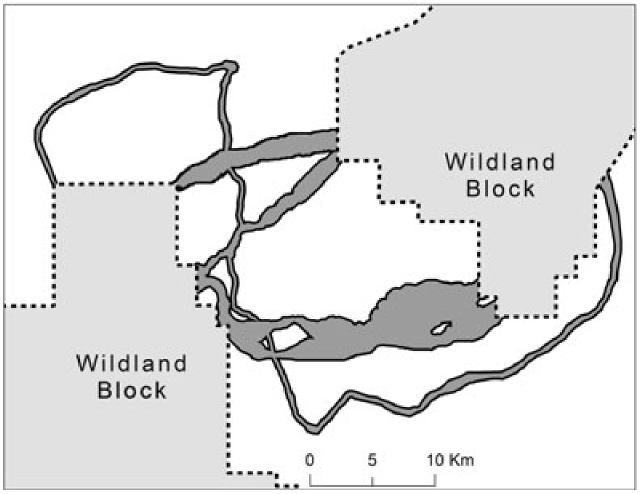

Figure 2. Example of single-species corridors joined into a preliminary linkage design. The needs of different focal species produce multiple strands. Facilitating landscape elements (such as riparian areas) can produce deeply looped strands.

Table 3. Sixteen key questions in linkage design and potential responses to each question.

Key question	*Recommendation (R), choices (C), and ranked options (C_n)**	*Product at this point of the analysis*
1. How should the analysis area be defined?	R: rectangle including facing edges of wildland blocks, intervening matrix, and facilitating elements	
2. How should focal species be identified?	R: multiple species, chosen to represent ecological processes, sensitivity to barriers, etc.	
3. What landscape factors should the model include?	R: use a comprehensive set of factors R: acknowledge when available data layers are not comprehensive	
4. What metric should be used for each factor?	R: report source, resolution, and accuracy of data	
5. How should resistance of each class of pixels be estimated?	C_1: from animal-movement data, genetic distance, or rates of interpatch movement C_2: from animal occurrence, density, or fitness C_3: literature review and expert opinion	resistance value for each class within each factor
6. How should factor resistances be combined?	C_1: geometric mean C_2: weighted sum C_3: weighted product R: display maps showing sensitivity of predicted linkage to this choice and previous choice	
7. How should a corridor terminus be delineated?	R: for analysis purposes, "pull back" facing edges of nearly touching blocks to give model "room to run" R: use a potential or known population for each terminus	
8. How should habitat patches be delineated?	R: map potential breeding patches to help define terminuses, increase likelihood the modeled corridor will encompass stepping stones, and as a tool to evaluate utility of the linkage design	
9. How should corridor dwellers be modeled?	R: assign minimum resistance to breeding patches within effective dispersal distance of patches already included	resistance for each pixel
10. How should continuous swaths of low-resistance pixels be identified?	C: lowest cumulative resistance C: individual-based movement model	cost map of matrix
11. How wide should a single-species corridor be?	R: for corridor dwellers, width should be substantially more than a home range width R: iterative mapping to identify acceptable number and severity of bottlenecks	least-cost corridor for one focal species
12. How should corridors of multiple focal species be combined?	R: union that covers all focal species, but trim redundant strands to minimize area and edge	preliminary linkage design
13. How wide should the linkage design be?	R: "no regret" standard R: add buffer against edge effects	
14. Is the best corridor any good?	C: description of habitat bottlenecks, interpatch distances, and habitat quality C: spatially explicit population model R: avoid a single summary number as a measure of quality	
15. How can the linkage design accommodate climate change?	C: use a dynamic landscape model C: maximize continuity of major topographic–edaphic elements	
16. How should the linkage design address barriers and management practices?	R: integrated prescriptions for land conservation, barrier mitigation, management practices	final linkage design

*_n, rank, with 1 being preferred, followed by 2, 3, etc._

them, and some additional area to allow the model to identify looping corridors. Constraining the analytical window too much may exclude potential source patches, stepping-stone patches, or other facilitating elements that lie outside the core habitat blocks and intervening matrix and thus may preclude optimal solutions (Adriaensen et al. 2003). On the other hand, if the goal is to identify a linkage across a landscape a few kilometers in length, it may be appropriate for the analysis area to exclude areas that may provide an alternative corridor that loops tens of kilometers outside this area.

Defining the wildland blocks to be connected is the critical first step in delineating the analysis area. Wildland blocks may be restricted to lands with the strongest conservation mandate (designated wilderness areas or strict nature reserves) or might include multiple-use natural lands with varying degrees of protection. As long as the areas to be connected are likely to remain wild for at least several decades, these blocks can be delineated on the basis of what conservation investors have an interest in protecting. Within a wildland block, habitat for each focal species may be limited in quality and amount, an issue we return to in questions 7 and 8.

2. HOW SHOULD FOCAL SPECIES BE IDENTIFIED?

We encourage the selection of focal species likely to collectively serve as an umbrella for all native species and ecological processes. For instance, Beier et al. (2006, 2007) invited agency, nongovernmental organizations, and academic biologists familiar with each linkage area to identify species that would serve as a collective umbrella for the biota. They sought to identify species requiring dispersal for metapopulation persistence, species with short or habitat-restricted dispersal movements, species tied to an important ecological process (e.g., predation, pollination, fire regime), species at risk of becoming ecologically trivial if connectivity is lost, and species reluctant to traverse barriers in the planning area. Each of their linkage designs had 10–20 focal species, often including reptiles, fishes, amphibians, plants, and invertebrates. In our experience, stakeholders understood the biota as well as we did, and the list developed with stakeholders was more comprehensive than the preliminary list we or any single stakeholder proposed.

Because large carnivores like bears and wolves live at low density and are among the first to be harmed by loss of connectivity, they are appropriate focal species for linkage design (Beier 1993; Servheen et al. 2001; Singleton et al. 2002). They also make popular flagship species to increase stakeholder support for a linkage. Large carnivores were the only focal species in 10 of 21 linkages designed for focal species (Table 1). Probably many of these carnivore corridors were intended to be implemented as part of a broader linkage design, but some seem to have been offered as designs for the entire biota. We argue against designing a linkage solely for large carnivores—or any single species. Many other species need linkages to maintain genetic diversity and metapopulation stability. Furthermore, most large carnivores are habitat generalists that can move through marginal and degraded habitats, and a corridor designed for them does not serve most habitat specialists with limited mobility (Newell 2006). Indeed, successful implementation of a single-species corridor for large carnivores could have a "negative umbrella effect" if land-use planners and conservation investors become less receptive to subsequent proposals for less charismatic species. The umbrella effect of large carnivores best serves biodiversity if these species are part of a linkage designed for a broad array of native species.

If stakeholders are concerned that a linkage may increase the spread of invasive species into wildlands, then one or more invasive species should be included in the suite of focal species. Any expected invasion via the linkage should be compared with invasion expected from edges and matrix land regardless of the conserved linkage (see question 14).

Delineating the analysis area (question 1) and identifying focal species (question 2) transform the general conservation goal (Conserve connectivity) to a specific one (Conserve connectivity for *these* species between *these* wildland blocks). Because stakeholders are ultimately responsible for defining the goal, the analyst may be reluctant to intrude on these premodeling issues. Nevertheless, in our experience stakeholders rarely share a clearly defined conservation goal, and modelers must actively work with them to address these questions (Beier et al. 2006).

3. WHAT LANDSCAPE FACTORS SHOULD THE MODEL INCLUDE?

Habitat for any species is defined on the basis of life requisites such as food, cover, nest sites, safety from hazards, and relationships with competing or facilitating species. Because these proximate habitat factors are rarely mapped for any species, [redacted] models have used available geographic information system (GIS) environmental data layers as proxies. Each linkage design incorporates at most 5 such proxy variables, typically land cover, 1 or 2 factors related to human disturbance, and 1 or 2 topographic factors (Table 1). Because land cover is related to food and cover and humans are an important hazard for many species, these layers are relevant. Nevertheless, to the extent that these factors fail to fully reflect all life requisites, GIS analysis can give misleading results (Malczewski 2000). How strongly the modeled layers correlate with habitat use or movement by most focal species is unknown.

What can be done about insufficiency of factors? In the short term, linkage designers can simply acknowledge the issue and factor uncertainty into the design. In the long term, the scientific community can encourage development of maps of soils, rock outcrops, permanent water sources, and other factors known to affect habitat use by focal species. In our work in the southwestern United States, these factors are important for focal species such as pronghorn (*Antilocapra americana*), bighorn (*Ovis canadensis*), prairie dogs (*Cynomys* sp.), and many reptiles. With reliable coverages of such features, models could be improved immediately.

4. WHAT METRIC SHOULD BE USED FOR EACH FACTOR?

Once factors are chosen, the analyst must choose resistance-relevant metrics for each factor. Metrics can be categorical (e.g., land-cover types, topographic classes) or continuous (e.g., elevation, distance from water). In most models (Table 1), each continuous variable (e.g., elevation) is converted into a categorical variable with a handful of classes (e.g., below, within, and above the published elevational limits of the species). Land-cover data may be available in a layer with 20–30 coarse classes (National Land Cover Database in the United States) or 70–100 classes (National Gap Analysis Program data layers in the United States).

Most wildlife habitat studies in which these maps were used present the data as if they represented reality (Glenn & Ripple 2004). Nevertheless, classification accuracy is typically 60% to 80% (Yang et al. 2001), and digital maps developed from different remotely sensed images produce markedly different depictions of vegetation (Glenn & Ripple 2004). We recommend that practitioners report resolution, accuracy, and source for land-cover data. We have found it useful to lump GAP classes into 25–50 classes because the GAP accuracy assessments indicate that many errors involve confusion between closely related land covers. Pooling these closely related types increases the classification accuracy of the map.

In most linkage designs, human disturbance was measured by road density within a moving window. Unfortunately, despite the seeming scale invariance of length per length squared, the calculated value of road density changes nonintuitively with the size of the moving window (D. R. Majka, unpublished data). Thus, it is difficult to reliably estimate resistance for road density classes, and published estimates of animal occurrence with respect to road density cannot be translated to a different-sized moving window. Distance to the nearest road avoids this problem and may be a more appropriate road-related metric of human disturbance. We discourage the practice of creating a separate class for road pixels that contain a potential crossing structure (e.g., bridge, culvert) and assigning a low resistance to those pixels. This practice forces the modeled corridor through the crossing structure, even when the structure is located in otherwise poor habitat. Thus it prevents the planner from identifying optimal locations for road-crossing structures.

Models can include one or more topographic metrics, such as elevation, aspect, insolation, slope, ruggedness, or topographic position, all of which are derived from a common set of digital elevation data. Some topographic metrics (e.g., elevation and aspect) probably affect animal movement by determining land cover, or (for poikilotherms) by influencing the thermal environment of the species. Other topographic metrics such as ruggedness and topographic position may directly affect animal movements. Topographic position can be estimated by classifying pixels into any number of classes, such as slope, ridgetop, or valley bottom (algorithms provided by J. Jenness [http://www.jennessent.com/]). The algorithms for ruggedness and topographic position require specifying window size (scale). Although it is appealing to model topography from the perspective of the focal species, the scale at which organisms assess topography is usually unknown. More important, most cost values are assigned by making inferences from scientific publications, which usually report animal response to topography as it was perceived by the human researcher. Dickson and Beier (2007) illustrate the use of topographic position and discuss the issue of window size and other procedural decisions. We encourage uncertainty analysis to address how these decisions affect a modeled corridor.

5. HOW SHOULD RESISTANCE OF EACH CLASS OF PIXELS BE ESTIMATED?

Setting resistance values is “the link between the non-ecological GIS information and the ecological-behavioral aspects of the mobility of the organism or process” (Adriaensen et al. 2003:234). As such it has received more attention from linkage designers than any other issue we discuss here.

Resistance of each class of land use, topography, or human disturbance is usually determined on the basis of expert opinion and literature review. Clevenger et al. (2002) emphasize the poor performance of expert opinion if it is not combined with literature review. In all published linkage designs, practitioners assigned scores on an arbitrary scale (typically 0 to 1, or 1 to 100). Because most of the relevant literature is on habitat use rather than animal movement (Chetkiewicz et al. 2006), one end of the scale reflects low resistance and high habitat quality, and the other end of the scale reflects high resistance and low habitat quality. In other words, one set of scores is interpreted as both a resistance model and a habitat-suitability model. This complementarity between resistance and habitat suitability reflects the assumption that animals choose travel routes on the basis of the same factors they use to choose habitat (Chetkiewicz et al. 2006). Although this seems reasonable, it may not always be true. For instance, Horskins et al. (2006) demonstrated that one corridor failed to provide gene flow for 2 species that occurred and probably bred within the corridor.

Following Walker and Craighead (1997), we urge linkage designers to explicitly state this as a crucial assumption and acknowledge that the assumption is untested.

Four types of empirical data (species occurrences, animal movement paths, interpatch movement rates, and genetic patterns among patches) can be analyzed in a resource-selection framework to provide estimates of resistance better than estimates from literature review and expert opinion. Unfortunately, resistance estimates derived from each type of data are subject to considerable uncertainty. Because this uncertainty is central to the interpretation of all resistance-based models, we address it in a separate section ("Subjective Translation and Other Problems").

Several designers have used uncertainty analyses to assess the impact of uncertainty in resistance estimates (Quinby et al. 1999; Schadt et al. 2002; Larkin et al. 2004; Newell 2006; Adriaensen et al. 2007). The results of most of these studies suggest that the location of the modeled corridor does not change significantly as long as the rank order of resistance values is assumed correct. Nevertheless, Schadt et al. (2002) attributed much of this insensitivity to the lack of alternative corridor locations in their highly urbanized potential linkage areas. In an extensive uncertainty analysis of the approach used by Beier et al. (2006), Newell (2006) found that modeled corridors were stable for 5 of 8 focal species in a large (50 × 35 km) potential linkage area relatively unconstrained by existing urbanization.

Uncertainty analysis can estimate the impact of uncertainty only for a particular focal species and landscape. Perhaps after many such analyses, general rules will be established about the types of species and landscapes that are insensitive to uncertainty. Until then we recommend that corridor designers routinely incorporate uncertainty analysis and present maps of model results under the most strongly divergent estimates of resistance, as Quinby et al. (1999) did.

6. HOW SHOULD FACTOR RESISTANCES BE COMBINED?

To estimate the overall resistance of a pixel, the analyst must combine resistance due to land cover with resistance due to human disturbance and other factors. To do so, the analyst must choose an arithmetic operation and assign a weight to each factor.

Most linkage designers have used a weighted sum to combine factor resistances, but Singleton et al. (2002) used a weighted product and Beier et al. (2007) used a weighted geometric mean. The geometric mean better reflects situations in which one factor limits wildlife movement in a way that cannot be compensated for by a lower resistance for another factor (U.S. Fish & Wildlife Service 1981).

Regardless of arithmetic operation, each factor is assigned a weight reflecting its contribution to the overall resistance of a pixel. In all published linkage designs, weights seem to have been assigned solely by expert opinion. The expert's task is complicated by the fact that a factor's weight reflects not only its importance, but also the factor's range of variation and units of measurement (Malczewski 2000). Use of a common scale (e.g., resistance units of 1–100) for each factor is common practice in least-cost modeling and eliminates differences among factors in range and units of measurement. Nevertheless, this presupposes that the resistance values for each factor were assigned in a way that compensates for differences among factors in range and units of measurement. Lacking evidence for this presupposition, we recommend that uncertainty analysis consider the simultaneous impact of uncertainty in both weights and class resistance scores, as was done by Quinby et al. (1999) and Newell (2006).

Although uncertainty analysis is a helpful short-term solution, in the future we hope that empirical, multivariate resource-selection studies will directly estimate weights and resistances and will suggest the proper way to combine factor resistances. Such studies could also reveal important interactions between factors.

7. HOW SHOULD A CORRIDOR TERMINUS BE DELINEATED?

A *terminus* is that part of a wildland block that forms or anchors one end of a modeled corridor. A terminus can be defined as a point (pixel), a linear edge (e.g., the wildland boundary), or a patch (e.g., a patch of high-quality focal-species habitat within the wildland block). There can be more than one potential terminus in each wildland block.

Some linkage designs use each wildland block in its entirety as a terminus for each single-species analysis. Nevertheless, in our experience this procedure sometimes produces a corridor that connects to a part of the wildland block far from any potential habitat for the focal species. This unreasonable result can be avoided by restricting terminuses to patches of known or potential breeding habitat (next section) within each wildland block.

Because distance is an important part of algorithms that are based on effective distance, in cases in which 2 wildland blocks nearly touch at one or more locations, these algorithms tend to identify the narrowest gap as the best corridor, even if the modeled corridor is low in habitat value or movement potential. To avoid this problem, we recommend giving the model "room to run" by identifying terminuses well inside the wildland blocks, behind parallel lines a few kilometers apart. Even if this modification does not change the modeled corridor for any focal species, it will demonstrate that the modeled corridor is not merely an artifact of boundary proximity.

8. HOW SHOULD HABITAT PATCHES BE DELINEATED?

Habitat patches are areas of habitat that can support reproduction by the focal species; they may occur within wildland blocks or matrix. Although linkage design does not require delineation of habitat patches, in our experience it is useful to delineate habitat patches as stepping stones within the matrix (next section), as terminuses within the wildland blocks (previous section), and as useful metrics for assessing functionality of a modeled linkage design (see question 14).

To delineate habitat patches, the analyst must specify a suitability threshold for habitat quality, the minimum area of suitable habitat necessary to sustain a breeding pair or population, and how nonhabitat pixels (at patch edges or islets within a patch) affect habitat quality (e.g., via edge effects). South Coast Wildlands (2003–2006), Southern Rockies Ecosystem Project (2005), Beier et al. (2007), and Girvetz and Greco (2007) illustrate procedures to identify pixels that are "good enough, big enough, and close enough together" to function as a habitat patch. To date, there has been no formal uncertainty analysis to determine how uncertainty in each of these 3 procedures affects either the map of habitat patches or the modeled corridor. Although we advocate such uncertainty analysis, we believe the procedures currently in use provide reasonable patch maps and that using these maps is better than ignoring the distribution of breeding habitat in the planning area.

9. HOW SHOULD CORRIDOR DWELLERS BE MODELED?

An unstated assumption in many corridor models is that an individual animal can move between wildland blocks in a single movement event of a few hours to a few weeks. Beier and Loe (1992) called such animals passage species and pointed out that other focal species—corridor dwellers—require more than one generation to move their genes between wildland blocks. They based their distinction on an interaction between the species and the landscape; thus, a particular species would be a passage species if the habitat blocks were within dispersal distance, but would be a corridor dweller in another landscape with habitat blocks more than one dispersal distance away. Corridor dwellers must find suitable breeding opportunities within the linkage.

To model movement by corridor dwellers, Wikramanayake et al. (2004), Beier et al. (2007), and Adriaensen et al. (2007) assigned the lowest resistance value to habitat patches (previous section). We recommend this procedure when modeling a species with a few habitat patches imbedded in a matrix dominated by poor habitat. In such situations the procedure tends to produce a corridor that links those patches in stepping-stone fashion. Nevertheless, if the habitat quality in a large fraction of the matrix is near the threshold between suitable and unsuitable, a slight decrease in the threshold can cause most of the matrix to be mapped as a habitat patch, resulting in a highly linear corridor that fails to include the highest-quality habitat. In these situations we discourage use of this procedure unless the analyst is confident that the threshold is precisely known.

The procedures of Wikramanayake et al. (2004) and Beier et al. (2007) could be improved by assigning the lowest resistance value only to potential breeding patches within effective dispersal distance of other potential breeding patches in the linkage. Nevertheless, "effective dispersal distance" in this context means dispersal distance in suboptimal habitat, and such data are available for only a few species. Even if such data (i.e., a frequency distribution of dispersal distances) were available, the data would not allow the analyst to infer the exact threshold at which interpatch connectivity is lost. A rigorous but data-hungry approach is suggested by van Langevelde (2000), who estimated this threshold distance from a time series of patch occupancy.

10. HOW SHOULD CONTINUOUS SWATHS OF LOW-RESISTANCE PIXELS BE IDENTIFIED?

Low-resistance pixels may not form a continuous swath (Fig. 3). To identify well-connected low-resistance pixels, all published corridor designs (Table 1) calculated each pixel's cost as the lowest possible cumulative resistance from that pixel to terminuses in each habitat block (Fig. 3). These cost values do form continuous swaths (modeled corridors).

Hargrove et al. (2004) present a promising alternative derived from individual-based movement models. Their approach simulates individual animals that leave each habitat block and explore the landscape with decision rules related to resistance of neighboring pixels until the individual either dies or reaches another habitat block. Pixels that are repeatedly chosen as part of successful paths are identified as part of the corridor. Corridors identified by this approach are intuitively appealing and consistently include the best habitat patches in the matrix (Hargrove et al. 2004). This approach also allows cost to vary with the direction of travel and thus can assess the extent to which the optimal corridor in one direction coincides with the optimal corridor in the opposite direction. The volume of movement in some corridors is predominantly unidirectional due to funneling effect of the landscape configuration (Ferreras 2001) or asymmetric population sizes (Dixon et al. 2006). This raises the possibility that the location of a modeled corridor may also depend on direction of movement. The main drawback of individual-based movement models is that the user must specify values for several elusive parameters. For instance, the model of Hargrove et al. (2004) requires estimates of the probability of abrupt reversal

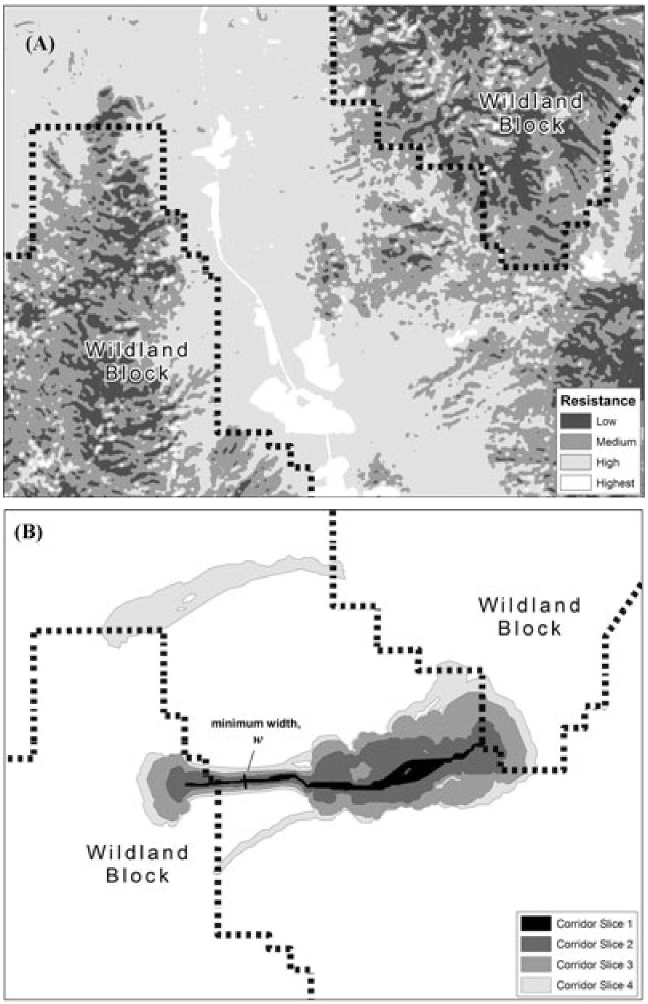

Figure 3. Modeling a corridor for a hypothetical focal species: (a) resistance of individual pixels (low-resistance pixels need not form a continuous swath) and (b) travel cost (cumulative resistance). Low-cost pixels always form continuous swaths and increasingly higher maximum costs define a nested set of increasingly broad "slices" of the landscape. As the cost threshold increases from slice 1 to slice 3 to achieve minimum width, w, the modeled corridor becomes very wide in areas outside the bottleneck. As the cost threshold increases even more (slice 4) the modeled corridor gains additional strands.

of direction, energy costs of movement, likelihood of finding food, and likelihood of mortality in each type of habitat. Uncertainty analyses should be used to describe and illustrate sensitivity of the corridor to uncertainty in these parameters.

11. HOW WIDE SHOULD A SINGLE-SPECIES CORRIDOR BE?

We discourage use of least-cost *paths* (one pixel in width, in contrast to broader *corridors*) for several reasons. First, a pixel-wide path could occur within otherwise inappropriate habitat. Thus it may be unlikely to be used and biologically irrelevant (Adriaensen et al. 2003). Furthermore, the location of a least-cost path is highly sensitive to pixel size and errors in classifying single pixels (Broquet et al. 2006). Finally, conservation biologists would rarely propose a pixel-wide path as a conservation measure.

Fortunately, the previous analytical steps produce a map in which increasingly wide corridors are displayed as nested polygons, each defined by the largest cost allowed in the polygon (Fig. 3b). As the cost threshold increases, multiple strands often emerge (e.g., swath 3 in Fig. 3b). Although a wider corridor is better in the sense that broad swaths include narrower ones, financial and other practical constraints favor smaller corridors. The analyst should present a graded cost map (e.g., Fig. 3b) to allow decision makers to appreciate trade-offs. Nevertheless, the decision maker typically wants the analyst to present a preferred alternative, namely a corridor that is just wide enough to work. The width of the single-species corridor is most critical when a conservation plan is built for a single species, but even for multiple-species linkage designs, a stopping rule is needed to map each single-species corridor.

Harrison (1992) suggests that a corridor for a corridor dweller should be roughly the width of the home range of a focal species or the square root of one-half of the home range area (assuming home ranges approximate a 2:1 rectangle). Nevertheless, if the focal species is strongly territorial, this could result in corridors fully occupied by home ranges where social interactions impede movement through the corridor (Horskins et al. 2006). Thus minimum corridor width for a corridor dweller should be substantially larger than a home range width.

A cost threshold that achieves a minimum width in a bottlenecked area may result in impractically broad swaths elsewhere (e.g., swath 4 in Fig. 3b). Therefore, corridor designers have used a variety of reasonable procedures to select an optimal or minimum corridor width. For example, Beier et al. (2007) required a minimum width through at least 90% of the corridor but allowed a few short bottlenecks. Quinby et al. (1999) presented a series of potential corridors corresponding to various cost percentiles and described the conservation implications of each option. Both approaches require iterative mapping and subjective evaluation. An objective set of decision rules, and an automated way to run them, would be significant advances. Nevertheless, given myriad possible landscape configurations and reasonable differences of opinion about when a corridor is "big enough," this may be an impossible goal.

12. HOW SHOULD CORRIDORS OF MULTIPLE FOCAL SPECIES BE COMBINED?

The previous procedures produce a least-cost corridor for a single species. All 8 studies in which multiple focal species were used (Table 1) present separate maps for each focal taxon. Only Singleton et al. (2002), Beier et al. (2006, 2007), and Adriaensen et al. (2007) joined the single-species corridors into a multiple-species linkage design. Singleton et al. (2002) used the median resistance value for each pixel type across the 4 focal species to develop a "general carnivore model." We discourage this approach, or other types of model averaging, because the general linkage may encompass none of the single-species corridors. Beier et al. (2006) took the union of all pixels included in one or more single-species corridor. Although this procedure fulfilled its goal of "no species left behind," it risked being larger than needed and thus needlessly expensive. To remedy this, Beier et al. (2007) trimmed pixels that served only one species as long as the deletion did not significantly affect corridor length or average habitat quality for that species. South Coast Wildlands (2003–2006) and Beier et al. (2007) also enlarged the multispecies linkage to include species-specific habitat patches if such an addition decreased the interpatch distances that dispersers would need to cross. Their trimming and adding procedures were subjective and only weakly quantitative. We encourage others to develop more rigorous procedures to minimize acquisition costs (area) and management costs (edge) without degrading the ability of the linkage design to serve all focal species.

13. HOW WIDE SHOULD THE LINKAGE BE?

Wide linkages are beneficial because they provide for metapopulations of linkage-dwelling species (including those not used as focal species); reduce pollution into aquatic linkages; reduce edge effects due to pets, lighting, noise, nest predation, nest parasitism, and invasive species; provide an opportunity to conserve ecological processes such as natural fire regimes; and help the biota respond to climate change. For these reasons, some or all strands of the linkage design should be wide enough to provide these benefits. Negative edge effects are biologically significant at distances of up to 300 m in terrestrial systems (25 studies summarized by Environmental Law Institute [2003]) and 50 m in aquatic systems (88 studies in the same review). We recommend the use of these distances as buffers added to the edges of a draft linkage design to minimize edge effects in the modeled linkage. In some situations, topographic features such as steep cliffs alongside a canyon-bottom linkage may block edge effects, reducing the need for a buffer. None of the designs in Table 1 rigorously justified a minimum width needed to conserve ecological processes because apparently there is no relevant literature.

Real-estate developers seeking government approval for their plans typically frame this question as, How narrow a linkage strand might possibly be useful to the focal species? Perhaps because they spend so much time negotiating with developers, some government planners frame the question the same way. In our view this is analogous to asking an engineer, What are the fewest number of rivets that might keep this wing on the airplane? We urge linkage designers to reframe the question as, What is the narrowest width that is not likely to be regretted after the adjacent area is converted to human uses? Although this no-regret standard is subjective, corridor designers have to draw the line somewhere, and we have found it helpful to reframe the issue this way.

14. IS THE BEST CORRIDOR ANY GOOD?

Least-cost procedures of GIS will always produce a least-cost corridor or path—even if the best is entirely inadequate for the focal species. Therefore linkage designs should assess how well the linkage design serves each species and how connectivity provided by the linkage after development compares with other benchmarks (such as connectivity under existing conditions, an alternative linkage design, or conversion of all matrix land to human uses). A conventional estimate of cost-weighted distance is a poor assessment metric because it does not indicate the level of interpatch movement or gene flow.

Until reliable resistance measures are developed, linkage designers must provide conservation investors and other stakeholders with meaningful descriptions of how well the linkage design is expected to serve each focal species. For example, Larkin et al. (2004) report the number of road crossings and the number and severity of bottlenecks in alternative corridors. Beier et al. (2007) provide frequency distributions of species-specific habitat quality in the linkage design and describe the longest distances an individual animal would have to move between potential breeding patches. In cases in which the interpatch distances exceeded the estimated dispersal ability of the species, South Coast Wildlands (2003–2006) and Beier et al. (2007) acknowledge that the linkage design probably would not provide meaningful connectivity for that species. South Coast Wildlands (2003–2006) and Beier et al. (2007) also used these descriptors to evaluate linkage utility for species (some birds, plants, and volant insects) for which habitat patches could be mapped but whose interpatch movement could not be modeled. Furthermore, they added patches of suitable habitat to the linkage design when such addition significantly reduced the length of interpatch dispersal movements required for one of these species.

J. Jenness recently developed an ArcMap extension (http://www.corridordesign.org/) that generates statistics on bottlenecks, interpatch distances, habitat quality, and other metrics for any linkage design polygon of interest to stakeholders. These statistics can help conservation investors compare the biological optimum in a set of parcels meeting a cost constraint or other conservation goal.

15. HOW CAN THE LINKAGE DESIGN ACCOMMODATE CLIMATE CHANGE?

All least-cost models include natural vegetation as a key driver; vegetation in turn is determined largely by climate, soils, and topography. Within the next 50 years, one of these factors, climate, will change enough to cause major shifts and reassembly of vegetation communities (Intergovernmental Panel on Climate Change 2001: Section 5.2.2.2). Williams et al. (2005) designed a linkage to allow endemic plants to shift their geographic range in response to climate change. Their procedure modeled suitable habitat at intervals of a decade and identified spatially and temporally contiguous chains of 2.9-km^2 grid cells with suitable habitat. Beier et al. (2006, 2007) assumed that a diversity of topographic elements (combinations of elevation, slope, and aspect, such as high-elevation flats, north-facing slopes, or lowland flats) would support relatively continuous strands of whatever native vegetation communities will be present after climate change. They therefore evaluated their linkage designs for continuity of major topographic elements and expanded the linkage design to increase such continuity as needed. Their procedure would be improved by considering soil type in addition to topography and by the use of an objective multivariate procedure to identify the major edaphic–topographic elements in a region. There is enormous room for innovation on this important issue.

16. HOW SHOULD THE LINKAGE DESIGN ADDRESS BARRIERS AND MANAGEMENT PRACTICES?

We advocate that linkage designs should comprehensively address land conservation, barrier mitigation, and land management practices. Unfortunately, most published linkage designs have one product, namely a map highlighting lands for conservation. There is a largely separate literature on wildlife-friendly highway crossing structures and other mitigations for highways and canals (e.g., National Highway Cooperative Research Program 2004; National Research Council 2005; Ventura County 2005; online proceedings of the International Conferences on Ecology and Transportation [www.icoet.net/]). Conserving land will not create a functional linkage if major barriers are not mitigated, an excellent crossing structure will not create a functional linkage if the adjacent land is urbanized, and an integrated project of land acquisition and highway mitigation could be jeopardized by inappropriate practices (e.g., predator control, fencing, artificial night lighting).

South Coast Wildlands (2003–2006) and Beier et al. (2007) used field observations to develop fine-scale recommendations for crossing structures and management practices to restore native vegetation and minimize the impact of exotic species, fences, pets, livestock, and artificial night lighting. In our experience this is the section of the report most avidly read and used by managers. Accordingly, the main body of each of our reports consists of a short (approximately 5 pages) description of how the linkage design will serve focal species (question 14) and 10–20 pages of management recommendations (question 16). Everything else is relegated to lengthy appendices. Georeferenced photographs help illustrate important recommendations.

Management recommendations are especially important where people already live in or adjacent to the linkage design and must be engaged as its stewards. An emerging issue is how to mitigate the impact of solid-steel fences, mowed strips, and stadium lighting designed to discourage human traffic on international borders.

Subjective Translation and Other Issues in Estimating Resistance

We introduce the term *subjective translation* to label an important problem that affects most resistance estimates. The problem is that resource selection metrics are usually translated into resistance estimates in a subjective way. The problem is most obvious for estimates derived from the literature and expert opinion, in which the analyst assigns a resistance score to each resource state by extrapolating from the literature on resource selection. Studies of resource selection produce results such as a ranked list of resource classes, probability of the species occurring in each class, 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 (Millspaugh & Marzluff 2001). If the focal animal is twice as likely to occur in pixel type A as in pixel type B, it is tempting to infer that B has twice the resistance of A. Nevertheless, such inference is valid only if the relationship between resistance and probability of occurrence is a linear, rather than exponential, logarithmic, or other function. There is no objective basis for choosing any one of these functions. Indeed, few linkage analysts even state how they translate resource-selection metrics into resistance. Even when they do (e.g., Ferreras 2001), the decision remains subjective.

Empirical data collected in the landscape of interest should provide a better basis than literature review for estimating resistance of various pixel classes, but some types of empirical data are still subject to the subjective translation problem. We considered 4 types of empirical data: species occurrence, animal movement, rates of interpatch movement, and genetic distances among populations. Kobler and Adamic (1999), Ferreras (2001), Bani et al. (2002), and Adriaensen et al. (2007) estimated resistance of land-use classes on the basis of empirical data on occurrence or abundance of focal species in each land-use class. Their approaches, and other approaches derived from resource-selection studies in the region of interest, improve on literature review or expert opinion because they use animal observations in the linkage planning area, but they are still affected by the subjective-translation problem.

Data on animal movement in the linkage area can yield resistance estimates free of subjective translation. Graham (2001) used data on daily movements of Keel-billed Toucans (*Ramphastos sulfuratus*) to assign resistance scores to 3 coarse land-cover classes. Graham's approach could be improved by including a more formal estimation procedure, a larger number of resource classes, and data on individuals moving between patches of breeding habitat (rather than daily movement within a home range).

If interpatch movement rates are a function of the resistance of each pixel type in the matrix between patches, multivariate methods can identify the set of resistance values (a vector in matrix algebra) that best explains observed movement rates. Nevertheless, Sutcliffe et al. (2003) noted 2 difficulties. First, unless the researcher samples the entire geographic range of the metapopulation, estimates will be distorted due to (unmeasured) movements from patches outside the study area but within the interacting group of patches. Second, if the resistance vector includes 3 or more classes, it may be impossible to solve for a single best vector. Sutcliffe et al. (2003) addressed this problem by starting with a handful of likely vectors derived from ecological knowledge of the focal species and determining which of these vectors was most consistent with observed rates of interpatch movement. Similarly, Verbeylen et al. (2003) used an information-theory approach to select which of 36 potential resistance vectors was most consistent with observed occupancy of putative sink patches. These ad hoc procedures were reasonable, but it is impossible to know whether the set of test vectors included the true vector or to obtain a unique mathematical solution if the number of resistances exceeds the number of patch pairs with data.

Epps et al. (2005) used genetic distances among populations to estimate the resistance that highways pose to movement by bighorn sheep by assigning each pixel of the matrix to 1 of 2 resistance classes (one for the highway, one for all other matrix pixels). Gerlach and Musolf (2000) similarly estimated resistance of a river to movement of bank voles (*Clethrionomys glareolus*) with genetic distances and a binary map. Epps et al. (2007) iteratively tested slope thresholds to estimate how steep a pixel had to be to facilitate gene flow among bighorn populations. These approaches have the same advantages and problems as the approach that uses data on interpatch movements. One additional complication is that genetic patterns reflect landscape pattern over an indeterminate number of generations; thus, they are difficult to interpret when new roads or land uses have recently changed the landscape (Berry et al. 2005; Epps et al. 2007).

RIGOROUS ESTIMATES OF RESISTANCE

Resistance estimates based on animal movement, interpatch movement, and genetic distances have biological meaning, such that a 50% increase in resistance corresponds with a 50% decrease in movement. Resistance estimates determined on the basis of interpatch movements have the advantage of reflecting a more relevant type of movement, namely, between-patch movement. Resistance determined on the basis of gene flow is most relevant because it reflects movement that resulted in gene flow. The advantages of resistances estimated from interpatch movement or genetic distance are offset by the computational difficulties of estimating long vectors from a single map (above). Until these computational issues are resolved, analysis of movement (e.g., of radio-tagged animals) may be an expedient empirical approach.

Analysts can improve on the pioneering efforts of Sutcliffe et al. (2003), Verbeylen et al. (2003), and Epps et al. (2007) in 2 ways. First, they should develop routines that explore more of the potential vector space and efficiently search for an optimal solution. Second, instead of evaluating pixelwide paths produced by each vector, they should evaluate all possible interpatch paths with models derived from circuit theory (McRae 2006; McRae & Beier 2007).

The subjective translation problem clouds the biological interpretation of resistance estimates derived from literature review and expert opinion or determined on the basis of species occurrence. Researchers based almost all designs in Table 1 on these less reliable types of resistance estimates because of time and funding constraints. In the future, more rigorous estimates should become the norm. Once the computational issues are resolved, data collection and analysis can be completed in as few as 3 years, and the cost would be vanishingly small compared with the amount conservation investors are wagering on the validity of the corridor design (S.A. Morrison & W.M. Boyce, unpublished).

Uncertainty Analysis

We have called for uncertainty analysis several times in this paper. The basic idea is to determine how much the corridor or linkage design changes when various options are chosen. We call attention to 3 issues in uncertainty analyses.

First, there are many possible interactions among choices. A small handful of options at each of the 16 choices described here will generate more combinations than anyone can feasibly subject to a sensitivity analysis (but see McCarthy et al. 1995). Therefore, most analyses will consider only 1 choice, or at most 3 choices in combination, holding other factors constant. This sort of analysis cannot reveal how the results would differ under different combinations of the other factors. Nevertheless, even a constrained analysis can suggest steps needed to reduce uncertainty and provide stakeholders with useful information. Any design robust to some assumptions is superior to a best guess that is not accompanied by uncertainty analysis.

Second, because uncertainty analysis is landscape specific, its results cannot be extrapolated to other landscapes. In any particular landscape, stakeholders may only want to know if a particular linkage design is robust to its assumptions, in which case generalizability is not an issue. Nevertheless, to advance the science of conservation planning, we recommend conducting uncertainty analyses on a diverse spectrum of artificial or real landscapes to identify the types of landscapes for which an approach is appropriate.

Third, the main questions for uncertainty analysis are how a choice affects the location of a modeled corridor or linkage and how well the design serves each focal species. Errors probably tend to be compounded through the processes reflected in the first 11 decision points. As a result, each single-species corridor is probably less robust than conservation biologists would like. Nevertheless, the processes reflected in the last 5 questions probably mitigate some error and uncertainty in the individual species models. In particular, adding focal species and widening the linkage to minimize edge effects or as a hedge against climate change will tend to decrease the risk that habitat important to any individual species is poorly covered by the linkage design.

Conclusions

Burgman et al. (2005) argue that choice of model frame (deciding what aspects of reality to model or ignore) is the most important type of uncertainty affecting conservation planning and that robust conservation plans must examine the choices, biases, and assumptions inherent in the model frame. We have called attention to several questions and assumptions that deserve serious attention. For instance, the idea that terrestrial animals choose movement routes using the same rules they use to select habitat seems reasonable. Nevertheless, Horskins et al. (2006) documented that a corridor with suitable habitat fails to promote gene flow, and Haddad and Tewksbury (2005) documented that low-quality habitat linkages promote wildlife movement. Although these results do not falsify this assumption, they do suggest that it is not universally true. We urge conservation biologists to be honest about uncertainties and assumptions, work to reduce uncertainty where possible, and describe the impact of uncertainty on the linkage design.

At only a few decision points do we feel confident in knowing the "right choice." For instance, we recommend the use of multiple instead of single focal species, special procedures for corridor dwellers in patchy landscapes, and considering the impact of climate change. But for most junctures, we have merely put up a road sign warning of an approaching intersection and what sort of hazards might lie there. We believe that the greatest progress will be made by building resistance models on the basis of factors that are comprehensive and developing an objective, biologically meaningful measure of resistance. We hope our roadmap will facilitate learning, provoke discussion and new approaches, improve the science of linkage design, and ultimately conserve biodiversity in a world increasingly dominated by human activity.

Acknowledgments

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