



# A Multiscale Network Analysis of Protected-Area Connectivity for Mammals in the United States

EMILY S. MINOR\* AND TODD R. LOOKINGBILL†

Appalachian Lab, University of Maryland Center for Environmental Science, 301 Braddock Road, Frostburg, MD 21532, U.S.A.

**Abstract:** *Protected areas must be close, or connected, enough to allow for the preservation of large-scale ecological and evolutionary processes, such as gene flow, migration, and range shifts in response to climate change. Nevertheless, it is unknown whether the network of protected areas in the United States is connected in a way that will preserve biodiversity over large temporal and spatial scales. It is also unclear whether protected-area networks that function for larger species will function for smaller species. We assessed the connectivity of protected areas in the three largest biomes in the United States. With methods from graph theory—a branch of mathematics that deals with connectivity and flow—we identified and measured networks of protected areas for three different groups of mammals. We also examined the value of using umbrella species (typically large-bodied, far-ranging mammals) in designing large-scale networks of protected areas. Although the total amount of protected land varied greatly among biomes in the United States, overall connectivity did not. In general, protected-area networks were well connected for large mammals but not for smaller mammals. Additionally, it was not possible to predict connectivity for small mammals on the basis of connectivity for large mammals, which suggests the umbrella species approach may not be an appropriate design strategy for conservation networks intended to protect many species. Our findings indicate different strategies should be used to increase the likelihood of persistence for different groups of species. Strategic linkages of existing lands should be a conservation priority for smaller mammals, whereas conservation of larger mammals would benefit most from the protection of more land.*

**Keywords:** biodiversity, conservation, dispersal, graph theory, reserve design, umbrella species

Un Análisis Multiescala de la Conectividad de Áreas Protegidas para Mamíferos en los Estados Unidos

**Resumen:** *Las áreas protegidas deben estar lo suficientemente cercanas, o conectadas, para permitir la preservación de procesos ecológicos y evolutivos a gran escala, como el flujo genético, la migración y los cambios de distribución en respuesta al cambio climático. Sin embargo, se desconoce si la red de áreas protegidas en los Estados Unidos está conectada de manera que preserve la biodiversidad en escalas temporales y espaciales grandes. Tampoco está claro si las redes de áreas protegidas que funcionan para especies mayores funcionarán para especies más pequeñas. Evaluamos la conectividad de las áreas protegidas en las tres biomas más grandes en los Estados Unidos. Con métodos derivados de la teoría de grafos – una rama de las matemáticas que trata con la conectividad y el flujo – identificamos y medimos redes de áreas protegidas para tres grupos diferentes de mamíferos. También examinamos el valor de la utilización de especies paraguas (típicamente mamíferos de talla grande y amplio rango de distribución) en el diseño de redes de áreas protegidas a gran escala. Aunque la cantidad total de terrenos protegidos varió enormemente entre biomas en los Estados Unidos, no fue así con la conectividad. En general, las redes de áreas protegidas estuvieron bien conectadas para mamíferos mayores pero no para mamíferos más pequeños. Adicionalmente, no fue posible predecir la conectividad para mamíferos pequeños con base en la conectividad para mamíferos mayores, lo que sugiere que el enfoque de especie paraguas puede ser una estrategia de diseño*

\*Current address: Department of Biological Sciences, University of Illinois at Chicago, M/C 066, 845 W. Taylor Street, SES 3346, Chicago, IL, U.S.A., email [eminor@uic.edu](mailto:eminor@uic.edu)

†Current address: Department of Geography and the Environment, University of Richmond, 108 Weinstein Hall, Richmond, VA 23173, U.S.A. Paper submitted June 16, 2009; revised manuscript accepted March 12, 2010.

*inapropiada para redes de conservación que intentan proteger muchas especies. Nuestros hallazgos indican que se deben utilizar diferentes estrategias para incrementar la probabilidad de persistencia de diferentes grupos de especies. La conexión estratégica de terrenos existente debe ser una prioridad para la conservación de mamíferos pequeños, mientras que la conservación de mamíferos mayores se beneficiaría más con la protección de más terrenos.*

**Palabras Clave:** biodiversidad, conservación, diseño de reservas, dispersión, especie paraguas, teoría de grafos

## Introduction

Long-term persistence of biodiversity is the ultimate goal of most conservation plans (Gaston et al. 2002; Wiersma & Nudds 2006). Managers often attempt to achieve this goal by maximizing numbers of species within a system of reserves, and conservation strategies focusing on species representativeness and complementarity have been successful in accumulating large numbers of species over the short term (Scott et al. 1993; Lawler et al. 2003). There are many challenges associated with conservation of multiple species over large spatial and temporal scales. First, planning is complicated by the various groups (e.g., federal government, state government, NGOs) that own and manage the discrete reserves comprising regional protected-area networks; these groups may or may not coordinate efforts or consider regional context when making conservation plans. Another difficulty is that species have different needs for the amount and spatial configuration of conservation areas (Hansson & Angelstam 1991). Finally, problems may arise during implementation of conservation plans if changes occur in the landscape surrounding reserves. These changes may reduce or eliminate immigration and lead to extinction in otherwise suitable habitat (Hansen & DeFries 2007). We evaluated the spatial distribution of regional protected-area networks in the United States and assessed whether they are able to sustain species with varying life histories and resource demands.

Long-term conservation of biological diversity requires preservation of large-scale ecological and evolutionary processes, such as gene flow, migration, and range shifts (Noss 2001; West et al. 2009). To accommodate these processes, and fully function as foraging and breeding grounds, protected areas must meet the minimum-area requirements of target species (Newmark 1987; Simberloff 1988). Gurd et al. (2001) suggest a minimum reserve area of 5037 km<sup>2</sup> is necessary to have a reasonable chance of preserving biodiversity in eastern North America. Other authors suggest guidelines of similar magnitude (Brashares et al. 2001; Wiersma et al. 2004; Marsden et al. 2005). Few protected areas, however, are this large. An alternative to large, contiguous reserves is a network of smaller protected areas that are close enough or connected so as to allow movement between them (Hilty et al. 2006). Because species have different minimum-area requirements and different movement

abilities, protected-area networks that are suitable for one species or group of species may be inappropriately scaled for other species. Thus, conservation planning should occur simultaneously at multiple spatial scales because designing protected-area networks for a single “umbrella species” (typically large-bodied, far-ranging mammals) may not ensure long-term persistence of biodiversity. The idea of using umbrella species or surrogate taxa as conservation targets has been evaluated extensively (e.g., Noss et al. 1996; Roberge & Angelstam 2004; Rodrigues & Brooks 2007) and has been applied to habitat reserves (Bifulchi & Lode 2005; Rondinini & Boitani 2006) and corridors (Beier et al. 2009). Nevertheless, the utility of the umbrella-species approach for measuring overall landscape connectivity has not been tested.

Scaling rules may be useful for examining issues of connectivity and umbrella species. For example, mammal dispersal distance and home range size are related to body mass (Lindstedt et al. 1986; Sutherland et al. 2000; Bowman et al. 2002). This relation suggests that conservation of small mammals may be more limited by distance between habitat reserves, whereas conservation of large mammals may be more limited by the area of suitable habitat in reserves. The concept of umbrella species relies on the assumption that reserves designed for the latter will also protect the former, but it is currently unknown whether protected-area networks that protect larger mammals will also protect smaller mammals, or vice versa. In fact, very little is known about connectivity of protected areas at large spatial scales for any species group. Related research by Holling (1992) suggests that landscape fragmentation differentially affects animals, depending on their body size and the spatial grain of the fragmentation. Nevertheless, more information is needed to assess how well protected areas in the United States can maintain biodiversity over the long term.

We assessed the functional connectivity of protected-area networks for biomes and ecoregions of the United States. We used methods from graph theory to determine whether the area and spatial configuration of protected areas are theoretically sufficient to allow for gene flow, migration, and range expansion of a variety of species and whether network connectivity is correlated for different groups of species. Graph theory provides a convenient tool for measuring the physical relations among landscape elements (i.e., structural connectivity) and how these relations affect the movement of organisms within

the landscape (i.e., functional connectivity). We assessed connectivity for mammals because sufficient data exist on their habitat requirements and movements to allow use of network analyses. Additionally, mammals as a group, and particularly large ones, have a high risk of extinction (Cardillo et al. 2005; Carrasco et al. 2009) and are frequently targets of conservation efforts.

## Methods

Spatial data about protected areas in the United States were obtained from the Conservation Biology Institute (CBI 2006). We used a geographic information system (GIS) to group these protected areas according to World Wildlife Fund (WWF) biomes and ecoregions (Olson et al. 2001) and used the three largest biomes in our analyses: (1) temperate broadleaf and mixed forest, (2) temperate grasslands, savannas, and shrublands, and (3) deserts and xeric shrublands. We refer to these biomes as the broadleaf, grassland, and desert biomes, respectively. Within these biomes, we analyzed protected areas with the highest level of biodiversity protection and permanent immunity from conversion of natural land-cover types. These sites have a land stewardship status 1 or 2 in the U.S. Geological Survey GAP analysis program (Maxwell et al. 2009) and are identified as such in the CBI data set. We analyzed protected-area networks at the ecoregion level and merged adjacent protected areas in the same ecoregion into a single unit for the network analysis. In cases where protected areas included two ecoregions, we split protected areas along biogeographic borders and assigned each part to its respective region. Within the contiguous United States, the number of ecoregions within biomes were as follows: broadleaf, 16; grassland, 15; desert, 8. The total amount of protected area and the area of the largest individual reserve were tallied for each biome and ecoregion.

The two primary inputs into our connectivity model were home range and dispersal distance of mammals. We explored the relation between these variables by compiling the data Bowman et al. (2002) used (found in Sutherland et al. 2000; Harestad & Bunnell 1979) and adding data from Corry and Nassauer (2005). We plotted these data and the least-square regression line (Fig. 1) to select our scales of analysis. We identified three positions along the regression line (Fig. 1) to represent three distinct scales of conservation planning: small scale, for mammals with small home ranges (1 ha) and short dispersal distances (1 km); intermediate scale, for mammals with intermediate home ranges (100 ha) and intermediate dispersal distances (10 km); and large scale, for mammals with large home ranges (1000 ha) and large dispersal distances (100 km). We did not assign individual species to a particular group. Instead, we used the round numbers (e.g., 1 ha home range and 1 km dispersal distance) to indicate the general relation. The three groups roughly corresponded to small, intermediate, and large body mass, and we refer to them as small mammals, intermediate mammals, and large mammals.

To define the protected-area networks for each group in each ecoregion, we included all reserves that met the minimum home range requirements of the mammals in that group (1 ha for small mammals, 100 ha for intermediate mammals, 1000 ha for large mammals). Therefore, within an ecoregion, reserves included in the large-mammal protected-area network were a subset of reserves in the intermediate-mammal protected-area network, which were a subset of reserves in the small-mammal protected-area network (Fig. 2). We considered reserves connected if they were as close as or closer than the maximum dispersal distance of the mammals in the group (1 km for small mammals, 10 km for intermediate mammals, and 100 km for large mammals). Distance between reserves was measured from the edge of one reserve to the edge of the other.

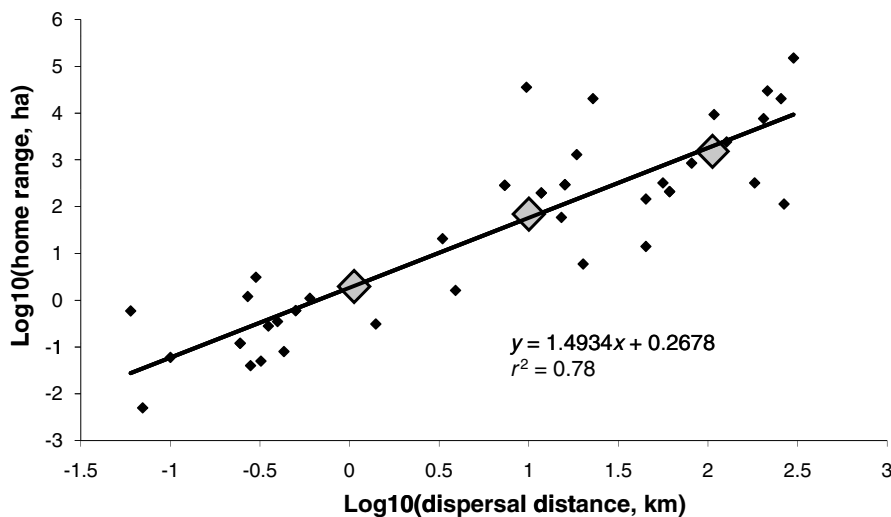


Figure 1. Relation between home range and dispersal distance of mammals derived from Bowman et al. (2002) (small diamonds, individual mammalian species; line and equation, linear least-square regression; large diamonds from left to right, small, intermediate, and large mammal groups used to analyze protected-area networks).



Figure 2. Protected-area network for large mammals (left), intermediate mammals (center), and small mammals (right) in the California Central Valley grasslands ecoregion (dots, centroid of individual reserves; lines, connectivity between reserves; shaded area in inset, location within United States).

We used a graph-theory approach (Urban et al. 2009) to measure and visualize network connectivity. Graph theory deals with connectivity and has been applied to many disciplines including computer science, social network analysis, and landscape ecology (Hayes 2000a, 2000b). A graph can represent a landscape of discrete habitat patches as a set of nodes (points) connected by individuals dispersing between them (Minor & Urban 2007). Using the LANDGRAPHS software package (Urban 2003), we drew lines between all connected reserves and identified groups of connected reserves called components. By definition, dispersal can occur between reserves within a component but not between components. The number of patches and total amount of habitat in the largest component may reveal information about population processes in that network; many small components suggest isolated subpopulations whereas few large components suggest a well-mixed population.

We quantified network connectivity within each ecoregion as the aggregate area of reserves in the largest component divided by the total area of reserves in that ecoregion, a value ranging from 0 to 1 (Ferrari et al. 2007). There are many other possible ways to measure network connectivity (Rothley & Rae 2005; Pascual-Hortal & Saura 2006; Minor & Urban 2008; Magle et al. 2009). Nevertheless, we believe our metric is one of the most intuitive and informative ways to capture large-scale population processes. For example, although we could have divided the area of all reserves in connected components by the total ecoregion reserve area, that metric would not have distinguished between an ecoregion with reserves that were all connected in a single component and an ecore-

gion with all reserves connected to only one other reserve (i.e., pairs of reserves). The two ecoregions are likely to have very different population processes as a result of their respective spatial patterns.

To consider the potential impact of highways on landscape connectivity, we conducted a separate, in-depth examination of connectivity in the broadleaf biome. We used the National Highway Planning Network data set, an annually updated and comprehensive database of the nation's interstate highway system, from the National Transportation Atlas. We spatially overlaid the interstate highways, which are multilane across all but a few brief stretches, with the protected areas data to identify those protected areas that were separated by highways. For this analysis, we considered all protected areas that were separated by interstate highways, regardless of the distance between them, as disconnected. After removing all prior connections that intersected highways, we reanalyzed the data with LANDGRAPHS software package to recalculate the land area in the largest component.

We analyzed our data in several different ways. To determine how connectivity increased the effective area of reserves in each protected-area network, we compared the area of individual protected reserves to the combined area of all units in the largest component of each network. We then used a linear mixed model to examine how the connectivity of protected-area networks varied among mammal groups and biomes. Network connectivity—as defined by the proportion of protected area in the largest component—was the response variable, and biome, mammal group, biome \* mammal group, and ecoregion were predictor variables. Biome and

mammal group were fixed effects and ecoregion was a categorical random effect nested within biome. To assess the potential impact of interstate highways on landscape connectivity, we used Wilcoxon rank-sum tests to compare our initial estimate of connectivity to a second measure of connectivity that incorporated interstate highways. Finally, to test the umbrella-species approach to reserve design, we assessed whether connectivity of protected-area networks for small and intermediate mammals was predictable from connectivity for large mammals. This analysis was accomplished using linear regression models to examine the relations among network connectivity for the different mammal groups in the 39 ecoregions.

## Results

The total amount of protected land varied among biomes (Table 1), increasing from grasslands (29,426 km<sup>2</sup> of protected areas; 1% of total biome), to broadleaf (68,811 km<sup>2</sup> of protected areas; 3% of total biome), to deserts (189,034 km<sup>2</sup> of protected areas; 12% of total biome). The mean area of the individual units in all three biomes was 1378 ha (median area = 27 ha), and a Kruskal-Wallis rank analysis of variance indicated significant differences among biomes ( $df = 2$ ,  $H = 586.5$ ,  $p < 0.001$ ). The area of individual reserves in the desert (mean = 5455 ha, median = 57 ha; Table 1) was significantly larger than reserves in the broadleaf (mean = 510 ha, median = 19 ha) or grassland biomes (mean = 756 ha, median = 47 ha) (Dunn's pairwise multiple comparison). Six sites were greater than 5037 km<sup>2</sup>; five of those were in the desert biome and one was in the grassland biome.

When considering the land area connected in network components ("effective reserve area") rather than individual units, connected area of protected land increased considerably in each biome. The amount of connected area in the largest component still varied significantly between biomes ( $df = 2$ ,  $H = 22.1$ ,  $p < 0.001$ ) and was largest in the desert (mean over all mammal groups = 13,615 km<sup>2</sup>, median = 5,581 km<sup>2</sup>; Table 1). The mean area of the largest component in the broadleaf biome was 2343 km<sup>2</sup> (median = 670 km<sup>2</sup>) and in the grassland biome was 965 km<sup>2</sup> (median = 358 km<sup>2</sup>).

Output from the linear mixed model indicated network connectivity—as measured by the proportion of reserve area that was connected in the largest component—varied among ecoregions and mammal groups (Table 2). Connectivity was significantly different across mammal groups (Fig. 3;  $df = 2$ ,  $F = 173.27$ ,  $p \ll 0.0001$ ). Mean connectivity of protected-area networks for large, intermediate, and small mammals was 0.85, 0.39, and 0.29, respectively. A likelihood-ratio test of the model with and without the random component confirmed the importance of the ecoregion variable to the model (LR = 21.3,  $p = 0.0016$ ). Nevertheless, after accounting for differences in total amount of protected area with our connectivity metric, there was no significant difference in connectivity between the three biomes ( $df = 2$ ,  $F = 0.09$ ,  $p = 0.91$ ); mean connectivity over all ecoregions and all mammal groups was 0.51. There was also not a significant interaction effect between mammal group and biome ( $df = 4$ ,  $F = 1.82$ ,  $p = 0.13$ ).

Incorporating interstate highways into the analysis affected connectivity for large mammals in the broadleaf biome but not for small mammals. Ignoring the possible effect of highways, mean connectivity over all ecoregions in the broadleaf biome was 0.26 (median = 0.21) for the small mammals and 0.87 (median = 0.99) for the large mammals. When protected areas separated by highways were considered unconnected, mean connectivity remained 0.26 (median = 0.20) for the small mammals but decreased to 0.54 (median = 0.48) for the large mammals. Wilcoxon rank-sum tests showed a significant change in connectivity for the large mammals when highways were included ( $n = 16$ ,  $U = 42.0$ ,  $p = 0.001$ ). Even with the negative effect of highways, connectivity for large mammals was still significantly higher than connectivity for small mammals ( $n = 16$ ,  $U = 178.0$ ,  $p = 0.001$ ).

A linear regression model showed that the relationship between connectivity for the largest mammals and connectivity for the intermediate mammals was statistically significant but lacked predictive power ( $n = 39$ ,  $p = 0.02$ ,  $r^2 = 0.13$ ). The relation between connectivity for the largest mammals and connectivity for the smallest mammals was not statistically significant ( $n = 39$ ,  $p = 0.19$ ). A plot of connectivity for large mammals versus small mammals showed that when connectivity was low for large mammals it was also low for small mammals,

**Table 1.** Summary statistics for protected areas in the three largest biomes in the contiguous United States.

Biome	Total protected land (ha) (% of all land in biome)	Mean area (ha) of individual protected lands	Mean area (ha) effective reserve*	No. of protected lands > 1; > 100; > 1000; > 503,700 ha
Temperate broadleaf and mixed forest	6,881,065 (3)	510	234,307	13,488; 3,334; 813; 0
Temperate grasslands, savannas, and shrublands	2,942,612 (1)	756	96,454	3,893; 1,417; 326; 1
Deserts and xeric shrublands	18,903,402 (12)	5,455	1,361,489	3,466; 1,763; 681; 5

\*Effective reserve area is the total combined area in the largest component averaged over all mammal groups.

**Table 2. Connectivity scores\* for each mammal group and other summary statistics for ecoregions included in the protected-area network analysis.**

Biome	Ecoregion	Total (ba) protected land (rank)	Mean (ba) of individual protected land (rank)	Connectivity			
				large mammals (rank)	intermediate mammals (rank)	small mammals (rank)	
Temperate broadleaf and mixed forest	Allegheny Highlands forests	1,004,133 (8)	2,402 (11)	1 (1)	0.68 (4)	0.48 (6)	
	Appalachian mixed mesophytic forests	523,482 (12)	426 (26)	1 (1)	0.40 (17)	0.19 (4)	
	Appalachian-Blue Ridge forests	1,055,762 (7)	1,178 (17)	0.98 (20)	0.15 (35)	0.08 (37)	
	central U.S. hardwood forests	498,533 (13)	245 (33)	0.92 (21)	0.10 (38)	0.06 (39)	
	east central Texas forests	10,757 (38)	489 (24)	1 (1)	0.34 (21)	0.30 (16)	
	eastern forest-boreal transition	959,539 (10)	2,492 (9)	1 (1)	0.99 (1)	0.96 (1)	
	eastern Great Lakes lowland forests	16,252 (36)	119 (37)	0.75 (30)	0.19 (32)	0.16 (27)	
	Mississippi lowland forests	238,916 (20)	1,225 (16)	0.84 (23)	0.20 (31)	0.20 (23)	
	New England-Acadian forests	453,202 (14)	253 (32)	1 (1)	0.60 (7)	0.23 (20)	
	northeastern coastal forests	237,358 (22)	84 (39)	0.79 (28)	0.25 (25)	0.13 (33)	
	Ozark Mountain forests	226,226 (23)	1,628 (13)	1 (1)	0.23 (28)	0.23 (20)	
	southeastern mixed forests	276,440 (18)	276 (31)	0.48 (37)	0.08 (39)	0.07 (38)	
	southern Great Lakes forests	120,747 (27)	168 (36)	0.35 (38)	0.22 (29)	0.17 (26)	
	upper Midwest forest-savanna transition	252,996 (19)	319 (30)	0.80 (26)	0.34 (21)	0.22 (22)	
	western Great Lakes forests	990,953 (9)	1,171 (18)	0.99 (19)	0.51 (13)	0.40 (11)	
	Willamette Valley forests	15,769 (37)	207 (35)	1 (1)	0.45 (14)	0.35 (13)	
	Temperate grasslands, savannas, and shrublands	California Central Valley grasslands	150,664 (6)	837 (23)	1 (1)	0.24 (26)	0.09 (36)
		Canadian aspen forests and parklands	5,323 (39)	409 (27)	1 (1)	0.54 (10)	0.51 (5)
		central and southern mixed grasslands	72,195 (31)	902 (21)	0.50 (36)	0.34 (21)	0.33 (15)
		central forest-grasslands transition	399,735 (15)	343 (29)	0.35 (38)	0.12 (37)	0.12 (34)
central tall grasslands		87,935 (28)	100 (38)	0.58 (35)	0.21 (30)	0.14 (30)	
Edwards Plateau savanna		133,171 (26)	4,162 (5)	1 (1)	0.57 (8)	0.57 (4)	
Flint Hills tall grasslands		34,857 (33)	1,584 (14)	0.86 (22)	0.62 (6)	0.48 (6)	
Montana Valley and foothill grasslands		283,590 (17)	958 (20)	1 (1)	0.14 (36)	0.10 (35)	
Nebraska Sand Hills mixed grasslands		67,373 (32)	2807 (8)	0.71 (33)	0.43 (15)	0.42 (8)	
northern mixed grasslands		87,558 (29)	1,510 (15)	0.80 (26)	0.27 (24)	0.27 (17)	
northern short grasslands		952,039 (11)	2,486 (10)	0.76 (29)	0.63 (5)	0.61 (2)	
northern tall grasslands		84,880 (30)	377 (28)	1 (1)	0.56 (9)	0.18 (25)	
Palouse grasslands		170,407 (24)	1,671 (12)	0.74 (31)	0.73 (3)	0.59 (3)	
Texas blackland prairies		18,213 (35)	467 (25)	1 (1)	0.36 (18)	0.36 (12)	
western short grasslands		394,672 (16)	1,002 (19)	0.82 (25)	0.43 (15)	0.42 (8)	
Deserts and xeric shrublands		Chihuahuan desert	1,239,599 (6)	3,635 (7)	0.60 (34)	0.36 (18)	0.24 (18)
		Colorado Plateau shrublands	4,426,823 (2)	4,974 (3)	1 (1)	0.54 (10)	0.41 (10)
		Great Basin shrub steppe	2,784,708 (4)	3,961 (6)	1 (1)	0.17 (33)	0.16 (27)
	Mojave desert	4,752,257 (1)	18,710 (1)	1 (1)	0.82 (2)	0.34 (14)	
	Snake-Columbia shrub steppe	3,100,303 (3)	4,461 (4)	1 (1)	0.54 (10)	0.14 (30)	
	Sonoran desert	2,331,993 (5)	13,402 (2)	1 (1)	0.24 (26)	0.24 (18)	
	Tamaulipan mezquital	32,321 (34)	226 (34)	0.74 (31)	0.35 (20)	0.14 (30)	
	Wyoming Basin shrub steppe	237,784 (21)	894 (22)	0.84 (23)	0.16 (34)	0.16 (29)	

\*Calculated as the percent (in area) of habitat reserves in an ecoregion that was contained in the largest component in that ecoregion.

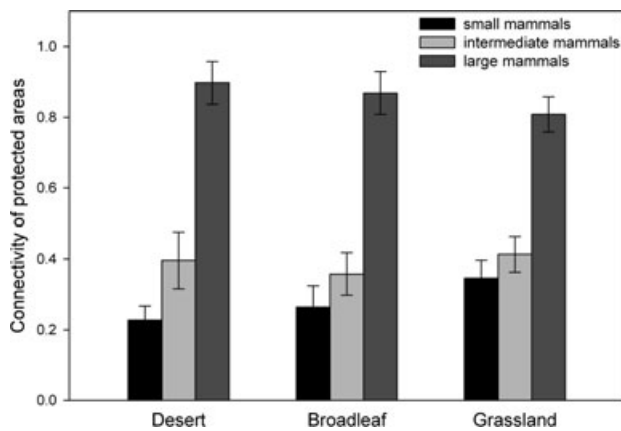


Figure 3. Connectivity scores of protected-area networks by biome and mammal group (whiskers, SE).

but when connectivity was high for large mammals it was impossible to predict the connectivity for small mammals (Fig. 4).

## Discussion

### Geographic Patterns of Conservation

The relative performance of protected areas for biodiversity conservation can be assessed for individual protected areas, portfolios of protected areas, or networks of protected areas (Gaston et al. 2008). At the scales of the individual reserve and the portfolio, the desert biome had the largest protected areas and the greatest total area of protected land (Table 1). The top six ecoregions in terms of total protected land and five of the top six ecoregions in terms of mean area of individual protected lands were in the desert (Table 2). Even for this biome, however, only five contiguous protected areas met Gurd et al. (2001) target of 5037 km<sup>2</sup> for long-term persistence of biodiversity. At the network scale, an alternative conservation strategy is to connect reserves into networks of sites collectively capable of maintaining long-term persistence (Brito & Grelle 2004; Cerdeira et al. 2005). This approach requires that protected lands be close enough for movement of animals between separate reserves and that the combined area of the connected reserves be large enough to sustain long-term species persistence. Our assessment of reserve connectivity showed that by combining protected sites in close proximity, the effective area of reserves increased substantially for all biomes, but the proportion of total protected land that was connected did not differ significantly among biomes (Fig. 3).

Protected-area networks are not the only source of wildlife habitat. Although <6% of the land area of United States (Scott et al. 2001) and the world (Jenkins & Joppa

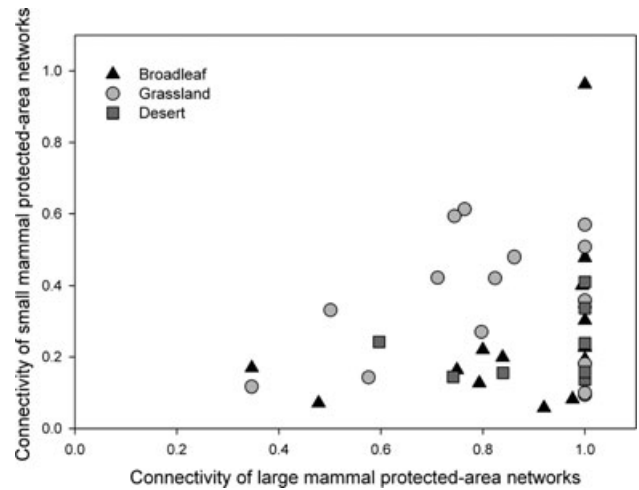


Figure 4. Connectivity scores for small mammals versus connectivity for large mammals by ecoregion.

2009) has strict protection for biodiversity, much of the remaining land has yet to be developed. For example, Riitters et al. (2002) estimated that  $2.5 \times 10^6$  km<sup>2</sup>, or approximately 31%, of the coterminous United States was forested. These undeveloped lands combine with protected areas to create a much larger and more connected network of habitat for native species than we considered here. Wiersma et al. (2004) suggest that the minimum area of protected land required for conservation of mammal species may be reduced by as much as one-third, to 3140 km<sup>2</sup>, if additional habitat surrounds the protected area. Nevertheless, at the current rate of population growth and development, these unprotected lands will not be undeveloped indefinitely. For example, approximately 47,000 km<sup>2</sup> of forest land in the United States was converted to other land cover classes from 1992 to 2001 (Wickham et al. 2008). Furthermore, Wade and Theobald (2009) showed that residential development patterns over the last several decades have substantially changed the land-use context around conservation areas across the United States. A primary conservation objective should therefore be to ensure that protected areas be sufficiently large and connected to allow long-term persistence of native biodiversity within these dynamic landscapes.

One strategy for accomplishing this objective is through the acquisition of additional protected lands. Site acquisitions adjacent to existing parks and reserves can help increase the overall functioning of park ecosystems (Jones et al. 2009). Our analysis suggests specific biomes (e.g., broadleaf) and ecoregions (e.g., northeastern coastal forest) where mean reserve area lags behind the rest of the country. Conversely, the grassland biome and various other ecoregions (e.g., Canadian aspen forests and parklands, east central Texas forests) suffer from an overall deficiency of protected area. Nevertheless,

the post hoc system of acquiring land for conservation within an entrenched mixed-use landscape generally precludes creation of super reserves large enough to meet the ecological demands of multiple species (Gaston et al. 2008). Graph theory can be used to guide a complementary conservation strategy that combines acquisition of smaller potential stepping-stone reserves (Minor & Urban 2007) with spatially focused matrix management (Lookinbill et al. 2010) to promote connectivity among constellations of protected areas (i.e., components). Because networks of protected areas are perceived differently by different groups of species, we subsequently assessed whether there were differences in the networks of protected areas for three different mammal groups.

### Taxonomic Patterns of Connectivity

For large mammals, connectivity was not the main conservation concern because the largest component in each ecoregion contained on average 85% of the protected land (Fig. 3). This indicates large mammals are probably able to access almost all the available land in an ecoregion. For mammals with large minimum-area requirements and long dispersal distances, the total amount of protected area is likely the most limiting factor in conservation. Although large mammals can move between most of the protected lands in an ecoregion, there may not be enough protected land for long-term persistence, especially in the grassland and broadleaf biomes (Table 1). Further conservation efforts for large mammals should focus on protecting more land wherever it is available.

The issue is different for smaller mammals, which appeared to be more limited by connectivity than available land. Connectivity decreased and total area and number of reserves increased in smaller mammal networks (e.g., Fig. 2). On average, <30% of the total protected area within an ecoregion was connected in the largest component for small mammals (Fig. 3). For intermediate mammals, the largest component contained an average of <40% of the protected land in each ecoregion. The fact that less than half of protected lands were connected for small and intermediate mammals suggests that connectivity may be the limiting factor for long-term persistence. Our results identified specific ecoregions for which connectivity was low for these mammal groups despite the relatively large mean reserve area (e.g., Appalachian-Blue Ridge forests, Great Basin shrub steppe; Table 2). Protecting additional land within close proximity to existing reserves, or increasing connectivity of nearby reserves through matrix management, would be a useful conservation strategy within these ecoregions.

For the sake of simplicity and because these effects have been shown to be species specific and difficult to quantify, we did not systematically consider how spatial variability in the matrix between protected areas could potentially affect connectivity. For example, there

is evidence that large (Dyer et al. 2002) and small mammals (Rondinini & Doncaster 2002) are reluctant to cross roads, but this barrier effect may be stronger for some species than others (Goosem 2001; Ford & Fahrig 2009). There has been little research examining the relative effect of roads as barriers for one group versus another and even less related to other potential barriers such as rivers. We did, however, examine the potential impact of highways on connectivity of protected area networks for a subset of our study region, assuming that highways would present equivalent (and absolute) movement barriers to all groups of mammals. Under these assumptions, large mammals would be more affected than small mammals because their longer movement pathways would more likely intersect with highways.

Our results indicate the umbrella-species approach may not be appropriate for designing multispecies protected-area networks. To our knowledge, only Beier et al. (2009) have investigated the utility of umbrella species for connectivity planning. Although they examined corridors rather than overall landscape connectivity, they also concluded that large carnivores do not represent movement of other species across a landscape. We offer further evidence that the level of connectivity for large mammals is not predictive of connectivity for smaller mammals. In poorly protected ecoregions with small and scattered reserves, the networks tended to be disconnected for all groups. On the other end of the spectrum, ecoregions with more total protected area generally had large reserves (e.g., ecoregions within the desert biome). Although movement among these large reserves was generally possible for large mammals, the reserves may or may not be close enough for small mammal dispersal and the ecoregions may or may not have the smaller reserves necessary to act as stepping stones between the larger sites. Therefore, it is not possible to predict connectivity for small mammals on the basis of connectivity for large mammals, which suggests that networks of protected areas need to be assessed separately for specific groups of species rather than generically designed for all species.

### Assumptions and Caveats

Our assessment of connectivity relies on several important assumptions. First, we assumed habitat quality was equal in all protected areas. Although limiting our analysis to protected areas with GAP status 1 or 2 (those areas with the highest level of biodiversity protection) should minimize the variability of habitat quality, habitat quality is probably not equal across the landscape. Varying habitat quality is likely to alter connectivity (Garroway et al. 2008) if high-quality patches act as population sources and low-quality patches have few emigrants. This effect may be local, however, and may not consistently bias our large-scale measures of connectivity. Additionally, by relying on the CBI protected areas database and only GAP



status 1 and 2 lands within the database, we may have excluded some county, state, and private lands that are potentially important to biodiversity conservation. The protected-area database is not complete and may lack consistency in coverage between states, but it is currently the most comprehensive source available.

For our comparison between biomes, we largely ignored the effect of the matrix on dispersal behavior and considered two reserves connected if they were within the maximum dispersal distance of the focal taxon. Nevertheless, roads, rivers, and other barriers may isolate a habitat reserve from the surrounding landscape (McRae et al. 2005; Goetz et al. 2009). In the broadleaf biome, highways may negatively affect connectivity for large mammals but not for small mammals. The effect of highways is likely to vary geographically because the highway network is most dense in the eastern part of the country. Furthermore, the effect of highways and other linear features is likely to vary by species. Although we assumed all mammals in a group have similar dispersal behavior, we know functional connectivity of a landscape can be highly species specific (Belisle 2005).

## Conclusion

Our findings indicate that different reserve design strategies should be used to increase the likelihood of persistence for different mammal groups. For smaller mammals, strategic linkages of existing lands should be a conservation priority. Relatively small habitat patches can sustain populations of small mammals, so many population processes may still be maintained without connectivity among patches. Nevertheless, the ability to move across the landscape may be crucial for range shifts in response to climate change and subsequent changes in distribution of suitable habitat. For these species, the location of newly protected lands may be more important than the amount of land, and new acquisitions should be located so that they serve as stepping stones between larger protected areas. For large mammals, acquiring additional land should be the focus. Location of the new land is not as much of a concern because current networks are reasonably connected for most ecoregions and large mammals have considerable dispersal abilities. These animals are more likely to be limited by their demands for large areas of habitat than by the connectivity of existing protected lands. Because different conservation strategies are more appropriate for different species groups, our results do not support the use of large, far-ranging mammals as umbrella species in the design of protected-area networks.

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