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RESEARCH ARTICLE

Using network theory to prioritize management in a desert bighorn sheep metapopulation

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Abstract Connectivity models using empirically-derived landscape resistance maps can predict potential linkages among fragmented animal and plant populations. However, such models have rarely been used to guide systematic decision-making, such as identifying the most important habitat patches and dispersal corridors to protect or restore in order to maximize regional connectivity. Combining resistance models with network theory offers one means of prioritizing management for connectivity, and we applied this approach to a metapopulation of desert bighorn sheep (*Ovis canadensis nelsoni*) in the Mojave Desert of the southwestern United States. We used a genetic-based landscape resistance model to construct network models of genetic connectivity (potential for gene flow) and demographic connectivity (potential for colonization of empty habitat patches), which may differ because of sex-biased dispersal in bighorn sheep. We identified high-priority habitat patches and corridors and found that the type of connectivity and the network metric used to quantify connectivity had substantial effects on prioritization results, although some features ranked highly across all combinations. Rankings were also sensitive to our empirically-derived estimates of maximum effective dispersal distance, highlighting the importance of this often-ignored parameter. Patch-based analogs of our network metrics predicted both neutral and mitochondrial genetic diversity of 25 populations within the study area. This study demonstrates that network theory can enhance the utility of landscape resistance models as tools for conservation, but it is critical to consider the implications of sex-biased dispersal, the biological relevance of network metrics, and the uncertainty associated with dispersal range and behavior when using this approach.

Keywords Colonization · Connectivity · Dispersal · Extinction · Fragmented population · Gene flow · Graph theory · Habitat patch · Landscape resistance

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Introduction

Connectivity is a beneficial or necessary component of many ecological processes, including gene flow,

migration, dispersal from natal ranges, range shifts in response to climate change, and metapopulation dynamics (Crooks and Sanjayan 2006). The past decade has seen rapid progress in the development of connectivity models that use resistance surfaces to explain effects of landscape features on animal movement (Chardon et al. 2003; Perez-Espona et al. 2008; Chetkiewicz and Boyce 2009). Numerous studies using resistance surfaces have demonstrated that effective distance (ED), which combines geographic distance and relative habitat resistance, is a better predictor of realized population connectivity than simple Euclidean distance (Cushman et al. 2006; Epps et al. 2007; McRae and Beier 2007). Resistance-based connectivity models have facilitated the identification of likely routes for dispersal and movement between habitat patches using methods such as least-cost path (LCP) analysis and circuit theory (Adriaensen et al. 2003; McRae et al. 2008). Although resistance models may perform poorly when resistance values are assigned to different habitats solely on expert opinion (Spear et al. 2010; Sawyer et al. 2011), landscape genetic analyses (e.g., Cushman et al. 2006; Epps et al. 2007) or resource selection models (e.g., Chetkiewicz and Boyce 2009; Epps et al. 2013) can be used to develop and optimize models with an empirical basis. Developing such models has become increasingly popular (Zeller et al. 2012) and empirically-derived resistance models have been used to evaluate or map prospective dispersal corridors (Cushman et al. 2010; Wasserman et al. 2012), but they have rarely been used to guide more systematic decision making. For instance, even knowing the likely location and ED of dispersal routes does not allow rigorous evaluation of their relative importance in metapopulations or other fragmented systems. Because conservation resources are always limited, methods for prioritizing actions are a critical component missing from many connectivity analyses.

Combining landscape resistance models with network theory offers a compelling potential solution. Network theory has risen to prominence in landscape ecology as a framework for quantifying the role that habitat patches and dispersal corridors play in linking fragmented populations (Urban et al. 2009). In this context, a network consists of "nodes" (habitat patches or populations) and "edges" (connections between populations). Information on actual or potential dispersal between patches determines which nodes are connected by edges, and in some cases the strength of the connection. Network theory offers a multitude of metrics to quantify contributions of individual nodes and edges to network connectivity, and thus could help guide decisions about where to manage, maintain, or restore connectivity. However, defining the location and strength of edges is problematic; many analyses connect nodes on the basis of rough approximations such as the maximum dispersal distance for the species according to telemetry data or expert opinion (e.g., Fortuna et al. 2006; Minor and Urban 2007), ignoring variation in the intervening landscape. As described above, landscape resistance models derived from empirical data allow the construction of network models with edge weight determined by ED rather than geographic distance. Less commonly, resistance models have also been used to estimate maximum effective dispersal distance (Epps et al. 2007; Parks et al. 2012), information that can be used to limit network edges in a more meaningful way. The resulting networks could provide a powerful tool for quantifying the relative importance of each patch and corridor to overall connectivity.

The need to prioritize conservation actions in fragmented systems raises another commonly-neglected point: distinguishing among different types of connectivity may be important. The potential for gene flow among populations (hereafter, "genetic connectivity") and the potential for re-colonization of habitat patches after local extinctions (hereafter, "demographic connectivity") are often cited as critical reasons to maintain connectivity among fragmented populations (Crooks and Sanjayan 2006; Mills 2007), but could potentially operate at different scales if species exhibit sex-biased dispersal. Levels of connectivity that allow for adequate gene flow may not allow for adequate re-colonization, and patches or corridors that are most important to genetic connectivity of a metapopulation may not coincide with those most important to demographic connectivity. This is especially relevant for species with highly sex-biased dispersal, where re-colonization potential may be limited by the more philopatric sex but gene flow is facilitated by both sexes.

Here, we combine resistance-based connectivity models and network theory to develop tools for prioritizing management options in a metapopulation of desert bighorn sheep (*Ovis canadensis nelsoni*) in the Mojave Desert of southern California and Nevada,

Fig. 1 Desert bighorn sheep habitat patches in the Mojave Desert region. *Gray polygons* are occupied patches, *white polygons* are unoccupied patches, and *hollow dashed polygons* are "buffer" patches outside the study area. Barriers to dispersal (interstate highways, urban areas, etc.) are shown in *black*. Patches are labeled with 3-letter abbreviations; for full patch names, see Table S1 in Supporting Materials
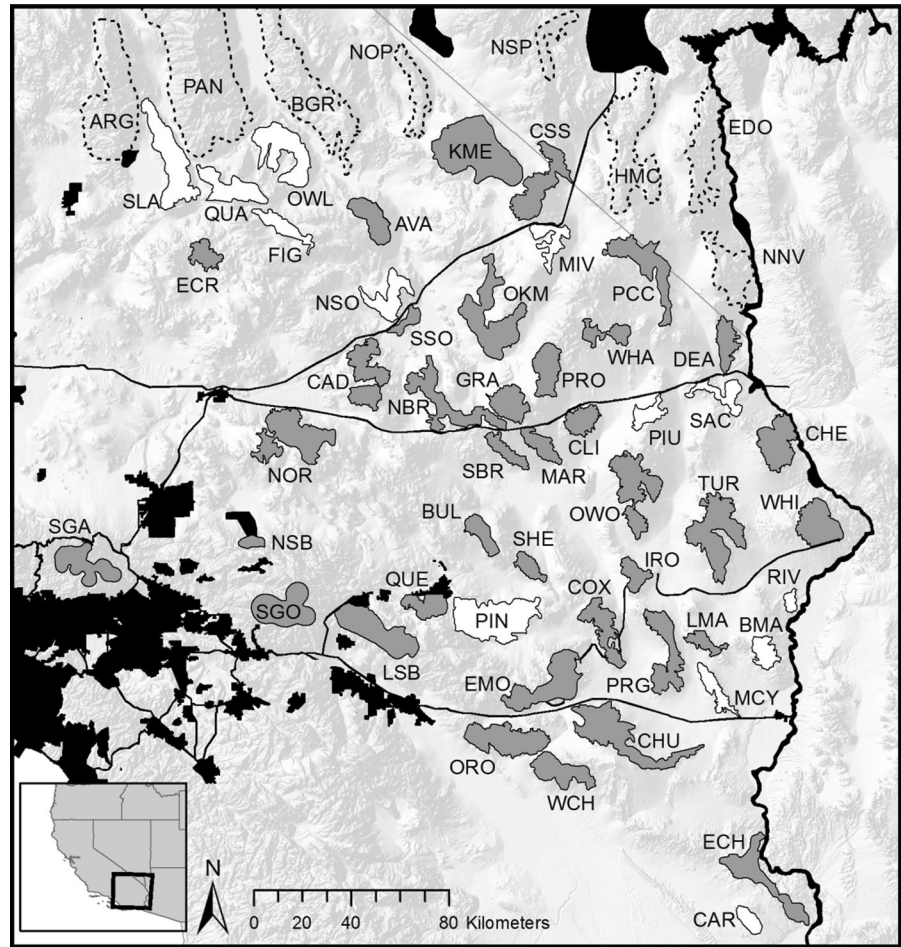
USA. Bighorn sheep exhibit sex-biased dispersal (Krausman et al. 1999); therefore, we consider genetic and demographic connectivity explicitly and separately. Bighorn sheep populations in this region occupy numerous small mountain ranges separated by broad expanses of relatively flat desert (Fig. 1), and their relative isolation and small size makes them vulnerable to loss of genetic diversity through genetic drift and inbreeding (Epps et al. 2005). Population extinctions occurred in nearly 40 % of central Mojave populations over a 60-year period during the 20th century (Torres et al. 1994), and there is a clear need to maintain connectivity between habitat patches to allow for re-colonization (Epps et al. 2010). Although core habitat where bighorn sheep reside, forage, and breed remains largely intact in the region, surrounding dispersal habitat has been fragmented over the past century by interstate highways, canals, urbanization,

mining operations, and other anthropogenic developments (Epps et al. 2005). In the absence of disease, connectivity is expected to positively affect metapopulation persistence and genetic diversity.

This landscape exemplifies the need for tools to prioritize management actions in fragmented systems. Current and proposed utility-scale renewable energy development could further compromise connectivity if energy facilities such as wind farms or solar arrays are sited in or near bighorn sheep habitat or along dispersal corridors (Lovich and Ennen 2011). Possible management actions to protect connectivity in this system include: (1) establishing additional protections for occupied habitat patches; (2) establishing additional protections for intact dispersal corridors; (3) reintroducing bighorn sheep populations in suitable habitat patches that are currently unoccupied; and (4) removing existing barriers to dispersal (e.g., installing

wildlife crossing structures). We use genetic-based landscape resistance models from the Mojave bighorn sheep metapopulation to construct network models with three objectives: (1) to establish priorities for maximizing desert bighorn connectivity in the region; (2) to determine how the prioritization process is influenced by the type of connectivity (genetic versus demographic); and (3) to evaluate the impact of model error and assumptions on prioritization results.

Methods

Our analysis followed three general steps. First, we used a least-cost path resistance model optimized from genetic data (Epps et al. 2007) to estimate connectivity among habitat patches in the Mojave Desert. Second, we combined these connectivity estimates with genetic estimates of dispersal thresholds to construct network models describing genetic or demographic connectivity. Third, we used network metrics to rank the importance of each patch and corridor with respect to network connectivity, and explored sensitivity of rankings to connectivity type, network metric, and modeling error.

Study area

We defined our study area to match the spatial extent of the analyses in Epps et al. (2007), including 37 habitat patches currently occupied by bighorn sheep populations (Fig. 1). Because bighorn sheep use steep terrain almost exclusively, patch boundaries were delineated on the basis of slope (>10 %) and effective distance to perennial water sources (see Appendix 2 of Epps et al. 2007); in some cases, boundaries were modified using expert opinion to include additional area known to be used by bighorn sheep. Each population was associated with a single patch and represented by a single network node because bighorn habitat is discretely distributed on the landscape, and previous genetic analyses supported these patch-based population definitions (Epps et al. 2005, 2007); thus, we hereafter use the terms "patch," "population," and "node" interchangeably. We also identified 13 "restorable patches" in the study area that currently do not support a bighorn sheep population but did in the past (Wehausen 1999; Epps et al. 2004) and are within dispersal range of an occupied patch.

Connectivity with patches beyond the boundary of our study area is likely, which creates the potential for bias in the network analysis: patches near the boundary may appear relatively unimportant even if they provide important connections to patches outside the boundary. To minimize this bias, we included occupied "buffer" patches adjacent to our study area ($n = 8$), but did not evaluate potential management actions among those buffer patches.

Genetic-based connectivity models

We inferred connectivity using a landscape resistance model developed by Epps et al. (2007) that used gene flow estimates among populations of desert bighorn sheep (392 individuals; 26 populations; 14 microsatellite loci) to test and optimize least-cost path connectivity models incorporating distance and topography and estimated dispersal thresholds in terms of ED from the best model. We believe least-cost path models better approximate ED for bighorn sheep in this system than alternative methods that incorporate less efficient dispersal routes (e.g., circuit theory, least-cost corridor) because habitat patches are discrete mountain ranges separated by desert flats, allowing bighorn sheep to see for long distances to other habitat patches within the scale of individual movements and to visually navigate between patches. Epps et al. (2007) used partial Mantel tests to compare 18 topography-based resistance models representing all combinations of three percent-slope cutoffs between high- and low-resistance slope categories, and six ratios of high: low resistance values. The strongest correlation between ED and gene flow occurred when areas of >15 % slope were assigned 1/10th the dispersal cost of areas of <15 % slope. The estimated maximum effective dispersal distance (ED_{MAX}) was 16.4 resistance units (referred to as "km-cost-units" in Epps et al. (2007); equivalent to 16.4 km of <15 %-slope terrain, or 164 km of >15 %-slope terrain).

Bighorn sheep exhibit sex-biased dispersal, with males moving between patches more frequently and over greater distances than females (Krausman et al. 1999). Because the Epps et al. (2007) model was developed from bi-parentally inherited genetic markers, it is suitable for describing gene flow but likely overestimates the potential for re-colonization or rescue, which are limited by female dispersal. Thus,

a female-specific estimate of ED_{MAX} was needed to characterize demographic connectivity. We estimated female ED_{MAX} using two sources of data: (1) observations of radio-collared females moving between patches, and (2) sharing of female mitochondrial haplotypes between patches, which indicate past female dispersal events given that mitochondrial DNA is maternally inherited (explained fully in Appendix S1 in Supplemental Material). The frequency distribution of ED for female dispersal events (Fig. S1) suggested female dispersal declined with ED at a rate similar to that observed by Epps et al. (2007) for male-limited gene flow, but with a smaller ED_{MAX}. We modified the equation from Epps et al. (2007) predicting gene flow as a function of ED to account for this reduced dispersal range, and explored sensitivity to errors of up to 30 % in the estimation of female ED_{MAX} (Appendix S2).

We calculated the ED of the least-cost paths between all pairs of habitat patches in the study area (including buffer patches and patches for which genetic data were unavailable) using the slope-based resistance model described above. Anthropogenic features acting as complete or nearly complete barriers to bighorn sheep dispersal based on anecdotal evidence (Bleich et al. 1996) or genetic analysis (Epps et al. 2005), including fenced interstate highways, urban areas, and aqueducts, were incorporated into resistance surfaces by assigning barrier cells a million times higher resistance than non-barrier cells; this ensured that the least-cost path between any pair of patches separated by a barrier had $ED > ED_{MAX}$. Least-cost paths were calculated in ArcGIS 10.0 (ESRI, Redlands, CA, USA). We then used ED values to predict expected gene flow (Nm; see Equation 2 in Epps et al. 2007) between each pair of patches. While the interpretation of F_{ST}-based estimates of Nm has been questioned (Whitlock and McCauley 1999; Holsinger and Weir 2009), we used Nm merely as a measure of relative differences in gene flow among pairs of habitat patches.

Network models

We generated two network models to explore genetic and demographic connectivity of the Mojave bighorn sheep metapopulation:

1. Genetic network: This network modeled the potential for gene flow among patches, which should be limited by male dispersal range. We included network edges representing dispersal corridors between all pairs of patches separated by $ED < 16.4$ resistance units (and hereafter use the terms "edge" and "corridor" interchangeably). We then assigned these corridors weights equal to their predicted Nm values (Appendix S1); thus, within the estimated maximum male dispersal range, the strength of dispersal varied with effective distance as predicted by the genetic-based resistance model. We assumed gene flow between connected patches was symmetrical; the validity of this assumption is discussed later.

2. Demographic network: This network modeled the potential for rescue or re-colonization of a patch from neighboring patches, which should be limited by female dispersal range. Accordingly, we included corridors between all pairs of patches separated by $ED < 10$ resistance units, our estimate of maximum female dispersal distance (Appendix S1). Similar to the genetic network, corridors were weighted by the female-specific Nm-ED equation (Appendix S1), and we assumed symmetrical dispersal. Thus, the demographic network was a sparser version of the genetic network, containing all of the same patches but only a subset of the corridors due to the more restricted movement of females.

Evaluating contribution of individual patches and corridors to connectivity

We used an iterative approach to evaluate the importance of patches and corridors to network connectivity. First, we identified subsets of network features that could be targeted for each of four possible management actions. The "patch protection" (PP) subset included all patches in the current network, and the "patch restoration" (PR) subset included all restorable patches within ED_{MAX} of a patch in the study area. The "corridor protection" (CP) subset included all corridors in the current network, and the "corridor restoration" (CR) subset included all potentially restorable corridors that are currently interrupted by an anthropogenic barrier but would otherwise connect two patches separated by $<ED_{MAX}$. These subsets

differed between the genetic and demographic networks because these networks included different numbers of restorable patches, corridors, and restorable corridors due to differences in ED_{MAX}.

For PP and CP, we deleted one patch or corridor at a time and then re-calculated network metrics (discussed below) to determine the effect of that specific feature on network connectivity. Patches and corridors whose removal resulted in larger decreases in network connectivity metrics were inferred to be more important contributors to genetic or demographic connectivity, and higher priority for protection. Because redundant corridors were excluded from the network (Appendix S1), our method assumed that the loss of a patch compromised all corridors passing through that patch. For PR and CR, we added one patch or corridor at a time and re-calculated network metrics; patches and corridors whose addition resulted in larger increases in network connectivity metrics were inferred to be higher priority for restoration.

Contributions of individual nodes and edges to network connectivity can be assessed using a wide variety of network metrics, but choosing a biologically appropriate metric to describe a particular aspect of connectivity is challenging (Pascual-Hortal and Saura 2006; Moilanen 2011). Global metrics that describe whole network-level properties can be used to describe the impact of specific network features on connectivity by comparing these metrics for networks with and without a particular node or edge. However, many global metrics are not calculable or not meaningful when applied to fragmented networks consisting of multiple disconnected subgroups of patches ("components"), which are common among anthropogenically-fragmented systems such as ours. We used two metrics that describe network-level connectivity but are unaffected by multiple components (see additional details in Appendix S3):

1. *Mean weighted closeness (MWC)* Closeness is a measure of how near a patch is to all other network patches along shortest paths and can be calculated in weighted networks using Dijkstra's (1959) algorithm, which accounts for the possibility that paths containing many steps of large weight may be more efficient than paths containing few steps of small weight. We used a formulation of weighted closeness for networks with disconnected components (Opsahl et al.

2010) and calculated the mean of this metric across all patches. MWC reflects the long-term potential for transfer of genes or individuals across the network because it considers all connections, including those between very distant patches that would require numerous dispersal steps. Network changes (e.g., patch or corridor additions) that increase MWC can be interpreted as increasing the efficiency of transfer for genes or individuals within the network over multiple generations.

2. *Effectively connected pairs (ECP)* We defined this metric as the number of pairs of patches connected by a total effective distance less than ED_{MAX} (i.e., <16.4 resistance units in the genetic network and <10 resistance units in the demographic network). This included pairs that are connected by a single corridor or a multi-corridor path with combined effective distance $<ED_{MAX}$. ECP describes the short-term potential for genetic or demographic connectivity among populations.

For each management action, we calculated the proportional change (hereafter, Δ value) in network metrics when each feature was removed from the network (for PP and CP) or added to the network (for PR and CR). Larger Δ values indicate features with a larger positive impact on connectivity.

To determine how the type of connectivity affected prioritization results, we calculated Spearman's rank correlation coefficient between genetic network Δ values and demographic network Δ values for each metric (ECP or MWC) and type of management action (PP, CP, PR, or CR). We also calculated the Spearman correlation between ECP- and MWC-based Δ values within each network to determine how metric choice affected prioritization. In cases where between-network comparisons involved different numbers of patches or corridors, we calculated correlations using Δ values for those features common to both networks. Lastly, we identified "high-priority" patches or corridors for each management action as those ranking among the top five in at least two of the four combinations of connectivity type and network metric.

Sensitivity analysis

We evaluated sensitivity to changes in male and female ED_{MAX} (which define corridor presence/

absence) by increasing or decreasing ED_{MAX} in 5-percent increments up to 30 % (male ED_{MAX}: 11.5–21.3, female ED_{MAX}: 7.0–13.0 resistance units). We then reanalyzed the data to produce new sets of Δ values at each error level, and we calculated the Spearman correlation between Δ values from original ED_{MAX} estimates and Δ values at each error level. We also examined how the set of features identified as potential targets for each management action changed as a function of ED_{MAX} (see Appendix S2 for further details).

Testing ecological relevance of network metrics

Connectivity measures, especially network metrics, have been criticized for having questionable relevance to ecological processes such as gene flow or colonization (Pascual-Hortal and Saura 2006; Moilanen 2011). We tested the relevance of our network-level metrics (ECP and MWC) by generating patch-level analogs and determining whether they predicted nuclear and mitochondrial genetic diversity of patches in the genetic and demographic networks, respectively. If the structures of our networks adequately represent gene flow and colonization, and ECP and MWC adequately capture these processes at the metapopulation level, then we would expect that patch-level analogs of ECP and MWC should be correlated with: (1) allelic richness (A) and expected heterozygosity (H_e) of patches in the genetic network, which should be influenced most by male-mediated gene flow, and (2) mitochondrial haplotype richness (HR) of patches in the demographic network, which should reflect female movements between populations because mitochondrial haplotypes are maternally inherited (see Appendix S4).

Results

As expected, the genetic network exhibited much greater connectivity than the demographic network (Fig. 2). The genetic network contained nearly twice as many corridors (gen: 66, dem: 38) and effectively connected pairs (gen: 122, dem: 65), and fewer than half as many components as the demographic network (gen: 5, dem: 13). MWC was nearly twice as high in the genetic network than the demographic network (gen: 11.57, dem: 5.83). We report additional network

properties in Appendix S5 to facilitate comparison with other ecological networks.

We identified 21 restorable corridors and 13 restorable patches in the genetic network, and 15 restorable corridors and 11 restorable patches in the demographic network. Prioritization of patches and corridors varied between genetic and demographic networks, and also between metrics (Tables 1, S3–S6; Figs. 2, S8–S11).

Correlations between Δ values from the genetic and demographic networks ranged from 0.62 to 0.95 depending on which management action and metric was considered. Within a network type, correlations between ECP- and MWC-based Δ values ranged from 0.35 to 0.95; for all management actions except corridor restoration, these between-metric correlations were higher in the demographic network than the genetic network. Although some of these correlation values were quite low, agreement among the top ranking features was generally much better than among the entire set of features (Tables 2, S3–S6). We identified at least four patches or corridors for each management action that met our criteria for high-priority features (Table 2).

Sensitivity analysis showed that Δ values were generally quite robust to errors in ED_{MAX}, although this varied across combinations of management action, connectivity type (genetic vs. demographic), and network metric (Fig. S4). The correlation of original Δ values with new Δ values remained above 0.75 within the range of ED_{MAX} values tested (±30 %), with the exception of MWC-based results in the genetic network, which changed considerably when ED_{MAX} was reduced by more than 20 %. However, changing ED_{MAX} led to changes in the subsets of nodes and edges identified as potential targets for each management action (Figs. S5, S6). For instance, decreasing female ED_{MAX} by 30 % meant that only 65 % of the restorable corridors identified in our analysis would still meet the criteria for a restorable corridor.

Patch-based analogs of our network metrics calculated for the genetic network predicted both A and H_e ($R^2 = 0.19$–0.34; $P = 0.002$–0.029), and those calculated for the demographic network predicted HR ($R^2 = 0.53$–0.56; $P < 0.0001$), for 25 populations within our study system (Appendix S4, Table S2). Our patch-level analogs of ECP and MWC explained
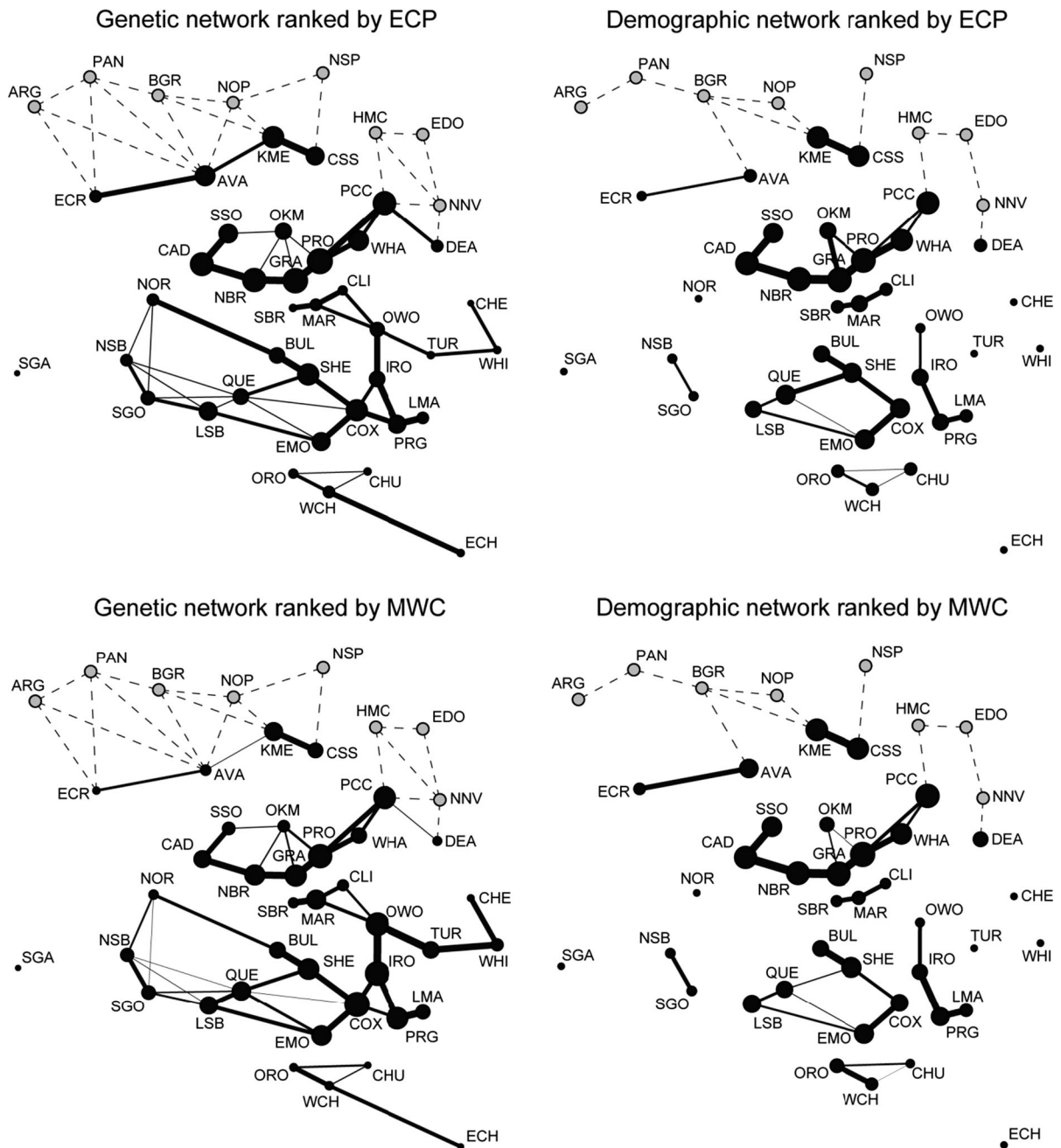
Fig. 2 Prioritization of patch and corridor protection according to network type (genetic or demographic) and network metric used to rank features (*ECP* effectively connected pairs, a measure of short-term network connectivity, *MWC* mean weighted closeness, a measure of long-term connectivity). *Black circles* and *lines* represent existing patches and corridors included in the prioritization analysis; circle size and line width are inversely proportional to rank (*larger circles* and *wider lines* are more important patches and corridors to protect). *White circles* and *dashed lines* represent "buffer" patches and associated corridors (not ranked). Patches are labeled with 3-letter abbreviations; for full patch names, see Table S1 in Supporting Materials

considerably more variation in all three genetic diversity indices than common centrality metrics (Table S2), suggesting that ECP and MWC have

greater ecological relevance as measures of connectivity, although much of the variation in genetic diversity remained unexplained.

Table 1 Correlation of prioritization results between networks and between metrics for each management action

Set 1			Set 2			Spearman correlation coefficient
Network	Mgmt. action	Metric	Network	Mgmt. Action	Metric	
Between-network correlations						
G	PP	ECP	D	PP	ECP	0.88
G	PP	MWC	D	PP	MWC	0.62
G	PR	ECP	D	PR	ECP	0.88
G	PR	MWC	D	PR	MWC	0.95
G	CP	ECP	D	CP	ECP	0.80
G	CP	MWC	D	CP	MWC	0.78
G	CR	ECP	D	CR	ECP	0.82
G	CR	MWC	D	CR	MWC	0.85
Between-metric correlations						
G	PP	ECP	G	PP	MWC	0.74
D	PP	ECP	D	PP	MWC	0.95
G	PR	ECP	G	PR	MWC	0.85
D	PR	ECP	D	PR	MWC	0.92
G	CP	ECP	G	CP	MWC	0.77
D	CP	ECP	D	CP	MWC	0.80
G	CR	ECP	G	CR	MWC	0.46
D	CR	ECP	D	CR	MWC	0.35

"Set 1" and "Set 2" describe the two sets of Δ values being compared. For instance, the first row of the table shows the correlation between ECP-based Δ values for patch protection in the genetic network ("Set 1") and ECP-based Δ values for patch protection in the demographic network ("Set 2")

G genetic network, *D* demographic network, *PP* patch protection, *PR* patch restoration, *CP* corridor protection, *CR* corridor restoration, *ECP* effectively connected pairs, *MWC* mean weighted closeness

Discussion

Recognition of the need to prioritize management (including restoration) of habitat patches and corridors at the landscape scale is increasing, as evidenced by recent publications addressing this issue using resistance- or network-based approaches (McRae et al. 2012; Theobald et al. 2012; Albert et al. 2013). Yet, very rarely have these two approaches been combined to achieve greater insight into the effects of potential management actions, as demonstrated by our analysis. One exception is Lookingbill et al. (2010), who used network theory to evaluate the relative importance of existing dispersal corridors and habitat patches for the Delarma fox squirrel (*Sciurus niger cinereus*); that analysis used an individual-based simulation model of dispersal across an expert opinion-based resistance surface to estimate connectivity among patches and construct a binary network. We further refined this methodology by: (1) utilizing an optimized, empirically-derived resistance model, (2) constructing weighted networks that incorporate differences in effective distances among corridors (i.e., edge weights); (3) considering patch and corridor restorations in addition to losses; and (4) evaluating multiple types of connectivity. This combined approach provides a useful framework for distinguishing among different processes related to connectivity, as well as an objective means of balancing those biological elements in our decision-making.

We observed large structural differences between networks based on genetic connectivity and those based on demographic connectivity (Fig. 2), with much higher levels of both short-term (ECP) and long-term (MWC) connectivity in the genetic network. Therefore, managing to maintain only genetic connectivity among bighorn sheep populations would not necessarily maintain natural re-colonization; likewise, important connections for gene flow might be missed if only colonization potential was considered. This

Table 2 High priority patches and corridors for protection or restoration in the genetic and demographic networks

Mgmt. action	Patch or corridor[a]	Genetic network			Demographic network		
		ECP	MWC	n	ECP	MWC	n
Patch protection	PRO	✔	✔	37	✔	✔	37
	PCC	✔	✔		✔	✔	
	GRA	✔			✔	✔	
	NBR	✔			✔	✔	
	CAD	✔			✔	✔	
Patch restoration	PIN	✔	✔	13	✔	✔	11
	OWL	✔	✔		✔	✔	
	FIG	✔	✔		✔	✔	
	SLA	✔	✔		✔	✔	
	QUA		✔		✔	✔	
Corridor protection	GRA–PRO	✔	✔	47	✔	✔	27
	GRA–NBR	✔	✔		✔	✔	
	CAD–NBR	✔			✔	✔	
	CSS–KME	✔			✔	✔	
	CAD–SSO	✔			✔	✔	
Corridor restoration	GRA–MAR	✔	✔	21	✔	✔	15
	NBR–SBR	✔	✔		✔	✔	
	EMO–ORO	✔			✔	✔	
	CLI–PRO		✔			✔	

High priority features are defined as those ranking among the top 5 (represented with a ✔ in the table) in at least two of the four combinations of connectivity type (genetic, demographic) and network metric (ECP, MWC)

n total number of features associated with a particular management action in the genetic or demographic network

[a] See Table S1 for 3-letter patch abbreviations and full patch names

pattern is probably common among species that exhibit strongly sex-biased dispersal. For such species, researchers and managers must give greater recognition to the type of connectivity that they are trying to model, preserve, or restore.

Considering different types of connectivity resulted in markedly different prioritization results for some management actions (Table 1, S3–S6). However, there was generally strong agreement among the highest ranking features in each network according to one or both of our metrics. For each management action, we found at least four high-priority features and at least two features that ranked in the top five across all four combinations of connectivity type and network metric (Table 2), suggesting that conservation actions could target patches or corridors that are highly important to both genetic and demographic connectivity and to both short- and long-term connectivity. Consistent with previous network-based

connectivity analyses (Jordán et al. 2003; Laita et al. 2011), prioritization also depended on the choice of network metric (Table 1), reinforcing the need to select biologically relevant network metrics. We chose our two metrics to represent local and long-distance transfer of genes or individuals in a bighorn sheep metapopulation, but recognize that these metrics cannot capture all aspects of those processes.

Our sensitivity analysis suggested that values of connectivity metrics were relatively robust to errors in estimating ED_{MAX} (Appendix S2). However, such errors were quite influential in determining which features should be candidates for a particular management action. For instance, the Avawatz–S. Soda (AVA–SSO) corridor was the highest ranking restorable corridor by MWC in the demographic network (Table S6), but if female ED_{MAX} was decreased by only 10 %, the AVA–SSO corridor's ED would be too large for it to be considered a restorable corridor. Thus,

even small errors in estimating dispersal thresholds or dispersal functions, or estimates that ignore landscape resistance, could affect conclusions about the relative importance of patches and corridors to network connectivity. Estimating dispersal functions and thresholds remains a challenging research need and a major limitation to many connectivity analyses (Parks et al. 2012).

Analytical limitations

Our networks were constructed using the topography-based Epps et al. (2007) landscape resistance model, and the parameterization of that landscape resistance model could affect our conclusions about the relative importance of network features. Incorporating other environmental variables in the resistance model could influence network rankings, although Epps et al. (2007) observed a strong relationship between genetic differentiation and effective distance using the topographic resistance model. Additionally, resistance models were tested using partial Mantel tests, which have been demonstrated to have inflated risk of type I error when applied to spatially autocorrelated data (Graves et al. 2013; Guillot and Rousset 2013); however, the best model was identified on the basis on Mantel r correlation, not statistical significance, and had a very small p value (<0.0001, unpublished data).

We assumed that dispersal between patches is symmetrical, but this may be an oversimplification. Because habitat quality varies among patches (Epps et al. 2004, 2006), source-sink dynamics could influence dispersal. Network theory can easily accommodate asymmetrical connectivity, but genetic methods for estimating directional dispersal are less well established.

Our prioritization assumed that only a single patch or corridor was added or removed to the existing network. Consequently, if multiple actions were taken simultaneously, it would be incorrect to conclude that the greatest benefit to connectivity would result from pursuing actions in order of their Δ values. For instance, if the two restorable corridors with the highest Δ values in the genetic network were restored (the Granite–Marble [GRA–MAR] and N. Bristol–S. Bristol [NBR–SBR] corridors; Table S6; Fig. S8), they would play nearly identical roles by linking the two largest network components across Interstate

Highway 40. Restoring the GRA–MAR corridor and a corridor across a different barrier (e.g., the Eagle–Orocopia [EMO–ORO] corridor across Interstate Highway 10) would be more useful. We strongly recommend grouping restorable corridors by the barrier feature with which they are associated, then using our results to prioritize within each group rather than on the basis of overall ranks.

Additional factors beyond the contribution of patches and corridors to metapopulation connectivity will need to be considered when prioritizing management. Monetary costs, conflicts with other land uses, effects on other species, effects on disease spread, and public support are all likely to vary by management action and location. Information on habitat quality (e.g., Epps et al. 2004) may also allow more efficient use of management resources than relying solely on network connectivity rankings. Consideration of these factors is beyond the scope of this analysis; here, we have sought only to provide input on the biological connectivity aspect of the overall prioritization process.

Recommended actions in the Mojave Desert region

Should conservation resources be allocated preferentially to patch- or corridor-focused actions? Using Δ values to compare patch protection versus corridor protection is not informative because our analysis assumed that the loss of a patch also compromised all associated corridors (a necessary assumption because network methods require that every edge connects two nodes). However, comparisons between patch restoration and corridor restoration effectiveness on the basis of Δ values are warranted. Corridor restorations had a much stronger effect on long-term connectivity (as measured by MWC) than patch restorations in both the genetic and demographic network: 18 of 21 restorable corridors in the genetic network and 9 of 15 in the demographic network would increase MWC more than the top-ranked restorable patch (Tables S5, S6). If increasing short-term connectivity is the goal, however, then patch restorations could be nearly as effective: only four restorable corridors in the genetic network and two in the demographic network would increase ECP more than the top-ranked restorable patch (Tables S5, S6). There may be fewer new opportunities for patch protection than corridor

protection in our study area because the current system of land protection (e.g., Wilderness designation) focuses more on core bighorn sheep habitats (i.e., mountain ranges) than infrequently used dispersal habitat. Yet, patch protection and restoration through natural colonization or population reintroductions are still vital to maintain metapopulation viability. Restoring corridors to unoccupied patches could be warranted when a patch contains favorable bighorn sheep habitat but has experienced a population extinction due to stochastic or temporary factors (e.g., local drought or disease outbreak) and has not had opportunity to be naturally recolonized; in such cases, restoring connectivity could make population reintroduction efforts unnecessary.

Our network approach is also amenable to evaluating conservation actions targeting multiple patches or corridors. For example, we used our models to quantify the effects of four plausible multi-feature restoration scenarios: (1) re-occupation of the N. Soda (NSO) patch and restoration of the NSO–SSO, GRA–MAR, and EMO–ORO corridors to mitigate barrier effects of three interstate highways; (2) re-occupation of four northern patches (Fort Irwin Granite [FIG], Owlshead [OWL], Quail [QUA], and Slate [SLA]) that are currently unoccupied but have low predicted extinction probabilities (Epps et al. 2004); (3) re-occupation of the Sacramento (SAC) and Piute (PIU) patches to provide stepping stones between eastern and central patches in the metapopulation; and (4) all of the above actions. Scenario 1 is the most efficient of the individual scenarios for increasing MWC because it links together the four largest components in the network (Table 3). Scenario 1 is also most efficient for increasing ECP in the genetic network, but slightly less efficient than Scenario 2 in the demographic network. Dramatic increases in metapopulation connectivity are possible by combining patch and corridor restorations: under Scenario 4, ECP and MWC would more than double in the genetic and demographic networks.

We suggest several actions to efficiently maximize genetic diversity and metapopulation persistence in the Mojave region. First, restore at least one connection across each of the three interstate highways that currently fragment the metapopulation, which will vastly improve the potential for long-distance gene flow in this system and restore important demographic links (Epps et al. 2005). Second, evaluate whether

Table 3 Effects of four multi-part conservation scenarios on connectivity of genetic and demographic networks, as measured by Δ values associated with each scenario for both network types and metrics

	Genetic network		Demographic network	
	ECP	MWC	ECP	MWC
Scenario 1: mitigate interstate highways	0.57	0.93	0.46	0.65
Scenario 2: re-occupy northern Mojave patches	0.35	0.18	0.48	0.33
Scenario 3: re-occupy stepping stone patches	0.07	0.06	0.05	0.02
Scenario 4: all actions in scenarios 1–3	1.16	1.27	1.02	1.07

existing infrastructure such as highway bridges over washes can be modified to encourage use by bighorn sheep; for instance, by removing highway fencing around bridged washes and strategically locating artificial water sources to lure sheep to the area, it may be possible to facilitate bighorn sheep crossings beneath highways in some locations. Third, maximize patch occupancy by protecting or improving habitat, protecting routes for natural re-colonization (even to currently unoccupied patches), or reintroducing populations where natural re-colonization is unlikely. Finally, we note that our rankings could be used to address situations where connectivity is potentially problematic. For instance, our rankings may indicate which populations or connections could have the greatest impact on disease spread, such as in response to a recent outbreak of respiratory disease within the study area (California Dept. of Fish and Wildlife, unpublished data).

Applying the network approach in conservation

Combining landscape resistance models with network analysis offers a means of evaluating conservation scenarios across complex systems. Other studies of genetic connectivity have used genetic data alone (e.g., pairwise genetic distances) to construct network models (Dyer and Nason 2004; Garroway et al. 2008; Rozenfeld et al. 2008). The advantage of this approach is that it quantifies genetic connectivity between populations more directly than the resistance-based approach we used. However, it can only be applied to

extant populations for which genetic data are available, and assumes that genetic distance reflects the current landscape configuration. In contrast, our resistance-based approach can be used to predict connectivity between any set of habitat patches and to evaluate effects of barrier mitigation or population reintroduction. However, we reiterate that evaluating how dispersal varies with effective distance is an important component when combining resistance models with network analysis, and better methods of estimating such relationships are needed.

Evaluating the relative importance of habitat patches and dispersal corridors by iterative removal from and addition to network models is particularly useful when the spatial footprint of potential threats to habitat or connectivity is unclear. For instance, the transitory nature of renewable energy development plans in the Mojave Desert makes it difficult to anticipate the specific locations and extents of energy facilities with any certainty. Incorporating anticipated landscape changes directly into resistance surfaces and re-analyzing network structure might be preferable, but it may be too late for meaningful conservation action by the time that final development plans are available. Instead, the iterative prioritization method can be used to evaluate landscape changes in accordance with the importance of the patches and edges likely to be affected due to their proximity.

Conservation applications of network theory have been criticized for overemphasizing the relevance of landscape connectivity (Moilanen 2011), which is only one of several factors contributing to regional persistence—the ultimate goal of most conservation programs. More complex metapopulation models allow for estimation of persistence probabilities and have also been used to prioritize habitat patches and dispersal corridors (Moilanen et al. 1998; Hoyle and James 2005); yet the data requirements for such models are prohibitive even in many well-studied systems, limiting their application to real-world conservation issues. For instance, the well-known incidence function model (Hanski 1994) requires estimates of patch-specific colonization and extinction rates that are typically obtained through multi-year occupancy surveys of all possible habitat patches. Obtaining these empirical estimates for species with slow population turnover rates, such as desert bighorn sheep, is simply not feasible within a short enough time frame to inform management decisions. For example, Epps et al. (2010) reported only four known desert bighorn colonization events in a 20 year period in the Mojave Desert. On the other hand, there is abundant evidence that: (1) re-colonization is critical for persistence of any fragmented system where population extinction is common (Levins 1969) such as the Mojave bighorn system (Epps et al. 2004); (2) genetic diversity affects fitness and ultimately population persistence, particularly for species with small effective population sizes (Reed and Frankham 2003; Frankham 2005); and (3) gene flow between populations is a primary driver of genetic diversity in this system (Epps et al. 2006) and other systems of small, partly-fragmented populations. Thus, clear biological reasons exist for attempting to maximize genetic and demographic connectivity through conservation actions, even when estimates of their effect on regional persistence are not possible.

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