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Evaluating resistance surfaces for modeling wildlife movement and connectivity

Katherine Zeller

EVALUATING RESISTANCE SURFACES FOR MODELING WILDLIFE MOVEMENT AND CONNECTIVITY

A Dissertation Presented

by

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MODELING WILDLIFE MOVEMENT AND CONNECTIVITY

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DEDICATION

To my mother and father and their unwavering belief in and encouragement of the education of their children.

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First of all, I would like to thank my husband, Tom, for his encouragement and support through this sometimes harrowing process. The journey to today would have been much harder (and possibly much longer!) without his steady belief in me. He helped make these last five years so very much easier simply by laughter and love.

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ABSTRACT

EVALUATING RESISTANCE SURFACES FOR MODELING WILDLIFE MOVEMENT AND CONNECTIVITY

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The continued growth of human populations and associated development in many areas of the world is causing persistent fragmentation of natural habitats. In response, wildlife corridors are often promoted as essential for the conservation of wildlife species. Wildlife corridors allow for the movement of individuals between habitat patches and confer many benefits including the maintenance of metapopulations and metapopulation dynamics, the maintenance of seasonal migratory routes, genetic exchange, and the potential for individuals and populations to shift their ranges in response to climate change.

Wildlife corridors are modeled across a resistance-to-movement surface where resistance represents the willingness of an organism to cross a particular environment, the physiological cost of moving through a particular environment, or the reduction in survival for the organism moving through a particular environment. Resistance surfaces can be estimated using a wide variety of methods yet, to date, there has been no in-depth

methodological comparison of these methods and their appropriateness for modeling connectivity.

My dissertation has two main objectives. The first was to determine the sensitivity of species-habitat models, resistance surfaces and corridors for pumas (*Puma concolor*) in southern California to six key factors: (1) data type used (point, step, or path data); (2) Statistical models employed; (3) Behavioral state of the individuals; (4) Spatial scale of analysis; (5) GPS collar acquisition interval; and (6) Thematic resolution and richness of the underlying geospatial layers. The second objective was to determine which combination of factors results in the most appropriate resistance surfaces for connectivity modeling.

I found that species-habitat models, resistance surfaces and corridors were extremely sensitive to all six of these factors – to the point where using one scale versus another or one data type versus another resulted in conflicting conclusions about habitat use and differences in the location of corridors. I recommend that, for modeling movement and corridors, path data be used in a context-dependent multi-scale modeling framework. I also recommend that many different geospatial layers at different thematic resolutions be examined to identify the most appropriate landscape definition for the species and study area of interest.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

ESTIMATING LANDSCAPE RESISTANCE TO MOVEMENT: A REVIEW

Introduction

Understanding animal movement is crucial for developing effective landscape-level conservation initiatives. Successful movement of animals across the landscape may fulfill a number of biological processes, including foraging, mating, migration, dispersal and gene flow, and is especially critical in allowing individuals and populations to adjust (e.g., redistribute) to a changing environment. However, animal movement is one of the most difficult behaviors to observe and quantify. When movement can be assessed, the number of individuals being studied is often small, and/or there may be large gaps of time between successive point locations along a movement path. Resistance to movement values are typically used to fill this gap in movement knowledge by providing a quantitative estimate of how environmental parameters affect animal movement. In this context, 'resistance' represents the willingness of an organism to cross a particular environment, the physiological cost of moving through a particular environment, the reduction in survival for the organism moving through a particular environment, or an integration of all these factors. Resistance estimation is most commonly accomplished by parameterizing environmental variables across a 'resistance' or 'cost' to movement continuum, where a low resistance denotes ease of movement and a high resistance denotes restricted movement, or is used to represent an absolute barrier to movement. 'Friction' and 'impedance' to movement or their inverse, 'permeability' and 'conductivity' to movement are also terms used to describe these travel surfaces (Singleton et al. 2002; Chardon et al. 2003; Sutcliffe et al. 2003). For simplicity, the term ‘resistance surface’ will be used to describe these movement surfaces for the remainder of the paper.

The use of resistance surfaces in landscape ecology and conservation biology has increased over the last decade. In particular, resistance surfaces are used in metapopulation and corridor studies to represent the landscape between populations or habitat patches. These studies have matured from simple ‘isolation by-distance’ or ‘isolation-by-barrier’ hypotheses to recognizing that animal movement between populations is influenced by the varying environmental conditions an individual encounters as it moves through a landscape (Ferreras 2001; Adriaensen et al. 2003). This is typically referred to as ‘isolation-by-resistance’ (McRae 2006). Resistance surfaces are a quintessential element to contemporary landscape genetics studies focused on assessing how landscape structure affects the flow of genes across the landscape (Manel et al. 2003; Spear et al. 2010).

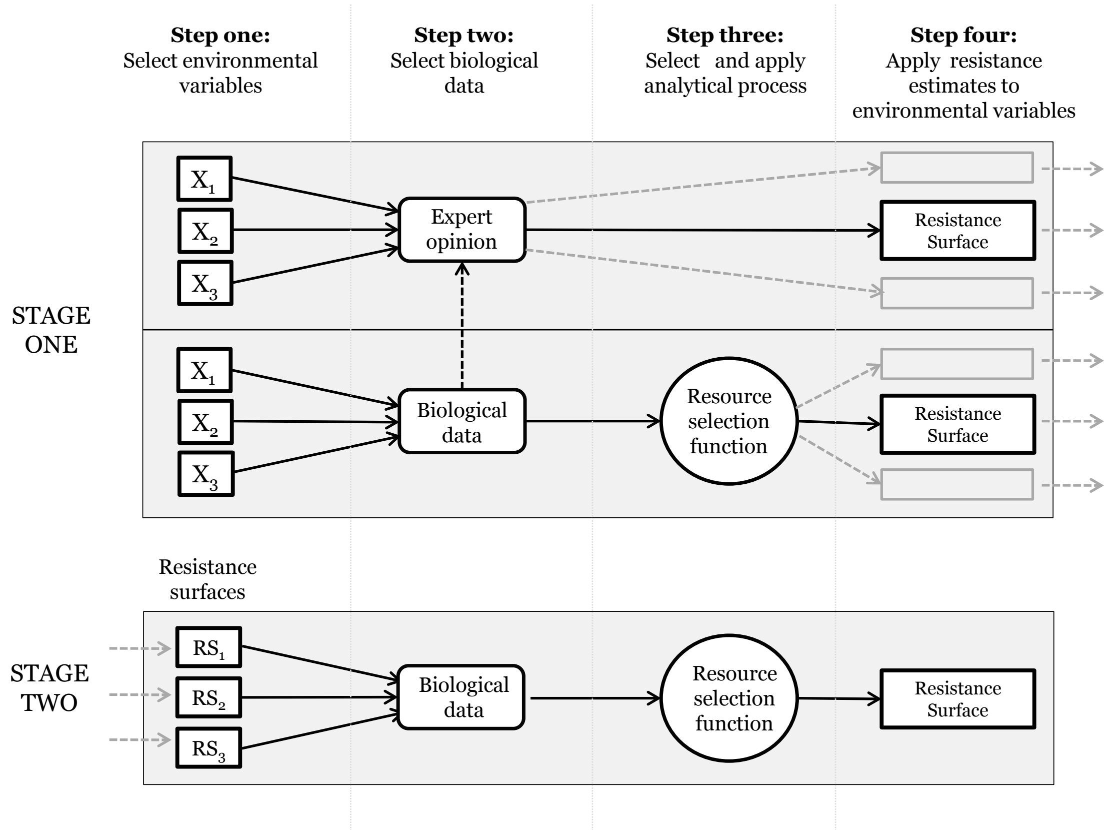
Myriad methods have been used to model landscape resistance to movement. Techniques range from very basic and data-light to complex and data-heavy. Moreover, no general consensus has been reached regarding the most accurate data sources and analytical methods for modeling resistance surfaces (Spear et al. 2010). A summary of the methods used and their pros and cons is needed in order to frame the current state of knowledge surrounding resistance surface modeling and provide guidance for future research. Here, we provide a comprehensive literature review of the data sources and analytical methods used for deriving resistance surfaces. We discuss common techniques, highlight unique approaches, and consider the strengths and weaknesses of these methods. Finally, we discuss directions for future research and methodological improvement.

Methods

We focused our literature review on papers that dealt explicitly with estimating resistance to movement values for wildlife. We searched for papers in the ISI Web of Science (ISI 2011) with the following search criteria from January 2000 to June 2011: Topic = (resistance OR cost OR effective distance OR landscape permeability) AND (corridor* OR connect* OR wildlife OR linkage); this resulted in 1,343 papers. We refined our results by restricting the search to the following subject areas: Genetics and Heredity, Biochemistry and Molecular Biology, Ecology, Environmental Sciences, Multidisciplinary Sciences, Environmental Studies, Zoology, Biology, Evolutionary Biology, Veterinary Sciences, Biodiversity Conservation, Forestry, Agriculture, Dairy and Animal Science, Management, Marine and Freshwater Biology, Entomology, Geography, Fisheries, Oceanography, Remote Sensing, and Ornithology. This restricted the result to 693 papers, which we further refined by excluding papers which were simulation exercises only, did not deal explicitly with wildlife, and/or did not estimate resistance values. This resulted in our final sample of 96 papers distributed across 26 different journals. We purport that, although this is not a full census of papers on resistance, the final set of papers we reviewed represent a comprehensive survey of current methods used to estimate resistance to movement for wildlife. References for the 96 papers are provided in Appendix A.

To summarize each paper, we recorded the following information: taxonomy and number of target species, number and type of environmental variables, grain and extent of analysis, type of biological input data, analytical approach, type of resource selection function (RSF), and final range of resultant resistance values. We distinguished among five types of biological input data: (1) expert opinion, (2) detection data, (3) relocation data, (4) pathway data, and (5) genetic data, as defined below (‘‘Biological data’’ section). We refer to ‘analytical approach’ as the analytical method(s) by which the environmental variables were interpreted and transformed into a final resistance surface. In this regard, we distinguished among three analytical approaches: (1) ‘one-stage expert approach’, in which the final resistance surface was derived in a single step based solely on expert opinion; (2) ‘one-stage empirical approach’, in which the final resistance surface was derived in a single step based on the analysis of biological data; and (3) ‘two-stage empirical approach’, in which a set of alternative resistance models were created based on expert opinion and/or the analysis of biological data in the first stage, followed by model selection based on the analysis of biological data in the second stage. We also distinguished among five types of RSFs that were used within the one-stage and two-stage empirical approaches: (1) point selection function (PSF), (2) home range selection function (HSF), (3) matrix selection function (MSF), (4) step selection function (SSF), and (5) path selection function (PathSF), as defined below (‘‘Resource selection functions’’ section). Lastly, although we reviewed 96 papers, several papers used more than one biological input data type or analytical approach. Consequently, we refer to the number of ‘instances’ in the text and tables, rather than number of papers, as appropriate.

Figure 1.1. Resistance surface methods. Biological data types and analytical processes commonly used to derive resistance surfaces.



Results and Discussion

Overview of modeling resistance surfaces

We provide a brief outline of the resistance surface modeling process as background for interpreting the literature review (Fig. 1.1).

In step one of the modeling process, one or more environmental variables are selected that are either known or assumed to influence movement of a target species. These variables are represented with geospatial layers that are either developed for the study area or are readily available. The geospatial layers are then scaled appropriately (e.g., resampled to a coarser spatial resolution) to the species/phenomenon of interest and are represented either as raw data, classified into a desired set of classes (e.g., land cover classes), or transformed using various functions (e.g., Gaussian transformation of elevation).

In step two, biological data on which the estimation of resistance values will be based are chosen and may include detection data (i.e., presence-only or presence–absence points), relocation data (e.g., capture– recapture), pathway data (i.e., travel paths), genetic data (i.e., genotypes of individuals), or a combination of these types. If empirical data are lacking, then expert opinion can be used in its place.

Once environmental and biological data are in hand, step three involves selecting an analytical approach by which to estimate resistance values. If biological data are unavailable, then an expert-only approach must be used and there is no analytical process per se. If biological data are available, the type of biological data will usually drive the selection of the analytical approach. However, the analytical approach may be chosen first and then the biological data collected to meet the requirements of the model. In either case, the analytical approach usually entails selecting an appropriate RSF given the type of biological data and researcher preference. In addition, the approach selected may include two stages: first to derive a set of candidate resistance surfaces, and second to select the ‘‘best’’ of the candidates.

In step four, once the resistance values are estimated, a final resistance surface is created by applying the results to the grids of the previously selected environmental variables. Depending on the biological data and analytical approach employed and the intended use of the resistance surface (e.g., corridor design, population modeling), multiple resistance surfaces (e.g., to reflect model uncertainty) may be retained for use in the subsequent application. However, some studies are only interested in assessing the degree to which environmental variables may be affecting movement and thus do not develop a 'final' resistance surface.

Taxonomic bias

Eight taxonomic classes, 25 orders, and 59 families were represented in our sample (Table 1.1). The Mammalia class (86 % of studies), the Carnivora order (46 % of studies), and the Felidae family (17 % of studies) were the most highly represented. Four studies used generic species as a proxy for real species (Adriaensen et al. 2003; Rae et al. 2007; Pinto and Keitt 2009; Watts et al. 2010). Of the 14 studies that modeled more than one species, resistance values were modeled separately for each species in 10 of the studies and were combined into a single resistance model in four of the studies. Not surprisingly, large and charismatic species of conservation concern were the focus of the majority of studies, although amphibians were also represented surprisingly well, while birds and invertebrates were less often the focus.

Table 1.1. Taxonomic focus (including Phylum, Class, Order and Family) in 96 studies aimed at producing a resistance surface.

Taxonomic Divisions		***Number of Papers*** [a]	***Percentage of Papers*** [b]
Phylum	Chordata	124	129%
	Arthropoda	10	10%
Class	Mammalia	83	86%
	Amphibia	7	18%
	Aves	16	17%
	Insecta	8	8%
	Reptilia	8	8%
	Arachinidia	1	1%
	Actinopterygii	1	1%
	Branchiopoda	1	1%
Order	Carnivora	45	46%
	Artiodactyla	19	20%
	Rodentia	13	14%
	Passeriformes	11	11%
	Anura	10	10%
	Caudata	7	7%
	Testudines	4	4%
	Lepidoptera	4	4%
	Squamata	4	4%
	Ephemeroptera	2	2%
	Proboscidea	2	2%
	Falconiformes	1	1%
	Trichoptera	1	1%
	Erinaceomorpha	1	1%
	Dasyuromorphia	1	1%
	Cypriniformes	1	1%
	Cladocera	1	1%
	Columbiformes	1	1%
	Hemiptera	1	1%
	Tubulidentata	1	1%
	Ixodida	1	1%
	Sirenia	1	1%
	Piciformes	1	1%
	Strigiformes	1	1%
	Galliformes	1	1%
Family	Felidae	16	17%
	Mustelidae	11	11%
	Cervidae	10	10%
	Ursidae	10	10%

Bovidae	6	6%
Ambystomatidae	6	6%
Bufonidae	5	5%
Canidae	4	4%
Sciuridae	4	4%
Ranidae	4	4%
Hyaenidae	3	3%
Acanthizidae	2	2%
Heteromyidae	2	2%
Parulidae	2	2%
Nymphalidae	2	2%
Elephantidae	2	2%
Cricetidae	2	2%
Colubridae	2	2%
Emydidae	2	2%
Families represented by	40	42%

[a] Number of approaches used is more than 96 since more than one approach was used in some papers.
[b] Percentage of approaches used, rounded to nearest whole number.

Environmental variables

Estimates of resistance to movement are predicated on the choice of environmental variables, and the choice of both thematic and spatial scale (grain and extent) for representing those variables. Despite the universal importance of these choices, there was surprisingly little attention given to the selection and representation of environmental variables in the majority of the studies reviewed. Thirty-nine different environmental variables were used to model resistance (Table 1.2). Land use/land cover was the most widely used variable, followed by roads, elevation, hydrology, and slope. In 36 studies, only a single environmental variable was used, in 54 studies two to five variables were used, and in the remaining six studies, 6–10 variables were used. In these multi-variable studies, with one exception (Wasserman et al. 2010), variables were combined after analyzing the variables individually or fit simultaneously in the statistical model (e.g., via multiple logistic regression) to produce a single resistance surface.

With regards to the choice of environmental variables, ideally only those variables that are believed to have an influence on the movement of the target species are included, but more often than not, this type of a priori knowledge is lacking. Furthermore, environmental variables may be chosen as a proxy for landscape characteristics that an individual actually perceives and responds to as it moves through the landscape. For example, if understory cover is not available as an environmental layer, secondary forest cover may be used as a proxy. However, in a review of least-cost models, Sawyer et al. (2011) criticized the use of proxies for landscape features that may affect animal movement due to weaknesses in predictive power.

In addition, the source and accuracy of environmental data varies widely among studies. Spatial data are sometimes collected via GPS units with varying degrees of accuracy, but the majority of spatial environmental data come from remotely-sensed (RS) satellite or aerial imagery, typically using either a manual ‘‘heads-up’’ mapping approach or a semi- automated classification method. Acceptable error rates (if error rates are assessed at all) in layers derived from RS imagery are not standardized (Loveland et al. 2000), and although the target of most classifications is 85 % correct classification, many fall short of that goal (Foody 2002). Because image interpretation takes specialized software and training, the majority of papers reviewed chose to use extant environmental data. Unfortunately, these extant data are typically derived from imagery that is years, if not decades, old. In study areas where the environmental variables have remained mostly constant during this time-lag, this may not be a problem, but in more dynamic study areas, temporal appropriateness of the data must be scrutinized. When using RS data to derive habitat characteristics, seasonality must also be considered, especially in areas that have pronounced wet and dry seasons, or with species that exhibit distinct ecological differences from one season to the next. Although the availability of timely and affordable RS images and associated environmental layers is increasing, this will likely remain an issue for layers that are only periodically updated like roads, housing, and census data.

To avoid errors associated with RS and GPS spatial data, one approach is to limit data layers to those with consistent and high accuracy rates. In the papers reviewed, nine studies restricted environmental variables to topographic variables like slope (Epps et al. 2007), aspect (Clark et al. 2008), bathymetry (Flamm et al. 2005), or elevation (Vignieri 2005) that were presumably more accurate than interpreted variables like vegetation cover. Another approach is to evaluate the environment within a buffer around each animal detection or movement pathway, where the buffer encompasses the positional error of the data (Adriaensen et al. 2003; Braunisch et al. 2010). Though these inaccuracies cannot, at the moment, be avoided, they should at least be acknowledged in studies of this type (Beier et al. 2008).

With regard to the choice of thematic scale for representing environmental variables, 65 of the papers reviewed used only categorical variables, 24 used a combination of categorical and continuous variables, and seven used only continuous variables (Table 1.2). In many cases, the thematic scale chosen differed from the scale of the raw data. There are myriad ways to transform the scale of the raw data to more appropriately represent how the target species perceives an environmental attribute. For example, discrete data such as points (e.g., houses) and lines (e.g., roads) can be transformed into a continuous surface by calculating the distance to the nearest feature or computing a kernel density estimate of the feature (Cushman and Lewis 2010). Categorical data can be altered by aggregating similar categories into a reduced number of classes (O'Brien et al. 2006). Continuous data can be converted into categorical data by binning it into ranges, although this should be done with caution as this can lead to bias and introduce artificial boundaries not perceived by the target species (McGarigal and Cushman 2005; Cushman and Landguth 2010). Lastly, continuous environmental data can be transformed using various mathematical functions (e.g., Gaussian, linear or power functions), often to reflect nonlinear relationships between the species and the environmental gradient (Cushman et al. 2006). Despite the myriad ways to transform the thematic scale of environmental data, in the studies reviewed, transformations were generally applied arbitrarily and without explicit consideration of their potential influence on the results. Indeed, only a handful of the studies in our review objectively compared alternative thematic scales of the same environmental variable.

With regards to the choice of spatial scale (grain and extent) for representing environmental variables, there was extreme variability among the studies reviewed; grain size ranged over four orders of magnitude (1 m to 50 km) (Table 1.2). Many studies simply adopted the grain of the source data (e.g., 30 m for land cover derived from Landsat imagery) without explicitly considering whether the grain should have been coarsened for the application. Ideally, grain size should be determined based on the scale at which the target species perceives and responds to heterogeneity in the environment (Wiens 1989). Estimates of this functionally relevant scale are typically based on expert opinion and/or previous autecological studies (Cushman et al. 2010), but objective methods can be used to determine the optimum grain size—at least above the lower limit set by the source data—when biological data are available (Thompson and McGarigal 2002). Surprisingly, only six of the papers reviewed adopted this approach (McRae and Beier 2007; Rae et al. 2007; Broquet et al. 2009; Koscinsky et al. 2009; Murphy et al. 2010; Nichol et al. 2010), and they often reached different conclusions regarding the best grain size, illustrating the point that one scale does not fit all species and that the finest scale available is not always the best scale for the target species. In addition, species may be responding to different environmental cues at different scales (Thompson and McGarigal 2002). Therefore, it may be more appropriate to identify the optimum grain for each environmental variable separately and to combine the results in the final resistance surface, as was done by Jaquiery et al. (2011), rather than try to find a single ‘‘optimum’’ grain for all variables.

Study area extent ranged over six orders of magnitude (2.36 km2 to 3.2 million km2) in the studies reviewed (Table 1.2). Study area extent is usually driven by research objectives; however, it is worth noting that choice of extent may influence the estimation of resistance values. For example, Short Bull et al. (2011) used genetic data to estimate resistance for black bears across 12 different study areas with different extents. The optimal resistance surface varied by study area. Attention must also be paid to choice of study area boundary. Koen et al. (2010) cautioned that the hard edges of study areas may cause a bias in the estimate of resistance values and recommended placing buffers at the edges of map boundaries to avoid these boundary effects.

Table 1.2. Geospatial data. Environmental variables, spatial grain, thematic scale and study area extent used in 96 studies aimed at producing a resistance surface.

Environmental Variable	***No. Papers***[a]
Land cover/land use	80
Roads and other linear features	37
DEM; Hydrology	22
Slope	18
Human development	
(e.g. Buildings, culverts/weirs)	11
Percent Canopy cover	6
Settlements; Aspect	5
Human population density	4
Compound Topographic Index; Traffic data; Land management/Zoning	3
Temperature; NDVI; Topographic exposure; Topographic Ruggedness Index; Precipitation	2
Already developed habitat/non-habitat map; Anisotropic surface; Bathymetry; Climactic suitability; Current velocity; Depth to bedrock; Distance from presence point; Flow rate; Percent rock; Persistent spring snow cover; Predation risk; Relief; Seral stage based on DBH; Soil density; Solar exposure; Substrate type; Topographic position; Topographic smoothness; Vapor density; Vegetation height; Water depth	1

No. Environmental Variables Used	***No. Papers***[a]
1	36
2 – 5	54
6 - 10	6

Thematic Scale	***No. Papers[a]***
Continuous	7
Categorical	65
Continuous & Categorical	24

Grain (m)	***No. Papers[a]***
0-1	7
2-5	8
6-10	11
11-20	9
21-30	22
31-50	5
51-100	16
101-500	11
501-1,000	7
1,001-5,000	4
5,001-50,000	1
Not provided	8

Study area extent (km^2)[b]	***No. Papers[a]***
0-10	10
11-20	6
21-50	3
51-100	8
101-500	17
501-1,000	10
1,001-5,000	23
5,001-10,000	7
10,001-20,000	6

20,001-50,000	6
50,001-100,000	6
100,001-500,000	11
>500,000	4
Not provided	2

[a] Total number of papers is greater than 96 due to the use of more than one parameter, grain size, or study area extent.
[b] If study area extent was not provided, where possible, the study area extent was estimated from the figure provided.

Biological data

Perhaps the most obvious difference among the studies reviewed was the type of biological data used, which included: (1) expert opinion, (2) detection data, (3) relocation data, (4) pathway data, and (5) genetic data (Table 1.3). Note, expert opinion is not biological data, but it is often used in place of biological data or in combination with biological data, so it is included here. These data types were typically used alone, but in some cases they were used in combination in a two- stage approach, as discussed below.

Expert opinion

Expert opinion was used in 76 instances, 33 of these combined expert opinion with another biological data type (Table 1.3). We assumed the use of literature to inform expert opinion in most cases. Additionally, we classified papers as using expert opinion if researcher opinion was used in any part of the estimation procedure. For example, in instances where estimation procedures were used that were not able to take advantage of full optimization techniques due to computational limitations, the parameter space and/or a priori resistance surfaces were based in part on expert opinion.

The main issue with expert opinion data is that, even though experts may be drawing from their own previous research, the data are not truly empirical, making it difficult to objectively evaluate performance. Expert opinion has generally been shown to provide suboptimal parameterization of environmental variables when compared to empirical approaches (Pearce et al. 2001; Clevenger et al. 2002; Seoane et al. 2005), and thus has been criticized for its use in the development of resistance models (Cushman et al. in press). Moreover, because experts are often drawing from experience with habitat selection of their target species and not movement per se, these values should be considered proxies for movement at best. However, given the paucity of empirical data on many species in many places, more often than not expert opinion is the only option available on which to base a resistance model, and in many cases the urgency of conservation action requires that expert opinion be used as an interim solution until empirical data can be obtained (Compton et al. 2007).

Table 1.3. Modeling approaches. Analytical approach, type of biological data and type of resource selection function used in 96 studies aimed at deriving a resistance surface. See text for a definition of data type and resource selection functions.

Analytical Approach	***Data Type***	***Resource Selection Function***	***No. of approaches [a] (%) [b]***
One-stage expert	Expert	none	43[c] (43%)
One-stage empirical	Detection	Point	12[d] (12%)
	Relocation	Home range	3 (3%)
	Relocation	Matrix	1 (1%)
	Genetic	Matrix	5[e] (5%)
	Detection	Matrix	1[f] (1%)
Two-stage expert-empirical	Expert - Genetic	Matrix	20 (20%)
	Expert - Detection	Matrix	6 (6%)
	Expert - Detection	Point	3 (3%)
	Expert - Relocation	Matrix	2 (2%)
	Expert - Pathway	Step	1 (1%)
	Expert - Pathway	Path	1 (1%)
Two-stage empirical	Detection - Genetic	Point - Matrix	1 (1%)
	Relocation - Genetic	Matrix - Matrix	2 (2%)

[a] Number of approaches used is more than 96 since more than one approach was used in some papers.
[b] Percentage of approaches used, rounded to nearest whole number.
[c] Four of these papers used empirical data to validate the expert-derived resistance surface.
[d] Three of these papers used genetic data or a measure of vocal dissimilarity to validate the resistance surface derived from detection data.
[e] Three of these did not involve optimization of resistance values, but calculated proportion of land cover types within a strip between populations and validated with genetic data. Technically, the resistance values were empirically derived from the locations of the genetic samples and thus could be classified as detection data.
[f] This study did not involve optimization of resistance values but calculated proportion of land cover types within a strip between populations and validated with detection data.

Detection data

Detection data are defined by single point locations of unknown individuals. If multiple locations of the same individuals are recorded (e.g., via telemetry or capture–recapture), but the individual locations are treated as independent detections in the analysis, then the data are still considered detection data.

Detection data were used in 23 instances (Table 1.3) and included both presence-only data (n = 19) and presence–absence data (n = 4). The main difference between presence-only and presence–absence data is that the latter contains observations assumed to represent true absences while the former do not, and the methods of statistical analysis may differ. In the papers reviewed, detection data were obtained in a wide variety of ways, including: sightings (Bartelt et al. 2010), pellet counts (Beazley et al. 2005), nests (Kuroe et al. 2011), vocalizations (Laiolo and Tella 2006), traps (Wang et al. 2008), hair snares (Cushman et al. 2006; Wasserman et al. 2010), tracks or other sign (Epps et al. 2011), and telemetry studies (Chetkiewicz and Boyce 2009). Note, presence points collected via telemetry studies likely represent locations from fewer individuals than are collected through other methods, so the assumption that the samples represent a random sample of the entire population is often harder to justify (Manly et al. 2010). Moreover, care must also be taken to ensure independence of points from telemetry studies since they are intrinsically serially autocorrelated (Cushman 2010). For these reasons, data from telemetry studies are probably best treated as pathway data (as discussed below).

While detection data are often the most easily- acquired empirical data, there are a variety of issues associated with using detection data to parameterize resistance surfaces.

Most importantly, detection data are point-specific, meaning that movement is inferred instead of directly measured. Also, there is no generally accepted method for translating habitat selection indices based on detections into resistance values for movement (Beier et al. 2008). Errors can arise from this inference because detections usually represent within-home range habitat use patterns and thus may not adequately reflect how environments affect animals during movements such as dispersal and migration (Cushman et al. in press), although in a recent study on cougar dispersal, it was shown that habitat preference of dispersers was similar to habitat preference of resident adults (Newby 2011). In addition, if detections are biased towards protected areas where individuals are disproportionately found, any measured habitat preferences may not be applicable to the matrix between them, especially if the range of environmental conditions differs in the matrix, as it is likely to do. This is particularly relevant if resistance to movement between protected areas is the focus of the conservation application (e.g., corridor design).

Relocation data

Though relocation data are sometimes associated with translocation of animals, we are defining relocation data as having two or more sequential locations of the same individual, but not at a sufficiently frequent interval to treat each sequence as a movement pathway. A commonly used example of relocation data is mark–recapture data. With relocation data, the focus is on the matrix between locations rather than the specific pathways between locations or the point locations themselves. Clearly, relocation data is preferred over static detection data when the focus is estimating resistance to movement of individuals through the landscape.

Relocation data were used in only eight instances (Table 1.3). The paucity of studies using relocation data reflects the greater difficulty of capturing, marking and re-capturing or re-sighting individuals compared to detecting species' presence. Relocation data were used in two different ways. In the first approach, relocation data were used to compute movement speeds (Stevens et al. 2006), homing rates (Desrochers et al. 2011), movement rates (Ricketts 2001), exchange rates (Sutcliffe et al. 2003), or dispersal rates (Michels et al. 2001) through various environments or between habitat patches without knowing the actual movement paths. In most of these studies, inferred travel routes (e.g., least cost paths) between locations were used to calculate resistance values that best explained the observed movement rates. However, Stevens et al. (2006) used a controlled laboratory experiment to calculate movement speeds of individuals across various homogeneous substrates. Caution should be exercised when using movement speed alone to infer resistance, as it may not account for all three components of resistance: willingness to cross, physiological cost and reduction in survival. The main issue with relocation data used in this manner is that the movement paths between points are unknown and therefore must be inferred. Thus, there is an added unknown level of uncertainty in the final estimates of resistance associated with the method of inferring movement paths.

In the second approach, relocation data were used to construct home ranges (Graham 2001; Kautz et al. 2006; Thatcher et al. 2009). In these studies, travel paths between relocations within the delineated home ranges were not inferred at all; rather, the composition of the home ranges was compared to that available within the study area to assign habitat preferences, which were then transformed into resistance values. A major issue with home range data, like detection data, is that movement is inferred instead of directly measured, and there is added uncertainty due to variability in the method of home range determination. Additionally, home range estimation commonly results in including expanses of area that are not actually used by individuals, especially when using the Minimum Convex Polygon home range estimator (Worton 1995). However, the main issue with the methods used in all of these studies is that there was no formal evaluation of alternative resistance values; the final resistance values were merely assigned based on the computed habitat preferences.

Pathway data

Pathway data is defined by having two or more sequential locations of the same individuals, but at a sufficiently frequent interval to treat each sequence as a movement pathway (under the assumption that it represents the true pathway). Here, the focus is squarely on the specific connections between locations rather than the ambiguous matrix between locations or the point locations themselves. Pathway data is much preferred over static detection data and relocation data when the focus is estimating resistance to movement of individuals through the landscape.

Despite the clear advantages of pathway data, it was used in only two instances (Cushman and Lewis 2010; Richard and Armstrong 2010). The paucity of studies using pathway data reflects practical and economic tradeoffs associated with obtaining relocations at frequent intervals, but also may reflect unfamiliarity with the methods for analyzing movement paths by researchers.

To obtain meaningful movement pathways and thus meet the implicit assumption of both step and path analyses (see below), the interval between point locations must be relatively short to reduce the uncertainty associated with the interval between locations. Unfortunately, there is no consensus on how short is short enough, because it depends on the species' vagility. For example, if a species has the ability to move 1 km in 1 h, and the spatial resolution of the environment is 100 m, then a fix interval of 1 h is probably far too long because there are too many possible pathways through the landscape that the species could take between two points say 500 m apart. However, a 10 min interval would likely capture the exact pathway at the resolution of 100 m. Because of this issue, pathway analyses are probably best suited to animals that can be monitored frequently, typically via GPS telemetry. Indeed, the advent of GPS telemetry has enabled the acquisition time interval between fixes to be dramatically reduced, enabling movement pathways to be generated for both short- and far-ranging species.

Using the entire pathway may confound different types of movement such as local movements within resource patches, movements between resource patches within home ranges, migration movements, and dispersal movements. This may translate to the final resistance surfaces if environmental variables confer different levels of resistance to different types of movement. Therefore, we recommend attempting to decouple these behaviors before the paths are used for estimating resistance to movement. While this issue is particularly evident with pathway data, it is an important issue in all resistance modeling studies regardless of the type of biological data used.

Genetic data

Movement need not refer to the movement of individuals directly; it can also refer to the movement of genes—by individuals over generations. Genetic data were used in 28 instances to derive resistance surfaces, plus an additional five instances to validate a resistance surface (Table 1.3). Genetic data consist of genetic samples collected at multiple locations and, in contrast to relocation and pathway data, genetic data does not require resampling individuals over time. Genetic data are used to measure the genetic distance between locations, either between individuals (Cushman et al. 2006) or between populations (Emaresi et al. 2011), and thus infer rates of gene flow, or to estimate gene flow directly (Wang et al. 2009). Genetic distance or estimates of gene flow are then evaluated against measures of geographic distance under alternative resistance models to find the best estimates of resistance. Of the 28 instances, 14 used a between-population measure of genetic distance, 12 used a between-individual measure, and two used a direct measure of gene flow between populations. Despite their prevalence, population-based methods have been criticized because individuals must be assigned to discrete populations even if the population is continuously distributed, and because they assume an island-matrix population structure that may be inappropriate for certain species or study areas (Shirk et al. 2010). Cushman and Landguth (2010) found that genetic distances between individuals provide the most robust estimates of resistance. However, population-based approaches may be the most practical means of analysis for some species and study areas (e.g., when populations are organized into discrete local populations). When migration rates among discrete local populations can be readily measured, a direct measure of gene flow, through siblingship and parentage assignments, may be the best approach (Wang et al. 2009).

In the past, the main issue with genetic data was the difficulty, inaccuracy and high cost of genotyping. However, in recent years these practical constraints have lessened dramatically, making genetic data a practical option in most cases. Consequently, the use of genetic data for parameterizing resistance surfaces appears to be on the rise (Spear et al. 2010). However, there are other issues with the use of genetic data. One issue is that estimates of gene flow may be temporally mismatched to the current landscape of interest (Landguth et al. 2010). Another is that resistance to movement of individuals (who are carrying genes across the landscape) is not measured directly, in contrast to relocation and pathway data. Estimates of gene flow between locations, whether inferred or not, reflect the movement of many individuals over many generations, presumably travelling along many different pathways. This makes genetic data appealing, since it effectively integrates the movements of many individuals over time and thus leads to a more synoptic measure of landscape resistance. Moreover, since gene flow reflects only successful movements, it integrates the movements that matter most to the species – those that result in successful breeding.

Analytical approaches

A wide variety of analytical approaches were used among the papers reviewed, which made any classification of approaches extremely challenging. Nevertheless, we found it useful to group papers into three categories: (1) ‘one-stage expert approach’, (2) ‘one- stage empirical approach’, and (3) ‘two-stage empirical approach’ (Fig. 1.1). Strictly speaking, the one- stage expert approach is not analytical, but it is in fact the most common approach used for deriving resistance surfaces, so it is included here.

One-stage expert approach

In the ‘one-stage expert approach’, expert opinion is used to derive the final resistance surface in a single step; no statistical modeling is used in the process. If biological data are used at all, it is used merely to inform expert opinion (Zimmermann and Breitenmoser 2007) or to validate the derived surface (Coulon et al. 2004).

A one-stage expert approach was used in 43 instances (Table 1.3). In these studies, experts were typically asked to provide numerical resistance values to each environmental layer from a bounded parameter space (e.g., 0–10 or 0–100) that would reflect resistance to movement during home range use, migration or dispersal. A final resistance surface was created by applying the resistance values to each environmental layer and summing the values. If weights were being used to reflect the relative importance of each environmental variable, these were incorporated via a weighted product (Singleton et al. 2002) or a weighted geometric mean (Beier et al. 2008). In some cases, experts were asked to derive a habitat suitability index from the environmental variables, and the inverse of the habitat suitability values were taken as the resistance values (LaRue and Nielsen 2008).

Because experts come from varying backgrounds and research experiences, they likely have diverging opinions regarding resistance or habitat suitability values (Johnson and Gillingham 2004). Consequently, various methods can be used to reduce the variation in expert opinion. For example, responses can be smoothed by simply averaging the submitted values or applying a trimmed mean by omitting the highest and lowest values (Compton et al. 2007). Variation can also be addressed through expert consensus, either by gathering the experts in one place or by using an iterative process where resistance values are re-compiled until a consensus is reached (Freeman and Bell 2011).

A more structured method of dealing with variation in expert opinion is to use an analytical hierarchy process (AHP) (Saaty 1980), where the assigned values are standardized through the use of decision-making trees. An advantage of the AHP process is that it produces an index of consistency. If consistency scores are below 0.1, then the responses among experts are deemed consistent; whereas, if they are above 0.1, then re-assessment may take place to reduce variability (Magle et al. 2009). Because environmental variables may differ in the magnitude of their influence on species movement, experts can be asked to weight variables in terms of their influence (Beier et al. 2009), or the weighting can be completed in the AHP process. For example, Estrada-Peña (2003) applied time weights to the resistance surface by increasing weights as a function of distance to emulate tick feeding time on hosts. Experts can also be asked to identify landscape attributes that are barriers to movement or to estimate the cumulative resistance value that would result in a barrier to movement (Rabinowitz and Zeller 2010).

A one-stage expert approach is perhaps the least quantitatively rigorous of the approaches used, because there is no way to objectively parameterize resistance surfaces. However, a one-stage expert approach should not be too easily dismissed, as it allows experts to synthesize knowledge about complex habitat relationships obtained from disparate studies that may otherwise be difficult to incorporate into a resistance surface.

One-stage empirical approach

In a 'one-stage empirical approach', a statistical model is confronted with biological data to find the optimum resistance surface given the data; usually, some combination of expert opinion and previously published research is used to select environmental variables, their scale, and the functional form of the relationship between each variable and resistance (e.g., Gaussian, linear, power).

A one-stage empirical approach was used in 22 instances; however, in seven of these instances the biological data were not used to optimize the resistance surface (Table 1.3). Most of the analytical studies developed a RSF based on detection data and then used the inverse of the selection index to obtain resistance values, but there was a wide variety of statistical methods used to create the RSF, including logistic regression analysis (Pullinger and Johnson 2010), maximum entropy and ecological niche factor analysis (Wang et al. 2008; Kuemmerele et al. 2011), and a variety of other less conventional approaches (e.g., Ferreras 2001; Flamm et al. 2005; Kindall and VanManen 2007; Kuroe et al. 2011). In three instances, relocation data were used to construct home ranges, which were the basis for a simple RSF that assigned resistance values based on measured habitat preferences without optimizing the surface (Graham 2001; Kautz et al. 2006; Thatcher et al. 2009). In five instances, genetic data were used to derive the RSF; however, three of these cases used a strip-based approach (where proportion of environmental features within a rectangular strip between populations were used) to estimate resistance values and no optimization was performed (Emaresi et al. 2011). Two studies developed RSFs based on genetic data and attempted to optimize resistance values in a single stage (Wang et al. 2009; Shirk et al. 2010).

These latter two studies are unique in their attempts to use landscape genetic techniques to sample the full parameter space. While the optimization of resistance based on detection data is relatively straightforward and computationally efficient using conventional statistical methods, this is not the case with movement data such as relocation data, pathway data, and genetic data. Because of the exponentially large number of possible resistance surfaces in multivariate analyses, and the computational demands of analyzing movement paths (either inferred or observed), a full optimization of all environmental parameters has not yet been achieved. However, Wang et al. (2009) and Shirk et al. (2010) have used two different landscape genetics techniques to successfully perform a constrained optimization. Wang et al. (2009) created a range of a priori resistance surfaces using three environmental variables. One parameter was always assigned a blanket resistance value of 1 (since resistance values are relative) and the other two layers were assigned every possible combination of resistance values from 1 to 10 in 0.1 unit increments. The relative least-cost distances between population pairs were compared with the 95 % confidence interval of relative rates of gene flow estimated from the molecular data. All resistance surfaces whose relative least-cost distances between all population pairs fell within their expected ranges, based on the molecular analysis, were considered to be biologically accurate. Shirk et al. (2010) developed a framework that allows for interactions among variables and non- linear responses using a quasi-unconstrained parameter space. First, they performed a univariate optimization of each of four environmental variables by systematically increasing and decreasing the resistance values until a unimodal peak of support (using genetic data) was reached. Then, they obtained a multivariate model by summing all the optimized univariate surfaces and systematically optimizing the parameters for one variable while holding the other layers constant, and iteratively repeating this process until the parameter estimates stabilized.

Two-stage empirical approach

In a ‘two-stage empirical approach’, expert opinion and/or biological data are used to derive a suite of alternative resistance surfaces in the first stage, which are confronted with biological data and a model selection procedure in the second stage to select the best resistance surface. Note, given the ubiquitous involvement of experts in all approaches, such as selecting environmental variables and choosing the functional form of the relationship between each variable and resistance, the distinction between this approach and the one-stage empirical approach is perhaps a matter of degree and not an absolute dichotomy.

A two-stage empirical approach was used in 36 instances, 33 of which used expert opinion in stage one to derive the alternative resistance surfaces (Table 1.3). In the majority of these studies (n = 28), expert opinion was used to derive a limited, often small, set of alternative resistance surfaces (i.e., candidate models) based on specific hypothesized relationships between the environment and resistance to movement—in the spirit of model selection and multi-model approaches to statistical inference (Burnham and Anderson 2002). This approach was combined with detection data (Chardon et al. 2003), relocation data (Desrochers et al. 2011), pathway data (Richard and Armstrong 2010) and genetic data (Koscinsky et al. 2009) in the second stage to select the best surface. In the remaining studies (n = 8), expert opinion was used to constrain the resistance parameter space, from which a priori resistance surfaces were constructed in sufficient number and distribution to effectively sample that parameter space. Here, expert opinion was used mainly to determine the range of plausible resistance values for each environmental variable; the candidate models or resistance surfaces were derived merely as a practical solution to model optimization within the constrained parameter space. This approach was combined with detection data (Janin et al. 2009), relocation data (Sutcliffe et al. 2003), pathway data (Cushman and Lewis 2010) and genetic data (Cushman et al. 2006) in the second stage to select the best surface. Finally, it should be noted that in both cases, expert opinion is used to select the environmental variables and the functional form of the relationship between each variable and resistance; thus, both are clearly expert-guided approaches.

Surprisingly, only three papers used empirical data to develop a suite of resistance surfaces, which were then subjected to model selection through the use of an independent empirical data set of a different data type (Table 1.3).

Resource selection functions

In the context of resistance surface modeling, we consider a RSF to be any model that yields estimates of environmental resistance or habitat selection based on patterns observed in biological data (Fig. 1.2).

Point selection function (PSF)

A PSF seeks to find the combination of environmental parameters that best explains the distribution of detections based on presence-only or presence– absence points. Importantly, it is the characteristics of the point locations themselves and not the connections between points that are assessed in a PSF. Resistance is typically given as the inverse of the final selection index.

A PSF was used in 16 instances (Table 1.3). In most of these cases (n = 12), the PSF was derived from detection data and optimized using an objective statistical procedure such as logistic regression (Chetkiewicz and Boyce 2009). However, in a few of these cases, alternative parameterizations of the PSF were derived by experts a priori and the detection data were used simply to select the parameters with the most biological support (Janin et al. 2009).

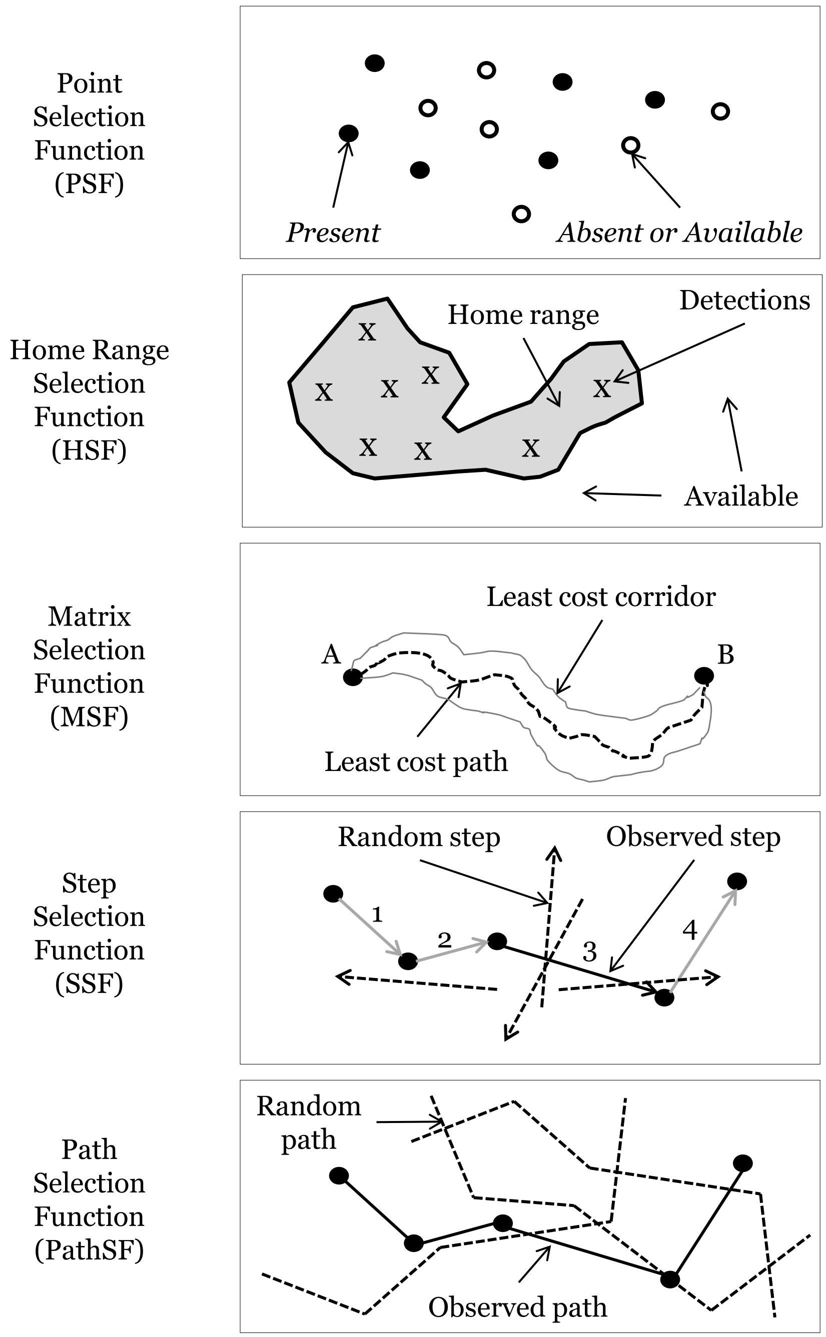
An important issue with any PSF derived from presence-only points is determining what constitutes the ‘‘available’’ environment. Regarding this, there appears to be no accepted standard, but methods such as paired logistic regression (also referred to as ‘conditional logistic regression’ and ‘case-controlled logistic regression’) that compare each presence point to what is locally available within a meaningful ecological neighborhood seem to us to be superior to other methods (Pullinger and Johnson 2010). Of course, a PSF derived from presence–absence points does not suffer this issue and seems to us to be superior than one derived from presence-only data. The main issue with any PSF is the need to infer resistance to movement from resource selection at point locations.

Home range selection function (HSF)

A HSF seeks to find the combination of environmental variables that best explains the distribution of home ranges derived from relocation data. Importantly, it is the characteristics of the home ranges and not the specific connections between relocations that are assessed in a HSF. Resistance is typically given as the inverse of the final selection index.

A HSF was used in only three instances (Table 1.3). None of these cases involved optimizing the HSF based on the home range data; in two of these cases they compared the composition of the home ranges to that of the study area in order to assign a habitat preference index to each environmental condition and then assigned resistance as the inverse of the preference index (Graham 2001; Kautz et al. 2006).

Figure 1.2. Resource Selection Functions used to derive resistance surfaces.



The issues with a PSF also apply to a HSF. However, at least conceptually, a HSF is closer to the ideal of addressing resistance to movement than a PSF because a home range includes the area an individual moves through to meet their local resource needs. Despite this conceptual advantage, however, a HSF does not overcome the fundamental limitation of having to infer resistance to movement from point data.

Matrix selection function (MSF)

A MSF seeks to find the combination of resistance parameters that best explains the movement of individuals or their genes between locations, but without knowing or assuming the actual movement paths between locations. Specifically, a MSF derives from a measure of the ecological distance between two points separated by a resistant matrix, where the ecological distance increases as the geographic distance and resistance between points increases. A MSF seeks to find the resistance parameters that maximize the correlation between the ecological distance and the frequency of movement of individuals or their genes between locations.

A MSF was used in 38 instances, making it by far the most commonly used RSF (Table 1.3). In most of these cases (n = 28), alternative parameterizations of the MSF were derived by experts a priori and either detection data (n = 6), relocation data (n = 2) or genetic data (n = 20) were used to select the parameters with the most biological support. The cases involving detection data seem contrary to the idea of a MSF; however, in these cases the MSF was used in the context of a metapopulation model to explain observed patch occupancy (or presence). In only three cases was the MSF optimized (within constraints) in a one-stage empirical approach using an objective statistical procedure based on either relocation data (n = 1) or genetic data (n = 2).

A MSF has several important features. First, a MSF evaluates environmental resistance directly, as opposed to a PSF that evaluates habitat selection directly and produces an index that must be translated into resistance post hoc. Second, a MSF evaluates the environmental resistance between locations without requiring information on the actual movement paths, which are required by both step and PathSFs (see below). Third, a MSF does not require the arbitrary designation of 'available', which is a challenge that confronts all other selection functions. Lastly, A MSF is the only selection function suited to multiple types of biological data, including detection data, relocation data and genetic data.

The main issue with any MSF is choosing a measure of ecological distance, and there are several, including: (1) least cost distance, which is equal to the cumulative cost along the least cost path between points (Epps et al. 2007); (2) least cost path length, which is equal to the geographic distance along the least cost path between points (Koscinsky et al. 2009); (3) least cost corridor, which is equal to the cumulative cost within the least cost corridor between points (Savage et al. 2010); (4) resistance distance, which is equal to the cumulative resistance of the matrix between points based on circuit theory (McRae 2006; Klug et al. 2011); and (5) resistant kernel distance, which is equal to the kernel-weighted (e.g., Gaussian) least cost distance between points (Compton et al. 2007). Currently, there is no one preferred measure of ecological distance. McRae and Beier (2007) compared how least cost distance and resistance distance performed and found resistance distance to be better, while Schwartz et al. (2009) found the opposite.

Savage et al. (2010) found the least cost corridor measure to outperform least cost distance. Foltete et al. (2008) did not find any difference between the least cost distance and least cost path length. In the studies reviewed, there were 23 instances of least cost distance, eight of least cost path length, one of least cost corridor, and four of resistance distance. Many studies used more than one measure of ecological distance. Regardless of the measure of ecological distance chosen, care must be taken to address the inherently high level of correlation with straight geographic distance (Cushman and Landguth 2010). Another issue with the MSF approach, as stated above, is that they are very computationally demanding which has, to date, prevented a full optimization of resistance estimates.

Step selection function (SSF)

A SSF seeks to find the combination of resistance parameters that best explains the movement of individuals between locations, and is derived from pathway data where specific movement paths can be meaningfully assigned and decomposed into discrete segments or steps between sequential locations. A SSF derives from a measure of the cost distance along each segment compared to the cost distance along random segments of equal length. Note, here the cost distance is measured along each segment of the observed pathway rather than along an arbitrary modeled path as in a MSF.

A SSF was used in only one instance, making it one of the two least commonly used types of RSF (Table 1.3). In this case, alternative resistance surfaces were derived by experts a priori and the pathway data were used to select the surface that best discriminated between observed and random segments (Richard and Armstrong 2010).

A SSF is one of the most powerful selection functions for deriving resistance surfaces, because it derives directly from observed movement pathways. As with any selection function that compares use to availability, one of the main issues with any SSF is choosing the spatial (and temporal) constraints on availability. For example, should the beginning point of each random segment be the same as the paired observed segment or should it be shifted by a random distance and direction and, if so, how far? The implications of these decisions on the final parameter estimates are unknown. Another issue arises when available steps are chosen close to the observed step, making the available steps highly correlated and representative of only habitat near the observed step. This runs the risk of omitting from the analysis important landscape characteristics that an individual is actually avoiding, making the analysis result in a gradient of resistance for preferred habitat types.

Path selection function (PathSF)

A PathSF is similar to a SSF except that the entire movement path is assessed as a single pathway as opposed to a series of steps. A PathSF was also used in only one instance (Table 1.3). In this case, alternative resistance surfaces were derived by experts a priori and the pathway data were used to select the surface that best discriminated between observed and random paths (Cushman and Lewis 2010).

A PathSF is arguably the most powerful selection function for deriving resistance surfaces, because inferences are made directly from observed movement pathways. One advantage of using the entire path as the observational unit rather than the individual segments is that fine-scale habitat selection can be captured and pseudoreplication and autocorrelation issues can be avoided by preserving the topology of the entire path (Cushman 2010). Another advantage is that a PathSF allows inferences to be made about environmental features between observed points. Despite these advantages, however, a PathSF cannot escape the issue of arbitrariness in the designation of 'available'. In Cushman and Lewis (2010), studying black bears (Ursus americanus) in northern Idaho, available paths were randomly shifted a distance between 0 and 20 km (based on a black bear's average dispersal distance) in latitude and longitude, and randomly rotated between 0° and 360°. An alternative to the approach used by Cushman and Lewis (2010) is to simulate individual movement paths by drawing from empirical distributions of number of steps, step length, step orientation and total path length (B. Compton and K. McGarigal, unpublished report). This approach is a trade-off between preserving the exact topology of the observed paths and representing the underlying 'population' from which the observed paths were drawn, but an empirical comparison of these two approaches has not been done.

Conclusions and recommendations

In this review, we assessed current practices for deriving resistance surfaces and have arrived at several conclusions in three overarching categories: (1) selection and definition of environmental variables, (2) use of biological data and analytical processes, and (3) evaluation of resistance surfaces. First, not surprisingly, there was tremendous variety of environmental variables used across studies owing to differences in the species and ecological systems under investigation (Table 1.2). In some cases, researchers used model selection procedures to select the number and combination of variables used to derive the resistance surface that best explained observed biological data. However, in most cases, little or no attention was paid to the sensitivity of the results to the choice and/or number of environmental variables used to construct the resistance surface. In addition, we discovered very few studies that evaluated choices for representing each environmental variable in terms of the measurement scale (continuous or categorical) and spatial resolution (i.e., grain size). For example, of the 22 papers that used elevation, none compared the representation of elevation as a continuous surface (or a continuous function of elevation) versus discrete elevation classes. Likewise, while there is no inherently correct spatial resolution for representing an environmental attribute, since it varies among species and ecological processes and is usually unknown to the researcher prior to the analysis, our review identified only a handful of studies that evaluated how spatial resolution affected the optimization of the resistance surface (McRae and Beier 2007; Rae et al. 2007; Broquet et al. 2009; Koscinsky et al. 2009; Murphy et al. 2010; Nichol et al. 2010). Indeed, this may not be as important as choice of thematic representation of environmental variables since the grain size may have little effect on the relative cumulative cost of a corridor (Cushman and Landguth 2010). However, given the almost unlimited number of ways to represent the environment in terms of the number and choice of variables and the spatial and thematic scale, there is a need for more comparative studies to determine sensitivity of results to these choices and to recommend robust methods for finding the optimal representation given that it cannot be known a priori.

Second, the papers reviewed used a wide variety of data types and analytical methods to reach the same goal—estimating resistance to movement (Table 1.3). Despite heavy criticism, expert opinion was used in 80 % of the papers reviewed and was the only source of information in 43 % of the papers. Reliance on expert opinion is likely to continue in the future as there are many species and/or systems for which empirical data do not yet exist and yet conservation concerns demand immediate action. Genetic data were the second most heavily used data type (38 % of papers) and its use appears to be increasing due to the increased ease, accuracy, and affordability of genotyping. The increasing appeal of genetic data may also be that it provides a measure of functionally relevant movement between populations or sites—movement that results in successful breeding. Detection data (consisting of both presence-only and presence– absence data) was the third most common data type (23 % of papers), despite the fact that resistance to movement must be inferred from detection data. Due to the prevalence of detection data in wildlife studies, it is likely that methods based on detection data will continue to figure prominently in resistance modeling in the foreseeable future. Since estimating resistance to movement was a putative goal of the studies reviewed, we found it alarming that movement data in the form of relocations (8 % of papers) or pathways (2 % of papers) was the least used data type. The paucity of individual movement data in such studies is likely due to the practical, logistical and/or economic difficulties of collecting movement data. However, with the increased availability of GPS telemetry, it is likely that the use of movement data will increase in the future.

Despite the dramatic differences among data types, there have been few attempts to critically and objectively evaluate these differences. Clevenger et al. (2002) found that empirical data generally outperformed expert opinion, Shirk et al. (2010) found that their optimized resistance model was superior to the expert-based model and Cushman and Lewis (2010) found that that using genetic distances between individuals resulted in a similar resistance surface to one developed using movement paths. Clearly, there is an urgent need for more comprehensive comparative studies that seek to clarify the tradeoffs associated with each data type.

Third, not surprisingly, given the variety of types of biological data used, a variety of RSFs were used to estimate resistance values. Indeed, one of the most challenging aspects of this review was trying to understand and organize the myriad analytical approaches used by researchers to derive the final resistance surface. We offer an organizational scheme that distinguishes among five basic types of RSFs, and we encourage future researchers to adopt this scheme. Each selection function corresponds to a different analytical framework for estimating the final resistance values, and each has inherent issues (discussed previously) that should be considered in every application. Two of these issues are particularly noteworthy. First, all of the selection functions except the MSF require the researcher to designate what constitutes 'available' for comparison with the 'use' data. This adds a degree of arbitrariness to the analysis that to our knowledge has not been addressed in the context of resistance surface modeling, but needs to be. Second, while PSFs derived from detection data have been over-utilized in resistance surface modeling, in our opinion, PathSFs derived from pathway data have been under-utilized. Pathway data are the only data type that provide unambiguous spatial representation of how animals move through the environment to meet their local resource needs and they may be constructed to assess within home range movements, dispersal or migration depending on the source data. MSFs derived from genetic data are complementary to PathSFs because they can assess multi-generational movement of effective dispersers (i.e., those that disperse and reproduce), albeit at the cost of having to infer resistance to movement through a matrix based on a chosen measure of ecological distance.

A pervasive issue in resistance surface modeling studies is that these methods rely on the assumption that animals make movement decisions based on the same preferences they use in selecting habitat. This may not be an issue if this assumption is true. However, if animals are driven by something other than resource selection during movement events, the two behaviors need to be separated when estimating resistance values. This issue is perhaps most apparent with pathway data. Because the use of local resources (e.g., food and cover) and movement through the environment to find and obtain those local resources are typically difficult to discern in pathway data, it is challenging to parse out environmental conditions associated with local resource use from those conferring resistance to movement. Moreover, the movement data may confound local movements within resource patches, movements between resource patches within home ranges, migration movements between seasonal use areas, and dispersal movements between natal and breeding sites or among breeding sites. There is no reason to assume that the environment will affect resource use and different types of movement the same. While this issue is most notable with pathway data, it also applies to other data types, with the possible exception of genetic data, which generally deals principally with movement associated with successful reproduction. We are not aware of any attempts to address this issue in resistance modeling studies and recommend that it be a priority in future studies.

Given the myriad sources of uncertainty in the modeling process and the propagation of errors from imperfect environmental data to the collection and analysis of the biological data, model sensitivity and uncertainty should be assessed in any study that uses resistance surfaces, especially when expert opinion is involved (Rae et al. 2007; Beier et al. 2009). Less than a third of the papers reviewed performed sensitivity analyses, either on corridor location resulting from the analysis (Rayfield et al. 2010) or on statistical differences between the resistance surfaces themselves (Compton et al. 2007). The incorporation of uncertainty into resistance models was much less common, with only a few papers creating models based on the probability distribution of parameter estimates (Kuroe et al. 2011). Performing sensitivity analyses or incorporating uncertainty in parameter estimates are especially important for research that will result in conservation recommendations or conservation action. Presumably, much of the research that seeks to estimate resistance will use the resultant resistance surfaces in connectivity modeling and these connections or corridors will be promoted to planners and land managers for implementation. Presenting the full range of possibilities for proposed actions adds transparency to the process and increases the likelihood of buy-in from land managers and the public alike.

Applying the resistance estimates in connectivity modeling was not the focus of this review, but it is worth mentioning that the use of these resistance estimates to identify corridors may have far-reaching consequences. Conservation and public resources may be used to implement wildlife corridors based upon resistance surfaces. To this end, we recommend more comparative research into each step of the resistance estimation process—the selection and definition of environmental variables, the choice of biological data type, and the analytical process. This will help to assess the relative influence of each step in the process and its influence on the accuracy of resistance estimates. Ultimately, comparative analyses will lead to filling in gaps in our knowledge around resistance surface modeling and lead to more effective and successful conservation measures.

Appendix

References for the 96 papers used in this review

Adriaensen, F., J.P. Chardon, G. De Blust, E. Swinnen, S. Villalba, H. Gulinck, and E. Matthysen. 2003. The application of 'least-cost' modeling as a functional landscape model. Landscape and Urban Planning 64: 233–247.

Bartelt, P.E., R.W. Klaver, and W.P. Porter. 2010. Modeling amphibian energetics, habitat suitability, and movements of western toads, *Anaxyrus (=Bufo) boreas*, across present and future landscapes. Ecological Modelling 221: 2675-2686.

Bauer, D.M., P.W.C. Paton, and S.K. Swallow. 2010. Are wetland regulations cost effective for species protection? A case study of amphibian metapopulations. Ecological Applications 20: 798-815.

Beazley, K., L. Smandych, T. Snaith, F. MacKinnon, P. Austen-Smith, Jr., and P. Dunker. 2005. Biodiversity considerations in conservation system planning: Map-based approach for Nova Scotia, Canada. Ecological Applications 15: 2192-2208.

Beier, P., D.R. Majka, and S.L. Newell. 2009. Uncertainty analysis of least-cost modeling for designing wildlife linkages. Ecological Applications 19: 2067-2077.

Braunisch, V., G. Segelbacher, and A.H. Hirzel. 2010. Modelling functional landscape connectivity from genetic population structure: a new spatially explicit approach. Molecular Ecology 19: 3664-3678.

Broquet, T., N. Ray, E. Petit, J.M. Fryxell, and F. Burel. 2009. Genetic isolation by distance and landscape connectivity in the American marten (*Martes americana*). Landscape Ecology 21: 877-889.

Bunn, A.G., D.L. Urban, and T.H. Keitt. 2000. Landscape connectivity: A conservation application of graph theory. Journal of Environmental Management 59: 265-278.

Chardon, J.P., F. Adriaensen, and E. Matthysen. 2003. Incorporating landscape elements into a connectivity measure: a case study for the Speckled wood butterfly (*Pararge aegeria* L.). Landscape Ecology 18: 561-573.

Chetkiewicz, C.-L.B., and M.S. Boyce. 2009. Use of resource selection functions to identify conservation corridors. Journal of Applied Ecology 46: 1036-1047.

Clark, R.W., W.S. Brown, R. Stechert, and K.R. Zamudio. 2008. Integrating individual behavior and landscape genetics: the population structure of timber rattlesnake hibernacula. Molecular Ecology 17: 719-730.

Compton, B.W., K. McGarigal, S.A. Cushman, and L.R. Gamble. 2007. A Resistant-Kernel Model of Connectivity for Amphibians that Breed in Vernal Pools. Conservation Biology 21: 788-799.

Coulon, A., J.F. Cosson, J.M. Angibault, B. Cargnelutti, M. Galan, N. Morellet, E. Petit, S. Aulagnier, and A.J.M. Hewison. 2004. Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual-based approach. Molecular Ecology 13: 2841-2850.

Cushman, S.A. and J.S. Lewis. 2010. Movement behavior explains genetic differentiation in American black bears. Landscape Ecology 25: 1613-1625.

Cushman, S.A., K.S. McKelvey, J. Hayden, and M.K. Schwartz. 2006. Gene-flow in complex landscapes: testing multiple hypotheses with causal modeling. American Naturalist 168: 486-499.

Cushman, S.A., K.S. McKelvey, and M.K. Schwartz. 2009. Use of empirically derived source-destination models to map regional conservation corridors. Conservation Biology 23: 368-376.

Dedecker, A.P., K. Van Melckebeke, P.L.M. Goethals, and N. DePauw. 2007. Development of migration models for macroinvertebrates in the Zwalm river basin (Flanders, Belgium) as tools for restoration management. Ecological Modelling 203: 72-86.

Desrochers, A., M. Bélisle, and J. Morand-Ferron. 2011. Integrating GIS and homing experiments to study avian movement costs. Landscape Ecology 26: 47-58.

Driezen, K., F. Adriaensen, C. Rondinini, C.P. Doncaster, and E. Matthysen. 2007. Evaluating least-cost model predictions with empirical dispersal data: A case-study using radiotracking data of hedgehogs (*Erinaceus europaeus*). Ecological Modelling 209: 314-322.

Emaresi, G., J. Pellet, S. Dubey, A.H. Hirzel, and L. Fumagalli. 2011. Landscape genetics of the Alpine newt (Mesotriton alpestris) inferred from a strip-based approach. Conservation Genetics 12: 41-50.

Epps, C.W., B.M. Mutayoba, L. Gwin, and J.S. Brashares. 2011. An empirical evaluation of the African elephant as a focal species for connectivity planning in East Africa. Diversity and Distributions 17: 603-612.

Epps, C.W., J.D. Wehausen, V.C. Bleich, S.G. Torres, and J.S. Brashares. 2007. Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44: 714-724.

Estrada-Peña, A. 2003. The relationships between habitat topology, critical scales of connectivity and tick abundance *Ixodes ricinus* in a heterogeneous landscape in northern Spain. Ecography 26: 661-671.

Fall, A. M.J. Fortin, M. Manseau, and D. O'Brien. 2007. Spatial graphs: Principles and applications for habitat connectivity. Ecosystems 10: 448-461.

Ferreras, P. 2001. Landscape structure and asymmetrical inter-patch connectivity in a metapopulation of the endangered Iberian lynx. Biological Conservation 100: 125-136.

Flamm, R.O., B.L. Weigle, I, E. Wright, M. Ross, and S. Aglietti. 2005. Estimation of manatee (Trichechus manatus latirostris) places and movement corridors using telemetry data. Ecological Applications 15: 1415-1426.

A.D. Flesch, C.W. Epps, J.W. Cain III, M. Clark, P.R. Krausman, and J.R. Morgart. 2009. Potential effects of the United States-Mexico border fence on wildlife. Conservation Biology 24: 171-181.

Foltête, J.C., K. Berthier, and J.F. Cosson. 2008. Cost distance defined by a topological function of landscape. Ecological Modelling 210:104-114.

Freeman, R.C., and K.P. Bell. 2011. Conservation versus cluster subdivisions and implications for habitat connectivity. Landscape and Urban Planning 101: 30-42.

Gonzales, E.K., and S.E. Gergel. 2007. Testing assumptions of cost surface analysis—a tool for invasive species management. Landscape Ecology 22:1155-1168.

Graham, C.H. 2001. Factors influencing movement patterns of keel-billed toucans in a fragmented tropical landscape in southern Mexico. Conservation Biology 15: 1789-1798.

Gurrutxaga, M., P.J. Lozano, and G. del Barrio. 2010. GIS-based approach for incorporating the connectivity of ecological networks into regional planning. Journal for Nature Conservation 18: 318-326.

Hagerty, B.E., K.E. Nussear, T.C. Esque, and C.R. Tracy. 2011. Making molehills out of mountains: landscape genetics of the Mojave desert tortoise. Landscape Ecology 26: 267-280.

Hepcan, S., C.C. Hepcan, I.M. Bouwma, R.H.G. Jongman, and M.B. Ozkan. 2009. Ecological networks as a new approach for nature conservation in Turkey: A case study of Izmir Province. Landscape and Urban Planning 90: 143-154.

Hokit, G.G., M. Ascunce, J. Ernst, L.C. Branch, and A.M. Clark. 2010. Ecological metrics predict connectivity better then geographic distance. Conservation Genetics 11: 149-159.

Huber, P.R., S.E. Greco, and J.H. Thorne. 2010. Spatial scale effects on conservation network design: tradeoffs and omissions in regional versus local scale planning. Landscape Ecology 25: 683-695.

Hurme, E., P. Reunanen, M. Monkkonen, A. Nikula, V. Nivala, and J. Oksanesn. 2007. Local habitat patch pattern of the Siberian flying squirrel in a managed boreal forest landscape. Ecography 30: 277-287.

Janin, A., J.P. Léna, N. Ray, C. Delacourt, P. Allemand, and P. Joly. 2009. Assessing landscape connectivity with calibrated cost-distance modelling: predicting common toad distribution in a context of spreading agriculture. Journal of Applied Ecology 46: 833-841.

Kautz, R., R. Kawula, T. Hoctor, J. Comiskey, D. Jansen, D. Jennings, J. Kasbohm, F. Mazzzotti, R. McBride, L. Richardson, and K. Root. 2006. How much is enough? Landscape-scale conservation for the Florida panther. Biological Conservation 130: 118-133.

Kindall, J.L., and F.T. VanManen. 2007. Identifying Habitat Linkages for American Black Bears in North Carolina, USA. Journal of Wildlife Management 71: 487-495.

Klug, P.E., S.M. Wisely, K.A. With. 2011. Population genetic structure and landscape connectivity of the Eastern Yellowbelly Racer (*Coluber constrictor flaviventris*) in the contiguous tallgrass prairie of northeastern Kansas, USA. Landscape Ecology 26: 281-294.

Koscinsky, D. A.G. Yates, P. Handford, and S.C. Lougheed. 2009. Effects of landscape and history on diversification of a montane, stream-breeding amphibian. Journal of Biogeography 36: 255-265.

Kuemmerle, T., K. Perzanowski, H. Resit Akcakaya, F. Beaudry, T.R. Van Deelen, I. Parnikoza, P. Khoyetskyy, D.M. Waller, and V.C. Radeloff. 2011. Cost-effectiveness of strategies to establish a European bison metapopulation in the Carpathians. Journal of Applied Ecology 48: 317-329.

Kuroe, M., N. Yamaguchi, T. Kadoya, and T. Miyashita. 2011. Matrix heterogeneity affects population size of the harvest mice: Bayesian estimation of matrix resistance and model validation. Oikos 120: 271-279.

Lada, H., J.R. Thompson, R. MacNally, and A.C. Taylor. 2008. Impacts of massive landscape change on a carnivorous marsupial in south-eastern Australia: inferences from landscape genetics analysis. Journal of Applied Ecology 45: 1732-1741.

Laiolo, P., and J.L. Tella. 2006. Landscape Bioacoustics allow detection of the effects of habitat patchiness on population structure. Ecology 87: 1203-1214.

Larkin, J.L, D.S. Maehr, T.S. Hoctor, M.A. Orlando, and K. Whitney. 2004. Landscape linkages and conservation planning for the black bear in west-central Florida. Animal Conservation 7: 23-34.

LaRue, M.A., and C.K. Nielsen. 2008. Modelling potential dispersal corridors for cougars in Midwestern North America using least-cost path methods. Ecological Modelling 212: 372-381.

Lee-Yaw, J.A., A. Davidson, B.H. McRae, and D.M. Green. 2009. Do landscape processes predict phylogeographic patterns in the wood frog? Molecular Ecology 18: 1863-1874.

LePichon, C., G. Gorges, P. Boet, J.Baudry, F.Goreaud, and T. Faure. 2006. A spatially explicit resource-based approach for managing stream fishes in riverscapes. Environmental Management 37: 322-335.

Li, H., D. Li, T. Li, Q. Qiao, J. Yang, and H. Zhang. 2010. Application of least-cost path model to identify a giant panda dispersal corridor network after the Wenchuan earthquake—Case study of Wolong Nature Reserve in China. Ecological Modelling 221: 944-952.

Magle, S.B., D.M. Theobald, and K.R. Crooks. 2009. A comparison of metrics predicting landscape connectivity for a highly interactive species along an urban gradient in Colorado, USA. Landscape Ecology 24: 267-280.

McRae, B.H., and P. Beier. 2007. Circuit theory predicts gene flow in plant and animal populations. Proceedings of the National Academy of Sciences 104: 19885–19890.

Michels, E., K. Cottenie, L. Neys, K. DeGelas, P. Coppin, and L. DeMeester. 2001. Geographical and genetic distances among zooplankton populations in a set of interconnected ponds: a plea for using GIS modelling of the effective geographical distance. Molecular Ecology 10: 1929-1938.

Murphy, M.A., R. Dezzani, D.S. Pilliod, and A. Storfer. 2010. Landscape genetics of high mountain frog metapopulations. Molecular Ecology 19: 3634-3649.

Murtskhvaladze, M., A. Gavashelishvili, and D. Tarkhnishvili. 2010. Geographic and genetic boundaries of brown bear (*Ursus arctos*) population in the Caucasus. Molecular Ecology 19: 1829-1841.

Nichol, J.E. M.S. Wong, R.Corlett, and D.W. Nichol. 2010. Assessing avian habitat fragmentation in urban areas of Hong Kong (Kowloon) at high spatial resolution using spectral unmixing. Landscape and Urban Planning 95: 54-60.

Nikolakaki, P. 2004. A GIS site-selection process for habitat creation: estimating connectivity of habitat patches. Landscape and Urban Planning 64: 77-94.

O'Brien, D., M. Manseau, A. Fall, and M.J. Fortin. 2006. Testing the importance of spatial configuration of winter habitat for woodland caribou: An application of graph theory. Biological Conservation 130:70-83.

Patrick, D.A., and J.P. Gibbs. 2010. Population structure and movements of freshwater turtles across a road-density gradient. Landscape Ecology 25: 791-801.

Pereira, M., P. Segurado, and N. Neves. 2011. Using spatial network structure in landscape management and planning: A case study with pond turtles. 100: 67-76.

Pinto, N., and T.H. Keitt. 2009. Beyond the least-cost path: evaluating corridor redundancy using a graph-theoretic approach. Landscape Ecology 24: 253-266.

Pullinger, M.G., and C.J. Johnson. 2010. Maintaining or restoring connectivity of modified landscapes: evaluating the least-cost path model with multiple sources of ecological information. Landscape Ecology 25: 1547-1560.

Purrenhage, J.L., P.H. Niewiarowski, and F.B.-G. Moore. 2009. Population structure of spotted salamanders (*Anbystoma maculatum*) in a fragmented landscape. Molecular Ecology 18: 235-247.

Rabinowitz, A. and K.A. Zeller. 2010. A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*. Biological Conservation 143: 939-945.

Rae, C., K. Rothley, and S. Dragicevic. 2007. Implications of error and uncertainty for an environmental planning scenario: A sensitivity analysis of GIS-based variables in reserve design. Landscape and Urban Planning 79: 210-217.

Ray, N., and M.A. Burgman. 2006. Subjective uncertainties in habitat suitability maps. Ecological Modelling 195: 172-186.

Richard, Y., and D.P. Armstrong. 2010. Cost distance modelling of landscape connectivity and gap-crossing ability using radio-tracking data. Journal of Applied Ecology 47: 603-610.

Richards-Zawacki, C.L. 2009. Effects of slope and riparian habitat connectivity on gene flow in an endangered Panamanian frog, *Atelopus varius.* Diversity and Distributions 15: 796-806.

Ricketts, T.H. 2001. The Matrix Matters: Effective Isolation in Fragmented Landscapes. The American Naturalist 158: 87-99.

Rodríguez-Freire, M., and R. Crecente-Maseda. 2008. Directional connectivity of wolf (*Canis lupus*) populations in Northwest Spain and anthropogenic effects on dispersal patterns. Environmental Modelling and Assessment 13: 35-51.

Rouget, M., R.M. Cowling, A.T. Lombard, A.T. Knight, and G.I.H. Kerley. 2006. Designing large-scale conservation corridors for pattern and process. Conservation Biology 20: 549-561.

Savage, W.K., A.K. Fremier, and H.B. Shaffer. 2010. Landscape genetics of alpine Sierra Nevada salamanders reveal extreme population subdivision in space and time. Molecular Ecology 19: 3301-3314.

Schadt, S., F. Knauer, P. Kaczensky, E. Revilla, T. Wiegand, and L. Trepl. 2002. Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. Ecological Applications 12: 1469-1483.

Schooley, R.L., and L.C. Branch. 2009. Enhancing the area–isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland mammal. Ecological Applications 19: 1708-1722.

Schooley, R.L., and J.A. Wiens. 2005. Spatial ecology of cactus bugs: Area constraints and patch connectivity. Ecology 86: 1627-1639.

Schwartz, M.K., J.P. Copeland, N.J. Anderson, J.R. Squires, R.M. Inman, K.S. McKelvey, K.L. Pilgrim, L.P. Waits, and S.A. Cushman. 2009. Wolverine gene flow across a narrow climatic niche. Ecology 90: 3222-3232.

Shanahan, D.F., H.P. Possingham, and C. Riginos. 2011. Models based on individual level movement predict spatial patterns of genetic relatedness for two Australian forest birds. Landscape Ecology 26: 137-148.

Shen, G., C. Feng, Z. Xie, Z. Ouyang, J. Li, and M. Pascal. 2008. Proposed conservation landscape for giant pandas in the Minshan Mountains, China. Conservation Biology 22: 1144-1153.

Shirk, A.J., D.O. Wallin, S.A. Cushman, C.G. Rica, and K.I. Warheit. 2010. Inferring landscape effects on gene flow: a new model selection framework. Molecular Ecology 19: 3603-3619.

Short Bull, R.A., S.A. Cushman, R. Mace, T. Chilton, K.C. Kendall, E.L. Landguth, M.K. Schwartz, K. McKelvey, F.W. Allendorf, and G. Luikart. 2011. Why replication is important in landscape genetics: American black bear in the Rocky Mountains. Molecular Ecology 20: 1092-1107.

Stevens, V.M., C. Verkenne, S. Vandewoestijne, R.A. Wesselingh, and M. Baguette. 2006. nGene flow and functional connectivity in the natterjack toad. Molecular Ecology 15: 2333-2344.

Sutcliffe, O.L., V. Bakkestuen, G. Fry, and O.E. Stabbetorp. 2003. Modelling the benefits of farmland restoration: methodology and application to butterfly movement. Landscape and Urban Planning 63: 15-31.

Thatcher, C.A., F.T. VanManen, and J.D. Clark. 2009. A habitat assessment for Florida panther population expansion into central Florida. Journal of Mammalogy 90: 918-925.

Verbeylen, G., L. DeBruyn, F. Adriaensen, and E. Matthysen. 2003. Does matrix resistance influence Red squirrel (*Sciurus vulgaris* L. 1758) distribution in an urban landscape? Landscape Ecology 18: 791-805.

Vignieri, S.N. 2005. Streams over mountains: influence of riparian connectivity on gene flow in the Pacific jumping mouse (Zapus trinotatus). Molecular Ecology 14: 1925-1937.

Vos, C.C., A.G. Antonisse-DeJong, P.W. Goedhart, and M.J.M. Smulders. 2001. Genetic similarity as a measure for connectivity between fragmented populations of the moor frog (*Rana arvalis*). Heredity 86: 598-608.

Walker, R.S., A.J. Novaro, and L.C. Branch. 2007. Functional connectivity defined through cost-distance and genetic analyses: a case study for the rock-dwelling mountain vizcacha (Lagidium viscacia) in Patagonia, Argentina. Landscape Ecology 22: 1303-1314.

Wang, I.J., W.K. Savage, and B. Shaffer. 2009. Landscape genetics and least-cost path analysis reveal unexpected dispersal routes in the California tiger salamander (*Ambystoma californiense*). Molecular Ecology 18: 1365-1374.

Wang, Y.H., K.C. Yang, C.L. Bridgman, and L.K. Lin. 2008. Habitat suitability modelling to correlate gene flow with landscape connectivity. Landscape Ecology 23: 989-1000.

Wasserman, T.N., S.A. Cushman, M.K. Schwartz, and D.O. Wallin. 2010. Spatial scaling and multi-model inference in landscape genetics: *Martes Americana* in northern Idaho. Landscape Ecology 25: 1601-1612.

Watts, K., A.E. Eycott, P. Handley, D. Ray, J.W. Humphrey, and C.P. Quine. 2010. Targeting and evaluating biodiversity conservation action within fragmented landscapes: an approach based on generic focal species and least-cost networks. Landscape Ecology 25: 1305-1318.

Wikramanayake, E., M. McKnight, E. Dinerstein, A. Joshi, B. Gurung, and D. Smith. 2004. Designing a conservation landscape for tigers in human-dominated environments. Conservation Biology 18: 839-844.

Zalewski, A., S.B. Piertnery, H. Zalewska, and X. Lambin. 2009. Landscape barriers reduce gene flow in an invasive carnivore: geographical and local genetic structure of American mink in Scotland. Molecular Ecology 18: 1601-1615.

Zetterberg, A., U.M. Mortberg, and B. Balfors. 2010. Making graph theory operational for landscape ecological assessments, planning, and design. Landscape and Urban Planning 95: 181-191.

Zimmermann, F., and U. Breitenmoser. 2007. Potential distribution and population size of the Eurasian lynx *Lynx lynx* in the Jura Mountains and possible corridors to adjacent ranges. Wildlife Biology 13: 406-416.

References

Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E (2003) The application of 'least- cost' modeling as a functional landscape model. Landsc Urban Plan 64:233–247

Bartelt PE, Klaver RW, Porter WP (2010) Modeling amphibian energetics, habitat suitability, and movements of western toads, Anaxyrus (= Bufo) boreas, across present and future landscapes. Ecol Model 221:2675–2686

Beazley K, Smandych L, Snaith T, MacKinnon F, Austen-Smith P Jr, Dunker P (2005) Biodiversity considerations in conservation system planning: map-based approach for Nova Scotia, Canada. Ecol Appl 15:2192–2208

Beier P, Majka DR, Spencer WD (2008) Forks in the road: choices in procedures for designing wildland linkages. Conserv Biol 22:836–851

Beier P, Majka DR, Newell SL (2009) Uncertainty analysis of least-cost modeling for designing wildlife linkages. Ecol Appl 19:2067–2077

Braunisch V, Segelbacher G, Hirzel AH (2010) Modelling functional landscape connectivity from genetic population structure: a new spatially explicit approach. Mol Ecol 19:3664–3678

Broquet T, Ray N, Petit E, Fryxell JM, Burel F (2009) Genetic isolation by distance and landscape connectivity in the American marten (Martes americana). Landscape Ecol 21:877–889

Burnham KP, Anderson D (2002) Model selection and multimodel inference (2nd edn). Springer, New York

Chardon JP, Adriaensen F, Matthysen E (2003) Incorporating landscape elements into a connectivity measure: a case study for the Speckled wood butterfly (Pararge aegeria L.). Landscape Ecol 18:561–573

Chetkiewicz C-LB, Boyce MS (2009) Use of resource selection functions to identify conservation corridors. J Appl Ecol 46:1036–1047

Clark RW, Brown WS, Stechert R, Zamudio KR (2008) Integrating individual behavior and landscape genetics: the population structure of timber rattlesnake hibernacula. Mol Ecol 17:719–730

Clevenger AP, Wierzchowski J, Chruszcz B, Gunson K (2002) GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. Conserv Biol 16:503–514

Compton BW, McGarigal K, Cushman SA, Gamble LR (2007) A resistant-kernel model of connectivity for amphibians that breed in vernal pools. Conserv Biol 21:788–799

Coulon A, Cosson JF, Angibault JM, Cargnelutti B, Galan M, Morellet N, Petit E, Aulagnier S, Hewison AJM (2004) Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual-based approach. Mol Ecol 13:2841–2850 Cushman SA (2010) Animal movement data: GPS telemetry, autocorrelation and the need for path-level analysis. In: Cushman SA, Huettmann F (eds) Spatial complexity, informatics, and wildlife conservation. Springer, New York, pp 131–149

Cushman SA, Landguth EL (2010) Spurious correlations and inference in landscape genetics. Mol Ecol 19:3592–3602 Cushman SA, Lewis JS (2010) Movement behavior explains genetic differentiation in American black bears. Landscape Ecol 25:1613–1625

Cushman SA, McKelvey KS, Hayden J, Schwartz MK (2006) Gene-flow in complex landscapes: testing multiple hypotheses with causal modeling. Am Nat 168:486–499

Cushman SA, Gutzweiler K, Evans JS, McGarigal K (2010) The gradient paradigm: a conceptual and analytical framework for landscape ecology. In: Cushman SA, Huettmann F (eds) Spatial complexity, informatics, and wildlife conservation. Springer, New York, pp 83–108

Cushman S, McRae B, Adriaensen F, Beier P, Shirley M, Zeller KA (in press) Biological corridors. In: MacDonald D, Willis K (eds) Key topics in conservation biology, vol II. Wiley

Desrochers A, Be´lisle M, Morand-Ferron J (2011) Integrating GIS and homing experiments to study avian movement costs. Landscape Ecol 26:47–58

Emaresi G, Pellet J, Dubey S, Hirzel AH, Fumagalli L (2011) Landscape genetics of the Alpine newt (Mesotriton alpestris) inferred from a strip-based approach. Conserv Genet 12:41–50

Epps CW, Wehausen JD, Bleich VC, Torres SG, Brashares JS (2007) Optimizing dispersal and corridor models using landscape genetics. J Appl Ecol 44:714–724

Epps CW, Mutayoba BM, Gwin L, Brashares JS (2011) An empirical evaluation of the African elephant as a focal species for connectivity planning in East Africa. Divers Distrib 17:603–612

Estrada-Pena A (2003) The relationships between habitat topology, critical scales of connectivity and tick abundance Ixodes ricinus in a heterogeneous landscape in northern Spain. Ecography 26:661–671

Ferreras P (2001) Landscape structure and asymmetrical inter- patch connectivity in a metapopulation of the endangered Iberian lynx. Biol Conserv 100:125–136

Flamm RO, Weigle BL, Wright IE, Ross M, Aglietti S (2005) Estimation of manatee (Trichechus manatus latirostris) places and movement corridors using telemetry data. Ecol Appl 15:1415–1426

Foltete JC, Berthier K, Cosson JF (2008) Cost distance defined by a topological function of landscape. Ecol Model 210:104–114

Foody GM (2002) Status of land cover classification accuracy assessment. Remote Sens Environ 80:185–201

Freeman RC, Bell KP (2011) Conservation versus cluster subdivisions and implications for habitat connectivity. Landsc Urban Plan 101:30–42

Graham CH (2001) Factors influencing movement patterns of keel-billed toucans in a fragmented tropical landscape in southern Mexico. Conserv Biol 15:1789–1798

ISI Web of Knowledge Thomson Reuters (2011) Web of Science. Retrieved June 16, 2011 from http://pcs.isi knowledge.com

Janin A, Le´na JP, Ray N, Delacourt C, Allemand P, Joly P (2009) Assessing landscape connectivity with calibrated cost-distance modelling: predicting common toad distribution in a context of spreading agriculture. J Appl Ecol 46:833–841

Jaquiery J, Broquet T, Hirzel AH, Yearsley J, Perrin N (2011) Inferring landscape effects on dispersal from genetic distances: how far can we go? Mol Ecol 20:692–705

Johnson CJ, Gillingham MP (2004) Mapping uncertainty: sensitivity of wildlife habitat ratings to expert opinion. J Appl Ecol 41:1032–1041

Kautz R, Kawula R, Hoctor T, Comiskey J, Jansen D, Jennings D, Kasbohm J, Mazzzotti F, McBride R, Richardson L, Root K (2006) How much is enough? Landscape-scale conservation for the Florida panther. Biol Conserv 130:118–133

Kindall JL, VanManen FT (2007) Identifying habitat linkages for American black bears in North Carolina, USA. J Wildl Manag 71:487–495

Klug PE, Wisely SM, With KA (2011) Population genetic structure and landscape connectivity of the Eastern Yellowbelly Racer (Coluber constrictor flaviventris) in the contiguous tallgrass prairie of northeastern Kansas, USA. Landscape Ecol 26:281–294

Koen EL, Garroway CJ, Wilson PJ, Bowman J (2010) The effect of map boundary on estimates of landscape resistance to animal movement. PLoS ONE 5:1–8

Koscinsky D, Yates AG, Handford P, Lougheed SC (2009) Effects of landscape and history on diversification of a montane, stream-breeding amphibian. J Biogeogr 36:255–265

Kuemmerle T, Perzanowski K, Resit Akcakaya H, Beaudry F, Van Deelen TR, Parnikoza I, Khoyetskyy P, Waller DM, Radeloff VC (2011) Cost-effectiveness of strategies to establish a European bison metapopulation in the Carpathians. J Appl Ecol 48:317–329

Kuroe M, Yamaguchi N, Kadoya T, Miyashita T (2011) Matrix heterogeneity affects population size of the harvest mice: Bayesian estimation of matrix resistance and model validation. Oikos 120:271–279

Laiolo P, Tella JL (2006) Landscape bioacoustics allow detection of the effects of habitat patchiness on population structure. Ecology 87:1203–1214

Landguth EL, Cushman SA, Schwartz MK, McKelvey KS, Murphy M, Luikart G (2010) Quantifying the lag time to detect barriers in landscape genetics. Mol Ecol 19:4179–4191

LaRue MA, Nielsen CK (2008) Modelling potential dispersal corridors for cougars in Midwestern North America using least-cost path methods. Ecol Model 212:372–381

Loveland TR, Reed BC, Brown JF, Ohlen DO, Zhu Z, Yang L, Merchant JW (2000) Development of a global land cover characteristics database and IGBP DISCover from 1 km

AVHRR data. Int J Remote Sens 21:1303–1330 Magle SB, Theobald DM, Crooks KR (2009) A comparison of metrics predicting landscape connectivity for a highly interactive species along an urban gradient in Colorado, USA. Landscape Ecol 24:267–280

Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. Trends Ecol Evol 18:189–197

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2010) Resource selection by animals: statistical design and analysis for field studies, 2nd edn. Kluwer, Amsterdam

McGarigal K, Cushman SA (2005) The gradient concept of landscape structure. In: Wiens J, Moss M (eds) Issues and perspectives in landscape ecology. Cambridge University Press, Cambridge, pp 112–119

McRae BH (2006) Isolation by resistance. Evolution 60:1551–1561 McRae BH, Beier P (2007) Circuit theory predicts gene flow in plant and animal populations. Proc Nat Acad Sci 104:19885–19890

Michels E, Cottenie K, Neys L, DeGelas K, Coppin P, DeMeester L (2001) Geographical and genetic distances among zooplankton populations in a set of interconnected ponds: a plea for using GIS modelling of the effective geographical distance. Mol Ecol 10:1929–1938

Murphy MA, Dezzani R, Pilliod DS, Storfer A (2010) Landscape genetics of high mountain frog metapopulations. Mol Ecol 19:3634–3649

Newby JR (2011) Puma dispersal ecology in the central Rocky Mountains. Master's thesis, University of Montana, Missoula, MT, pp 1–111

Nichol JE, Wong MS, Corlett R, Nichol DW (2010) Assessing avian habitat fragmentation in urban areas of Hong Kong (Kowloon) at high spatial resolution using spectral unmixing. Landsc Urban Plan 95:54–60

O'Brien D, Manseau M, Fall A, Fortin MJ (2006) Testing the importance of spatial configuration of winter habitat for woodland caribou: an application of graph theory. Biol Conserv 130:70–83

Pearce JL, Cherry K, Drielsma M, Ferrier S, Whish G (2001) Incorporating expert opinion and fine-scale vegetation mapping into statistical models of faunal distribution. J Appl Ecol 38:412–424

Pinto N, Keitt TH (2009) Beyond the least-cost path: evaluating corridor redundancy using a graph-theoretic approach. Landscape Ecol 24:253–266

Pullinger MG, Johnson CJ (2010) Maintaining or restoring connectivity of modified landscapes: evaluating the least- cost path model with multiple sources of ecological information. Landscape Ecol 25:1547–1560

Rabinowitz A, Zeller KA (2010) A range-wide model of landscape connectivity and conservation for the jaguar, Panthera onca. Biol Conserv 143:939–945

Rae C, Rothley K, Dragicevic S (2007) Implications of error and uncertainty for an environmental planning scenario: a sensitivity analysis of GIS-based variables in reserve design. Landsc Urban Plan 79:210–217

Rayfield B, Fortin MJ, Fall A (2010) The sensitivity of least-cost habitat graphs to relative cost surface values. Landscape Ecol 25:519–532

Richard Y, Armstrong DP (2010) Cost distance modelling of landscape connectivity and gap-crossing ability using radio-tracking data. J Appl Ecol 47:603–610

Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. Am Nat 158:87–99

Saaty TL (1980) The analytic hierarchy process. McGraw-Hill, New York

Savage WK, Fremier AK, Shaffer HB (2010) Landscape genetics of alpine Sierra Nevada salamanders reveal extreme population subdivision in space and time. Mol Ecol 19:3301–3314

Sawyer SC, Epps CW, Brashares JS (2011) Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? J Appl Ecol 48:668–678

Schwartz MK, Copeland JP, Anderson NJ, Squires JR, Inman RM, McKelvey KS, Pilgrim KL, Waits LP, Cushman SA (2009) Wolverine gene flow across a narrow climatic niche. Ecology 90:3222–3232

Seoane J, Bustamente J, Diaz-Delgado R (2005) Effect of expert opinion on the predictive ability of environmental models of bird distribution. Conserv Biol 19:512–522

Shirk AJ, Wallin DO, Cushman SA, Rica CG, Warheit KI (2010) Inferring landscape effects on gene flow: a new model selection framework. Mol Ecol 19:3603– 3619

Short Bull RA, Cushman SA, Mace R, Chilton T, Kendall KC, Landguth EL, Schwartz MK, McKelvey K, Allendorf FW, Luikart G (2011) Why replication is so important in landscape genetics: American black bear in the Rocky Mountains. Mol Ecol 20:1092–1107

Singleton PH, Gaines WL, Lehmkuhl JF (2002) Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least- cost corridor assessment. Research Paper PNW-RP-549. U.S. Forest Service Pacific Northwest Research Station, Portland, OR

Spear SF, Balkenhol N, Fortin MJ, McRae BH, Scribner K (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Mol Ecol 19:3576–3591

Stevens VM, Verkenne C, Vandewoestijne S, Wesselingh RA, Baguette M (2006) Gene flow and functional connectivity in the natterjack toad. Mol Ecol 15:2333–2344

Sutcliffe OL, Bakkestuen V, Fry G, Stabbetorp OE (2003) Modelling the benefits of farmland restoration: methodology and application to butterfly movement. Landsc Urban Plan 63:15–31

Thatcher CA, VanManen FT, Clark JD (2009) A habitat assessment for Florida panther population expansion into central Florida. J Mammal 90:918–925

Thompson CM, McGarigal K (2002) The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York. Landscape Ecol 17:569–586

Vignieri SN (2005) Streams over mountains: influence of riparian connectivity on gene flow in the Pacific jumping mouse (Zapus trinotatus). Mol Ecol 14:1925–1937

Wang YH, Yang KC, Bridgman CL, Lin LK (2008) Habitat suitability modelling to correlate gene flow with landscape connectivity. Landscape Ecol 23:989–1000

Wang IJ, Savage WK, Shaffer B (2009) Landscape genetics and least-cost path analysis reveal unexpected dispersal routes in the California tiger salamander (Ambystoma californiense). Mol Ecol 18:1365–1374

Wasserman TN, Cushman SA, Schwartz MK, Wallin DO (2010) Spatial scaling and multi-model inference in landscape genetics: Martes Americana in northern Idaho. Landscape Ecol 25:1601–1612

Watts K, Eycott AE, Handley P, Ray D, Humphrey JW, Quine CP (2010) Targeting and evaluating biodiversity conservation action within fragmented landscapes: an approach based on generic focal species and least-cost networks. Landscape Ecol 25:1305–1318

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385–397

Worton BJ (1995) A convex hull-based estimator of home-range size. Biometrics 51:1206–1215

Zimmermann F, Breitenmoser U (2007) Potential distribution and population size of the Eurasian lynx Lynx lynx in the Jura Mountains and possible corridors to adjacent ranges. Wildl Biol 13:406–416

CHAPTER 2

SENSITIVITY OF LANDSCAPE RESISTANCE ESTIMATES BASED ON POINT SELECTION FUNCTIONS TO SCALE AND BEHAVIORAL STATE: PUMAS AS A CASE STUDY

Introduction

Estimating landscape resistance to animal movement is the foundation for connectivity modeling and the identification of conservation corridors. In this context, 'resistance' represents the willingness of an organism to cross a particular environment, the physiological cost of moving through a particular environment, the reduction in survival moving through a particular environment, or an integration of all these factors. As reviewed in Zeller et al. (2012), methods for empirically estimating resistance to movement use either point locations collected independently or extracted from telemetry data, steps or paths derived from telemetry data, or genetic markers. Typically, when points, steps, or paths are employed, a resource selection function is developed and then used to predict probability of use across the area of interest. The inverse of this probability is then used as an estimate of resistance. The assumption here is that low resistance areas are preferred while high resistance areas are avoided.

Resource selection functions based on points, or point selection functions (PSFs), are widely used to analyze wildlife-habitat relationships (Boyce et al. 2002) and, although PSFs do not explicitly represent movement, they are one of the most common ways to empirically estimate resistance to movement for a species (Zeller et al. 2012). At the core of any PSF, and resource selection functions in general, is a ‘used’ versus ‘available’ design where ‘preferred’ habitats are used in greater proportions than their availability and vice versa (Manly et al. 2002). Use of PSFs in ecology have traditionally been based on one or two scales of analysis (Wheatley and Johnson 2009), and inferences are made across all data points regardless of the behavioral state of an individual. However, PSFs, particularly those based on GPS telemetry data, have the potential for examining a range of scales and behavioral states to model increasingly realistic relationships between individuals and their environments through ‘context-dependent’ modeling.

Context-dependent modeling acknowledges that an animal’s interaction with its environment depends on its location, its surroundings, and its behavioral state (Dalziel et al. 2008), and thus accounts for the landscape and behavioral context of an individual. A simple, but effective way to model context-dependent PSFs is to use conditional logistic regression. Conditional logistic regression, also called case- controlled or paired logistic regression, pairs each used point or area with a relevant available area (Compton et al. 2002). The available area is often defined based on the acquisition interval of GPS collars. For example, with a 1-h acquisition interval, the extent of the available area is defined as some upper quantile of the distribution of step lengths at 1-h (Boyce 2006). However, in conditional logistic regression, the chosen extent of available habitat also determines the scale of the analysis (ignoring grain size), and the collar acquisition interval is rarely chosen with a priori knowledge of the scales at which a species responds most strongly to its environment (following Holland et al. (2004), we use the term ‘characteristic scale’ to reference this strongest scale of response). Furthermore, there may be different characteristic scales for each habitat type or landscape feature.

Therefore, using a single scale may result in inaccurate estimates of selection and resistance (Wheatley 2010; Norththrup et al. 2013) and a continuum of scales should be examined so as to capture the true characteristic scale(s). If multiple characteristic scales are found, a multi-scale model may be more appropriate to model context-dependent resource selection (Meyer and Thuiller 2006; DeCesare et al. 2012; Martin and Fahrig 2012).

Historically, PSFs were modeled using all data points, regardless of the behavior of the animal at the time the points were collected. However, it is reasonable to assume that selection of habitat for feeding or denning, for example, may be different than selection of habitat for movement between resource patches. Combining data from different behavioral states in a single analysis almost certainly biases inferences about resource selection and estimates of landscape resistance. Fortunately, the availability of high resolution GPS data now allows for approaches that incorporate different behavioral states. Distance, or rate of movement, and turning angle have been the primary criteria used to discern between two main behavioral states, variously defined as active versus resting (Squires et al. 2013), or static versus traveling (Dickson et al. 2005). While a few studies have begun to compare resource selection during different behavioral states (e.g. Dickson et al. 2005; Squires et al. 2013), there are no comparative studies on how behavior influences resistance estimates.

We investigated the influence of scale and behavioral state on context-dependent PSFs and the resistance estimates derived from these PSFs using GPS collar data from pumas (*Puma concolor*) in southern California. The GPS collars were programmed at a high sampling intensity (5-min intervals), allowing us to empirically examine a continuum of scales, from a very fine scale to the scale of a typical home range for a puma in the region (Dickson and Beier 2002). First, we hypothesized that PSF inference would be sensitive to the extent of available habitat and that pumas would have different characteristic scales for different land cover types. Second, we hypothesized that using all data points or partitioning points based on behavioral state (resource use versus movement) would influence interpretation of how pumas were responding to their environment. Third, we hypothesized that resistance estimates based on context-dependent PSFs would be sensitive to both scale and behavioral state. Fourth, we hypothesized that a multi-scale model would be more appropriate for modeling resistance to movement than a single-scale model. Lastly, we hypothesized that results from a context-independent model would differ from the results of our context-dependent models, both in model performance and estimates of resistance.

Methods

Study area and data collection

The study area encompassed 4,089 km2 in the Santa Ana Mountains and surrounding lowlands in southern California, including portions of Orange County, Riverside County and San Diego County. The Santa Ana mountains are a coastal range with elevation ranging from sea level to 1,734 m and a Mediterranean climate defined by hot dry summers and mild wetter winters.

Eight pumas (five female and three male) were collared between October 2011 and February 2012 and were fit with Lotek 4400 S GPS collars programmed to acquire locational fixes every 5 min (Lotek Wireless Inc., Canada). Collar duration ranged from

12 to 71 days (median = 24). Long-term collar accuracy from manufacturer tests is 5 to 10 m, though vegetation types and topographical conditions may decrease accuracy (Chang, personal communication). Therefore, two- dimensional fixes with a PDOP [5 were removed to avoid the use of data that may have large spatial errors, as recommended by Lewis et al. (2007), resulting in a mean data loss of 2.96 %. Missed fixes from failure of the collar to record a GPS location resulted in a mean data loss of 15.87 %, bringing our total mean data loss to 18.83 %. Citing various studies, Frair et al. (2010) have cautioned that coefficients of selection become statistically different when there is a 10–25 % loss of data from positional or habitat bias. However, our losses were relatively consistent across individuals and if biases were introduced, they were likely uniform in nature. The final data set consisted of 61,115 fixes across the eight individuals (range 1,650–20,433; median = 5,846). Due to the low number of individuals, sexes were pooled in the analyses, and a mixed-effects model was used to account for inter-individual differences (see ‘‘Statistical analysis’’ section).

We used land cover types from the California Wildlife Habitat Relationship database as independent variables in our PSFs. The Wildlife Habitat Relationship data were obtained from the CalVeg geospatial data set (USDA Forest Service 2007) in vector format at the 1:24,000 scale, which we rasterized at a 30-m resolution. There were 25 mapped land cover types present in the study area, but many types had very low occurrence (<1 %). In order to avoid issues with data sufficiency, we aggregated these 25 types into nine classes based on provided descriptions from the California Department of Fish and Game (1988). The final land cover classes and their percentages of the study area were as follows: chaparral (45 %), urban (19 %), coastal scrub (14 %), annual grassland (6 %), coastal oak woodlands (5 %), agriculture (5 %), riparian areas (3 %), perennial grassland (2 %), and naturally barren or open areas (1 %).

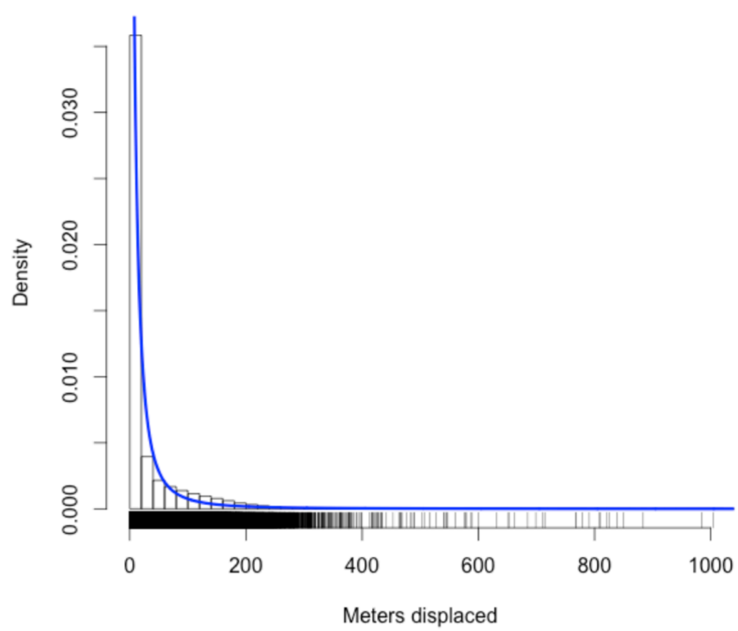
Used and available habitat

All data analysis was performed using R software (R Core Team 2013). Our used and available habitat were defined in a paired design to allow for the use of conditional logistic regression (Compton et al. 2002). For each telemetry point, we designated 'used' habitat as a 30-m fixed-width buffer around the pixel where a point was located. We calculated the proportions of land cover types across these nine pixels. This definition of used habitat allowed us to meet two goals: (1) it provided a buffer that helped to account for small locational errors in the telemetry points (Rettie and McLoughlin 1999), and (2) it allowed us to incorporate the immediate environment around each point into the area of used habitat. The latter goal was based on the assumption that an individual may not only be selecting habitat at the used pixel, but may be selecting a particular pixel because of its immediate surroundings. This may be especially important for puma that are known to utilize edge habitats (Laundré and Hernández 2003; Laundré and Loxterman 2007).

'Available' habitat for each used point was defined as follows. We calculated the straight-line distances between consecutive points, which gave us a distribution of displacement distances. Breaks in the data due to poor fixes or missing fixes were taken into account in the calculation of these distances. We then fit a generalized Pareto distribution to the empirical distribution of displacement distances using the POT package (Ribatet 2012). The Pareto distribution fit the empirical distribution well due to its characteristic steep curve and long right tail (Fig. 2.1). We then placed a Pareto kernel over each used point, thresholded this kernel at the 97.5 percentile of the Pareto distribution or the maximum observed displacement distance, whichever was smaller, calculated the intensity of each land cover type, and converted these intensities to proportions. Our approach allowed us to census the entirety of land cover types within the available area in their correct proportions, as opposed to what is commonly done in PSFs where a random sample of points are selected within the available area. This alleviates issues with selecting a sample size for available points and associated biases in inference (Norththrup et al. 2013). In addition, the use of the Pareto kernel allowed us to weight land cover within an ecological neighborhood (sensu Addicott et al. 1987) around each used point based on probability of use. To explore the effect of acquisition interval and associated extent of available habitat on PSF inference and estimates of resistance, we implemented 36 additional extents as defined by acquisition intervals from 10- to 360-min at 10-min intervals. For each new acquisition interval, we calculated the displacement distances by subsetting the 5-min data at that interval and calculating the straight-line distance between consecutive points. We then fit a new Pareto distribution to each empirical distribution, defined a maximum threshold and calculated the proportion of available habitat within the Pareto kernel as described above (online Appendix A). It is important to note here that all of the original 5-min points were used in the PSF analyses for each of our 37 scales; the subsetting of points was performed only to acquire the distributions of displacement distances for the additional 36 scales.

GPS collars programmed at a high sampling intensity produce data that are autocorrelated, making it difficult to meet the independence assumption inherent to logistic regression. When this assumption is violated, the standard errors of the parameter estimates may be deflated resulting in inflated type 1 error rates (Legendre 1993) and the parameter estimates themselves may or may not be biased (Dormann et al. 2007; Hawkins et al. 2007). However, because we were primarily concerned with the predictive ability of the models, and were not testing the significance of the parameters in a traditional hypothesis testing framework, we opted not to alter our data structure or our models to account for autocorrelation in our data (though see ''Behavioral states'' section where some correlation may be addressed in our parameterization of resource use points).

Figure 2.1. Pareto distribution. Distribution of displacement distances and fitted Pareto distribution (blue line) at the 5-min acquisition interval. Displacement distances were calculated as the straight-line distance between consecutive points. Pareto distributions were fit to the data at each of our 37 acquisition intervals.



Behavioral states

We distinguished between two behavioral states: (1) resource use, and (2) movement. A static or slow and tortuous trajectory more likely reflected resource use, such as acquiring food and seeking and using day beds, than a faster and more direct trajectory, which more likely reflected purposeful movement through the landscape between resource use patches. Because we did not know, a priori, if a telemetry point was recorded during a movement or resource use behavior, we used a range of definitions for each behavioral state based on the distances between locations. Distance thresholds were defined along a geometric progression from 12.5 to 200 m with a common ratio of two (Table 2.1). The largest distance threshold was capped at 200 m due to an insufficient number of data points beyond this distance. At the 12.5 m distance threshold, any point 12.5 m or closer to the previous point was identified as a resource use point and any point further than 12.5 m from the previous point was identified as a movement point. Consecutive resource use points within the 12.5-m threshold distance of each other were considered part of the same resource use cluster. This same procedure was performed for each distance threshold.

Our range of definitions for each behavioral state ran the continuum from least conservative to most conservative. The 12.5-m distance threshold required resource use points to be very close to one another and the definition of resource use at this threshold likely did not include any true movement points. Therefore, this was considered our most conservative definition of resource use. Conversely, the 12.5-m distance threshold was considered our least conservative definition for movement since there were likely many true resource use points included with the designated movement points. At the opposite end of our continuum, 200 m, the movement points were considered to be relatively pure. For the remainder of the paper we will refer to resource use and movement points along this continuum as follows: RU1 and M1 are the resource use and movement points, respectively, based on the least conservative definition for each behavioral state (RU = 200 m; M = 12.5 m), whereas RU5 and M5 are based on the most conservative definitions (RU = 12.5 m; M = 200 m).

Table 2.1. Behavioral states, alternative definitions of behavioral states, and associated attributes used in the PSF analyses.

Behavioral State	Alternative definition	Distance Threshold (meters)	Number of data points	Number of clusters
All behaviors		0	61,115	-
Movement	M1	12.5	17,614	-
	M2	25	12,436	-
	M3	50	8,800	-
	M4	100	4,212	-
	M5	200	507	-
Resource Use	RU1	200	60,608	268
	RU2	100	56,903	1,382
	RU3	50	52,315	1,933
	RU4	25	48,679	2,381
	RU5	12.5	43,501	3,892

Statistical analysis

At each scale and for all definitions of each behavioral state, as well as for all points regardless of behavioral state, we conducted a conditional mixed-effects logistic regression with individual cat as a random effect. We performed both simple regressions for each land cover type and multiple regressions including all land cover types. For the multiple regressions, we used the land cover type with the weakest effect in the simple regressions as the reference class. In conditional logistic regression, there is no model intercept, therefore the reference land cover type was simply omitted from the analysis.

We confirmed that correlation among our predictor variables was relatively low prior to performing the multiple regressions (maximum Pearson correlation coefficient = -0.48). We also created a multi-scale model using the characteristic scale for each land cover type as identified from the simple regressions (see below).

We used the lmer (or glmer) function in the lme4 package (v. 0.999999-2, Bates et al. 2013) for performing conditional mixed-effects logistic regression in R. The use of lme4 requires the differences between the used and available for each variable to be calculated at each point prior to analysis and that the response variable equals one for each data point [as described in Agresti (2002)]. The full model specification in R is provided in online Appendix B. Online Appendix B also provides a discussion of other options for conditional mixed-effects logistic regression in R along with an example of the R code used to conduct this analysis.

For the movement data, each point was given equal weight in our models. For the resource use data, each point in a cluster was down-weighted by its proportional contribution to that cluster. For example, in a cluster with 10 points, each point was assigned a weight of 0.1 and thus each cluster, regardless of the number of points, received an effective weight of one.

We defined the characteristic scale for each land cover type as the scale with the largest absolute regression coefficient and/or largest deviation from an odds ratio of one. To evaluate the predictive performance of the models, we performed a tenfold cross-validation using the methods recommended by Johnson et al. (2006). These methods are based on the Hosmer–Lemeshow approach, but are adapted for use with RSFs. For each model, we calculated the utilization value for each RSF bin using the Pareto kernel that corresponded to the extent of available for that model (results were similar when we used a uniform kernel). We quantified predictive performance of the models using Lin's (1989) concordance correlation coefficient (CCC). For a good model, the predicted observations should fall close to the expected observations on a line originating at 0 with a slope of 1 (Johnson et al. 2006). The CCC statistic measures how correlated two points are based on their deviance from this 45-degree line. We based the interpretation of results on the square of the CCC statistic.

To determine if results from context-dependent models differ from context-independent models, we focused on the multi-scale models since we assumed they might be more appropriate than the single-scale models. To derive the context-independent model, we ran a mixed-effects logistic regression in an unpaired framework using lmer with all data points. We compared model performance amongst our context- dependent multi-scale models and the context-independent multi-scale model.

Estimation of resistance

Resistance estimates from PSFs are typically calculated by taking the inverse of the predicted probability of presence. These estimates are often truncated at some upper value or re-scaled to a range, say from 1 to 10 or 1 to 100 (e.g., Ferreras 2001; Pullinger and Johnson 2010). Truncation and rescaling may alter the relative relationships between resistance estimates by introducing unnecessary subjectivity. To avoid this subjectivity, we used the inverse of the predicted probability of presence as our resistance estimates without any data standardizations. Because estimating a complete resistance surface for the full factorial of models was computationally prohibitive, we generated 20,000 random points across the study area, predicted the probability of presence across these points, and used the inverse of these values as our estimates of resistance.

To determine how sensitive resistance estimates were to the choice of scale, we calculated the absolute proportional difference in resistance estimated at each scale from that estimated at the 5-min/250-m scale. Similarly, to determine how sensitive resistance estimates were to behavioral state, we calculated, at each scale, the absolute proportional difference in resistance estimates based on the most conservative definition of each behavioral state (RU5 and M5) from that estimated based on all points and from each other. We explored how different the single-scale estimates of resistance were from the multi-scale estimates by calculating the absolute proportional differences in resistance estimated by each single-scale model from that estimated by the multi-scale model. Finally, we calculated the absolute proportional difference in resistance estimates between our multi-scale contextindependent model and our context-dependent models.

Results

Characteristic scales

The simple conditional mixed-effects logistic regression models revealed different characteristic scales among land cover types, including four general patterns of response: (1) a fine-scaled response where the strongest response occurred at the finest scale(s) (e.g., Fig. 2.2a); (2) a unimodal response where the strongest response occurred at an intermediate scale (e.g., Fig. 2.2c); (3) an asymptotic threshold response, where the response was weak at fine scales, and became stronger and eventually reached an asymptote as scale increased (e.g., Fig. 2.2h); and (4) a coarse-scaled response where the strength of response increased with scale without reaching an asymptote (e.g., resource-use curves, Fig. 2.2e). This last pattern may be due to the true characteristic scale being at a coarser scale than we examined. The multiple regression models showed the same patterns.

Despite pronounced differences in effect size, characteristic scale, regardless of preference or avoidance, remained relatively consistent across behavioral states for several land cover types (Fig. 2.2). For example, across most definitions of each behavioral state, grassland had its strongest effect at the 5-min/ 250-m scale (Fig. 2.2a); coastal oak woodland, coastal scrub, and perennial grassland types had their strongest effects at the 10-min/530-m scale (Fig. 2.2c, f, g, respectively); barren had its strongest effect at the 40-min/2,350-m scale (Fig. 2.2b); and agriculture had its strongest effect at the 360-min/9,890-m scale (Fig. 2.2e). In contrast, some cover types exhibited marked differences in characteristic scale between behavioral states. For example, chaparral exhibited a fine-scale response for all movement states, but an increasingly coarse-scale response for the more conservative resource use states (Fig. 2.2d). Conversely, riparian exhibited a fine-scale response for all resource use states, whereas the response was weakest at the finest scales for all movement states (Fig. 2.2i).

Figure 2.2 Simple Regressions. Beta estimates and odds ratios from simple conditional mixed-effects logistic regressions for each land cover type across scales and behavioral states. Movement and resource use 1 were the least conservative definitions of those behavioral states and movement and resource use 5 were the most conservative.

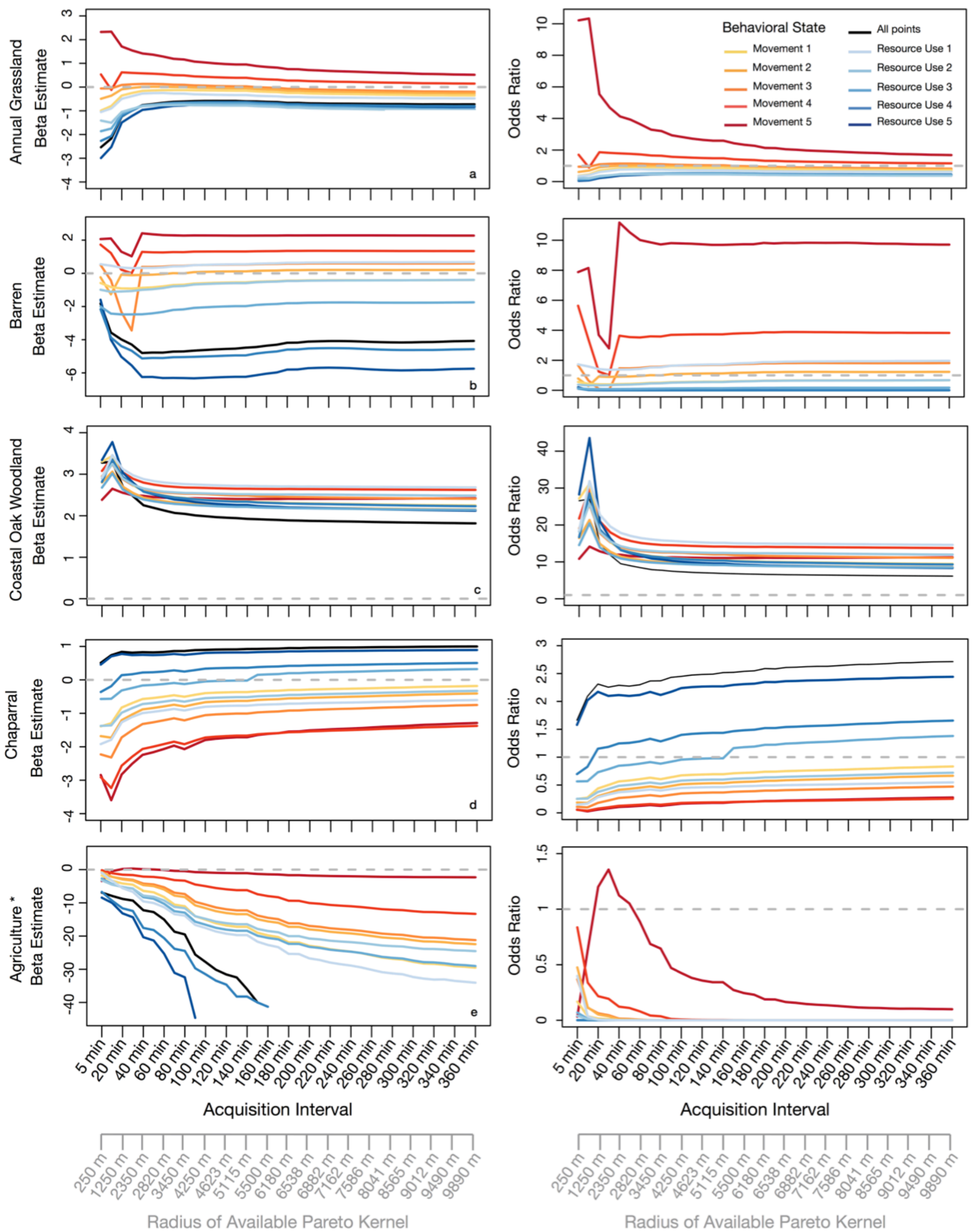
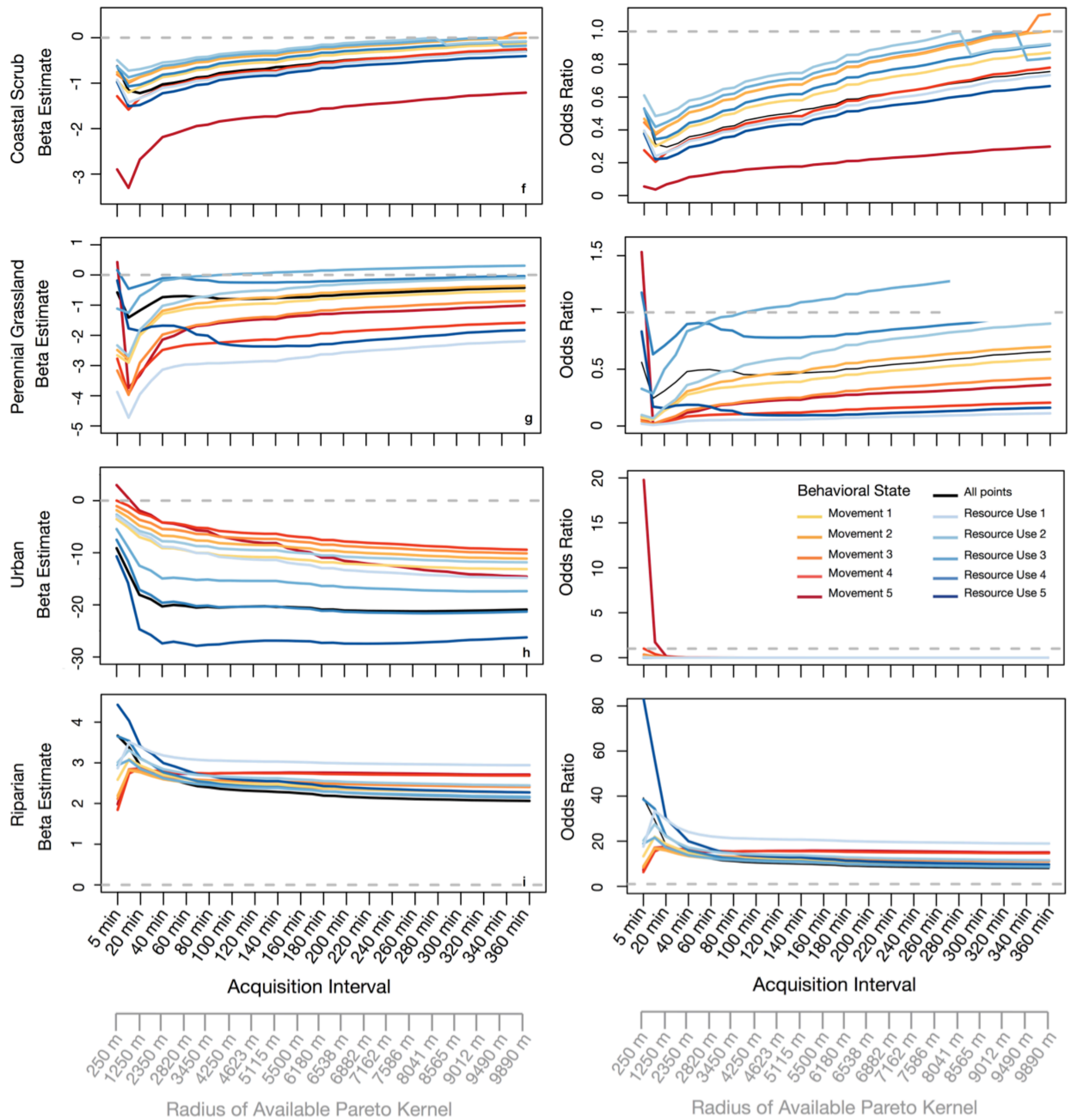


Figure 2.2 Continued



Behavioral states

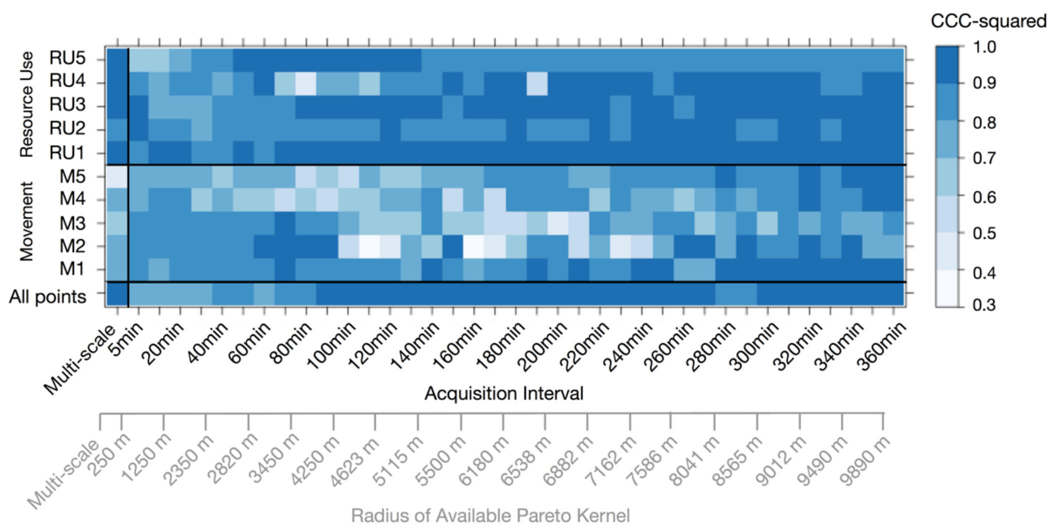
Behavioral state had a strong but variable influence on the magnitude and nature of the effect attributed to each land cover type. In some cases, the effect was consistently positive (i.e., exhibiting selection for the land cover type) or negative (i.e., exhibiting selection against the land cover type), but the magnitude of effect (i.e., effect size) varied markedly between definitions of the two behavioral states. For example, with agriculture and urban, there was a consistent negative effect and the effect size was greater for the resource use state compared to movement, but the effect size generally increased as the definition of the resource use state became more conservative, whereas it generally decreased as the definition of the movement state became more conservative (Fig. 2.2e, h). In other cases, the effect was relatively similar across behavioral states (e.g., coastal oak woodland, Fig. 2.2c, and riparian, Fig. 2.2i), indicating that selection for or against some land cover types may not be that sensitive to choice of behavioral state. Importantly, in some cases, using movement points versus resource use points led to opposite conclusions regarding habitat selection. For example, with annual grassland, the strength of effect weakened but remained negative as the behavioral state moved along the continuum from the most conservative definition of resource use (RU5) to the least conservative (RU1)(Fig. 2.2a). However, for the movement states, the response was still weakly negative for the least conservative definitions, but became increasingly positive for the most conservative definitions. We observed a similar pattern of reversal in habitat selection between behavioral states for barren and chaparral land cover types (Fig. 2.2b, d).

Lastly, models based on all data points (i.e., that did not distinguish between behavioral states) tended to reflect the average relationship observed across the continuum of definitions of the resource use behavioral state (Fig. 2.2). This was perhaps not too surprising given the disproportionate sample sizes attributed to resource use versus movement (Table 2.1), but it has serious implications for the development of resistance surfaces intended to reflect resistance to movement for purposes of connectivity modeling.

Model performance

Regardless of scale or behavioral state, all the models performed reasonably well (Fig. 2.3). The lowest squared CCC was 0.39, or a CCC of 0.62. In general, the resource use models performed better (mean squared CCC of 0.924) than the movement models (mean squared CCC of 0.820). We also observed an increase in model performance with scale, such that at the coarsest scale all the models (across all behavioral states) had a squared CCC of 0.75. However, both trends were not entirely consistent.

Figure 2.3. Concordance Correlation Coefficient (CCC). Squared CCC across scales and behavioral states. A high squared CCC indicates good model performance.

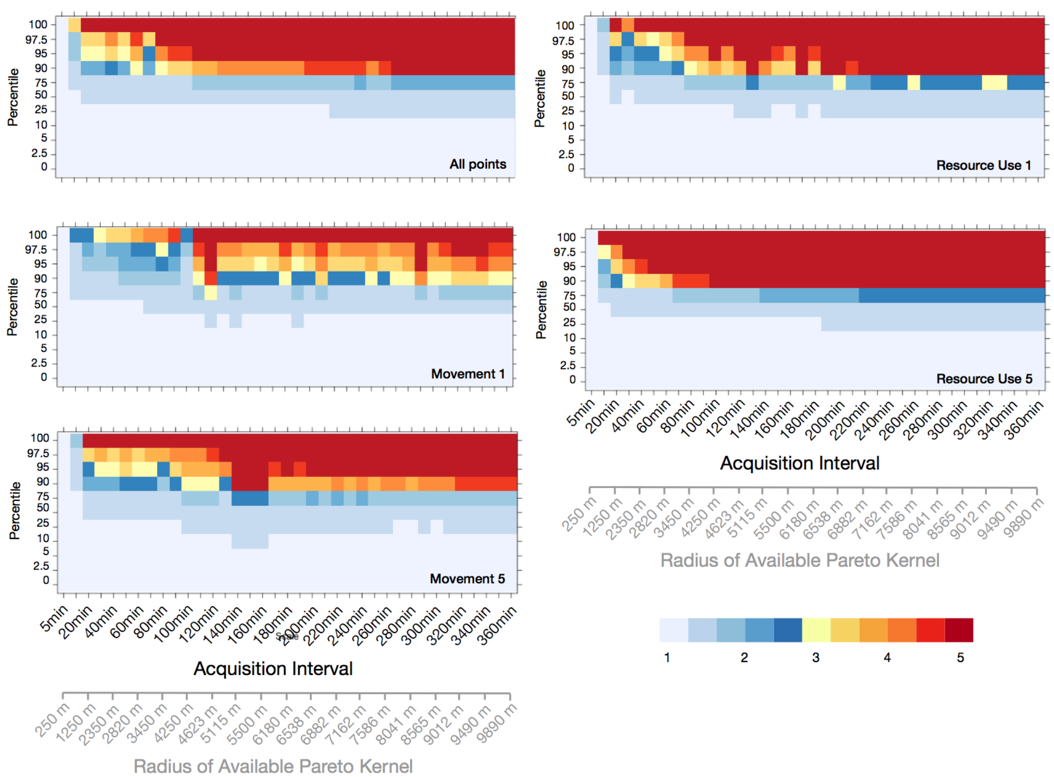


The multi-scale model generally performed as well or better than any single-scale model in modeling selection during resource use or both behaviors combined; however, for movement data, the single- scale models at coarser scales tended to perform better than the multi-scale model (Fig. 2.3). The squared CCC for the context-independent multi-scale model was 0.564. Therefore, the context-dependent multi-scale models clearly outperformed the context-independent model for all points and all definitions of each behavioral state with the exception of M5, where model performance was roughly equivalent (squared CCC of 0.527).

Sensitivity of resistance estimates

Resistance estimates were highly sensitive to scale. Holding behavioral state constant, proportional differences in resistance ranged from 0 to 245 (or 24,500 %) across scales (Fig. 2.4). In Fig. 2.4, each plot represents either all points or a subset of the points selected to represent a particular behavioral state. Within each plot (i.e., holding behavioral state constant), the x-axis represents the extent of available habitat assessed (representing the data acquisition interval and corresponding extent of available) and the y-axis represents various percentiles of the distribution of absolute proportional difference in resistance values between the reference surface (the 5-min/250- m scale as an arbitrary reference) and the surface estimated at each of the remaining scales. The color intensity in each cell represents the magnitude of the absolute proportional difference (on a natural log scale) between each surface and the reference surface. This figure reveals two important patterns. First, regardless of scale and behavioral state, the extreme differences in resistance were in the upper 20 % of the distribution, meaning that a relatively small portion of the landscape was most sensitive to the choice of scale. Second, estimates of resistance based on the most conservative definitions of each behavioral state were somewhat more sensitive than those based on the least conservative definitions. Thus, restricting the data to points clearly representing either movement or resource use resulted in estimates of resistance that were highly sensitive to scale.

Figure 2.4. Resistance differences among scales. Log proportional differences in resistance estimates as measured from the smallest scale (5 min/ 250 m) for models using all points and Movement 1, Movement 5, Resource Use 1, and Resource Use 5 points. The y-axis represents a range of percentiles for the distribution of proportional differences. The legend represents the log proportional differences. Warmer colors indicate larger differences. Please refer to ''Sensitivity of resistance estimates'' section for an in-depth description of this plot.



Resistance estimates were also highly sensitive to behavioral state. Holding scale constant, proportional differences in resistance ranged from 0 to 245 (or 24,500 %) between behavioral states (Fig. 2.5). The interpretation of Fig. 2.5 is similar to Fig. 2.4, but the reference surface is either all points (Fig 2.5a, b) or M5 (Fig. 2.5c). Figure 2.5 indicates that, across all scales, estimates of resistance differed more between all points and movement points than between all points and resource use points, and in both cases the sensitivity was greatest at the upper quantiles. Also, estimates of resistance based on the most conservative definitions of the two behavioral states were more different from each other than either one was from all points. This pattern was generally consistent across all scales and most evident at the upper quantiles. Considering both scale and behavioral state, we found resistance estimates to be slightly more sensitive to scale than behavioral state.

Given the results from the regression analyses, it seemed intuitive that the multi-scale model would be more appropriate for the PSFs and, thus, for the resistance estimates. Therefore, we evaluated the sensitivity of resistance to the choice of multi-scale versus single-scale models for all points and the data subsets based on the most conservative definitions of movement (M5) and resource use (RU5). As expected, resistance estimates were sensitive to the choice of single- versus multi-scale modeling approaches regardless of data subset (Fig. 2.6). The greatest differences in estimates of resistance were between the multi-scale model and the finer single-scale models and at the upper quantiles. In addition, estimates of resistance for the movement points were more sensitive than either all points or the resource use points.

Lastly, we compared resistance estimates between the multi-scale context-independent model and the multi-scale context-dependent model for all points, M5 and RU5, and observed that resistance estimates were sensitive to whether context-dependent or - independent inference was used. As seen in the other resistance results, differences in resistance estimates between the two methods were greatest at the upper quantiles of the resistance distributions (online Appendix C).

Figure 2.5. Resistance differences among behavioral states. Log proportional differences in resistance at each scale between models using a) all points and Movement 5, b) all points and Resource Use 5, and c) Movement 5 and Resource Use 5. The y-axis represents a range of percentiles for the distribution of proportional differences. The legend represents the log proportional differences. Warmer colors indicate larger differences.

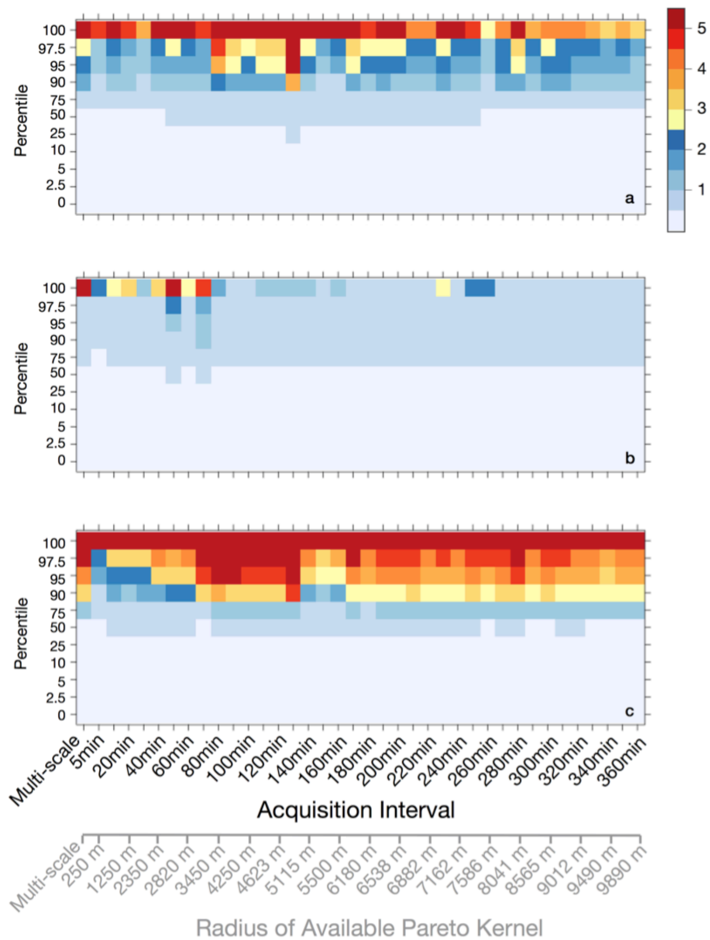
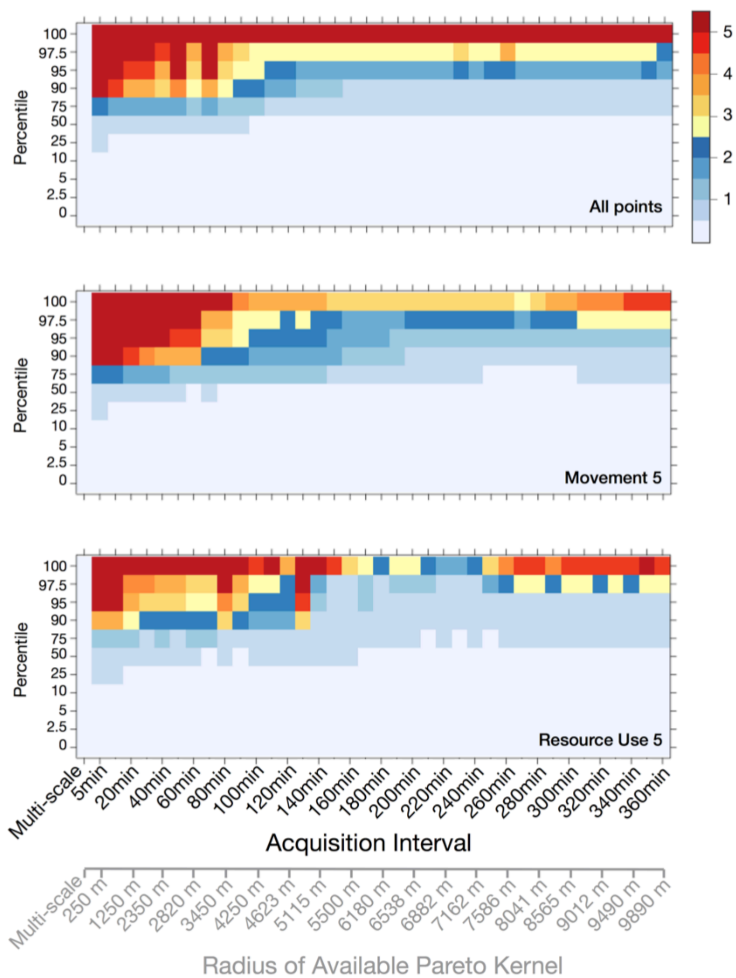


Figure 2.6. Resistance differences among model framework. Log proportional differences in resistance between the multi-scale model and each single scale model for models using all points, Movement 5 and Resource Use 5 points. The y-axis represents a range of percentiles for the distribution of proportional differences. The legend represents the log proportional differences. Warmer colors indicate larger differences. Please refer to ''Sensitivity of resistance estimates'' section for an in-depth description of this plot.



Discussion

Our findings highlight the utility of context-dependent modeling for PSFs and resistance estimation. With such modeling, both scale (spatial and temporal) and behavioral state (e.g. resource use versus movement) can be used to produce a more detailed, context- dependent estimation of resource selection and resistance to movement (Dalziel et al. 2008). It has long been recognized that species respond to their environment at different scales and that no single scale can capture the relationship between a species and its environment (reviewed in Levin 1992). Instead, it is more realistic to assume there are multiple characteristic scales along the continuum from feeding site to species range, and that adopting Wien's (1989) 'domains of scale' concept allows for more flexibility in modeling the true scales at which a species responds to its environment. By examining a range of scales, we found multiple characteristic scales across land cover types. For example, pumas in the study area responded more strongly to annual and perennial grassland, coastal oak woodland, coastal scrub and riparian areas at fine scales (250–530 m), to barren areas at mid scales (2 km), and to agricultural and urban areas at coarse scales (7.6–9.9 km). This suggests a mostly bi- modal scale of habitat selection; pumas appear to be selecting certain land cover types in their immediate perceptual range, while avoiding large agricultural and urban areas, reflecting what has been published in the literature on puma resource selection in coastal mountain habitat of California (Dickson and Beier 2002; Sweanor et al. 2008; Burdett et al. 2010; Wilmers et al. 2013).

In addition to identifying a single characteristic scale for each land cover type, we observed a dramatic effect of scale on the effect size (i.e., the magnitude of the regression coefficient and corresponding odds ratio) for most land cover types. For example, based on the simple regression model using data representing the most conservative definition of movement (M5), the odds ratio for annual grassland was roughly 10 when the scale was 10 min/530 m and decreased to roughly 2 when the scale was 360 min/9,890 m (Fig.

2.2a). Thus, the inferred preference for annual grassland during movement was dramatically greater at finer scales than coarser scales. This has implications for estimating resistance (and modeling connectivity), since this would translate into dramatically lower resistance to movement if the resistance surface were derived from finer-scale data than if it were derived from coarser-scale data. Similar sensitivities to scale were observed for most land cover types.

One of our more startling findings was a reversal from preference to avoidance of some land cover types as the scale varied. For example, based on a simple regression using data representing the most conservative definition of movement (M5), the odds ratio for agriculture was close to zero (indicating strong avoidance) at the finest scales, increased to roughly 1.3 (indicating a weak preference) at the 30-min/ 1,590-m scale, but then decreased to less than one (indicating avoidance) at scales beyond 60 min/ 2,820 m (Fig. 2.2e). These results have important implications for inferences regarding habitat selection (preferred vs. avoided), and, by extension, estimates of resistance.

Given the above findings, we suggest that context- dependent modeling should involve an exploration of multiple scales, echoing previous recommendations by Wheatley (2010) and Martin and Fahrig (2012). Though many GPS collar studies may not be intensive enough to acquire an empirical distribution of movement distances at the 5-min sampling intervals we had in our study, it should not prevent the examination of multiple scales. Whether the scales are empirically- derived or not, a continuum of scales should be used to approximate the true characteristic scale of response.

Though our definitions of behavioral state were relatively simplistic, since they relied solely on displacement distances, our findings provide evidence that resource use and movement behaviors are likely to be confounded in most PSF studies. For our study animals, this appeared to be less of an issue for resource use inference than movement inference since, when all points were used, results were often similar to those obtained via resource use points only. However, differences were readily apparent when evaluating movement behavior. This has ramifications when modeling resistance to movement since, if all points are used, it may be concluded that a species routinely avoids a habitat type, when in fact that type may be tolerated, or even preferred, during movement events. This may lead to artificially inflated or deflated resistance estimates for certain land cover types. By decoupling resource use from movement, we found that pumas had notably different responses to annual grassland, barren and chaparral land cover types depending on their behavioral state. For example, pumas had a negative response to annual grassland and barren areas during resource use behaviors, but had a positive relationship to these land cover types with our most conservative definitions of movement. Published RSF studies on pumas have shown only that they avoid these two habitat types (e.g., Dickson and Beier 2002). The opposite trend was observed for chaparral, where for our two most conservative definitions of resource use, chaparral was preferred, likely due to its use for day beds, but it was strongly avoided for our two most conservative definitions of movement. Chaparral habitat is notoriously difficult for humans to travel through and it is not unrealistic to assume the same difficulty would be faced by a puma. Our results based on resource use points may be biased toward day bed locations, especially for models based on RU5 points. Parsing out daybed locations, from resource use, from movement may reveal further important puma-habitat relationships. Though we removed GPS points that are prone to large spatial errors, small errors may have introduced some bias in our behavioral state definitions, particularly for RU5.

Regardless of behavioral state, we found that our study animals largely avoided agricultural and urban areas. However, these areas were avoided more strongly during resource use behavior than movement behavior. As in previous studies, we found that pumas preferred coastal oak woodland and riparian areas and avoided coastal scrub (Burdett et al. 2010; Wilmers et al. 2013), and the use of these three land cover types did not appear to be sensitive to the choice of behavioral state. In the same study area, Dickson et al. (2005) compared resource selection functions for pumas between static points and travel points and found that although there were no statistical differences in habitat selection between the two behavioral states, that chaparral and riparian vegetation types were used more often as resting locations than during travel. Our results reflect these behavioral differences across all scales for chaparral and across fine scales for riparian habitat. Though many of our findings regarding behavioral state are intuitive, they demonstrate that resource selection depends on the behavioral state of the study animal. Our findings point to a need for more attention to be paid to the behavioral context of study animals for future PSF and resistance analyses.

Failing to use the appropriate behavioral state for the question at hand may be due to the paucity of empirical definitions for different behavioral states. Knowing when an individual is using resources or moving, or simply moving slowly to acquire resources, may mostly be guesswork, so there is a need for methods that will aid in the identification of different behavioral states. Previous studies have modeled moving versus resting or resource use states based on movement distance and turning angles (Morales et al. 2004; Squires et al. 2013) or fractal dimensions (Fritz et al. 2003). State space models, as described in Patterson et al. 2008 have also been used to distinguish behavioral states. For pumas in particular, there have been studies that have attempted to identify states of predation and feeding (Ruth et al. 2010; Wilmers et al. 2013) and denning and communication behaviors (Wilmers et al. 2013) through cluster sampling. Though these studies are highly informative, more research on this topic is needed. The increased use of accelerometers on GPS collars may aid greatly in this effort (Brown et al. 2012).

We found resistance estimates were also sensitive to scale and behavioral state. This sensitivity was especially evident at the upper quantiles of the differences in resistance values, indicating that choice of scale and behavioral state has the largest effect on *20 % of the landscape. In addition, estimates of resistance were more sensitive when attempting to decouple movement points from all points than when decoupling resource use points from all points. These results have important implications for modeling connectivity, because in most cases the objective is to estimate resistance to movement rather than resource use.

Though our results are specific only to pumas in southern California, we believe the lessons learned herein can be applied to other species and study areas. Context-dependent models allow for habitat selection and resistance to be estimated at each cell across the study landscape based on its location, surrounding environment, and the behavioral state of the individual. Thus, the resistance assigned to a particular cover type will vary across the landscape depending on the local context. Most current methods for estimating resistance are context-independent and resistance estimates are static for each landscape feature (e.g. land cover type), regardless of its landscape context. Using context-dependent models to estimate a resistance surface is more computationally intensive than context-independent methods since they require a unique resistance value to be calculated for each grid cell in a landscape. Our results provide empirical evidence that context-dependent models generally outperform context-independent models indicating the extra computational time is warranted. For future habitat selection and resistance models based on PSFs, we recommend context-dependent models that explore a continuum of scales and consider using the appropriate behavioral state for the question at hand.

Step or path data may be more appropriate than point data for modeling resistance since it explicitly represents animal movement. Resource selection functions from these data would likely be sensitive to scale and behavioral state as well. However, further research is needed into this topic to determine the degree of sensitivity. A further concern with step and path data is the GPS collar acquisition interval. Step and path data incorporate information along the straight line between consecutive telemetry points. Short intervals may be adequate to represent resource use for an individual, but as intervals increase, the straight line between points may be too coarse to truthfully reflect resource use during movement. We are currently exploring these questions and the utility of step and path data for estimating resistance.

In closing, although our findings indicate that inferences regarding habitat selection and landscape resistance derived from PSFs are highly sensitive to both the choice of scale for assessing availability of habitat and the choice of data filters for decoupling behavioral states, the following challenges remain regarding the implications of these findings for modeling connectivity. First, while we can confirm that estimates of habitat selection and landscape resistance derived from PSFs vary among scales and behavioral states, it is unclear how best to determine which scale(s) and/or behavioral state is the most ecologically meaningful for purposes of modeling connectivity, since it will undoubtedly depend on the objective and method of modeling connectivity. However, it seems likely that decoupling movement from resource use will be important in most applications, since the former is typically the focus for connectivity modeling, and that adopting a multi-scale approach will lead to the most robust inferences. Second, our findings indicate that while most of the landscape exhibits some sensitivity to the choice of scale and behavior, only a relatively small portion of the landscape exhibits extreme sensitivity, and it is unknown how this will affect measured connectivity given the differences among methods such as least- cost path modeling to identify corridors between a set of well-defined nodes and a more synoptic modeling approach based on resistant kernels in which connectivity is evaluated from every location to every other location. Lastly, our results were based on a single categorical predictor (land cover) at a single resolution. Choice of thematic content and resolution and the spatial grain of the predictor variables will likely also have a large effect on PSF inference and resistance estimates.

Appendices

Appendix A. Acquisition intervals and associated radii of Pareto kernels used to define available habitat for PSFs

Acquisition interval (minutes)	Radius of Pareto kernel (meters)
5	250
10	530
20	1250
30	1590
40	2350
50	2470
60	2820
70	3345
80	3450
90	4040
100	4250
110	4475
120	4623
130	4725
140	5115
150	5236
160	5500
170	5676
180	6180
190	6214
200	6538
210	6678
220	6882
230	7029
240	7162
250	7345
260	7586
270	7843
280	8041
290	8229
300	8565
310	8873
320	9012
330	9228
340	9490
350	9677
360	9890

Appendix B. Conditional mixed-effects logistic regression models in R and example R code

We were aware of three main options for performing conditional mixed-effects logistic regression in R. Though no examples were found in the published literature, one option was to use the lme4 package (v. 0.999999-2, Bates et al. 2013). Within this package, the lmer (or glmer) function can be used, specified as described in Agresti (2002). This specification is equivalent to a conditional generalized linear model with a binomial probability distribution.

Lme4 model formulation is as follows:

lmer(Y ~ −1+diff100+…(-1+diff100+…|Individual), data=data, family='binomial')

where *Y* equals one for each data point, −1 specifies a no-intercept model, *diff100* equals the difference between the proportion of used and available for a land cover type at each data point, the expression in parentheses specifies a random slope effect with *Individual* as the unique identifier for each animal, *data* references the data set to use, and the *family* argument identifies the probability distribution, in this case, the binomial. Note, this model formulation with more recent versions of lme4 (v. 1.0-4 and above) will result in an error. Archived versions of lme4 can be accessed here: http://cran.r-project.org/src/contrib/Archive/lme4/.

A second option was to use the coxme function from the package by the same name (Therneau 2012). Coxme is based on the Cox proportional hazards model (Cox 1972) which models individual survival based on the amount of time that passes before an event occurs. Time to event is related to one or more covariates. By setting time equal to 1 for all data points, the Coxme function performs as a conditional mixed-effects regression (Therneau pers. comm.; Elliot et al. submitted).

Finally, there was the approach used by Craiu et al. (2011), which uses a two-step approach to execute a conditional mixed-effects logistic regression. The R package, called TwoStepCLogit (Craiu et al. 2013), implements a fixed effects logistic regression for each individual in the first step, which are then combined in the second step through a restricted maximum likelihood estimation procedure.

Due to interpretation difficulties with the two-step approach, we ran the models with lmer and coxme. For the simple regressions, and for multiple regressions including up to four variables, the results from the two approaches were comparable, if not identical. However, we were unable to successfully run coxme with greater than four variables, likely due to model complexity or idiosyncrasies of our data set. Therefore, we used lmer, as specified above, for all our conditional mixed-effects logistic regression models.

Program R code and description.

```
## This R software code allows for the estimation of used habitat via
## a fixed-width buffer around each telemetry point, the estimation of
## available habitat via a Pareto-weighted kernel around each telemetry
## point. These data are then used in a conditional mixed-effects
## logistic regression to model resource selection.

library(sp)
library(raster)
library(rgdal)
library(POT)
library(lme4)
library(gridio)
## This last library (gridio) was developed by Ethan Plunkett and is available upon  #
request from the UMASS Landscape Ecology Lab
# http://www.umass.edu/landeco/index.html). Please put 'gridio' in the
# subject line of these communications. Gridio requires running the 32-bit version #of R,
among other requirements. The code using Gridio functions is subject to
# change with updates to the gridio library. Gridio is only needed if a non-uniform
# kernel is desired (e.g. a Gaussian kernel or a Pareto kernel as used below).
#Otherwise, the raster library may be used to estimate a uniform kernel (in other
# words, to estimate the available habitat as proportions in fixed-width buffer
# around each used point).

##  SOURCE THE PARETO KERNEL FUNCTION OR RUN SCRIPT PROVIDED
BELOW
source('make.pareto.kernel.5.r')

## DEFINE THE DATA PROJECTION
dataproj<-"+proj=utm +zone=11 +ellps=GRS80 +datum=NAD83 +units=m +no_defs"

## READ IN DATA and prep data frame for input from 9 different habitat types. The
# following code assumes:
# 1) That all individuals are in a single data frame
# 2) That the data frame has an ID field with a unique identifier for each individual
# 3) That the time and distance between points has been calculated and added to
#       the data frame. In addition, an 'mpermin' field is also needed that represents,
#       for each point (except the first point for each individual) the meters moved per
#       minute from the previous point.
# 4) That for each point there is a LongitudeUTM and LatitudeUTM field with the
```

```
#	lat/long in UTM

used<-paste0('used', (seq(100,900,by=100)))
cats[ ,used]

avail<-paste0('avail', (seq(100,900,by=100)))
cats[ ,avail]

diff<-paste0('diff', (seq(100,900,by=100)))
cats[ ,diff]

## READ IN LAND COVER LAYER
# read in ascii land cover and convert to raster object

habitat<-readGDAL("habitat.asc")
habitat<-raster(habitat)
projection(habitat)<-dataproj

## CALCULATE USED HABITAT AROUND EACH POINT
# create spatial points object from cats

cats.xy<-cats[,c("LongitudeUTM","LatitudeUTM")]
cats.xy<-SpatialPoints(cats.xy,CRS(dataproj))

# extract used habitat a from a 30m buffer around each telemetry point
usedhabitat<-extract(habitat,cats.xy,buffer=30)

# place 0 or 1 in used column for appropriate habitat type
for (i in 1:length(usedhabitat)){
  cats$used100[i]<-length(which(usedhabitat[[i]]==100))/length(usedhabitat[[i]])
  cats$used200[i]<-length(which(usedhabitat[[i]]==200))/length(usedhabitat[[i]])
  cats$used300[i]<-length(which(usedhabitat[[i]]==300))/length(usedhabitat[[i]])
  cats$used400[i]<-length(which(usedhabitat[[i]]==400))/length(usedhabitat[[i]])
  cats$used500[i]<-length(which(usedhabitat[[i]]==500))/length(usedhabitat[[i]])
  cats$used600[i]<-length(which(usedhabitat[[i]]==600))/length(usedhabitat[[i]])
  cats$used700[i]<-length(which(usedhabitat[[i]]==700))/length(usedhabitat[[i]])
  cats$used800[i]<-length(which(usedhabitat[[i]]==800))/length(usedhabitat[[i]])
  cats$used900[i]<-length(which(usedhabitat[[i]]==900))/length(usedhabitat[[i]])
}
```

```
## CALCULATE AVAILABLE HABITAT FOR EACH POINT
# Calcualte shape and scale parameters for the Pareto kernel
move.rate.pareto<-fitgpd(cats$distance[-1],0.01) # the 0.01 sets the minimum
# allowable movement distance
pareto.scale.cats<-move.rate.pareto$param[[1]]
pareto.shape.cats<-move.rate.pareto$param[[2]]

# Initialize the gridio package and read in a separate grid for each habitat type. To   #
calculate the Pareto kernel, each habitat type must be binary (1s in grids where    # the
habitat is present and 0s elsewhere)
gridinit()
habitat100<-read.ascii.grid("habitat100.asc",as.matrix=F)
habitat200<-read.ascii.grid("habitat200.asc",as.matrix=F)
habitat300<-read.ascii.grid("habitat300.asc",as.matrix=F)
habitat400<-read.ascii.grid("habitat400.asc",as.matrix=F)
habitat500<-read.ascii.grid("habitat500.asc",as.matrix=F)
habitat600<-read.ascii.grid("habitat600.asc",as.matrix=F)
habitat700<-read.ascii.grid("habitat700.asc",as.matrix=F)
habitat800<-read.ascii.grid("habitat800.asc",as.matrix=F)
habitat900<-read.ascii.grid("habitat900.asc",as.matrix=F)

habitatlist<-list(habitat100, habitat200, habitat300, habitat400, habitat500, habitat600,
                  habitat700, habitat800, habitat900)

cellsize<-habitat100$cellsize

# Make and calculate pareto kernel
(max.r = qgpd(0.95,scale=pareto.scale.cats, shape=pareto.shape.cats)) # check to be sure
this is reasonable

pareto.kern<-make.pareto.kernel(scale=pareto.scale.cats, shape=pareto.shape.cats,
                                max.r = max.r, cellsize=cellsize)
for (j in 1:nrow(cats)){
  for (k in 1:length(habitatlist)){
    hab<-habitatlist[[k]] # note that this is a raster with 0s and 1s
    cats[j,25+k]<-calc.kernel(hab, pareto.kern, x=cats$LongitudeUTM[j],
y=cats$LatitudeUTM[j])
  }
}
```

```
## DIFFERENCE USED AND AVAILABLE
cats$diff100<-cats$used100-cats$avail100
cats$diff200<-cats$used200-cats$avail200
cats$diff300<-cats$used300-cats$avail300
cats$diff400<-cats$used400-cats$avail400
cats$diff500<-cats$used500-cats$avail500
cats$diff600<-cats$used600-cats$avail600
cats$diff700<-cats$used700-cats$avail700
cats$diff800<-cats$used800-cats$avail800
cats$diff900<-cats$used900-cats$avail900

## SIMPLE AND MULTIPLE MIXED-EFFECTS LOGISTIC REGRESSIONS
# Simple regressions (GLM was used to get starting values for mixed-effects model)

cats$status<-1
mod1<-glm(status~-1+diff100,data=cats,family='binomial')
mod2<-glm(status~-1+diff200,data=cats,family='binomial')
mod3<-glm(status~-1+diff300,data=cats,family='binomial')
mod4<-glm(status~-1+diff400,data=cats,family='binomial')
mod5<-glm(status~-1+diff500,data=cats,family='binomial')
mod6<-glm(status~-1+diff600,data=cats,family='binomial')
mod7<-glm(status~-1+diff700,data=cats,family='binomial')
mod8<-glm(status~-1+diff800,data=cats,family='binomial')
mod9<-glm(status~-1+diff900,data=cats,family='binomial')

mod1<-lmer(status~-1+diff100+(-
1+diff100|Lion),data=cats,family='binomial',start=mod1$coef)
mod2<-lmer(status~-1+diff200+(-
1+diff200|Lion),data=cats,family='binomial',start=mod2$coef)
mod3<-lmer(status~-1+diff300+(-
1+diff300|Lion),data=cats,family='binomial',start=mod3$coef)
mod4<-lmer(status~-1+diff400+(-
1+diff400|Lion),data=cats,family='binomial',start=mod4$coef)
mod5<-lmer(status~-1+diff500+(-
1+diff500|Lion),data=cats,family='binomial',start=mod5$coef)
mod6<-lmer(status~-1+diff600+(-
1+diff600|Lion),data=cats,family='binomial',start=mod6$coef)
mod7<-lmer(status~-1+diff700+(-
1+diff700|Lion),data=cats,family='binomial',start=mod7$coef)
```

```
mod8<-lmer(status~-1+diff800+(-
1+diff800|Lion),data=cats,family='binomial',start=mod8$coef)
mod9<-lmer(status~-1+diff900+(-
1+diff900|Lion),data=cats,family='binomial',start=mod9$coef)

# Multiple regression. One habitat type was left out
model.full<-lmer(status~-
1+diff100+diff200+diff300+diff400+diff500+diff700+diff800+diff900+
          (-1+diff100+diff200+diff300+diff400+diff500+diff700+diff800+
            diff900|Lion),data=cats,family='binomial')


## PREDICT PROBABILITY OF USE AT RANDOM POINTS (or a whole surface)
#  Random points (or a point for each grid cell across the desired area) must have
#  been generated prior to this step. In addition the 'used', 'available', and ‘difference’ #
between used and available must have been calculated for these points prior to
#   prediction.

rand.points<-read.csv('rand.points.csv')
mn = model.matrix(terms(model.full),rand.points)
newrand = mn %*% fixef(model.full)
pred<-plogis(newrand)

## CALCULATE RESISTANCE
resist<-1/pred


## MAKE PARETO KERNEL FUNCTION TO RUN PRIOR TO THE SCRIPT
ABOVE OR
#    TO SOURCE

make.pareto.kernel<-function(scale, shape, max.r = 100,
                      cellsize = 1) {
  require("POT")
  max.r.cells <- max.r/cellsize
  size = ceiling(max.r.cells) * 2 + 1
  center = ceiling(max.r.cells) + 1
  kernel <- new("matrix", 0, size, size)
  for (i in 1:size) for (j in 1:size) {
    r = sqrt((i - center)^2 + (j - center)^2) * cellsize
```

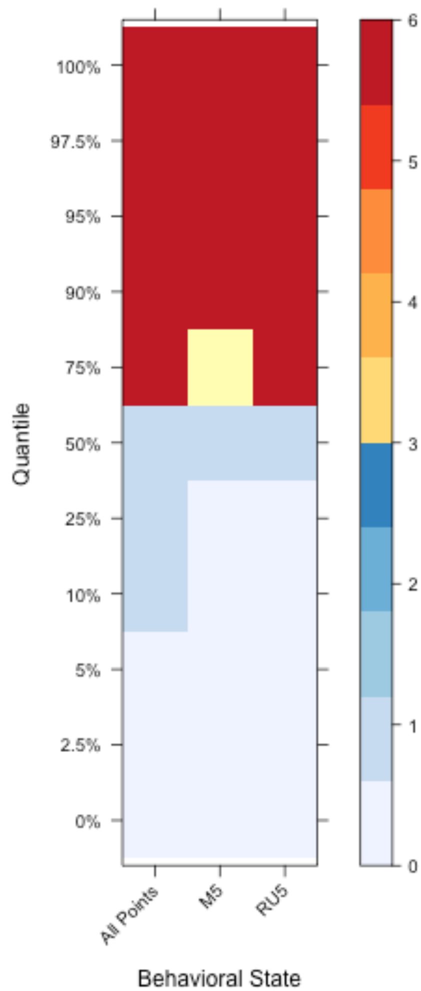
```
    if (r <= max.r)
      kernel[i, j] <- dgpd(r,scale=scale,shape=shape,log=FALSE)
  }

  kernel[center, center] <- 1/scale


  kernel <- kernel/sum(kernel)
  # This last part deletes the cells at the edge if they are all zero
  if (all(kernel[1, ] == 0, kernel[, 1] == 0,
        kernel[nrow(kernel),] == 0, kernel[, ncol(kernel)] == 0))
    kernel <- kernel[2:(nrow(kernel) - 1), 2:(ncol(kernel) - 1)]
  return(kernel)
}
```

Appendix C. Log proportional differences in resistance between the multi-scale context-dependent model and the multi-scale context independent model for models using all points, Movement 5 points, and Resource Use 5 points

The y-axis represents a range of percentiles for the distribution of proportional differences. The legend represents the log proportional differences. Warmer colors indicate larger differences.



References

Addicott JF, Aho JM, Antolin MF, Padilla DL, Richardson JS, Soluk DA (1987) Ecological neighborhoods: scaling environmental patterns. Oikos 49:340–346

Agresti A (2002) Categorical data analysis, 2nd edn. Wiley, Hoboken, p 419

Bates D, Maechler M, Bolker B (2013) Linear mixed-effects models using S4 classes. (R package). http://cran.r-project. org/web/packages/lme4/index.html. Accessed 20 April 2013

Boyce MS (2006) Scale for resource selection functions. Divers Distrib 12:269–276

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA (2002) Evaluating resource selection functions. Ecol Model 157:281–300

Brown DD, LaPoint S, Kays R, Heidrich W, Kummeth F, Wilelski M (2012) Accelerometer-informed GPS telemetry: reducing the trade-off between resolution and longevity. Wildl Soc Bull 36:139–146

Burdett CL, Crooks KR, Theobald DM, Wilson KR, Boydston EE, Lyren LM, Fisher RN, Vickers TW, Morrison SA, Boyce WM (2010) Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere 1: Article 4, p 1–21

California Department of Fish and Game (1988) A guide to wildlife habitats of California. In Mayer KE, Laudenslayer WF Jr (eds) State of California Resources Agency. Department of Fish and Game, Sacramento, p 166. http:// www.dfg.ca.gov/biogeodata/cwhr/wildlife_habitats.asp# Tree. Accessed 29 Jan 2013

Compton BW, Rhymer JM, McCollough M (2002) Habitat selection by wood turtles (Clemmys insculpta): an application of paired logistic regression. Ecology 83:833–843

Dalziel BD, Morales JM, Fryxell JM (2008) Fitting probability distributions to animal movement trajectories: using artificial neural networks to link distance, resources, and memory. Am Nat 172:248–258

DeCesare NJ, Hebblewhite M, Schmiegelow F, Hervieux D, McDermid GJ, Neufeld L, Bradley M, Whittington J, Smith KG, Morgantini LE, Wheatley M, Musiani M (2012) Transcending scale dependence in identifying habitat with resource selection functions. Ecol Appl 22:1068–1083

Dickson BG, Beier P (2002) Home-range and habitat selection by adult cougars in southern California. J Wildl Manag 66:1235–1245

Dickson BG, Jenness JS, Beier P (2005) Influence of vegetation, topography, and roads on cougar movement in southern California. J Wildl Manag 69:264–276

Dormann CF, McPherson JM, Araújo MB, Bivand R, Bollinger J, Carl G, Davies RG, Hirzel A, Jetz W, Kissling WD, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Shröder B, Schurr FM, Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609–628

Ferreras P (2001) Landscape structure and asymmetrical inter- patch connectivity in a metapopulation of the endangered Iberian lynx. Biol Conserv 100:125–136

Frair JL, Fieberg J, Hebblewhite M, Cagnacci F, DeCesare NJ, Pedrotti L (2010) Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Phil Trans R Soc B 365:2187–2200

Fritz H, Said S, Weimerskirch H (2003) Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. Proc R Soc Lond B 270:1143–1148

Hawkins BA, Diniz-Filho JAF, Bini LM, De Marco P, Blackburn TM (2007) Red herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology. Ecography 30:375–384

Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. Bioscience 54: 227–233

Johnson CJ, Nielsen SE, Merrill EH, McDonald TL, Boyce MS (2006) Resource selection functions based on use-availability data: theoretic motivation and evaluation methods. J Wildl Manag 70:347–357

Laundre JW, Hernandez L (2003) Winter hunting habitat of pumas Puma concolor in northwestern Utah and southern Idaho, USA. Wildl Biol 9:123–129

Laundre JW, Loxterman J(2007) Impact of edge habitat on summer home range size in female pumas. Am Midl Nat 157:221–229

Legendre P (1993) Spatial autocorrelation—trouble or new paradigm? Ecology 74:1659–1673

Levin SA (1992) The problem of pattern and scale in ecology: the Robert H MacArthur Award lecture. Ecology 73: 1943–1967

Lewis JS, Rachlow JL, Garton EO, Vierling LA (2007) Effects of habitat on GPS collar performance: using data screening to reduce location error. J Appl Ecol 44:663–671

Lin LI (1989) A concordance correlation coefficient to evaluate reproducibility. Biometrics 1:255–268

Manly BF, McDonald L, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies, 2nd edn. Kluwer Academic Publishers, Dordrecht

Martin AE, Fahrig L (2012) Measuring and selecting scales of effect for landscape predictors in species-habitat models. Ecol Appl 22:2277–2292

Meyer CB, Thuiller W (2006) Accuracy of resource selection functions across spatial scales. Divers Distrib 12:288–297 Morales JM, Haydon DT, Frair J, Holsinger KE, Fyxell JM (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. Ecology 85:2436–2445

Norththrup JM, Hooten MB, Anderson CR Jr, Wittemyer G (2013) Practical guidance on characterizing availability in resource selection functions under a use-availability design. Ecology 94:1456–1463

Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J (2008) State-space models of individual animal movement. Trends Ecol Evol 23:87–94

Pullinger MG, Johnson CJ (2010) Maintaining or restoring connectivity of modified landscapes: evaluating the least- cost path model with multiple sources of ecological information. Landscape Ecol 25:1547–1560

R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/. Accessed 15 May 2013

Rettie WJ, McLoughlin PD (1999) Overcoming radio telemetry bias is habitat-selection studies. Can J Zool 77:1175–1184 Ribatet M (2012) Generalized pareto distribution and peaks over threshold. (R package). http://cran.r-project.org/web/packages/POT/index.html. Accessed 15 Nov 2012

Ruth TK, Buotte PC, Quigley HB (2010) Comparing ground telemetry and global positioning system methods to determine cougar kill rates. J Wildl Manag 74:1122–1133

Squires JR, DeCesare NJ, Olson LE, Kolbe JA, Hebblewhite M, Parks SA (2013) Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. Biol Conserv 157:187–195

Sweanor LL, Logan KA, Bauer JW, Millsap B, Boyce WM (2008) Puma and human spatial and temporal use of a popular California state park. J Wildl Manag 72:1076–1084

USDA Forest Service (2007) CalVeg: FSSDE.Eveg- Tile47A_02_v2. Pacific Southwest Region Remote Sensing Lab, McClellan

Wheatley M (2010) Domains of scale in forest-landscape metrics: implications for species-habitat modeling. Acta Oecol 36:259–267

Wheatley M, Johnson C (2009) Factors limiting our understanding of ecological scale. Ecol Complex 6:150–159

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385–397

Wilmers CC, Wang Y, Nickel B, Houghtaling P, Shakeri Y, Allen ML, Kermish-Wells J, Yovovich V, Williams T (2013) Scale dependent behavioral responses to human development by a large predator, the puma. PLoS ONE 8:e60590. doi:10.1371/journal.pone.0060590

Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landscape Ecol 27:777–797

CHAPTER 3

USING STEP AND PATH SELECTION FUNCTIONS FOR ESTIMATING RESISTANCE TO MOVEMENT: PUMAS AS A CASE STUDY

Introduction

Given increasing human development and the frag- mentation of natural habitats, wildlife populations are becoming ever more isolated. Wildlife corridors can mitigate this isolation by maintaining the exchange of individuals and their genes between populations (Crooks and Sanjayan 2006). Modeling corridors often requires resistance-to-movement surfaces where 'resistance' represents the opposition an organism may encounter as it moves through a landscape, either in terms of movement ability, survival or both.

Though resistance is commonly estimated with static detection points, the use of observed movement steps or paths is considered more appropriate as the these data explicitly represent passage through the landscape (Richard and Armstrong 2010; Zeller et al. 2012). Movement may be defined as the straight-line steps between consecutive points (Fortin et al. 2005), or the entire pathway of an individual (Cushman and Lewis 2010; Elliot et al. 2014). These are referred to as step selection functions (SSFs) and path selection functions (PathSFs), respectively. Both methods are derived from classic resource selection functions (RSFs) that employ a 'used' versus 'available' design to estimate species–habitat relationships (Manly et al. 2002), and are analogous to modeling selection at Johnson's third order of habitat selection (selection of habitat patches within the home range; Johnson 1980). In SSFs, the 'used' data are the landscape variables measured along each step between consecutive points. ‘Available’ data are obtained by generating random steps (drawn from the empirical distribution of step lengths and turning angles) from the start point of each used step (Fig. 3.1a). Landscape variables are then measured along these random steps. In PathSFs, the entire path is used to calculate the ‘used’ data and that same path is randomly shifted and rotated from the used path to generate ‘available’ paths (Fig. 3.1b). SSFs and PathSFs are modeled in a conditional (a.k.a. case- controlled) logistic regression framework where each used step or path is paired with those that are randomly generated (Agresti 2002; Fortin et al. 2005). This framework allows for a realistic comparison between used and available (Compton et al. 2002; Fortin et al. 2005) and allows for context-dependent modeling (Zeller et al. 2014). The regression models are then used to predict the relative probability of movement across a study area at each grid cell, the inverse of which is used as the resistance surface. It is important to note that, though these predictions are made using the regression coefficients from the conditional logistic regression models, they are applied to the study area in an unpaired framework (more on this below).

For SSFs, the acquisition interval of the GPS collar determines the temporal scale of analysis, which, in turn, is inextricably tied to the spatial scale of analysis (Thurfjell et al. 2014). For example, at a 1-h acquisition interval, the distribution of random steps will represent movements only ranging as far as the steps achieved over that hour-long period. The sampling of the landscape at this 1-h interval becomes the spatial scale of the analysis (ignoring grain size), regardless of whether this matches the strongest scale, or ‘characteristic scale’ (Holland et al. 2004) of response of the target species. The current SSF framework only allows for the examination of a single scale and thereby runs the risk of missing the true scale, or scales, of response. In turn, this may lead to inaccurate estimates of selection and resistance (Wheatley and Johnson 2009; Norththrup et al. 2013). This issue also affects most PathSFs, in that only a single coarse scale is examined. However, Elliot et al. (2014) shifted the random paths at varying distances from the used path to explore various scales and construct multi-scale models. This is an improvement to the single-scale PathSF, but it does not allow for examination of scales that are smaller than the radius of the path, which can be quite large, and precludes investigating finer spatial scales to which an individual may be responding. Given the importance of multi-scale modeling for habitat selection and resistance, SSFs and PathSFs would be much improved if various scales, from fine to coarse, could be examined and included in the models.

Using SSFs and PathSFs to estimate resistance first involves predicting the relative probability of movement across the study area. In current SSF and PathSF applications, relative probability of movement has been predicted across a surface through the following formula (following Manly et al. 2002):

$$\hat{w}(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \ldots + \beta_p x_p) \tag{1}$$

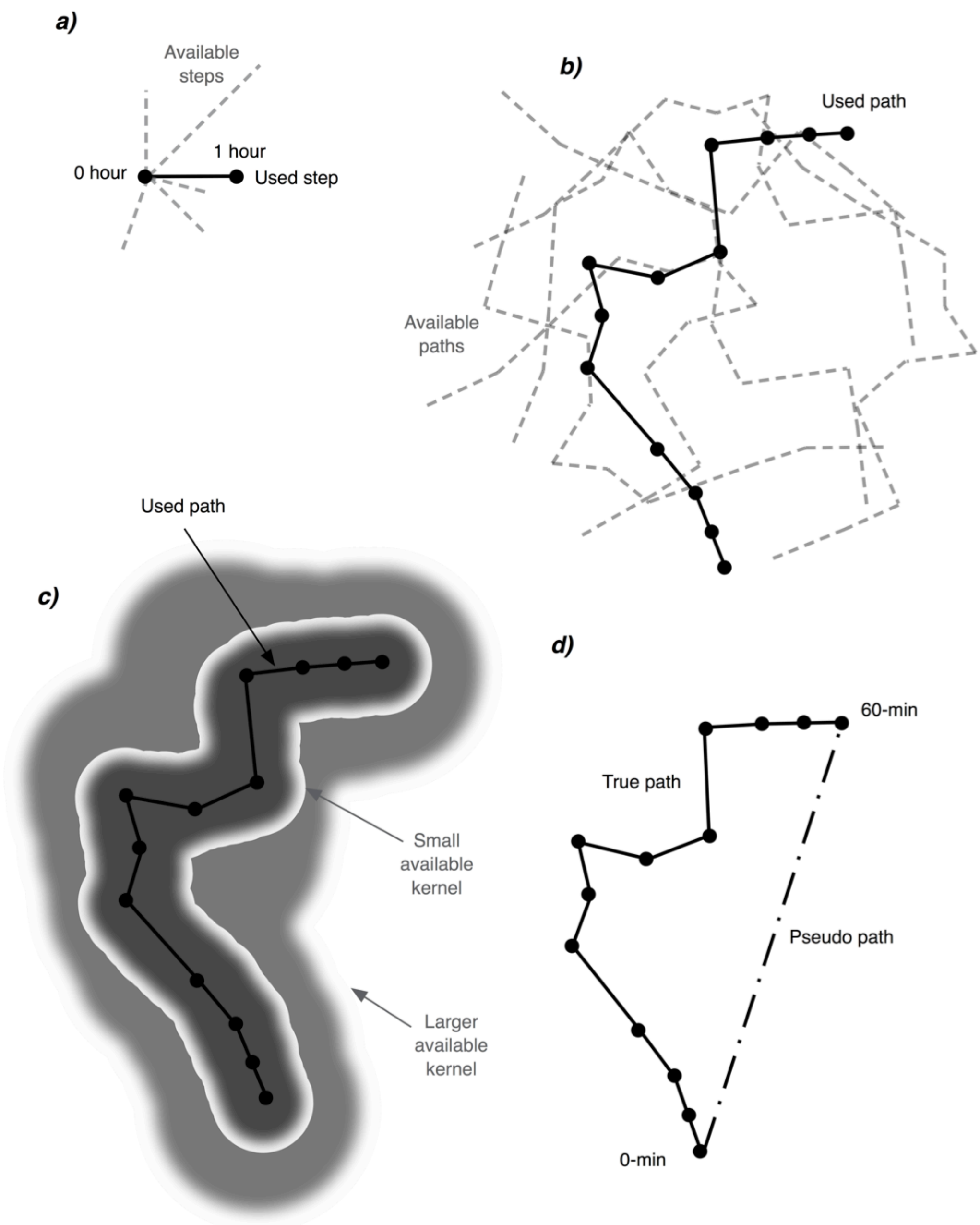
Here, the regression coefficients are those derived from the conditional logistic regression models, which are multiplied by the predictor variables (x) as measured at each pixel in the landscape. Though the regression coefficients are estimated from assessing what is along each used step or path and what is available around each step or path, the predictions are made in the absence of available data—in an unpaired framework. This results in each pixel of a given landscape feature (e.g., forest) having the same relative predicted probability of movement, regardless of its surroundings. By incorporating the available data around each pixel in the landscape, probability of movement can be estimated in a truly paired context- dependent framework. This allows for a unique probability of movement to be estimated for each pixel in the landscape, where the value of a pixel reflects the attributes of that pixel as well as the attributes surrounding that pixel (e.g., a pixel of forest surrounded by an urban area would likely have a much different relative probability value than a pixel of forest surrounded by forest). To determine the utility of a paired framework for predicting movement and estimating resistance for wildlife, this approach should be explored and compared to the unpaired framework.

SSFs and PathSFs have become more accessible due to the increased use of GPS telemetry collars and their ability to acquire relatively accurate, consistent, and frequent locations. However, GPS collar acquisition intervals can vary widely, from less than 5 min to 6 h and beyond. Fortin et al. (2005) and Coulon et al. (2008) state that SSFs do not assume an individual follows the straight line between points, but rather test whether selection of steps is related to what lies between these points. Still, predictor variables are most-often measured on the straight line, or a buffered area around the line (Thurfjell et al. 2014). Therefore, SSFs and PathSFs may be subject to bias when the acquisition interval is too long to accurately reflect movement for a species. Though no studies to date have examined the potential bias introduced by acquisition intervals for SSFs and PathSFs, studies focused on movement distance and home range size have found that as sampling intervals increase (1) paths of individuals become less tortuous and exponentially shorter in length (Mills et al. 2006), (2) movement rates decrease (Joly

2005), (3) minimum convex polygon home range estimates become smaller (Mills et al. 2006; Brown et al. 2012), and (4) areas utilized by an individual may be underrepresented, while areas avoided by an individual may be overrepresented (Brown et al. 2012). This final finding is of particular concern for inference from SSFs and PathSFs, and further research is needed to determine how sensitive movement models, resistance surfaces and corridors are to GPS collar acquisition interval.

Our objective is to explore these potential issues of scale, prediction framework, and GPS collar acquisition interval when using SSF and PathSFs for modeling movement and resistance. We use GPS collar data from pumas (Puma concolor) in southern California acquired at 5-min intervals, to (1) present a novel SSF/PathSF method that can examine movement at multiple scales, (2) use this new method to identify the characteristic scale(s) of response of pumas and create both single and multi-scale models, (3) predict probability of movement and resistance across our study area in a both a paired and an unpaired framework, and (4) investigate whether acquisition intervals greater than 5 min introduce bias in habitat selection and resistance results. We also determine the sensitivity of resistance surfaces to scale, prediction framework, and acquisition interval. Finally, as an illustration of how differences in scale, prediction framework, and acquisition interval may affect conservation decisions, we use circuit theory to model connectivity across a subsection of our study area for several scales of analysis including multi-scale models.

Figure 3.1. Step and path selection functions. Conceptual illustration of (a) used and available steps for a traditional step selection function, (b) used and available paths for a traditional path selection function, (c) our proposed multi-scale method for step and path selection functions, using a kernel to estimate different scales of available habitat and (d) the true 5-min path used by an individual over an hour-long period and the pseudopath over that same time period. The pseudopath represents the path that one would obtain with a 60-min GPS collar fix interval.



Methods

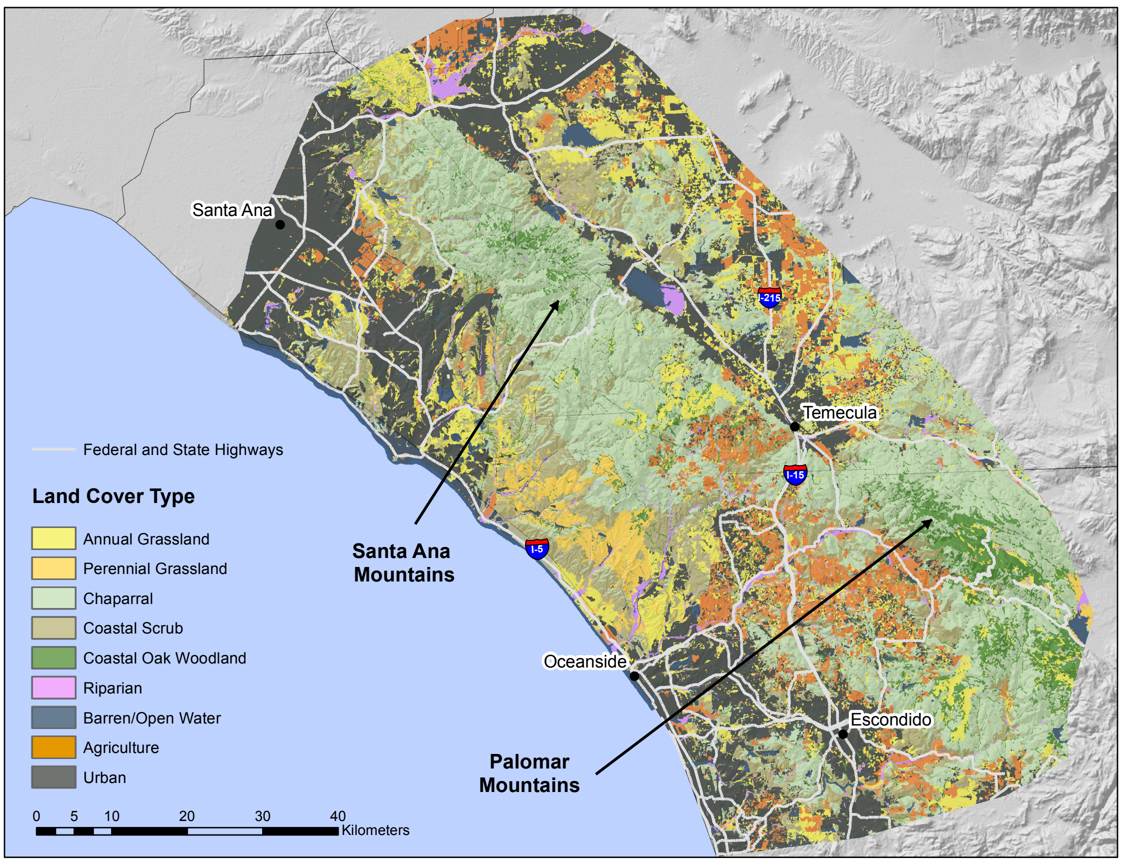
Study area and data collection

The study area, as previously described in Zeller et al. (2014), was located in the Santa Ana Mountains of southern California (Fig. 3.2). Between October 2011 and March 2014, ten pumas (six female and four male) were fitted with Lotek 4400 S GPS collars programmed to acquire locational fixes every 5 min (Lotek Wireless, Inc., Canada). Collar duration ranged from 9 to 71 days (median = 29). Long-term positional accuracy of the GPS collars from manufacturer tests is 5–10 m, though accuracy may decrease with certain vegetation types and topographical conditions (Chang personal communication). Two-dimensional fixes with a positional dilution of precision [5 were removed to avoid the use of data that may have large spatial errors, as recommended by Lewis et al. (2007). The final data set consisted of 75,716 fixes across the 10 individuals (range = 1650–18,464; median = 7147). Due to the low number of individuals, sexes were pooled in the analyses.

We used land cover types from the California wildlife–habitat relationship database as independent variables in our RSFs. These categorical habitat data were obtained from the CalVeg geospatial data set (USDA Forest Service 2007) in vector format at the 1:24,000 scale, which we rasterized at a 30 m resolution. Though there were 25 mapped land cover types present in the study area, many types had very low occurrence (<1 %), therefore, we aggregated these 25 types into nine classes based on descriptions from the California Department of Fish and Wildlife (1988). The aggregated land cover classes and their percentages of the study area were as follows: chaparral (45 %), urban (19 %), coastal scrub (14 %), annual grassland (6 %), coastal oak woodlands (5

%), agriculture (5 %), riparian areas (3 %), perennial grassland (2 %), and naturally barren or open areas (1 %) (Fig.3.2). There has been little vegetation change in the study area between the time the CalVeg data set was produced and the time the puma data was collected. Though the Santiago Fire affected portions of the western flank of the Santa Ana Mountains, the vegetation types remained the same pre- and post-fire.

Figure 3.2. Study area in southern California showing land cover types used in the analysis.



Multi-scale SSF and PathSF method

SSFs and PathSFs traditionally use random steps or paths for estimating ‘available’, thus constraining the available area to the longest step/path lengths observed.

When we free ourselves from using random steps and paths, we have more flexibility to explore multiple scales. Specifically, if we use a density kernel around the step or path we obtain a census of the proportion of available land cover types and avoid issues of selecting a certain number of steps or paths from the random sample (Norththrup et al. 2013). The density kernel may be weighted by an appropriate distribution; in our case, we used an empirically- derived Pareto distribution as our kernel (as described in Zeller et al. 2014), representing different distances traveled over specific time intervals (e.g., 5, 60 min, etc.). At the 5-min interval, the radius of the Pareto kernel was small resulting in a small available area sampled around each step or path (e.g., Fig. 3.1c). The radii of the Pareto kernel increased with increasing time intervals (e.g., Fig. 3.1c), thereby allowing us to sample different scales around each step or path. A more detailed description of our method is provided below.

Used steps

All data analyses were performed using R software (R Core Team 2013). We first calculated the distance of each step between consecutive points and identified all steps that measured 200 m or more; the 200 m distance threshold was to ensure that steps represented actual 'movement' through the landscape rather than local 'resource use' (see Zeller et al. 2014). We buffered each movement step by a 30 m fixed-width buffer to account for GPS error (Rettie and McLoughlin 1999) and incorporate the immediate environment around each step. We calculated our 'used' data for the SSFs as the proportion of land cover types along each buffered step.

Used paths

Because we only had 10 individuals, using the entire path for our path analysis would have resulted in an insufficiently small sample size. Therefore, we subset the entire path of each individual into 24-h paths, which resulted in a more reasonable sample size of n = 315. As with the steps, we buffered the paths by a 30 m fixed- width buffer and calculated the proportion of land cover types within this buffer. This was the 'used' data for our PathSFs. Because inferences about habitat use and resistance might be affected by the time of day at which a 24-h path begins, we ran 12 subsets; the first subset started at midnight, the next subset started at 2 a.m., etc. We ran a PathSF model (more on this below) for each subset separately and we averaged the regression coefficients across all 12 subsets to obtain a final model.

Available areas/scales of analysis

As described above and in Zeller et al. (2014), we estimated 'available' using a Pareto-weighted kernel around each step or path. To model multiple scales, we increased the time interval over which the Pareto distribution parameters were estimated and calculated available areas for each interval/scale separately. We estimated the parameters of the Pareto distribution as follows:

(1) We selected 19 different time intervals over which to empirically estimate the Pareto kernel. These intervals consisted of the 5-min time interval, the 20-min interval, and then every 20 up to 360 min (6 h).

(2) We subset the 5-min data at these different time periods and calculated the displacement distance between each point. This provided us with the distribution of displacement distances for each time period.

(3) We then fit a generalized Pareto function to the distribution of displacement distances for each time interval using the gpd.fit function in the gPdtest package (Estrada and Alva 2011). We set the radius of the available area at the 97.5 percentile of the Pareto distribution, or the maximum observed displacement distance, whichever was smaller.

Hereafter, we refer to the radius of each Pareto kernel as the scale of analysis. Our scale reflects the size or extent of the ecological neighborhood (as defined by the kernel) around the step/path, not the spatial grain of the data, which we held constant at 30 m for all analyses. These scales ranged from 532 to 7390 m (Appendix A). To obtain a kernel around a step or path for a scale, we distributed points uniformly along each step or path at a distance determined by the radii of the Pareto kernel for that scale. We then placed the Pareto kernel over each point and calculated the proportion of land cover types weighted by the Pareto kernel. The available data for each step or path at each scale was obtained by calculating the mean proportion of land cover types across all the Pareto kernels distributed along its length. Note, because the available areas are weighted by the Pareto distribution, they more heavily weight areas closer to the used step or path and the scales should not be thought of as a uniform buffer around each used step or path.

Statistical analysis

We provide a flow chart summarizing our statistical analyses procedure in Appendix B.

For the step and path data we paired each used step or path with the available area for that same step or path at a scale and ran conditional logistic regression models. We specified the conditional logistic regression models as described in Zeller et al. (2014), using the differences in the proportion of each land cover type between each used step or path and its corresponding available area as the predictor variables. In this specification, the response variable is always 1 and there is no model intercept (Agresti 2002). Because we are using the proportion of each land cover type as predictor variables, we do not have a single land cover variable with the categories coded as dummy variables, but instead have a single predictor variable for each of our nine land cover types.

We ran simple conditional logistic regression models at each scale for each land cover type separately. We also ran multiple conditional logistic regression models at each scale using the land cover type with the weakest effect in the simple regressions as our reference class. Correlation among our predictor variables was relatively low (maximum Pearson correlation coefficient = -0.48), allowing us to retain all predictor variables in our models. We attempted to run conditional logistic mixed effects logistic regression models, using individual puma as the random effect, but our models often failed to converge. Therefore, we did not use the mixed effects framework and simply used the glm function in R for our modeling.

To develop the conditional multi-scale logistic regression models, we identified the characteristic scale of response from the simple conditional logistic regression models as the scale with the largest absolute regression coefficient. We then used the characteristic scale for each land cover type to construct a multi- scale, multiple logistic regression model for our step and path data.

Model performance

For each of our single- and multi-scale multiple logistic regression models, we performed a 10-fold cross validation using the methods recommended by Johnson et al. (2006) and evaluated the predictive performance of the models using Lin's (1989) concordance correlation coefficient (CCC) as applied in Zeller et al. (2014). Because the SSFs and PathSFs had different sample sizes, we could not use an information criterion approach for model selection across all step and path models. Within the SSFs and PathSFs, however, we did have the same sample sizes and therefore calculated Akaike's information criterion (AIC; Burnham and Anderson 2002) for SSFs and PathSFs separately.

Predicting probability of movement and resistance

As noted in the ‘‘Introduction’’ section, previous SSFs and PathSFs that have used the have predicted the relative probability of movement values across an area of interest in an unpaired framework, using only the attributes at each pixel. This method does not consider the attributes of surrounding pixels. In order to predict probability of movement in the fully paired framework that was used to develop the models, we first calculated the proportion of land cover types in a 30-m fixed-width buffer at each pixel in our study area (which is akin to the ‘used’ data in the regression models). For a scale of interest, we then placed a Pareto kernel around each pixel and calculated the proportion of land cover types within this kernel (which is akin to the ‘available’ data in the regression models). We calculated the differences in the proportion of land cover types between each focal pixel and the surrounding kernel and used these as our predictor variables. Incorporating the information around each pixel allowed us to predict a unique probability of movement for every pixel across the study area using all the information that went into building the model. We also predicted the relative probability of movement in the traditional unpaired framework for comparison.

For our paired and unpaired probability of movement surfaces, we calculated resistance by taking the inverse of the probability of movement values. We did not rescale or truncate these values because we did not want to introduce any unnecessary subjectivity into the resistance surfaces. We chose to estimate resistance instead of conductance (which would simply be the raw predicted surface) because resistance surfaces are one of the most popular ways to estimate connectivity and model corridors (Zeller et al. 2012). We estimated paired and unpaired resistance surfaces at the 532, 2618, 3505, 4296, 5275, and 7390 m scales as well as for the multi-scale models for steps and paths.

Acquisition interval bias/pseudo paths

To investigate possible bias introduced by longer acquisition intervals, we subset the 5-min data so that it only contained point locations every 60 min. These data represent the steps/paths one would obtain with an hourly GPS collar acquisition interval. We refer to the 5-min data as the true steps/paths and the 60-min data as our pseudo steps/paths (Fig. 3.1d). We calculated used and available for the pseudo steps and paths, ran simple and multiple conditional logistic regressions for SSFs and PathSFs, and predicted resistance in the paired framework as described above. We considered the paths from the 5-min data as our truth and assessed bias by calculating the mean absolute difference between the regression coefficients obtained from the models using the 5-min paths and those using the pseudo paths for each land cover type at each scale as well as for the multi-scale model. We then averaged the differences across cover types at each scale to measure overall bias.

Sensitivity of predicted resistance surfaces and corridor locations to scale, prediction framework, and acquisition interval

We visually assessed the resistance surfaces from our different scales, prediction frameworks, and acquisition intervals and noted disparities. We also compared the distribution of resistance values between resistance surfaces.

To get a cursory sense of how differences in resistance surfaces might translate to differences in corridors, we performed a connectivity analysis in the Temecula corridor region within our study area. This area has received much attention as the last viable link between the Santa Ana puma population and populations in the Peninsular Range of southern California (Ernest et al. 2014; Vickers et al. 2015). Although there is no standard way to evaluate congruence among predicted corridors, recent conservation attention has been paid to identifying locations for road crossing structures across interstate 15 (I-15), the major barrier in this linkage. Therefore, we chose locations where modeled corridors cross I-15 as a simple but meaningful way to compare model predictions (Cushman et al. 2014). We used CircuitScape (McRae et al. 2013) to create current density maps (McRae et al. 2008) between protected areas on either side of I-15. We then identified the top 20 pixels along I-15 with the most current flow that might be considered as locations for road crossing structures. In this context, 'current flow' represents the number of random walkers that would move through a pixel as they passed between protected areas. We noted the location of each of these pixels for each resistance model as well as differences in these locations between resistance models. We recognize there are myriad methods for modeling connectivity across resistance surfaces (Cushman et al. 2013), but as this was not the focus of our paper, we only selected the one method as an illustrative example of how differences in resistance surfaces may translate into differences in connectivity.

Results

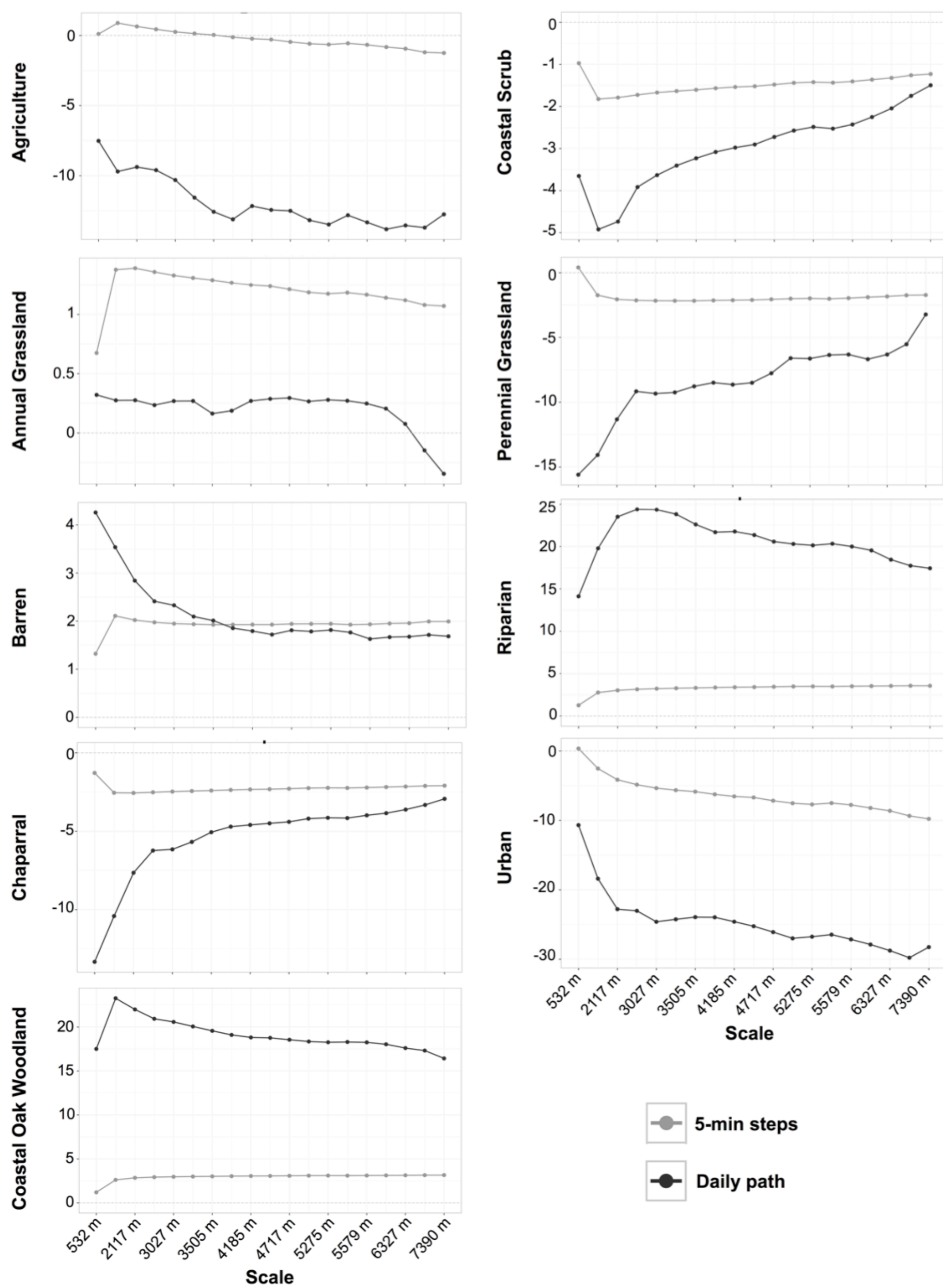
Characteristic scales of response and step versus path selection functions

The regression coefficients were sensitive to scale. Although puma response to most land cover types was consistently positive or negative across scales, annual grassland and agriculture resulted in a change of sign with scale (Fig. 3.3).

For both SSFs and PathSFs, pumas responded most strongly to annual grassland, barren, chaparral, coastal scrub, and perennial grassland at finer scales and to agriculture and urban at coarser scales (Fig. 3.3). Despite these general similarities, the exact characteristic scale between SSFs and PathSFs differed for every cover type except chaparral (Fig. 3.3). The land cover types that exhibited the greatest difference in characteristic scales between SSFs and PathSFs were coastal oak woodland and riparian (Fig. 3.3).

The simple conditional logistic regression models from the SSF and PathSFs resulted in different regression coefficients (Fig. 3.3). These differences could be pronounced, as evidenced by riparian and urban land cover types. With the exception of annual grassland, the PathSFs generally resulted in much larger (positive or negative) regression coefficients than the SSFs.

Figure 3.3 Simple regression results. Regression coefficients for land cover types used in the simple conditional logistic regression SSF and PathSF models across the 19 scales of analysis.



Model performance

Both SSFs and PathSFs performed well across scales, with the exception of the PathSF model for the 532 m scale (Fig. 3.4). Model performance for both SSFs and PathSFs tended to increase as scale increased and with the exception of the finest scale, the PathSFs outperformed the SSFs (Fig. 3.4). The best model performance for the SSFs was achieved at the 6555 m scale (0.976) and for the PathSFs at the 7390 m scale (0.992). Interestingly, the multi-scale models did not have the highest CCC value, though for both SSFs and PathSFs they were similar to the best model (0.943 and 0.982, respectively). We also calculated AIC values for the models. Because the SSFs and PathSFs had different sample sizes, we could not compare AIC values between the two methods, but within SSFs and PathSFs, AIC values decreased with increasing scale (Appendix C). The multi-scale model had the lowest AIC value for the SSFs and the 6555 m scale had the lowest AIC value for the PathSFs.

Acquisition interval bias

Our 60-min pseudo data (representing GPS data collected at an hour-long acquisition interval) resulted in biased regression coefficients compared with our 5-min data (Fig. 3.5; Appendix D). As expected, biases were higher for the PathSFs than the SSFs (Fig. 3.5). Appendix D provides the regression coefficients for each land cover type for the SSFs using the true step data and using the 60-min pseudo steps. In general, for land cover types that were preferred, the pseudo steps crossed these cover types less frequently, resulting in smaller regression coefficients and sometimes resulting in a change in sign from preference to avoidance. In fact, for the annual grassland and barren cover types, the true steps show a consistent preference for these types across scales while the pseudo steps show a consistent avoidance across scales. The opposite effect was generally seen for land cover types that were avoided. For these, the pseudo-steps crossed more of these cover types than were actually used, resulting in reduced avoidance, and in the case of coastal scrub, preference.

Figure 3.4. Concordance Correlation Coefficient (CCC). Predictive performance, as measured by CCC, of multiple conditional logistic regression SSF and PathSF models at all scales and for the multi- scale model.

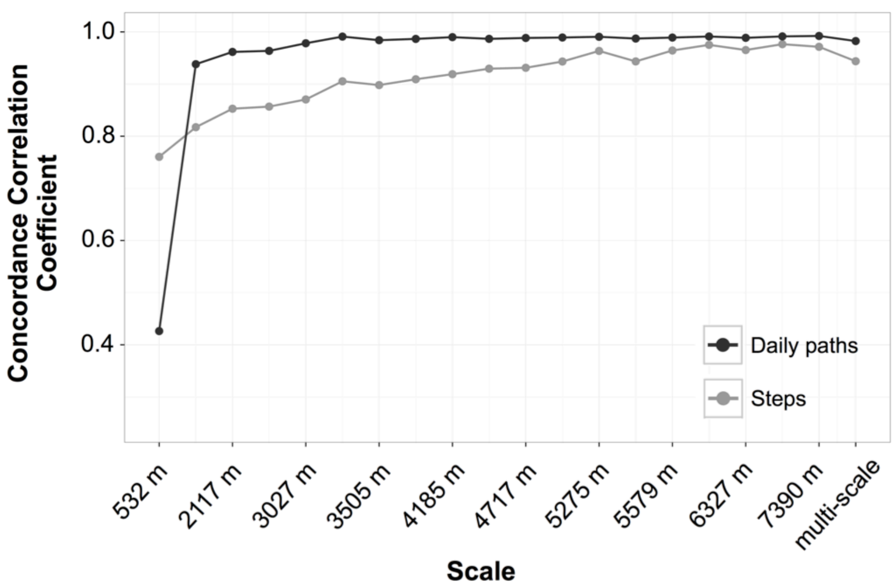
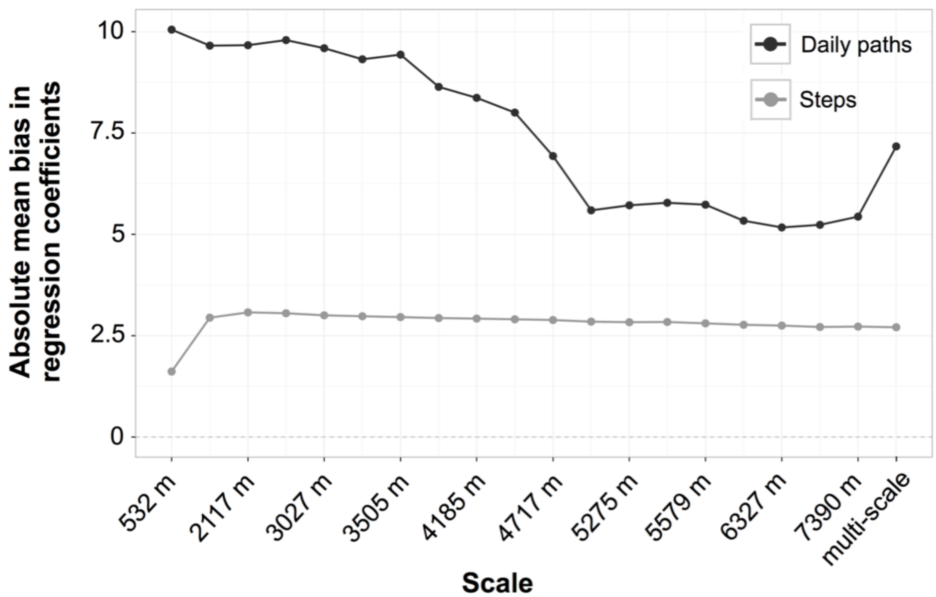


Figure 3.5. Bias in regression coefficients at a 60-min acquisition interval. Bias was calculated by taking the mean absolute difference between the regression coefficients obtained from the multiple SSF and PathSF models using the true 5-min data and those using the 60-min pseudo data for each land cover type at each scale and for the multi-scale models. We then averaged the differences across cover types at each scale.



Sensitivity of predicted resistance surfaces and corridors to scale, prediction framework, and acquisition interval

There were notable differences in the ranges of resistance values between SSFs and PathSFs, among scales, and among prediction frameworks (e.g., paired and unpaired; Fig. 3.6; Appendices E, F). In keeping with the regression coefficient results above, resistance values derived from PathSFs tended to be higher than those derived from SSFs (Fig. 3.6; Appendices E, F). Also, resistance values at finer scales were generally smaller than resistance values at coarser scales. Increasing resistance with scale can be explained by the generally increasing strength of avoidance with scale. As avoidance of a land cover type increased, the relative predicted probability of movement decreased. Taking the inverse of these small values to predict resistance resulted in high resistance values. Note that increasing selection with scale does not result in dramatic changes to the resistance surface since, using the method described above, the lowest value possible will always be 1.

The maximum resistance values from predicting resistance in the paired framework tended to be larger than those obtained from predicting resistance in the unpaired framework (Appendix E). The other notable difference between the frameworks was that, since the unpaired framework was not context-dependent, it resulted in the same resistance value for a cover type regardless of its context. Because urban, comprising 19 % of the study area, was the most avoided land cover type and resulted in the highest resistance values, the 91st–100th quantiles for the unpaired surfaces were the same (Appendix E). We can visualize the consistency among cover types in the first columns of Fig. 3.6 (SSF results) and Appendix F (PathSF results). The resistance surfaces from the paired frameworks are context dependent and rely not only on what is at each pixel, but what is surrounding each pixel. For example, when a puma is in a pixel that is comprised of coastal oak woodland, a land cover type they prefer, moving from coastal oak woodland to less optimal habitat will result in an increased resistance. This is seen in the second columns of Fig. 3.6 and Appendix F in the southeastern part of the study area where coastal oak woodland patches have the lowest resistance but are surrounded by a band of high resistance. Another example is in urban areas. Moving into an urban area has a high resistance, however, once inside an urban area, there is no difference between the proportion of urban in the used and available and thus, the resistance is not as high. In general, the resistance surfaces derived from the paired models are characterized by much greater spatial heterogeneity in resistance and a much greater range of resistance values (Fig. 3.6; Appendix F).

From the CircuitScape current density surfaces, we identified the top 20 pixels along I-15 that had the most current, or greatest flow of individuals. These locations are shown, along with the current surfaces in Fig. 3.7 (SSFs) and Appendix G (PathSFs). Locations varied among SSFs and PathSFs and among scales. Locations were more similar at the same scale across methods (SSFs vs. PathSFs) and frameworks (unpaired vs. paired) than within the same method or framework across scales, indicating scale is a major factor in connectivity differences.

Using the 60-min pseudo paths in the SSFs and PathSFs resulted in sometimes markedly different resistance surfaces and biased the road crossing locations (last column, Figs. 3.6, 3.7; Appendices F, G). For example, resistance surfaces tended to be biased high, particularly for SSFs. In addition, for the SSF models, crossing locations for the biased SSFs (based on the pseudo steps) tended to miss potential crossing locations in the middle section of I-15 that were picked up with the models based on true paths. These biased SSFs also identified crossing locations that were not present in any of the models that used the true paths (Fig. 3.7).

Figure 3.6. Resistance surfaces from the SSF models. The first column contains the resistance surfaces predicted in the unpaired framework, the second column contains resistance surfaces predicted in the paired framework, and the last column contains resistance surfaces predicted with pseudo steps in the paired framework. The first row contains the resistance surfaces from the smallest scale model, the middle row the mid-scale model, and the last row the multi-scale model. Resistance surfaces for the PathSFs are provided in Appendix E.

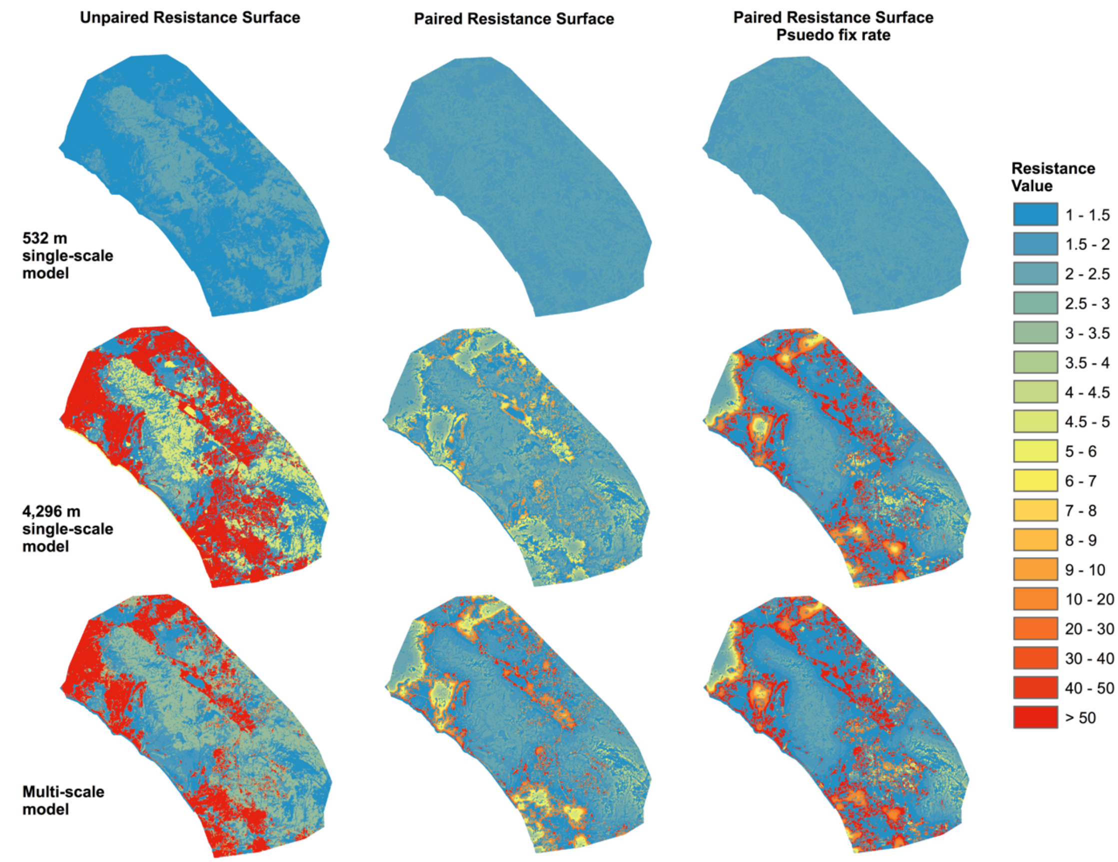
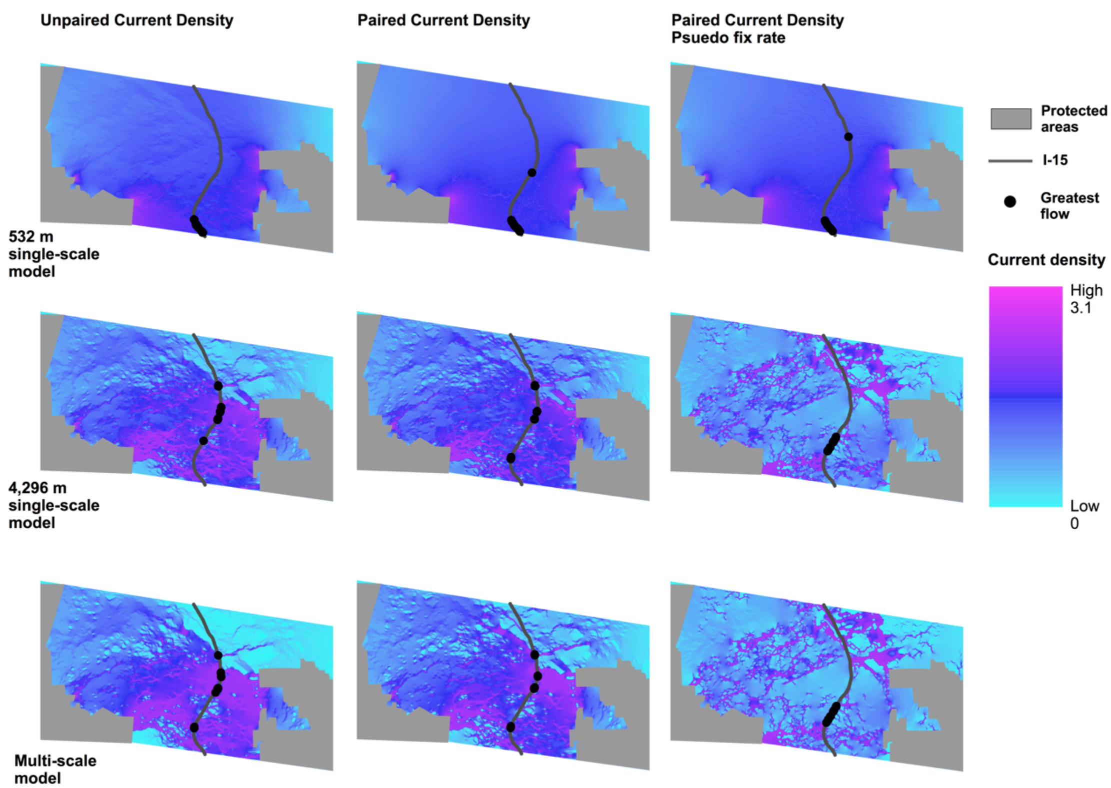


Figure 3.7. Road crossing locations from the SSF models. CircuitScape current density surfaces (log10 transformed) and road pixels with the highest current densities. The vertical line represents interstate-15, the black dots represent the top 20 pixels along I-15 with the highest current density. The first column contains current maps resulting from predicting resistance in the unpaired framework, the second column contains maps predicted in the paired framework, and the last column contains maps predicted with 60-min pseudo steps in the paired framework. The first row contains the current maps from the smallest scale model, the middle row the mid- scale model, and the last row the multi-scale model. Current density maps for the PathSFs are provided in Appendix F.



Discussion

We found that pumas have multiple characteristic scales during movement events. In our population, pumas exhibited a mostly bi-modal response to scale; characteristic scales were at a coarse scale for urban and agriculture, and at a fine scale for the remaining cover types, highlighting the importance of modeling movement at multiple spatial scales. We found regression coefficients to be extremely sensitive to scale. For example, for the PathSFs, regression coefficients ranged from -10 to -30 for the urban cover type, and -4 to -15 for the chaparral cover type. Regression coefficients also were prone to sign changes for some cover types, indicating different conclusions may be reached regarding habitat preference or avoidance with different scales. We found that regression coefficients from the PathSF models were generally greater than those from the SSF models and that characteristic scales differed between the SSFs and the PathSFs, indicating that choice of method may influence inference about movement and resistance (more on this below).

With the exception of the finest scale, SSF and PathSF models performed well across all scales (CCC [0.8) and PathSF models outperformed SSF models. Though the multi-scale models performed extremely well, they did not outperform some of the coarser, single-scale models.

Resistance surfaces differed between SSFs and PathSFs, with the PathSFs having higher resistance values than the SSFs. This was undoubtedly due to the greater avoidance of some cover types in the PathSFs compared with the SSFs.

Resistance surfaces also differed across scales. The finest scale produced the lowest range of resistance values, especially for the SSFs, and resistance generally increased with scale. This is again a reflection of the coefficients becoming more negative for certain cover types as scale increased. Increase in selection or avoidance with scale may be attributed to the fact that more of the landscape is sampled at larger scales. For example, when smaller scales are used, the available areas are more similar to the used areas and the models do not have much power to discern between selection and avoidance, resulting in weak regression coefficients. As scales broaden, the available areas represent a wider pool of conditions, enabling the model to more powerfully reflect differences in selection choices made by individuals.

The greatest conceptual difference in resistance surfaces was seen between predicting resistance in the unpaired versus the paired framework. In the unpaired resistance surfaces, it is evident that each cover type had a single resistance value regardless of its landscape context, whereas in the paired framework, each pixel had a unique value depending on its landscape context. This created more heterogeneous surfaces (more on this below). We found these differences among SSFs and PathSFs, scale, and prediction framework carried through to estimates of connectivity and road crossing locations.

Lastly, we found that regression coefficients, resistance surfaces, and corridors were sensitive to GPS collar acquisition interval. There was a consistent 3–4- fold difference in regression coefficients between the true 5-min steps/paths and the 60-min steps/paths. For some land cover types, using a longer acquisition interval resulted in a change of sign in the regression coefficient. Not surprisingly, CircuitScape current maps and road crossing locations were different between models that used the true paths versus those that used the pseudo paths. Therefore, a mismatch between GPS collar acquisition interval and species vagility may ultimately bias corridor conservation planning when using SSFs and PathSFs.

There is ample literature demonstrating that organisms select habitat at multiple spatial scales (see review by McGarigal et al. accepted). These multi- scale relationships have traditionally been modeled using RSFs based on point, or detection, data (e.g., DeCesare et al. 2012; Martin and Fahrig 2012; Zeller et al. 2014), not movement data. We believe this is due to the fact that methodological limitations with SSFs and PathSFs have constrained the exploration of scaling relationships and multi-scale models. However, there has been some exploration of scales with PathSFs. After Cushman et al. (2010) presented the first PathSF methodology which, involves shifting and rotating random paths to sample available habitat (Fig. 3.1b). Reding et al. (2013) was the first to incorporate more than one scale. Their paper on bobcats used buffers of two sizes around both the used and available paths in order to compare selection at these scales and combine the two scales into a single model. Elliot et al. (2014) used the original Cushman et al. (2010) method but changed the extent to which paths were shifted in order to explore multiple scales and construct multi-scale models. However, the Elliot et al. (2014) method does not allow for examination of fine scales. Here, we offer an improvement to SSF and PathSF methods for modeling habitat selection during movement at multiple scales and with multi-scale models. Our method is easily reproducible and can accommodate any number of biologically justified scales.

With our method, we found that individuals were not always operating at a single scale during movement and that multi-scale responses may be present. For some land cover types, we obtained stronger responses at coarser spatial and temporal scales. This is similar to Elliot et al. (2014) who found that lions in southern Africa select preferred vegetation types at fine spatial scales, and avoided anthropogenic risk, such as urban areas, at broad spatial scales. For our pumas, the coarse-scale response to urban and agricultural areas may be due to knowledge of the landscape including the location of large areas of human development. We used data from pumas that had established home ranges; however, results may vary with data from pumas that are dispersing in areas previously unknown to them. For dispersing individuals, it would not be surprising to find that habitat selection during movement occurs at much finer scales, since an individual may be reacting only to what is in their immediate perceptual range, not prior knowledge. Further research is needed to determine if characteristic scales for pumas differ between resident and dispersing individuals.

When estimating resistance, detection data is the most often-used data type, mainly due to the fact that it is relatively easy to acquire compared with movement data (Zeller et al. 2012). However, using step or path data to estimate resistance is conceptually more appealing since it explicitly represents movement. When step data is available, path data is typically available as well since it is simply a series of steps and one is left to select one approach over the other. Cushman et al. (2010) promoted PathSFs as being superior to SSFs given the fact that spatial and temporal autocorrelation of observations can be avoided, while maintaining the biologically important spatial patterns of movement. Given the larger regression coefficients and better model performance of PathSFs compared to SSFs, our results also support the use of PathSFs over SSFs. The differences in regression coefficients and resistance surfaces between SSFs and PathSFs may reflect the different types of movement these two approaches represent. We used a distance threshold for our step data so that the steps in our SSF explicitly represented movement events. Conversely, our paths represent all the behaviors in which an individual was engaged throughout the course of a day. Though the paths, as a trajectory of movement over a time period, are a representation of movement, they capture both the directed movement an individual may take when traveling between resource use patches as well as the slow, more tortuous movement an individual may take while acquiring resources. For estimating resistance, it may be argued that, as an individual moves about the landscape, they may be making directed movement as well as acquiring resources, again indicating that PathSFs may be the method of choice.

To our knowledge, this was the first study to conduct a PathSF for pumas and only the third to conduct an SSF. Dickson et al. (2005) and Dickson and Beier (2007) used an SSF approach to estimate habitat selection during movement for pumas in our same study area. Their steps were at 15-min intervals and they used a compositional analysis to rank cover types (from most to least preferred) as riparian, scrub, chaparral, grassland, woodland, and urban. With the exception of scrub and chaparral, these results agree with what we found in our SSFs. Differences may be due to different sample sizes, or the fact that compositional analyses cannot be conducted in the conditional logistic regression framework used herein. As noted in Dickson et al. (2005), previous research using point data found pumas avoid grasslands, apparently due to lack of stalking cover. However, during movement pumas may prefer grassland for increased mobility. Similarly, we found pumas to prefer naturally barren areas during movement. These results highlight the importance of accounting for behavioral state in modeling habitat selection since inferences based on movement can be different from those based on resource use (Squires et al. 2013; Elliot et al. 2014; Zeller et al. 2014). As this paper was aimed at testing various considerations for running SSF and PathSF models, we wanted to simplify the models and results by using only land cover classes as predictor variables. Future analyses for pumas in this study area could be improved by using other geospatial layers known to affect puma habitat selection including slope, topographic ruggedness, and roads (Burdett et al. 2010; Kertson et al. 2011; Wilmers et al. 2013).

The conditional logistic regression models allow for a biologically relevant comparison between used and available (Compton et al. 2002; Fortin et al. 2005) and the potential for using a context-dependent modeling approach (Zeller et al. 2014). For these reasons, extending the conditional framework to predicting the relative probability of movement and resistance is attractive. In previous studies, conditional logistic regression has been used to estimate the regression coefficients for the independent variables in a model, however these regression coefficients are then used in an unpaired framework to predict the relative probability of movement across a study area. We incorporated the available area around each pixel in the study area in our predicted surfaces for a truly paired approach to modeling resistance. In such a surface, resistance was estimated from each location on the landscape, putting the individual in the context of their surroundings. These surfaces are clearly applicable for individual-based modeling where individuals are making choices as they move through the landscape. However, using the paired approach needs further exploration. These surfaces may pose problems for modeling connectivity in certain landscapes because they may not adequately account for the absolute fitness costs of making any particular decision. For example, in the paired resistance surfaces the difficulty of entering an urban area (a strongly avoided land cover type) from an adjacent, preferred habitat reflects not only the relative fitness tradeoffs of moving into the urban area (i.e., the relative cost of moving into the urban area is high compared to moving away from the urban area), but also perhaps the ‘‘absolute’’ fitness costs of making that decision (i.e., moving through urban land cover confers a high fitness cost). However, once an individual moves inside the urban area, the context-dependent resistance is low because the relative cost of moving to another cell of urban is relatively low since the tradeoffs are all the same, even though the absolute fitness costs of moving through any cell of urban is still very high. The paired surface also produced concerning rings of high resistance around urban areas which, for moving into an urban area makes biological sense, but does not make biological sense for moving out of an urban area. In general, the paired resistance surfaces capture the relative fitness costs of making context-dependent decisions, whereas the unpaired surfaces capture the absolute fitness costs of making any decision. Given these issues, the utility of these surfaces used singly or in combination for corridor modeling is an area ripe for further research.

GPS collar acquisition intervals are often selected by weighing the desire to collect fixes at regularly short intervals against the desire for a long-lasting collar. We found, for studying movement in the context of SSFs and PathSFs, that collecting fixes at short intervals was critical in reducing bias in regression coefficients and resistance estimates. In previous SSFs, acquisition intervals have ranged from 1 min (Potts et al. 2014) to 1 day (Richard and Armstrong 2010) for birds, 1 h (van Beest et al. 2012) to 6 h (Coulon et al. 2008) for ungulates, and 30 min (Squires et al. 2013) to 4 h (Roever et al. 2010) for carnivore species. More research is needed to determine the appropriate intervals for studying movement for a species, but in general the optimal interval will be short (no more than a few minutes) for highly vagile species that do not travel on straight paths. Indeed, it is possible that an interval \5 min would be better for pumas than the 5-

min data used in this paper. Thurfjell et al. (2014) recommended performing pilot studies to determine the appropriate acquisition interval and highlighted the relative ease with which this may be done given remote options for downloading data and programming the GPS collars. Employing SSFs and PathSFs as we have done here, by calculating predictor variables along the step or path, should be done with great caution if it is suspected that the acquisition interval is too infrequent to capture true movement paths. Investigating the use of Brownian bridge models between points (Thurfjell et al. 2014) may alleviate bias, but at the cost of diluting specific species–habitat relationships along true movement paths.

The method we present for conducting SSFs and PathSFs is promising for modeling multi-scale species–habitat relationships during movement. It is also promising for estimating resistance, since using movement data in the form of steps or paths (vs. static point data) may be the most appropriate way to build resistance surfaces. However, many questions remain. First, like previous research teams, we have assumed that the inverse of the predicted relative probability of presence from RSFs translates directly to resistance, but there is no empirical evidence that this is the case. Second, more inquiry is needed to determine whether predicting resistance in the paired framework is superior to the unpaired framework, or whether some hybrid of these two resistance surfaces, representing a combination of relative and absolute fitness costs, is more appropriate. Related to these two points, methods are needed to compare amongst resistance surfaces derived via different data types and methods (Beier et al. 2008). Cushman et al. (2014) provide a robust method to compare the ability of resistance surfaces to predict actual crossing locations of individuals, however, methods are needed to assess the performance of entire resistance surfaces (not just road crossing locations). Third, more research is warranted to determine the appropriate GPS collar acquisition interval for species so as to reduce bias. Finally, more research is needed to determine how species respond to landscape features at different scales during movement.

We hope the results provided herein will be useful for further inquiry into how wildlife respond to landscape features during movement events. We provide a novel method for modeling movement at multiple scales within SSFs and PathSFs. Given our results, when there is a choice, we recommend PathSF models be used over SSF models. Due to the sensitivity of movement models and resulting resistance surfaces to scale, prediction framework and GPS collar schedule, much care should be used when modeling corridors for conservation purposes using these methods.

Appendices

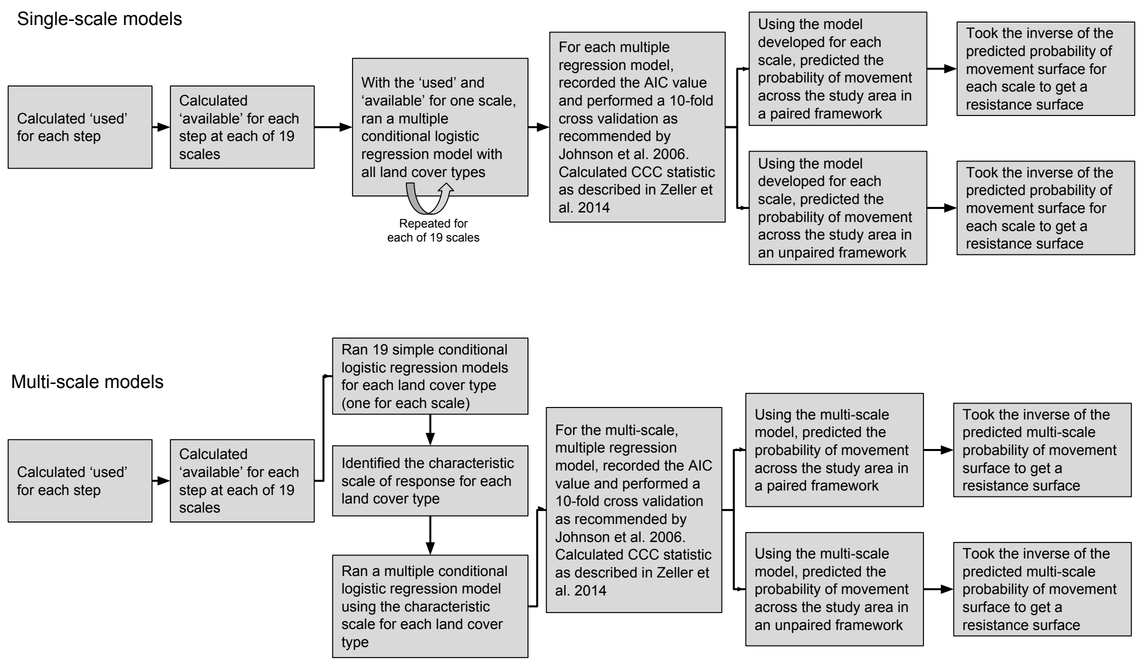
Appendix A. Time-intervals and associated radii of Pareto kernels used to define available habitat for the SSFs and PathSFs

We fit a Pareto distribution to the empirical distribution of displacement distances at each time-period and defined the maximum radii of the Pareto distribution by either using the 97.5 quantile of the distribution, or the maximum observed displacement distance, whichever was smaller.

Time-interval (minutes)	Radius of Pareto kernel (meters)
5	532
20	1351
40	2117
60	2618
80	3027
100	3278
120	3505
140	3834
160	4185
180	4296
200	4717
220	5064
240	5275
260	5486
280	5579
300	5802
320	6327
340	6555
360	7390

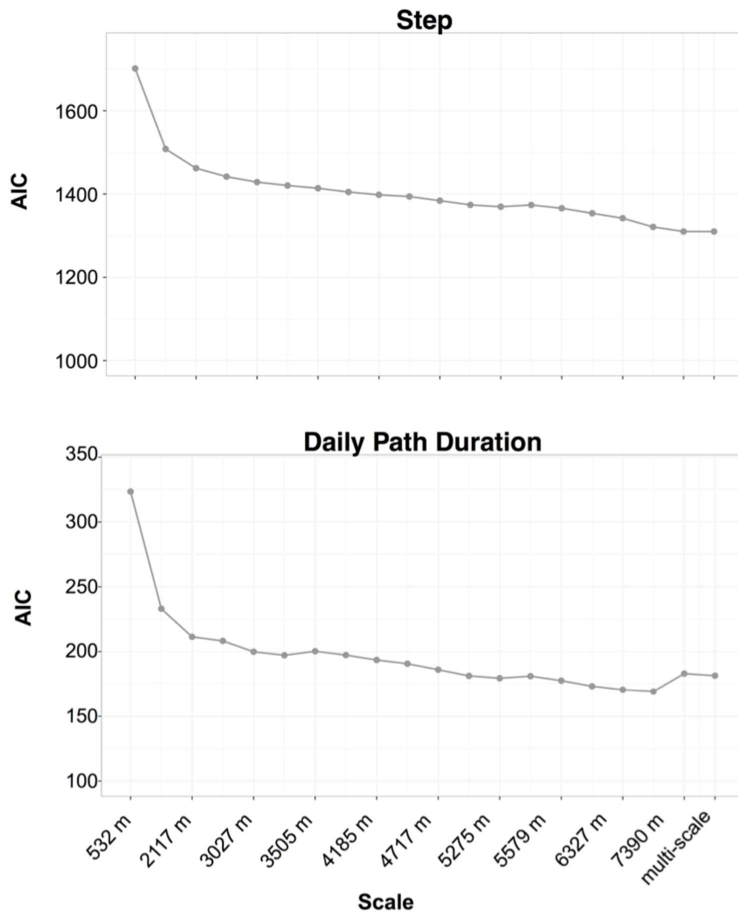
Appendix B. Flow chart depicting the statistical analysis procedure for our step data

The same procedure was followed for our path data. For further information please refer to the methods section of the main paper.

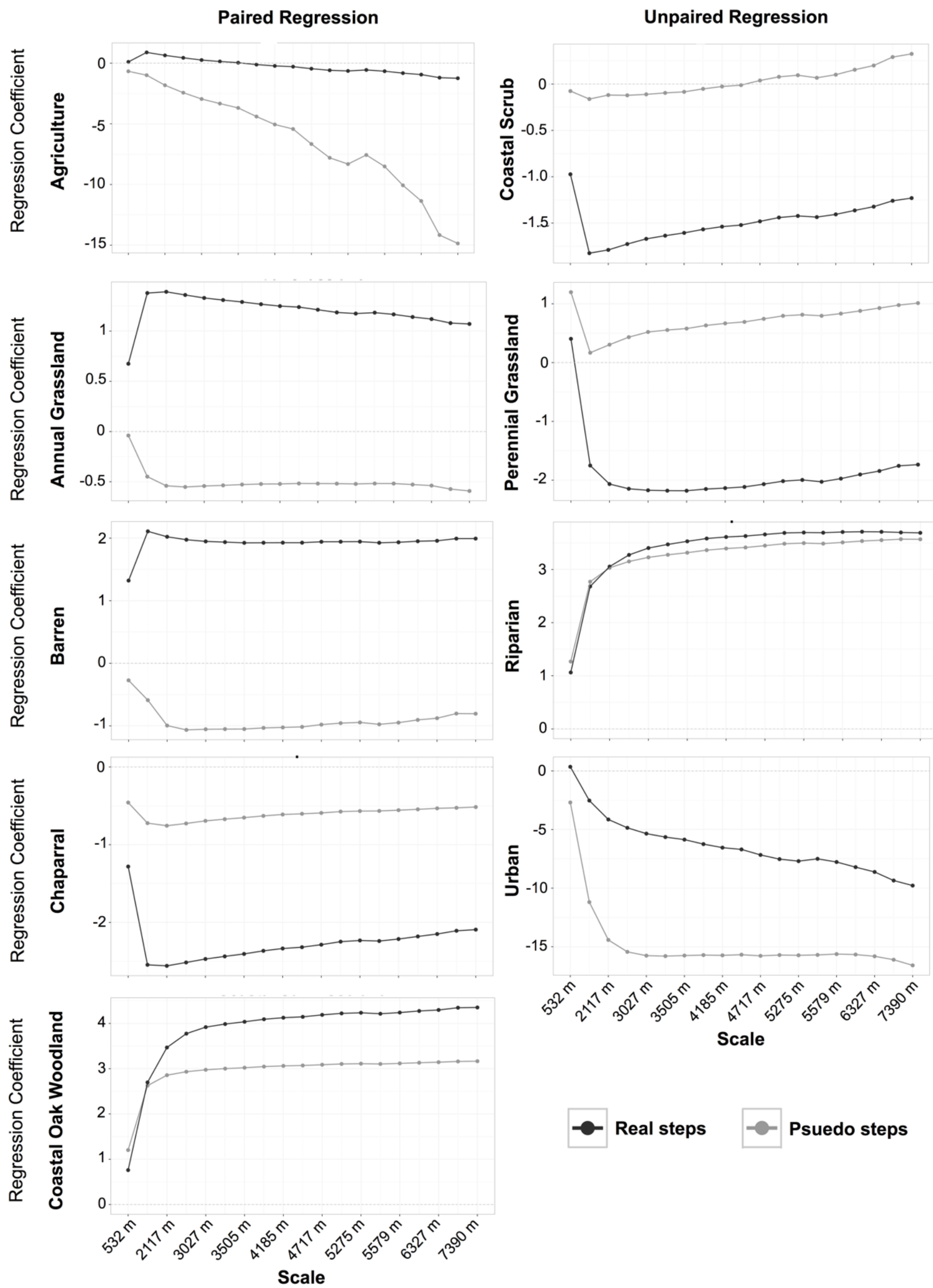


Appendix C. **AIC values for the single scale and multi-scale multiple regression SSFs and PathSFs**

Note, AIC values between the SSFs and PathSFs cannot be compared due to different sample sizes.



Appendix D. Regression coefficients for the simple paired logistic regression SSF models across the 19 scales of analysis for the true steps and the 60-min pseudo steps



Appendix E. Quantiles of (a) SSF and (b) PathSF resistance surfaces predicted in the paired and unpaired frameworks at select scales

a)

Resistance Value

Quanitle	SSF Paired Scale (m)					SSF Unpaired Scale (m)				
	532	2618	4296	7390	Multi-scale	532	2618	4296	7390	Multi-scale
1%	1.64	1.12	1.05	1.01	1.01	1.07	1.04	1.04	1.06	1.06
5%	1.79	1.23	1.13	1.05	1.06	1.16	1.06	1.1	1.12	1.09
10%	1.88	1.34	1.21	1.11	1.13	1.21	1.15	1.2	1.26	1.22
25%	1.99	1.65	1.51	1.35	1.38	1.31	1.35	1.6	1.8	1.78
50%	2	2.14	2.11	1.98	1.95	1.33	2.35	2.58	2.74	3.19
75%	2.02	2.58	2.88	3.24	3.18	2	3.25	5.4	22.79	21.98
90%	2.11	3.39	5.14	13.66	12.95	2.32	10.91	43.03	864	855
95%	2.24	4.15	7.63	32.19	30.33	2.32	10.91	43.03	864	855
99%	2.61	6.5	15.41	134	125	2.32	10.91	43.03	864	855
100%	7.3	36.68	168	3897	3923	2.32	10.91	43.03	864	855

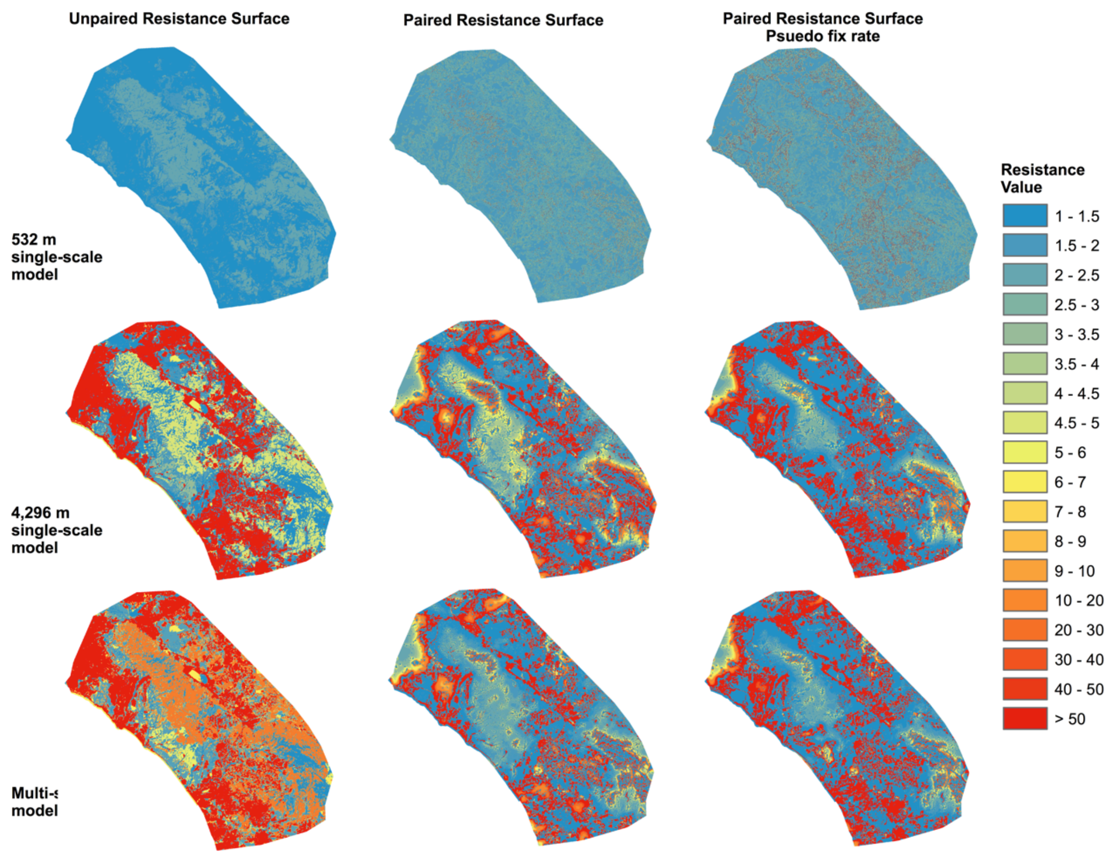
b)

Resistance Value

Quanitle	PathSF Paired Scale (m)					PathSF Unpaired Scale (m)				
	532	2618	4296	7390	Multi-scale	532	2618	4296	7390	Multi-scale
1%	1.03	1	1	1	1	1	1	1	1	1
5%	1.19	1	1	1	1	1	1	1	1	1
10%	1.41	1	1	1	1	1	1	1.01	1.03	1.13
25%	1.9	2.15	1.05	1.05	1.07	1.03	1.44	2	2	2.32
50%	2	2.64	2.58	2.37	3.12	2	4.6	4.6	4.6	3011
75%	2.2	10.6	31.97	29.09	33.91	4.6	7470	5.8xe^{4}	7.8xe^{5}	3.0xe^{4}
90%	3.08	123	113	1034	606	6.59	4.1xe^{7}	1.6xe^{9}	3.1xe^{10}	3.0xe^{7}
95%	5.34	632	1.1xe^{4}	9849	3570	6.59	4.1xe^{7}	1.6xe^{9}	3.1xe^{10}	3.0xe^{7}
99%	42.17	1.3xe^{4}	5.9xe^{5}	5.1xe^{5}	9.3xe^{4}	6.59	4.1xe^{7}	1.6xe^{9}	3.1xe^{10}	3.0xe^{7}
100%	2.8xe^{4}	1.1xe^{10}	2.6xe^{12}	3.3xe^{11}	1.4xe^{11}	6.59	4.1xe^{7}	1.6xe^{9}	3.1xe^{10}	3.0xe^{7}

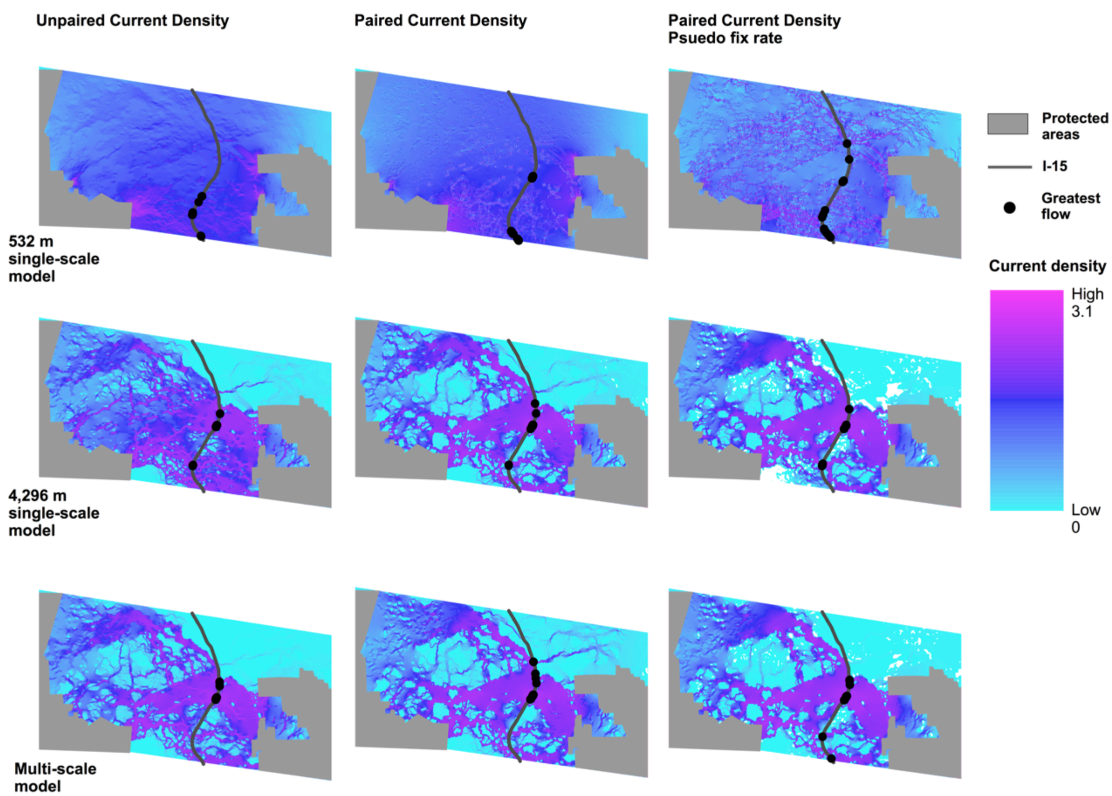
Appendix F. Resistance surfaces obtained from the PathSF models

The first column contains the resistance surfaces predicted in the unpaired framework, the second column contains resistance surfaces predicted in the paired framework, and the last column contains resistance surfaces predicted with pseudo paths in the paired framework. The first row contains the resistance surfaces from the smallest scale model, the middle row, the mid-scale model, and the last row the multi-scale model., and the last row the multi-scale model.



Appendix G. PathSF CircuitScape current density surfaces (log10 transformed) and road pixels with the highest current densities

The vertical line represents Interstate-15, the black dots represent the top 20 pixels along I-15 with the highest current. The first column contains current maps resulting from predicting resistance in the unpaired framework, the second column contains maps predicted in the paired framework, and the last column contains maps predicted with the 60-min pseudo paths in the paired framework. The first row contains the current maps from the smallest scale model, the middle row, the mid-scale model, and the last row the multi-scale model.



References

Agresti A (2002) Categorical data analysis, 2nd edn. Wiley, Hoboken, p 419

Beier P, Majka D, Spencer WD (2008) Forks in the road: choices in procedures for designing wildlife linkages. Conserv Biol 22:836–851

Brown DD, LaPoint S, Kays R, Heidrich W, Kummeth F, Wikelski M (2012) Accelerometer-informed GPS telemetry: reducing the trade-off between resolution and longevity. Wildl Soc Bull 36:139–146

Burdett CL, Crooks KR, Theobald DM, Wilson KR, Boydston EE, Lyren LM, Fisher RN, Vickers TW, Morrison SA, Boyce WM (2010) Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere 1:1–21

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York. ISBN 978-0-387- 22456-5

California Department of Fish and Game (1988) A guide to wildlife habitats of California. In: Mayer KE, Laudenslayer Jr WF (eds) State of California Resources Agency. Department of Fish and Game, Sacramento, p 166. http://www.dfg.ca.gov/biogeodata/cwhr/wildlife_habitats.asp#Tree. Accessed 29 Jan 2013

Compton BW, Rhymer JM, McCollough M (2002) Habitat selection by wood turtles (Clemmys insculpta): an application of paired logistic regression. Ecology 83:833–843

Coulon A, Morellet N, Goulard A, Cargnelutti B, Angibault JM, Hewison AJM (2008) Inferring the effects of landscape structure on roe deer (Capreolus capreolus) movements using a step selection function. Landscape Ecol 23:603–614

Crooks KR, Sanjayan M (2006) Connectivity conservation: maintaining connections for nature. In: Crooks KR, Sanjayan M (eds) Connectivity conservation. Cambridge University Press, Cambridge, p 1

Cushman SA, Lewis JS (2010) Movement behavior explains genetic differentiation in American black bears. Landscape Ecol 25:1613–1625

Cushman SA, Chase M, Griffin C (2010) Mapping landscape resistance to identify corridors and barriers for elephant movement in South Africa. In: Cushman SA, Huettmann (eds) Spatial complexity, informatics, and wildlife conservation. Springer, Japan, pp 349–367. ISBN 978-4-431- 87770-7

Cushman SA, McRae B, Adriaensen F, Beier P, Shirley M, Zeller K (2013) Biological corridors and connectivity. In: Macdonald DW, Willis KJ (eds) Key topics in conservation biology 2. Wiley-Blackwell, Hoboken, pp 384–404

Cushman SA, Lewis JS, Landguth EL (2014) Why did the bear cross the road? Comparing the performance of multiple resistance surfaces and connectivity modeling methods. Diversity 6:844–854

DeCesare NJ, Hebblewhite M, Schmiegelow F, Hervieux D, McDermid GJ, Neufeld L, Bradley M, Whittington J, Smith KG, Morgantini LE, Wheatley M, Musiani M (2012) Transcending scale dependence in identifying habitat with resource selection functions. Ecol Appl 22:1068–1083

Dickson BG, Beier P (2007) Quantifying the influence of topographic position on cougar (Puma concolor) movement in southern California, USA. J Zool 271:270–277

Dickson BG, Jenness JS, Beier P (2005) Influence of vegetation, topography, and roads on cougar movement in southern California. J Wildl Manag 69:264–276

Elliot NB, Cushman SA, Macdonald DW, Loveridge AJ (2014) The devil is in the dispersers: predictions of landscape connectivity change with demography. J Appl Ecol. doi:10. 1111/1365-2664.12282

Ernest HB, Vickers TW, Morrison SA, Buchalski MR, Boyce WM (2014) Fractured genetic connectivity threatens a southern California puma (Puma concolor) population. PLoS ONE 9(10):e107985. doi:10.1371/journal.pone. 0107985

Estrada EG, Alva JAV (2011) Package gPdtest: bootstrap goodness-of-fit test for the generalized Pareto distribution. http://cran.r-project.org/web/packages/gPdtest/index.html. Accessed 11 Feb 2015

Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330

Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. Bioscience 54:227–233

Johnson D (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71

Johnson CJ, Nielsen SE, Merrill EH, Mcdonald TL, Boyce MS (2006) Resource selection functions based on use-availability data: theoretic motivation and evaluation methods. J Wildl Manag 70:347–357

Joly K (2005) The effects of sampling regime on the analysis of movements of overwintering female caribou in east-central Alaska. Rangifer 25:67–74

Kertson BN, Spencer RD, Marzluff JM, Hepinstall-Cymerman J, Grue CE (2011) Cougar space use and movements in the wildland-urban landscape of western Washington. Ecol Appl 21:2866–2881

Lewis JS, Rachlow JL, Garton EO, Vierling LA (2007) Effects of habitat on GPS collar performance: using data screening to reduce location error. J Appl Ecol 44:663–671

Lin LI (1989) A concordance correlation coefficient to evaluate reproducibility. Biometrics 1:255–268

Manly BF, Mcdonald L, Thomas DL, Mcdonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies, 2nd edn. Kluwer Academic Publishers, Dordrecht

Martin AE, Fahrig L (2012) Measuring and selecting scales of effect for landscape predictors in species–habitat models. Ecol Appl 22:2277–2292

McGarigal K, Wan H, Zeller KA, Timm BC, Cushman SA (accepted) Multi-scale habitat modeling: A review and outlook. Landscape Ecol

McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724

McRae BH, Shah VB, Mohapatra TK (2013) Circuitscape 4 user guide. The Nature Conservancy. http://www.circuitscape. org. Accessed 19 May 2015

Mills KJ, Patterson BR, Murray DL (2006) Effects of variable sampling frequencies on GPS transmitter efficiency and estimated wolf home range size and movement distance. Wildl Soc Bull 34:1463–1469

Norththrup JM, Hooten MB, Anderson CR Jr, Wittemyer G (2013) Practical guidance on characterizing availability in esource selection functions under a use-availability design. Ecology 94:1456–1463

Potts JR, Mokross K, Stouffer PC, Lewis MA (2014) Step selection techniques uncover the environmental predictors of space use patterns in flocks of Amazonian birds. Ecol Evol 24:4578–4588

R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/. Accessed 15 May 2013

Reding DM, Cushman SA, Gosselink TE, Clark WR (2013) Linking movement behavior and fine-scale genetic structure to model landscape connectivity for bobcats (Lynx rufus). Landscape Ecol 28:471–486

Rettie WJ, McLoughlin PD (1999) Overcoming radio telemetry bias is habitat-selection studies. Can J Zool 77:1175–1184

Richard Y, Armstrong DP (2010) Cost distance modeling of landscape connectivity and gap-crossing ability using radio-tracking data. J Appl Ecol 47:603–610

Roever CL, Boyce MS, Stenhouse GB (2010) Grizzly bear movements relative to roads: application of step selection functions. Ecography 33:1113–1122

Squires JR, DeCesare NJ, Olson LE, Kolbe JA, Hebblewhite M, Parks SA (2013) Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. Biol Conserv 157:187–195

Thurfjell H, Ciuti S, Boyce MS (2014) Applications of step- selection functions in ecology and conservation. Mov Ecol 2:4

USDA Forest Service (2007) CalVeg: FSSDE.Eveg- Tile47A_02_v2. Pacific Southwest Region Remote Sensing Lab, McClellan

Van Beest FM, Van Moorter B, Milner JM (2012) Temperature- mediated habitat use and selection by a heat-sensitive northern ungulate. Anim Behav 84:723–735

Vickers TW, Sanchez JN, Johnson CK, Morrison SA, Botta R, Smith T, Cohen BS, Huber PR, Ernest HB, Boyce WM (2015) Survival and mortality of pumas (Puma concolor) in a fragmented, urbanizing landscape. PlosONE. doi:10. 1371/journal.pone.0131490

Wheatley M, Johnson C (2009) Factors limiting our understanding of ecological scale. Ecol Complex 6:150–159

Wilmers CC, Wang Y, Nickel B, Houghtaling P, Shakeri Y, Allen ML, Kermish-Wells J, Yovovich V, Williams T (2013) Scale dependent behavioral responses to human development by a large predator, the puma. PLoS ONE. doi:10.1371/journal.pone.0060590

Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landscape Ecol 27:777–797

Zeller KA, McGarigal K, Beier P, Cushman SA, Vickers TW, Boyce WM (2014) Sensitivity of landscape resistance estimates based on point selection functions to scale and behavioral state: pumas as a case study. Landscape Ecol 29:541–557

CHAPTER 4

SENSITIVITY OF RESOURCE SELECTION AND CONNECTIVITY MODELS TO LANDSCAPE DEFINITION

Introduction

Assessing species-habitat relationships and modeling connectivity require creating a spatially-explicit landscape model as a formal representation of (1) the types of landscape features that may affect habitat use and movement, (2) the spatial heterogeneity of those landscape features, and (3) the spatial scale of those landscape features. This 'landscape definition' is the basis for all habitat use and connectivity models (Cushman et al. 2013), yet the sensitivity of these models to landscape definition has received scant attention in the literature.

Landscape ecologists have long been aware that observed pattern-process relationships are highly sensitive to the spatial scale of the landscape model (Weins 1989; Wu 2004). Spatial scale is the marriage of two components: extent and grain. Wildlife biologists have traditionally been more focused on the former of these two scale components, the spatial extent, for wildlife-habitat inference (McGarigal et al. 2016). Here the most common approach is to summarize landscape features within buffers or kernels of varying size (aka 'ecological neighborhoods'; sensu Addicott et al. 1987) in order to determine the characteristic spatial scale of selection for a landscape feature (e.g., Holland et al. 2004). It is increasingly recognized that failure to identify the characteristic spatial scale of selection with regards to both grain and extent may bias wildlife-habitat inference (McGarigal et al. 2016).

Wildlife biologists are just beginning to examine the effects of spatial grain (also often referred to as "resolution") on species-habitat models. Varying the grain size of the geospatial layers has been used to both determine the characteristic scale of selection for a landscape feature (Thompson & McGarigal 2002) and to determine how spatial grain affects overall model performance (Karl et al. 2000; Seoane et al. 2004; Venier et al. 2004; Guisan et al. 2007; Cushman & Landguth 2010a; Gottshcalk et al. 2011). In general, these studies have found model performance decreases with increasing grain size, though the effect of grain size on model predictive performance remains equivocal (Tobalske 2002; Seoane et al. 2004; Guisan et al. 2007).

Thematic resolution of the geospatial layers used for a landscape definition has received far less attention than spatial scale in modeling species-habitat relationships. Thematic resolution refers to the level of heterogeneity of the geospatial layers. In many cases landscape features can be represented as a continuous gradient, which is thought to more closely mimic real world landscapes and reduce subjectivity (McGarigal & Cushman 2005; Cushman et al. 2010b). With continuous gradients, the thematic resolution is at its greatest given the precision of the raw data. However, landscape features can also be represented categorically, as in the classic patch-mosaic model of landscape structure (Forman 1995). When categorical layers are used, decisions must be made regarding the number and breakpoints of the classes. Lawler et al. (2004) found that species distribution models had similar fit between different thematic resolutions, but that predictions in various geographic locations differed. Seoane et al. (2004) found that finer thematic resolutions resulted in better predictive performance of species distribution models. Cushman & Landguth (2010a) found that the strength of the relationship between gene-flow and landscape features increased as the thematic resolution of the layers increased from the lowest resolution of two classes to the highest resolution (continuously scaled layers). They also found that thematic resolution was the dominant factor over spatial grain and spatial extent in defining the landscape for landscape genetic analyses.

Selecting the spatial grain and thematic resolution of the geospatial layers are not the only decisions one must contend with when defining the landscape. The layers themselves must be selected (i.e., thematic content; e.g., elevation, land cover type, etc.) along with the data source of each layer. Selection of geospatial layers is often determined *a priori* given previous knowledge of the target species or through model selection procedures such as Akaike's Information Criterion (AIC; Akaike 1973; Burnham & Anderson 2002). In addition, multiple data sources may be available for the chosen layers. For example, there may be multiple data source options for land cover type that have similar accuracy, but trade-offs may exist across the study area such that one data source may be very good at representing riparian areas but not as good at differentiating scrub from grassland, while another source may be very good at representing forested areas but not meadows. Source of the data layers in species-habitat models is often not discussed, though when layers from different sources have been compared (e.g., Seoane et al. 2004; Chust et al. 2004; Cushman et al. 2010a), the comparison is often confounded with spatial grain. For example, one data source will be available at 30m grain (e.g., Landsat) and another at 250m grain (e.g., CORINE; European Environmental Agency). Therefore, the effect of these choices on species-habitat models remains unclear.

Defining the landscape for modeling species-habitat relationships is not a straightforward task and one is faced with many choices, all of which may affect the resulting models and conclusions about species-habitat use. We are not aware of any studies that have looked at how species-habitat models are affected by all four of these landscape definition choices: (1) spatial grain, (2) thematic resolution, (3) which and how many geospatial layers to include in a definition, and (4) which data source to include for each geospatial layer.

Because our collective interest is in modeling wildlife movement and connectivity, we used GPS data from pumas (*Puma concolor*) in southern California to explore the sensitivity of multi-scale Path Selection Function (PathSF) models (Cushman & Lewis 2010; Cushman et al. 2010b; Zeller et al. 2015) to landscape definition. We hypothesized that model performance (as defined below) would be sensitive to landscape definition and, specifically, that model performance would increase with (1) decreasing spatial grain, (2) increasing thematic resolution, and (3) increasing number of geospatial layers, provided all the layers are true drivers of habitat selection. We also predicted that some data sources would improve model performance measures more than others.

<u>**Methods**</u>

Study Area and puma data

Our study area (4,089 km2) includes the Santa Ana Mountains of southern California and surrounding lowlands. This coastal mountain range experiences a Mediterranean climate with hot dry summers and mild wetter winters. Between October 2011 and March 2014, we fit ten pumas (six female and four male), with Lotek 4400S GPS collars programmed at a 5 min acquisition interval (Lotek Wireless, Inc. Canada).

Manufacturer tests indicate that long-term positional accuracy of the GPS collars is 5–10 m, though this may vary with certain vegetation types and topographical conditions (Chang, personal communication). To avoid the use of data that may have large spatial errors, we removed two-dimensional fixes with a PDOP > 5 (Lewis et al. 2007). This data filtering resulted in a final data set of 75,716 fixes across the 10 individuals (range = 1,650–18,464; median = 7,147). We pooled sexes in the analysis due to the low number of individuals. Daily paths were constructed for each puma by connecting consecutive 5-min points with straight-line segments over a 24-h period. This resulted in 315 daily paths for use in the PathSFs (see *Statistical Analyses* section below).

Geospatial data

We used the following seven geospatial layers which have been shown to influence puma habitat use: (1) elevation (Alexander et al. 2006; Allen et al. 2014; Burdett et al. 2010; Wilmers et al. 2014), (2) percent slope (Dickson & Beier 2006; Dickson et al. 2005; Wilmers et al. 2014), (3) terrain ruggedness (represented as total curvature; Burdett et al. 2010), (4) land cover type (Burdett et al. 2010; Wilmers et al. 2014), (5) percent vegetative cover (Holmes & Laundré 2006; Kissling et al. 2009), (6) roads (Dickson et al. 2005; Wilmers et al. 2014; Gray et al. 2016), and (7) human development (represented here as percent impervious surface; Burdett et al. 2010; Wilmers et al. 2014). We derived Percent slope and Terrain ruggedness from the National Elevation Dataset (USGS 2009) using the Percent slope and Total Curvature tools in the DEM Surface Tools Extension for ArcMap (Jenness 2013).

Some of the geospatial layers were available across our study area from multiple sources. To examine the possible effect of data source in our analyses, we selected three different sources for land cover type and percent vegetative cover, and two different sources for roads. We assumed most available elevation layers would have little error and be very similar to each other. Therefore, we selected only one data source for elevation and its derived layers (percent slope and terrain ruggedness). All geospatial layers and their sources are provided in Table 4.1.

We represented layers that were available in a continuous format (elevation, percent slope, terrain ruggedness, percent vegetative cover, and percent impervious surface) with four thematic resolutions: continuous, 3 classes, 4 classes, and 5 classes. Class breakpoints were determined using the Jenks optimization method (Jenks 1967). This method identifies breakpoints that minimize the within-class variance and maximize the between-class variance. Classifications of each continuous layer are provided in Appendix A. We represented land cover type, a categorical-only layer, using five or eight classes. These classes were determined based on the dominant vegetative classes in the study area and earlier resource selection functions conducted on pumas in the study area (Zeller et al. 2014; Zeller et al. 2015). We represented roads, another categorical-only layer, with two, three, or four classes. This allowed us to represent (1) primary and secondary roads only, (2) primary, secondary and tertiary roads only, and (3) all roads. Classification crosswalks for each categorical layer are provided in Appendix B. We recognize that vector features such as land cover and roads may be represented continuously by using moving windows to summarize each feature within a window. However, our PathSF analysis summarizes data within a weighted kernel around each used and available area — making an initial smoothing or weighting of the surface an extra, unnecessary step.

All raster layers were available at a 30m spatial grain size and we rasterized all vector layers to a 30m grain size. To examine a suite of spatial grains, we upscaled each 30m layer to 60m, 120m, 180m, and 240m using the majority rule for categorical layers and the focal mean for continuous layers. Each landscape definition was restricted to a single spatial grain.

Table 4.1. Data source and year of geospatial data layers used to model puma movement in southern California. County roads data were merged across the four counties in our study area to create a single coverage. *Raster* or *vector* indicate the original format of the data.

Geospatial data layer	***Source***	***Year***	***Citation***
Elevation	National Elevation Dataset *(raster)*	2009	USGS 2009
Percent Slope	Calculated from the National Elevation Dataset	-	
Terrain Ruggedness	Calculated from the National Elevation Dataset	-	
Percent Impervious Surface	National Land Cover Database *(raster)*	2011	Jin et al. 2013
Land Cover Type	CalVeg *(vector)*	2014	USDA 2007
	LandFire, Existing Vegetation Type *(raster)*	2012	LandFire 2012b
	National Land Cover Database *(raster)*	2011	Jin et al. 2013
Percent Vegetative Cover	LandFire, Existing Vegetation Cover *(raster)*	2012	LandFire 2012a
	Landsat, Vegetation Continuous Fields *(raster)*	2005	Sexton et al. 2013
	National Land Cover Database *(raster)*	2011	Jin et al. 2013
Roads	Open Street Map *(vector)*	2014	Open Street Map 2014
	County Roads Data		
	Orange County *(vector)*	2011	OCTA 2011
	Riverside County *(vector)*	2013	Riverside GIS 2013
	San Bernadino County *(vector)*	2014	San Bernadino 2014
	San Diego County *(vector)*	2013	SanGIS 2014

Landscape definitions

Varying the data source, thematic resolution, and spatial grain provided multiple representations of each geospatial layer. For example, elevation had a single data source, four different thematic resolutions and five different spatial grains, for a total of 20 different representations (Fig. 1). Likewise, percent slope, terrain ruggedness, and percent impervious surface also had 20 representations each. Percent vegetative cover had three data sources for the same combination of thematic resolutions and spatial grains, for a total of 60 representations. Roads had two data sources, three thematic resolutions and five spatial grains, for a total of 30 representations. Land cover type had three data sources, two thematic resolutions and five spatial grains, for a total 30 representations.

The ultimate landscape definition for puma could consist of a single geospatial layer or any combination of geospatial layers represented at any of the available spatial grains, thematic resolutions and data sources, all of which are plausible and realistic alternatives for modeling puma movement. Given the vast number of layer representations and combinations, analyzing a full factorial of landscape definitions ($N{\sim}5^8$) was not possible. Therefore, we performed a random selection procedure that we assumed would capture the general patterns of how landscape definition affects inference about puma movement. To generate a single landscape definition we:

(1) randomly selected the spatial grain (30m, 60m, 120m, 180m, 240m) for all layers included in the landscape definition;

(2) randomly selected the number of layers to include (1-7);

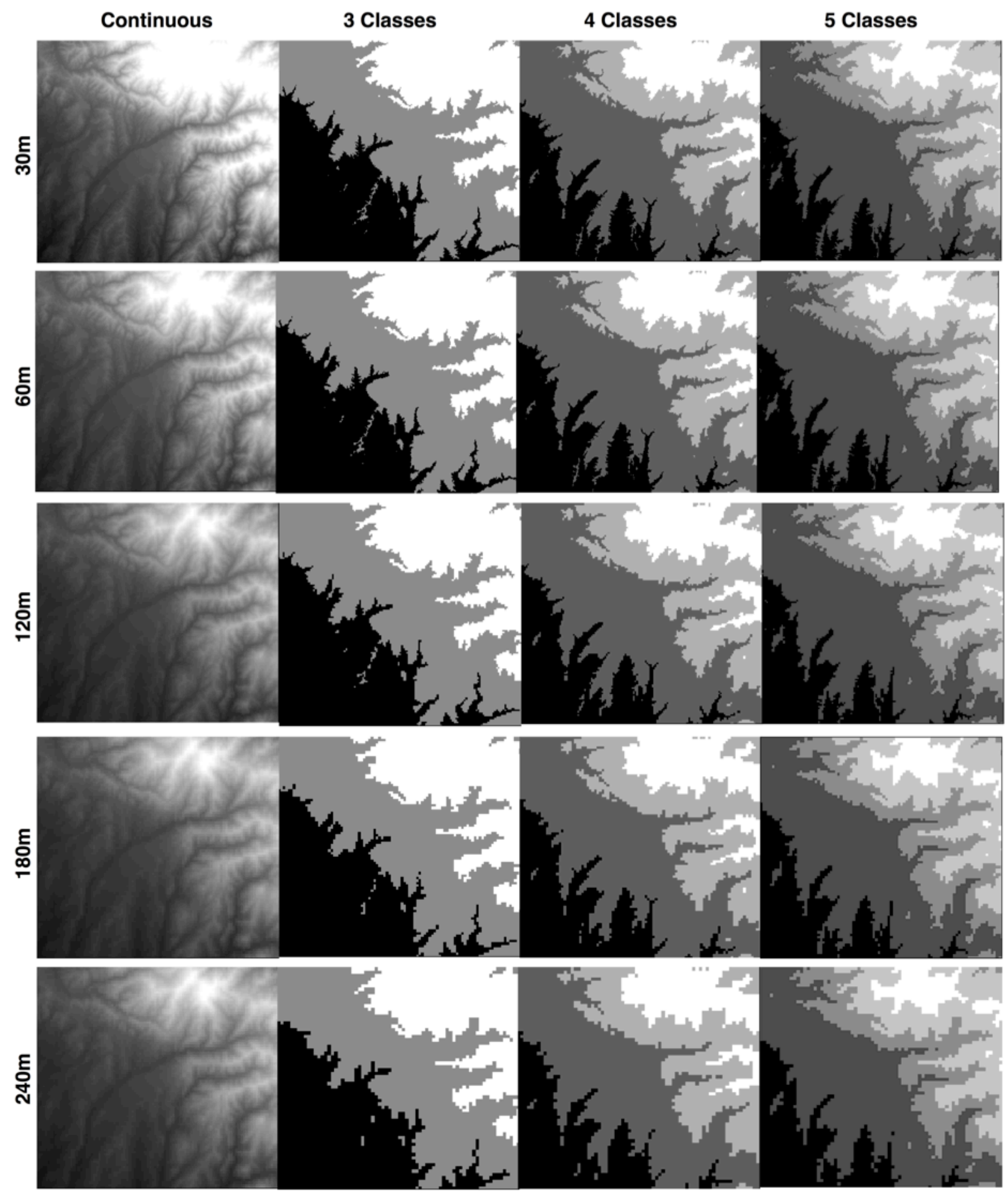
(3) randomly selected, without replacement, which layer(s) to include (elevation, percent slope, terrain ruggedness, land cover type, percent vegetative cover, roads, percent impervious surface);

(4) randomly selected the data source for each layer, as appropriate; and

(5) randomly selected the thematic resolution of each layer.

We repeated this process 2,000 times to generate 2,000 unique landscape definitions.

Figure 4.1. Twenty possible representations of elevation in a subset of the study area. Elevation was represented at four thematic resolutions (continuous, three classes, four classes, and five classes) and each thematic resolution was represented at five different spatial grains (30m, 60m, 120m, 180m, 240m).



Statistical Analyses

We conducted all statistical analyses in the R software environment (R Core Team 2013). We used multi-scale Path Selection Functions (PathSFs) as described in Zeller et al. (2015) to model landscape use and connectivity for pumas in our study area. PathSF's are analyzed in the 'used'/'available' framework typical of resource selection functions where the proportion of used to available for a landscape feature indicates preference or avoidance of that feature (e.g., Cushman and Lewis 2010). For each of our layer representations, we calculated the used data within a 30m fixed-width buffer around each daily path. Available data were calculated using a Pareto-weighted kernel around each daily path (Zeller et al. 2015). If a layer had a categorical representation, we calculated the proportion of each category within the used or available area. If a layer had a continuous representation, we calculated the mean. Therefore, all predictor variables in the statistical models were continuous in nature. If a geospatial layer was continuous, it was included in the model as a single variable. If a geospatial layer was categorical, the number of categories equaled the number of variables it contributed to the model (since each category was treated as a separate variable). This is worth noting since we later take a closer look at the number of layers used in each landscape definition, which varied from 1-7 (elevation, percent slope, terrain ruggedness, percent vegetative cover, percent impervious surface, land cover type, and roads) versus the number of variables in each landscape definition, which varied from 1-24.

Pumas in our study area select different landscape features at different scales (Zeller et al. 2014), therefore we developed multi-scale PathSF models (Zeller et al. 2014, 2015). To represent different scales, we varied the radii of the Pareto kernel at 10 different spatial extents from 500m to 7500m (Zeller et al. 2014). To compare scales, we ran univariate conditional logistic regression models for each layer representation at each scale. To identify the characteristic scale of selection we identified the scale with the lowest corrected AIC value (AICc; Akaike 1973; Burnham and Anderson 2002; Appendix C). This scale was then used in building the multivariate conditional logistic regression models for each of our 2,000 landscape definitions.

For a single landscape definition, we took each layer that comprised that definition and calculated used and available data (at the appropriate scale) for the puma paths. If there were multiple layers for a definition and correlations ≥0.7 were found between layers, we dropped the first from each pair of correlated layers. We then ran a conditional logistic regression model. Occasionally models produced complete separation warnings or convergence errors. When this was encountered we dropped the model from the analysis, a new unique landscape definition was generated, and the model was re-run. This was repeated for all 2,000 landscape definitions, resulting in 2,000 fitted models.

We calculated AICc for each model to compare overall model performance and to select the top models. We calculated percent deviance explained (D2) to compare the strength of the overall fit of the models (Franklin 2009), and we used the concordance correlation coefficient (CCC; Lin 1989) to evaluate the calibration of the predictive models. For a well-calibrated model, the predicted observations should fall close to the expected observations on a line originating at 0 with a slope of 1 (Johnson et al. 2006). The CCC statistic measures how correlated two points are based on their deviance from this 45-degree line, with CCC values closer to 1 indicating better calibrated models.

We determined the sensitivity of model selection, model fit, and prediction calibration to landscape definition by modeling the corresponding performance criteria (AICc, D2, and CCC) as a function of the following landscape definition options: (1) spatial grain (30m, 60m, 120m, 180m, 240m), (2) number of layers used in the model (1-7), (3) number of variables (1-24), and (4) whether the variables were all represented continuously, all represented categorically, or whether a mix of continuous or categorical representations were present. Specifically, we conducted Likelihood Ratio Tests comparing the full model with each of these four definition options left out in turn. Note, because roads and land cover class could only be represented categorically, we omitted landscape definitions with these variables to assess thematic resolution. We wanted to compare only models where a layer could be represented both categorically and continuously. We also produced mean and standard error plots to assess the relative influence of each of these four definition options on each of the performance criteria.

Using AICc values, we identified the top landscape definitions for pumas in our study area. We calculated odds ratios for the top model variables by predicting the probability of movement for each variable at the 25th and 75th percentile of the variable distribution while keeping the other variables in the model at their means and taking the ratio of the 75th percentile predicted probability to that of the 25th percentile.

To assess the importance of layer representations and determine whether some layer representations influenced model performance more than others; we identified paired models with and without each layer representation. We subtracted the AICc of the model with the layer representation from that of the model without the layer representation and took the mean of this difference across model pairs. The greater the mean value, the more important that layer representation is for modeling pumas in our study area. We also used this layer importance metric to determine whether some layer sources influenced model performance more than others. Note, we found it uninformative to use AIC weights to assess variable importance due to only having four models with any AIC weight.

To determine the sensitivity of probability of movement values (and thus inferred habitat selection) obtained from the different landscape definitions, we randomly sampled 1,000 pixels throughout the study area and predicted the probability of movement at each pixel for each of our 2,000 models. We then used various data exploration metrics (standard deviation, coefficient of variation, range, interquartile range) to determine the sensitivity of predicted values to landscape definition.

Modeling Connectivity and Road Crossing Locations

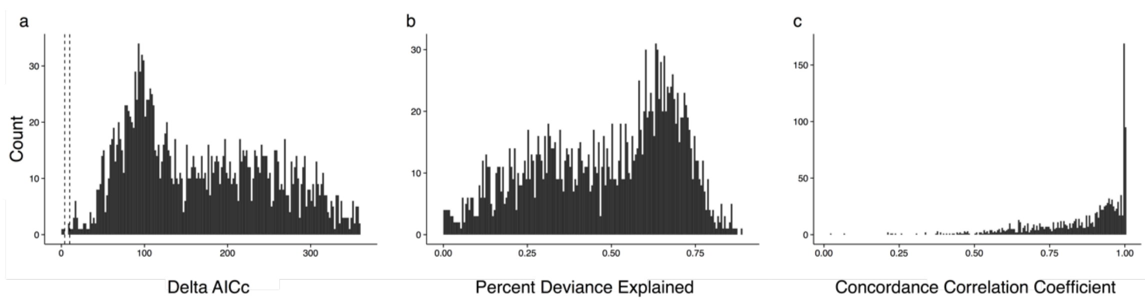
To provide a cursory example of how landscape definition may affect connectivity and corridor modeling, we selected landscape definitions across the model performance continuum at the 0^{th}, 25^{th}, 50^{th}, 75^{th} and 100^{th} percentile of AICc values. We predicted the relative probability of movement from each of these five models across our study area as described in Zeller et al. (2015). We assumed that this relative probability of movement could be used as a proxy for landscape conductance (McRae et al. 2008). For example, a pixel with a high probability of movement would have high conductance and vice versa. We visually examined the probability of movement/conductance surfaces to highlight differences.

We modeled connectivity across the Temecula corridor region, which is a subset of our study area. This region has been identified as the last viable, though highly threatened, link between the Santa Ana Mountain and the Palomar Mountain puma populations (Ernest et al. 2014; Vickers et al. 2015). An eight-lane highway, Interstate 15 (I-15), bisects the two mountain ranges and recent conservation attention has been paid to identifying locations for road crossing structures along its length. Therefore, as an example of how landscape definition might affect conservation agendas, we sought to identify road-crossing locations for each of the five selected models. First, we used CircuitScape (McRae et al. 2013) to create current density maps (McRae et al. 2008) across each conductance surface between nationally protected lands on either side of I-15. We then identified the top 10 pixels along I-15 with the most current flow, which might be considered preferred locations for constructing road-crossing structures. In this context, 'current flow' represents the number of random walkers that would move through a pixel as they passed between protected areas. We noted the location of the road-crossing pixels for each of our five landscape definitions as well as differences in these locations among landscape definitions.

Results

Delta AICc, D2 and CCC of the 2,000 conditional logistic regression models varied widely with landscape definition (Fig 4.2). The top model had only one competing model within 4 AICc units and two others within 10 AICc units; all other models were greater than 10 delta AICc units from the top model. Thus, only 4 (<1%) of the models were at all competitive out of the 2,000 evaluated, and the great majority of models were vastly inferior with delta AICc values greater than 100. D2 followed similar patterns, and even though the vast majority of models explained an ecologically meaningful percent of the deviance, the range in absolute explanatory power among models extended from 0.002 to 0.887. CCC was much less sensitive to landscape definition than AICc and D2, with most models having well-calibrated predictions, but nonetheless revealing that many models had unacceptably poorly calibrated predictions.

Figure 4.2. Model performance. Histograms of (a) delta AICc, (b) percent deviance explained (D2), and (c) concordance correlation coefficient (CCC) across our 2,000 landscape definitions associated with modeling puma movement in southern California. The first and second vertical dashed lines in (a) represent a delta AICc of 4 and 10 respectively.



Likelihood ratio tests indicated that spatial grain significantly influenced both AICc and D2 values (AICc: df=4, X^2=534.18, p<2.2e-16; D2: df=4, X^2=519.45, p<2.2e-16), with finer spatial grain resulting in better AICc and D2 values (Figs. 4.3a-4.4a; Appendix Ea). The number of layers included in a landscape definition also significantly influenced both AICc and D2 (AICc: df=6, X^2=456.69, p<2.2e-16; D2: df=6, X^2=437.79, p<2.2e-16), with greater number of layers resulting in better AICc and D2 values (Figs. 4.3c-4.4b, Appendix Ec). The number of variables in a landscape definition significantly influenced D2, but not AICc (AICc: df=26, X^2=22.08, p=0.684; D2: df=26, X^2=42.75, p=0.021), with greater number of variables resulting in higher D2 value (Fig. 4.3d,

Appendix Ed). This was expected as adding more variables will improve D2, but the addition of weak and/or spurious variables will be penalized using AICc. Similarly, model form significantly influenced D2, but not AICc (AICc: df=2, X^2=5.26, p=0.072; D2: df=2, X^2=6.65, p=0.0.036), indicating landscape definitions with a mix of continuous and categorical layers resulted in higher D2 values than landscape definitions with only continuous or only categorical layers (Figs. 4.3b-4.4c; Appendix Eb). None of the definition options significantly affected CCC (Appendix D & F).

Figure 4.3. Mean and standard error in model AICc as a function of spatial grain, variable form, number of geospatial layers, and number of variables in a landscape definition associated with modeling puma movement in southern California.

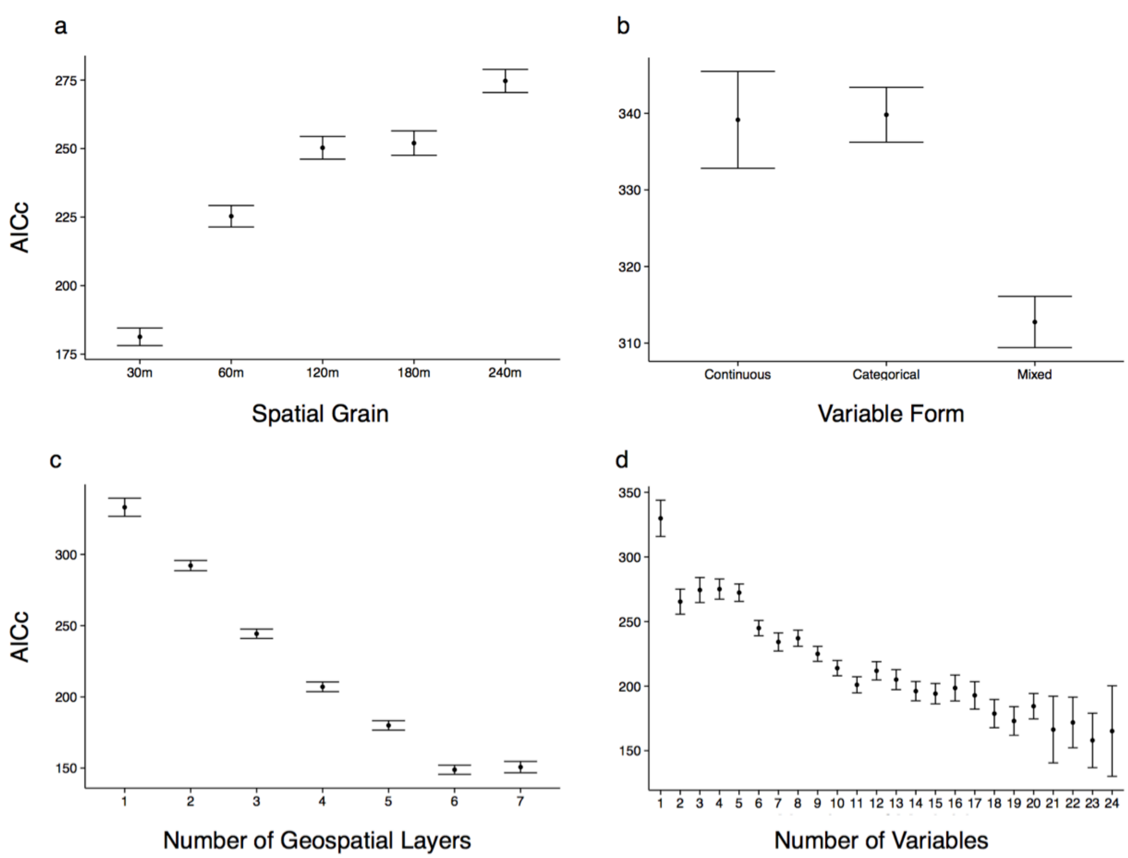
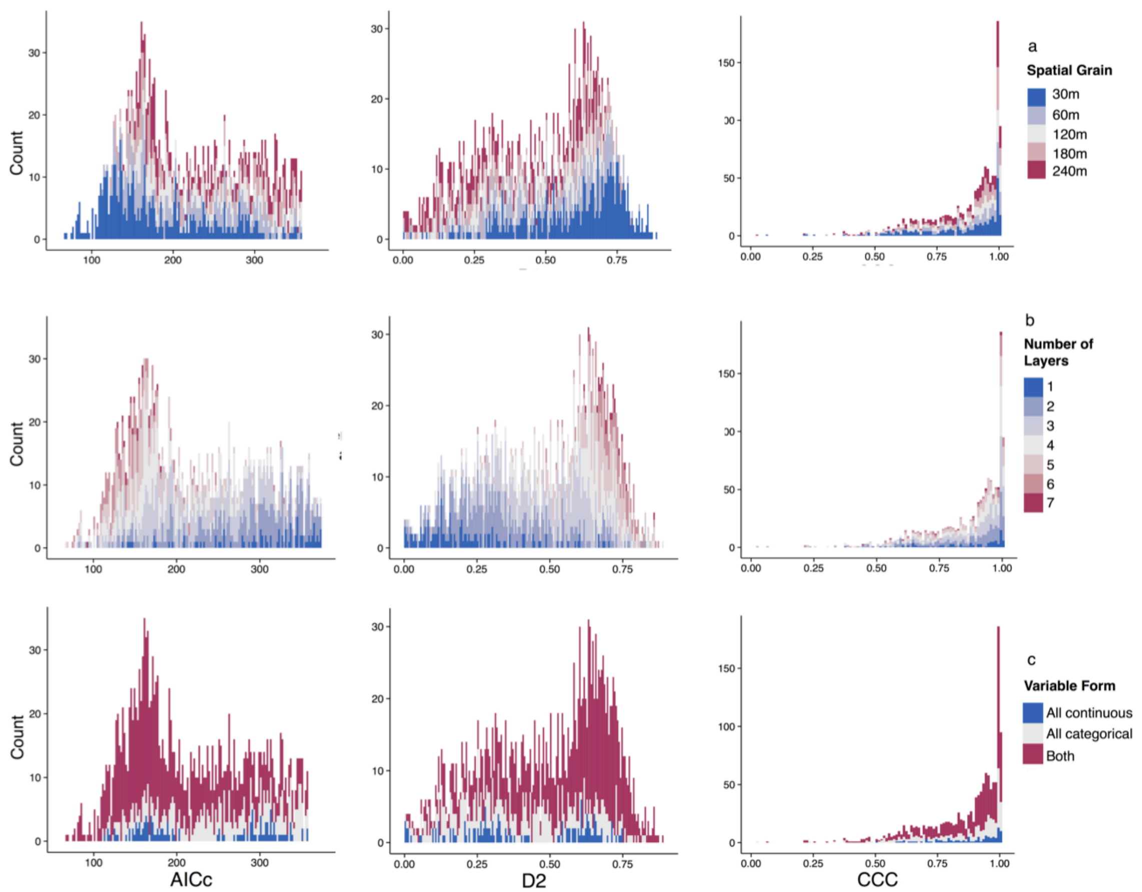


Figure 4.4. Model performance by definition option. AICc, percent deviance explained (D2), and concordance correlation coefficient (CCC) values for Path Selection Function models derived with 2,000 different landscape definitions associated with modeling puma movement in southern California. Histograms are color-coded according to (a) the spatial grain of the landscape definition (30m, 60m, 120m, 180m, 240m), (b) the number of geospatial layers included in a landscape definition (1-7), and (c) the form of the variables in the landscape definition (whether they are represented continuously, categorically, or both).



The top four models (based on delta AICc: 0, 2.85, 8.82, 9.81) and their associated landscape definitions and variable odds ratios are provided in Table 4.2. These top four models had D2>0.86 and CCC> 0.95, and thus all four of these models had exceptionally strong explanatory power and well-calibrated predictions. These top-ranked models included 4-5 geospatial layers and a mix of continuous and categorical layer representations for a total of 5-10 variables per model. All four of these models were at a spatial grain of 30m and included percent slope defined continuously. All four of these models also included roads defined with two classes (primary and secondary roads); however, the source of the roads data varied among models. Elevation, terrain ruggedness, percent impervious surface and percent vegetative cover were included in various forms in some but not all of these models. Only land cover type was not included in any of the top four models. The exact interpretation of these models requires coupling the characteristic scale of each variable (Appendix C) with the corresponding regression coefficient or, preferably, the odds ratio (Table 4.2). Briefly, across these top four models, pumas strongly avoided areas with steep slopes evaluated over intermediate scales (1500 m). Pumas showed weak preference for lower elevations evaluated over intermediate scales (1500-2000m). Pumas generally avoided less rugged terrain at intermediate scales (1500m) and strongly avoided more rugged terrain at very coarse scales (7500m). Pumas showed very weak preference for increasing percent vegetative cover evaluated over coarse scales (6500m). Pumas strongly selected areas with the lowest percentage of impervious surfaces (0 – 12%) evaluated over coarse scales (7500m). Lastly, pumas showed strong avoidance of primary and secondary roads evaluated over coarse scales (7500m).

Table 4.2. Top four landscape definitions, as indicated by AICc values, for modeling puma movement in southern California and the associated geospatial layers, thematic resolutions, thematic class (variables in the model) and associated odds ratio. All geospatial layers were at a 30m spatial grain. NLCD=National Land Cover Database. OSM=Open Street Map. Note, some landscape definitions do not contain the full set of classes for a layer because the absent variables were highly correlated (>=0.7) with other variables in the same model.

Layer	Thematic Resolution	Class	Model 1 Odds Ratio	Model 2 Odds Ratio	Model 3 Odds Ratio	Model 4 Odds Ratio
Percent Slope	*Continuous*	-	*0.004*	*0.07*	*0.006*	*0.067*
Elevation	*Continuous*	-		*0.99*	*0.91*	
Elevation	*Four Classes*	*1*	*1.16*			
		3	*1.0*			
		4	*0.99*			
Elevation	*Five Classes*	*1*				*1.0*
		3				*0.99*
		4				*0.99*
		5				*1.0*
Terrain Ruggedness	*Three Classes*	*1*	*0.64*			
		2	*0.99*			
		3	*0.0007*			
Terrain Ruggedness	*Four Classes*	*1*			*1.01*	
		2			*1.06*	
		3			*1.01*	
		4			*0.003*	
NLCD Percent Vegetative Cover	*Continuous*	-				*1.01*
NLCD Percent Vegetative Cover	*Three Classes*	*1*			*0.99*	
		3			*1.0*	
Percent Impervious Surface	*Four Classes*	*1*		*17.16*		*7.19*
OSM Roads	*Two Classes*	*1*	*0.0005*	*0.098*		*0.61*
		2	*0.0011*	*0.077*		*0.13*
County Roads	*Two Classes*	*1*			*0.002*	
		2			*0.17*	

Our layer importance results indicate that most geospatial layer representations improved model performance (positive values, Table 4.3, Mean difference in AICc). However, some layer representations resulted in worse model performance (negative values, Table 4.3, Mean difference in AICc). We expected the layer representations present in our top four models to also have high importance as judged by our criterion, but this expectation was not consistently supported. For example, the most important layer representation (LandFire land cover represented with five classes) was not present in any of our top four models. In addition, one layer representation that was present in our top four models even had a negative average importance value (terrain ruggedness represented categorically with three classes). We believe these results are due to the fact that our top-ranked models were outliers in the distribution of our 2,000 model definitions, and that these results more closely reflect the relative importance of layer representations in the center of the model distribution.

Similarly, we expected some geospatial data sources to improve AICc values more than others. However, we did not see any consistent improvement in model performance due to data source (Table 4.3). For example, the LandFire data source for land cover type was associated with both the most important layer representation (represented with 5 classes) and the 32nd most important layer (represented with 8 classes) out of the 40 representations.

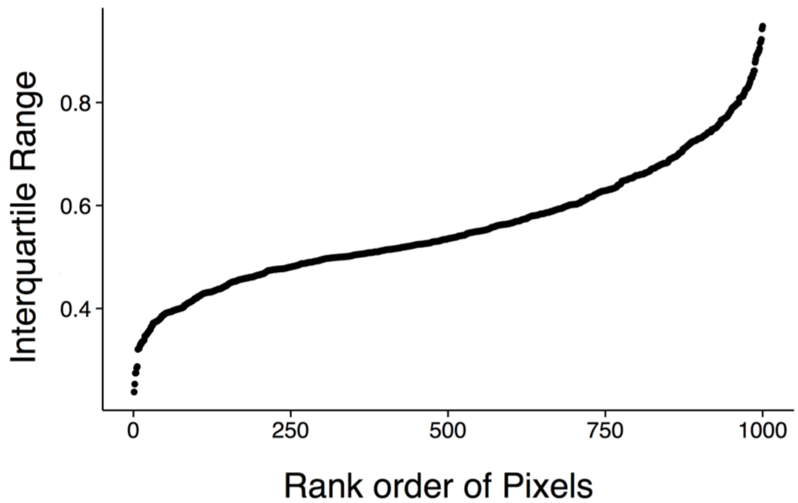
Probability of movement/conductance values at the 1,000 randomly selected pixels varied widely across the 2,000 landscape definitions (Fig. 4.5). The interquartile range at a pixel ranged from 0.2 to 1, with most of the pixels varying between 0.5 – 0.65. This indicates that probability of movement/conductance values are highly sensitive to the landscape definition used in the model.

Table 4.3. Relative importance of geospatial layer representations across spatial grains in generalized linear models predicting puma movement in southern California.

Layer	Thematic Resolution	Mean Difference in AICc
LandFire Land Cover Type	5 Classes	73
Percent Impervious Surface	4 Classes*	67
LandFire Percent Vegetative Cover	4 Classes	41
NLCD Percent Vegetative Cover	3 Classes*	38
Landsat Percent Vegetative Cover	3 Classes	32
NLCD Percent Vegetative Cover	4 Classes	31
NLCD Percent Vegetative Cover	Continuous*	27
County Roads	2 Classes*	25
Percent Slope	5 Classes	25
Percent Slope	4 Classes	24
Terrain Ruggedness	4 Classes*	22
Percent Impervious Surface	Continuous	22
Percent Slope	Continuous*	21
LandFire Percent Vegetative Cover	5 Classes	20
Landsat Percent Vegetative Cover	4 Classes	19
Landsat Percent Vegetative Cover	5 Classes	18
Landfire Percent Vegetative Cover	Continuous	17
Terrain Ruggedness	5 Classes	16
Elevation	5 Classes*	13
CalVeg Land Cover Type	5 Classes	12
Terrain Ruggedness	Continuous	12
Elevation	Continuous*	11
OSM Roads	2 Classes*	10
OSM Roads	3 Classes	9
NLCD Land Cover Type	8 Classes	8
LandFire Percent Vegetative Cover	3 Classes	6
County Roads	3 Classes	4
Percent Slope	3 Classes	4
Elevation	4 Classes*	4
Elevation	3 Classes	3
CalVeg Land Cover Type	8 Classes	1
LandFire Land Cover Type	8 Classes	-1
OSM Roads	4 Classes	-1
Percent Impervious Surface	5 Classes	-2
Terrain Ruggedness	3 Classes*	-4
NLCD Land Cover Type	5 Classes	-7
NLCD Percent Vegetative Cover	5 Classes	-14
Percent Impervious Surface	3 Classes	-22
County Roads	4 Classes	-33

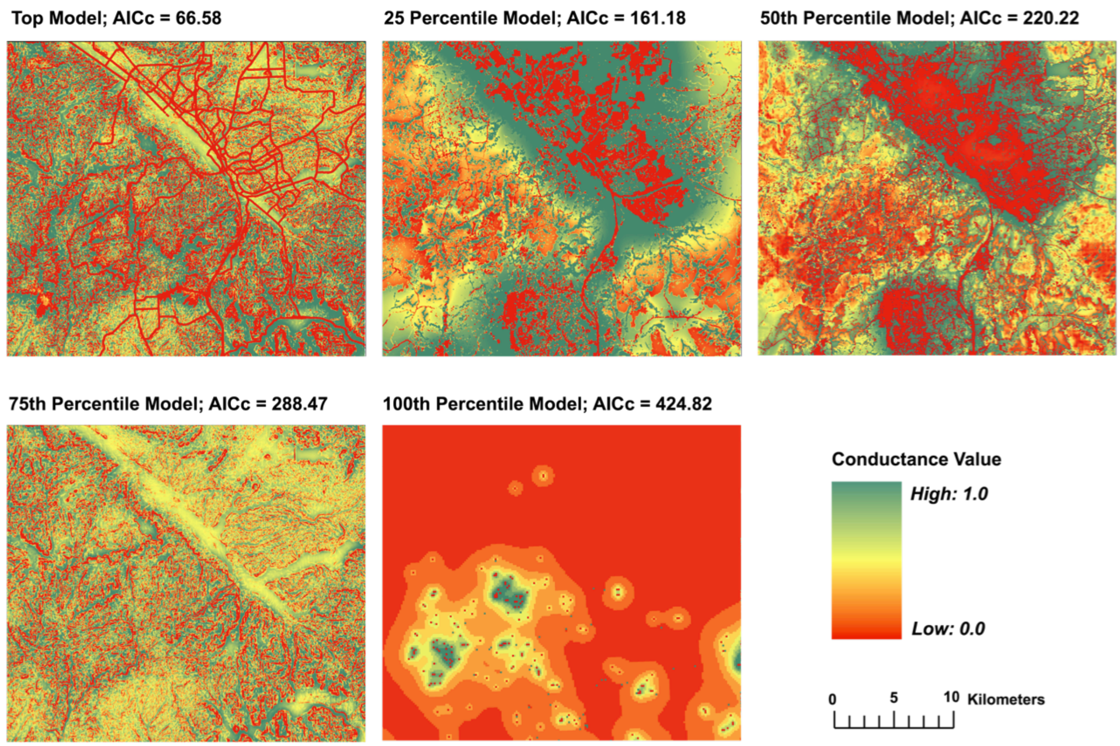
* Indicates a layer representation that was present in one of the top four models

Figure 4.5. Interquartile range of probability of movement values. Empirical distribution plot of the interquartile range of probability of movement (or conductance) values across the 2,000 models of puma movement in southern California for 1,000 randomly selected pixels across the study area.



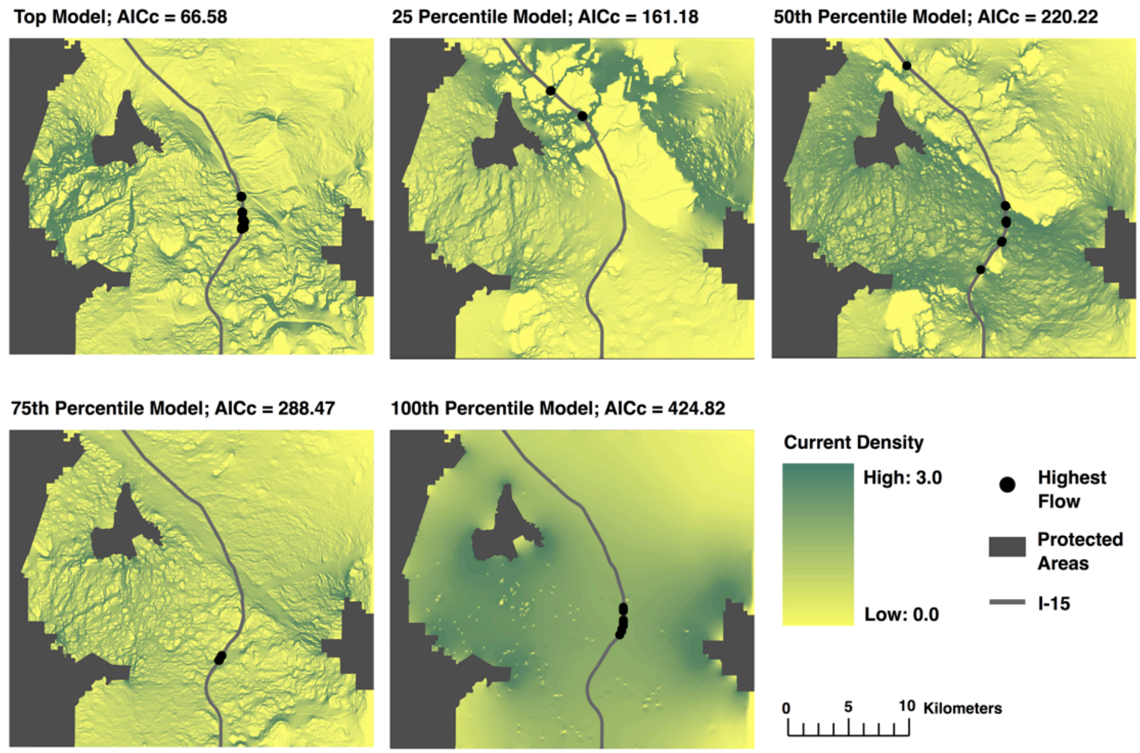
Probability of movement/conductance surfaces for the top model and the 25th, 50th, 75th, and 100th percentile of AICc values also varied widely visually (Fig. 4.6). Probability of movement/conductance was relatively evenly distributed across the study area in the top model. The 25th percentile model showed stark contrast between areas with high and low conductance, with fairly high conductance immediately surrounding (but not in) urban areas and lower conductance in the more natural mountainous areas. A similar pattern was observed in the 50th percentile surface. Most of the 75th percentile surface showed a medium to high conductance relatively evenly distributed across the study area, while most of the 100th percentile surface showed a very low conductance throughout the study area except in a few locations. The model results of these five example landscape definitions are included in Appendix G.

Figure 4.6. Probability of puma movement/conductance surfaces for a subset of the study area in southern California for the top-ranked model and models with the 25th, 50th, 75th, and 100th percentile of AICc values.



CircuitScape current density surfaces and the locations of the top 10 pixels along I-15 that had the most current, or greatest inferred flow of individuals, differed markedly according to landscape definition (Fig. 4.7).

Figure 4.7. Road crossing locations. CircuitScape current density surfaces associated with modeling puma movement in southern California and the point locations along I-15 with the 10 highest current densities.



Discussion

As landscape ecologists we are keenly aware of the importance of scale in wildlife-habitat inference and the preeminent importance of landscape definition in any landscape ecological analysis. As such, we conducted this study with the full expectation that puma habitat selection during within-home range movements in southern California would be somewhat sensitive to landscape definition. What our study revealed in this regard, however, was quite startling -- that inferred habitat selection, probability of movement/conductance surfaces and resultant connectivity models were exceptionally sensitive to landscape definition. Indeed, despite all 2,000 of the alternative landscape definitions evaluated being plausible and realistic given our current understanding of pumas in southern California, the weight of empirical evidence (based on AICc) was overwhelmingly in support of only a few of the alternative models. Moreover, the absolute explanatory power (based on percent deviance explained, D2) of the alternative models varied widely. Interestingly, despite the dramatic differences among alternative models in their relative and absolute explanatory power, the vast majority of the alternative models produced predictive surfaces very well calibrated to the landscape (based on the concordance correlation coefficient, CCC). Overall, these results suggest that there may be many alternative ways to define the landscape that will produce well-calibrated predictive surfaces that individually are significantly better than random, but that there may be very few clearly superior ways to the define the landscape. Indeed, there are a vast many more ways to define the landscape relatively poorly than there are to "get it right", even though all definitions seem plausible a priori.

These findings naturally extend to probability of movement/conductance surfaces and connectivity modeling. In our case study of pumas, the relative predicted probability of movement/conductance values, for most pixels, ranged nearly from 0 to 1 across alternative landscape definitions, indicating that different landscape definitions may result in polar opposite conclusions regarding probability of movement/conductance for the same location. This can have profound implications for connectivity modeling that is based on surface conductance. Indeed, predicted road crossing locations from various landscape definitions in our connectivity modeling exercise were strikingly different. Our findings align with those of Cushman et al. (2010a) who predicted road-crossing locations for black bears with two different resistance surfaces (one derived from genetic data and one derived from path data). Despite the fact that both resistance surfaces included the same variables and were very highly correlated, they produced very different road crossing locations. Consequently, recommended locations for constructing wildlife road crossing structures strongly depends on the chosen landscape definition.

We conducted this study with the expectation that some geospatial layers and digital representations of them (e.g., at certain spatial grains and thematic resolutions based on one particular data source) would marginally outperform others. Specifically, we hypothesized that model performance would increase with (1) decreasing spatial grain, (2) increasing thematic resolution and (3) increasing number of geospatial layers, and (4) that some data sources would improve model performance more than others. Consistent with our first hypothesis, our puma model performance was most sensitive to the spatial grain of the landscape definition, with finer spatial grains resulting in better model performance. These findings agree with other studies that have examined the effect of spatial grain on performance of species-habitat models (Karl et al. 2000; Seoane et al. 2004; Venier et al. 2004; Guisan et al. 2007; Cushman and Landguth 2010a; Gottshcalk et al. 2011). In contrast to model performance, we found the calibration of our predictions to be insensitive to spatial grain, similar to Guisan et al. (2007) who found no effect of spatial grain on the predictive performance of their species distribution models. Though Seoane et al. (2004) and Tobalske (2002) found an increase in predictive performance of species distribution models with decreasing spatial grain. Landscape definitions at our coarsest grain size (240m) generally resulted in poorer performing models, which is noteworthy because this spatial grain is very close to many freely available data platforms such as MODIS and CORINE (both 250m). Overall, our results indicate that finer-grained geospatial data are superior for modeling puma movement in southern California; however, we cannot say whether this finding is generalizable to other contexts.

Support for our second hypothesis regarding thematic resolution was equivocal. The best performing models tended to have a mix of layers defined continuously and categorically. Based on our previous work we expected models with all continuous layers to outperform categorical-only and mixed definition models (McGarigal and Cushman 2005; Cushman et al. 2010a; Cushman et al. 2010b; Cushman & Landguth 2010a). Moreover, we generally expected finer thematic resolutions to have greater model performance than coarser resolutions of that same layer, as in Cushman & Landguth (2010a) and Seoane et al. (2004). Perhaps our results differed from the previous studies because pumas in our study area are responding to more broadly defined landscape patterns, which are sometimes better reflected as categorical layers, than more finely detailed landscape structure. Another possibility is that pumas are responding to some variables in a non-linear, step-wise form and the categorical nature of some variables better captured this relationship than continuous variables. The issue of thematic resolution was first addressed in McArthur et al. (1966) who found that bird species in one location appeared to respond to a higher number of vegetation classes than bird species in another location. Given the many decades that have passed since this paper was published it is surprising that more research has not been conducted on how thematic resolution of geospatial layers affects species-habitat models. The equivocal results of thematic resolution on model performance found here and by Lawler et al. (2004) indicate that this is an area ripe for further research.

In support of our third hypothesis, our puma model performance was very sensitive to the number of geospatial layers in the landscape definition, with increasing number of layers resulting in better model performance. However, there was no clarity in our variable importance results in terms of which layers and associated layer representations were better than others. While the results likely reflected layer importance for the bulk of the model distribution, they did not adequately capture the layers in the top models. These results further highlight that our top models were outliers in our suite of landscape definitions.

With regards to our last hypothesis, we did not find an effect of data source on our puma model performance. This is in contrast to previous studies (Chust et al. 2004; Seoane et al. 2004). However, these studies confounded data source with spatial grain, indicating that spatial grain may have been more influential than the actual sources of data. Though not wildlife-specific, Cushman et al. (2010a) evaluated the ability of different land cover maps to predict the distribution of plant species. In their analysis, they did not confound grain and data source and found large differences in the explanatory power of the different data sources. For pumas in our study area, other landscape definition options were more influential than data source, though weighing the pros and cons of different data sources is surely an important consideration when selecting geospatial layers.

Our comprehensive empirical evaluation of alternative landscape definitions for modeling puma movement in southern California allowed us to identify clearly superior landscape definitions among the pool of viable candidates, which we contend led to stronger inference about puma habitat selection during movement in the study area than had we a priori selected a single landscape definition. We learned from our top-ranked models that slope was better represented as a continuous variable and that pumas showed a strong avoidance of steep slopes, as has been previously documented (Beier 1995; Dickson et al. 2005; Dickson & Beier 2006; Wilmers et al. 2013). All top-ranked models also included at least one of the other two topographic variables, elevation (represented either continuously or categorically) and terrain ruggedness (better represented categorically), indicating that pumas are strongly influenced by topography, as has been previously documented (Alexander et al. 2006; Allen et al. 2014; Burdett et al. 2010; Wilmers et al. 2014). Our top-ranked models also indicated a strong avoidance of primary and secondary roads by pumas, echoing previous research (Dickson et al. 2005; Wilmers et al. 2014). Two of our top-ranked models also included percent impervious surface represented categorically and indicated that pumas strongly selected for the lowest class of imperviousness (0-12%; Burdett et al. 2010).

One of our most noteworthy findings with regards to puma habitat selection was the apparent lack of strong selection for vegetation composition and structure in the top models, which was the sole basis for defining the landscape in our previous modeling work in this system (Zeller et al. 2014, 2015). Only one of our top-ranked models included any type of vegetative characteristic and, moreover, selection was weak, with pumas slightly avoiding areas with low percent cover and slightly preferring areas with high percent cover. Land cover type (actually, the relative abundance of individual land cover types) was not in any of the top-ranked models. Overall, our results suggest pumas in our study area respond more strongly to topographic variables and human development in the form of roads and other impervious surfaces than other landscape characteristics related to the composition and structure of vegetation. This finding aligns somewhat with recent findings by Gray et al. (2016) that showed that distance from roads (as a proxy for human development) could be used to accurately model puma occurrence and landscape permeability. The similarities to our findings may be due to the fact that both our study areas had relatively high levels of human development. However, these results are also similar to other studies on large felids. Elliot et al. (2014) showed vegetation was much weaker than roads, towns, and agricultural lands in predicting lion movement and Krishanmurthy et al. (*in press*) showed agricultural areas and villages were more important for predicting tiger movement than natural vegetation. Importantly, our findings do not mean that pumas during within-home range movement do not select for vegetation composition and structure, but rather that, comparatively, selection is much stronger for terrain and human development than vegetation. Note, it is also possible that vegetation cover attributes were not selected in the top-ranked models because topographic variables served as a proxy for vegetation cover types, as has been observed in previous studies (Burrough et al. 2001; Beier & Brost 2010). To examine this hypothesis further, we conducted a variance partitioning using the ecospat package in R (Broennimann et al. 2015) to portion the explained variance in the top model (with land cover type added as a predictor) between the terrain and human development predictors and land cover type predictors. Terrain and human development independently accounted for 8.7% of the explained variance, land cover independently accounted for 5.7% of the explained variance, and these predictors jointly accounted for 86% of the explained variance. Thus, the vast majority of the explained variance was confounded between the two sets of predictors and we are therefore unable to say whether terrain is acting as a proxy for vegetative characteristics or vice versa.

In summary, our findings have tremendous implications for both research and conservation planning. First, we had expected to find that our alternative landscape definitions would produce only slight differences in model performance in our case study on pumas in southern California. Instead, we found massive differences in model performance among the alternatives, with only a handful of competing landscape definitions among the 2,000 models evaluated. If we were able to run the full factorial of landscape definitions, we may have found that there were indeed a greater number of competing models and perhaps an even better performing top model. However, most researchers will only be able to compare a limited set of landscape definitions. Our results indicate that, at least for PathSFs, researchers may need to evaluate many different landscape definitions to find the optimal landscape representation for a study area and target species. Evaluating habitat and movement relationships with thematic resolution, thematic content, and grain that do not match the organisms' ecology and perceptions can greatly reduce model performance and the interpretations gained from models of landscape conductance.

This finding is relevant in consideration of Type I and Type II errors and the issue of affirming the consequent (Cushman & Landguth 2010b), in which a result that is consistent with a hypothesis is incorrectly accepted as demonstration that the hypothesis is true. Specifically, high sensitivity of model performance to variable grain and thematic resolution that we observed suggest elevated risk of Type II errors (failing to see an effect when it is present) when using variables at suboptimal definition. In addition, the high inherent correlation among variables increases the difficulty of distinguishing effects such that the risk of affirming spurious correlations and making Type I errors is elevated.

The practice of dropping variables from correlated pairs reduces variance inflation and Type I error rate in the full model, but can result in affirming spurious correlations if the incorrect variable is dropped. The high dependence of variable influence on landscape definition compounds the challenge of resolving this.

Second, given that many resource selection functions are used to predict the relative probability of use across a study area to identify resource use areas for conservation purposes, the wide differences among predicted values at the same pixels across landscape definitions is very disconcerting, and indicates different landscape definitions result in huge differences in predicted quality of locations for movement. In our case study on pumas we were specifically modeling probability of within-home range movement, which may be more sensitive to landscape definition than modeling probability of use, but further research is needed to determine this. Additionally, previous studies have found that dispersal of individuals is less constrained by landscape features than home-range use (Elliot et al. 2014; Mateo Sánchez et al. 2014), which might suggest that connectivity estimates derived from dispersal data would be less sensitive to landscape definition than within home-range data.

Differences in the predicted probability of movement /conductance surfaces also translated into differences among modeled connectivity surfaces (derived using CircuitScape) and the optimal road crossing locations, again in agreement with Cushman et al. (2010a). It was reassuring that our top model identified road crossing locations that have been approached by pumas in our study area and that were also identified by a consensus of road ecology and puma experts (Vickers et al. unpublished report). However, the alternative landscape definitions were highly variable in identifying optimal road crossing locations, in some cases agreeing with the top model and in other cases indicating very different locations. Thus, had we a priori selected only a single landscape definition, there is a very good chance we would have produced a very different probability of movement/conductance surface, derived very different optimal road crossing locations, and possibly inspired a multi-million dollar crossing structure in a suboptimal location.

Lastly, the way the landscape is represented is at the heart of all species-habitat models. Landscape definition will ultimately affect inference about species-habitat relationships, probability of use surfaces, and connectivity estimates. Therefore, defining the landscape to the best of our ability is of utmost importance. To our knowledge, this is the first study to assess model performance across all of the following four landscape definition choices: (1) spatial grain, (2) thematic resolution, (3) number of geospatial layers, and (4) source of geospatial layers. More research is needed to determine the effect of landscape definition on other species-habitat models such as point and step selection functions, species distribution models, and occupancy models. Research is also needed to more effectively tease apart the effects of thematic resolution and layer source on species-habitat models. Regardless, our results demonstrate the profound effect of landscape definition on species-habitat models. When possible, we recommend that researchers examine a variety of landscape definitions and at the very least put a great deal of thought into how the landscape is defined for their species and question of interest.

Appendices

Appendix A. Classes and class breakpoints for all continuous geospatial layers (elevation, percent slope, terrain ruggedness, percent impervious surface, and percent vegetative cover).

Continuous layers were represented continuously and with 3, 4, or 5, classes. Value ranges of classes were determined with the Jenks optimization method.

Elevation

Number of Classes	**Class**	**Value Range (meters)**	
		From	*To*
3 Classes	1	0	327
	2	327	783
	3	783	1,871
4 Classes	1	0	275
	2	275	570
	3	570	974
	4	974	1,871
5 Classes	1	0	260
	2	260	504
	3	504	775
	4	775	1,158
	5	1,158	1,871

Percent slope

Number of Classes	**Class**	**Value Range (percent)**	
		From	*To*
3 Classes	1	0	17
	2	17	43
	3	43	179
4 Classes	1	0	12
	2	12	30
	3	30	55
	4	55	179
5 Classes	1	0	10
	2	10	25
	3	25	41
	4	41	64
	5	64	179

Terrain Ruggedness

Number of Classes	Class	Value Range (total curvature)	
		From	*To*
3 Classes	1	0	0.011
	2	0.011	0.042
	3	0.042	0.42
4 Classes	1	0	0.008
	2	0.008	0.027
	3	0.027	0.065
	4	0.065	0.42
5 Classes	1	0	0.006
	2	0.006	0.022
	3	0.022	0.044
	4	0.044	0.086
	5	0.086	0.42

Percent Impervious Surface

Number of Classes	Class	Value Range (percent)	
		From	*To*
3 Classes	1	0	20
	2	20	50
	3	50	100
4 Classes	1	0	12
	2	12	38
	3	38	64
	4	64	100
5 Classes	1	0	10
	2	10	30
	3	30	50
	4	50	70
	5	70	100

Percent Vegetative Cover

Number of Classes	Class	Value Range (percent)	
		From	*To*
3 Classes	1	0	10
	2	10	25
	3	25	100
4 Classes	1	0	7
	2	7	20
	3	20	30
	4	30	100
5 Classes	1	0	7
	2	7	17
	3	17	25
	4	25	40
	5	40	100

Appendix B. Crosswalks for categorical geospatial data (roads and land cover type).

There were two data sources for roads, Open Street Map and County roads (across 4 counties). There were three data sources for land cover type (National Land Cover Data Base, LandFire, and CalVeg). Original roads data were classified into 2, 3, or 4 categories. Original land cover data were classified into 5 or 8 categories.

Roads

Open Street Map

Road Type	Road Classification; 2-categories
Bridleway	Unpaved/Trail (Category 4)
Construction	Tertiary (Category 3)
Cycleway	Unpaved/Trail (Category 4)
Footway	Unpaved/Trail (Category 4)
Living street	Tertiary (Category 3)
Motorway	Primary(Category 1)
Motorway link	Primary(Category 1)
Path	Unpaved/Trail (Category 4)
Pedestrian	Tertiary (Category 3)
Platform	Tertiary (Category 3)
Primary link	Secondary (Category 2)
Primary	Secondary (Category 2)
Residential	Tertiary (Category 3)
Rest area	Tertiary (Category 3)
Road	Tertiary (Category 3)
Scale	Unpaved/Trail (Category 4)
Secondary	Secondary (Category 2)
Secondary link	Secondary (Category 2)
Service	Tertiary (Category 3)
Tertiary	Tertiary (Category 3)
Tertiary link	Tertiary (Category 3)
Track	Unpaved/Trail (Category 4)
Trunk	Secondary (Category 2)
Trunk link	Secondary (Category 2)
Unclassified	Tertiary (Category 3)

County Roads

San Diego

Road Type	Road Classification
Freeways and ramps	Primary(Category 1)
Light, 2 lane collector	Tertiary (Category 3)
Rural collector	Tertiary (Category 3)
Major 4-lane road	Secondary (Category 2)
Primary arterial	Primary(Category 1)
Private street	Tertiary (Category 3)
Recreational parkway	Tertiary (Category 3)
Rural mountain road	Tertiary (Category 3)
Alley	Tertiary (Category 3)
Class I bike path	Unpaved/Trail (Category 4)
4-lane collector	Secondary (Category 2)
2-lane major road	Tertiary (Category 3)
Expressway	Primary(Category 1)
Freeway	Primary(Category 1)
Local road	Tertiary (Category 3)
Military road	Unpaved/Trail (Category 4)
6-lane road	Secondary (Category 2)
Transit way	Tertiary (Category 3)
Unpaved road	Unpaved/Trail (Category 4)
Pedestrian	Unpaved/Trail (Category 4)

San Bernadino

NS_Code	Road Classification
4	Tertiary (Category 3)
5	Tertiary (Category 3)
6	Tertiary (Category 3)
7	Secondary (Category 2)
9	Secondary (Category 2)
A	Unpaved/Trail (Category 4)
C	Tertiary (Category 3)
E	Primary(Category 1)
F	Primary(Category 1)
L	Tertiary (Category 3)
P	Tertiary (Category 3)
R	Tertiary (Category 3)
S	Tertiary (Category 3)
T	Primary(Category 1)

Riverside

Road Definition	Road Classification
Interstate	Primary(Category 1)
Interstate ramp	Primary(Category 1)
State highway	Primary(Category 1)
State highway ramp	Primary(Category 1)
Expressway	Primary(Category 1)
Expressway ramp	Primary(Category 1)
Major road	Secondary (Category 2)
Arterial road	Secondary (Category 2)
Collector road	Tertiary (Category 3)
Residential road	Tertiary (Category 3)

Orange

Road Definition	Road Classification
Collector	Secondary (Category 2)
Major	Secondary (Category 2)
Primary	Secondary (Category 2)
Secondary	Tertiary (Category 3)
Principal	Secondary (Category 2)
Freeway	Primary(Category 1)

Land Cover Type

CalVeg

Type	Classification; 8-categories	Classification; 5-categories
Urban	Urban	Urban/Agriculture
Deciduous orchard	Agriculture	Urban/Agriculture
Annual grassland	Grassland	Grassland
Chamise redshank chaparral	Chaparral	Chaparral
Eucalyptus	Agriculture	Urban/Agriculture
Valley foothill riparian	Riparian	Woodland/Riparian
Montane riparian	Riparian	Woodland/Riparian
Coastal oak woodland	Woodland	Woodland/Riparian
Saline emergent wetland	Riparian	Woodland/Riparian
Freshwater emergent wetland	Riparian	Woodland/Riparian
Barren	Natural barren	Natural barren/Scrub
Pasture	Agriculture	Urban/Agriculture
Evergreen orchard	Agriculture	Urban/Agriculture
Perennial grassland	Grassland	Grassland
Coastal scrub	Scrub	Natural barren/Scrub
Mixed chaparral	Chaparral	Chaparral
Closed cone pine cypress	Chaparral	Chaparral
Lacustrine	Natural barren	Natural barren/Scrub
Desert riparian	Riparian	Woodland/Riparian
Crop	Agriculture	Urban/Agriculture
Montane hardwood conifer	Woodland	Woodland/Riparian
Vinyard	Agriculture	Urban/Agriculture
Montane chaparral	Chaparral	Chaparral
Sagebrush	Scrub	Natural barren/Scrub
Desert wash	Natural barren	Natural barren/Scrub
Sierran mixed conifer	Woodland	Woodland/Riparian
Montane hardwood	Woodland	Woodland/Riparian
Wet meadow	Riparian	Woodland/Riparian
Desert scrub	Scrub	Natural barren/Scrub
Juniper	Chaparral	Chaparral
White fir	Woodland	Woodland/Riparian

National Land Cover Database

Code:Type	Classification; 8-categories	Classification; 5-categories
11: Open water	Natural barren	Natural barren/Scrub
21: Developed, open space	Urban	Urban/Agriculture
22: Developed, low intensity	Urban	Urban/Agriculture
23: Developed, medium intensity	Urban	Urban/Agriculture
24: Developed, high intensity	Urban	Urban/Agriculture
31: Barren	Natural barren	Natural barren/Scrub
41: Deciduous forest	Woodland	Woodland/Riparian
42: Evergreen forest	Woodland	Woodland/Riparian
43: Mixed forest	Woodland	Woodland/Riparian
52: Shrub/scrub	Scrub	Natural barren/Scrub
71: Grassland/herbaceous	Grassland	Grassland
81: Pasture/hay	Agriculture	Urban/Agriculture
82: Cultivated crops	Agriculture	Urban/Agriculture
90: Woody wetlands	Riparian	Woodland/Riparian
95: Emergent herbaceous wetlands	Riparian	Woodland/Riparian

LandFire

Code:Type	Classification; 8-categories	Classification; 5-categories
3002: Mediterranean California Sparsely Vegetated Systems	Natural barren	Natural barren/Scrub
3004: North American Warm Desert Sparsely Vegetated Systems	Natural barren	Natural barren/Scrub
3014: Central and Southern California Mixed Evergreen Woodland	Woodland	Woodland/Riparian
3015: California Coastal Redwood Forest	Woodland	Woodland/Riparian
3019: Great Basin Pinyon-Juniper Woodland	Woodland	Woodland/Riparian
3027: Mediterranean California Dry-Mesic Mixed Conifer Forest and Woodland	Woodland	Woodland/Riparian
3028: Mediterranean California Mesic Mixed Conifer Forest and Woodland	Woodland	Woodland/Riparian
3029: Mediterranean California Mixed Oak Woodland	Woodland	Woodland/Riparian
3034: Mediterranean California Mesic Serpentine Woodland and Chaparral	Chaparral	Chaparral
3082: Mojave Mid-Elevation Mixed Desert Scrub	Scrub	Natural barren/Scrub
3087: Sonora-Mojave Creosotebush-White Bursage Desert Scrub	Scrub	Natural barren/Scrub
3088: Sonora-Mojave Mixed Salt Desert Scrub	Scrub	Natural barren/Scrub
3092: Southern California Coastal Scrub	Scrub	Natural barren/Scrub
3096: California Maritime Chaparral	Chaparral	Chaparral
3097: California Mesic Chaparral	Chaparral	Chaparral
3098: California Montane Woodland and Chaparral	Chaparral	Chaparral
3099: California Xeric Serpentine Chaparral	Chaparral	Chaparral
3105: Northern and Central California Dry-Mesic Chaparral	Chaparral	Chaparral
3108: Sonora-Mojave Semi-Desert Chaparral	Chaparral	Chaparral
3110: Southern California Dry-Mesic Chaparral	Chaparral	Chaparral
3112: California Central Valley Mixed Oak Savanna	Woodland	Woodland/Riparian
3113: California Coastal Live Oak Woodland and Savanna	Woodland	Woodland/Riparian
3118: Southern California Oak Woodland and Savanna	Woodland	Woodland/Riparian
3128: Northern California Coastal Scrub	Scrub	Natural barren/Scrub
3129: California Central Valley and Southern Coastal Grassland	Grassland	Grassland

3130: California Mesic Serpentine Grassland	Grassland	Grassland
3131: California Northern Coastal Grassland	Grassland	Grassland
3135: Inter-Mountain Basins Semi-Desert Grassland	Grassland	Grassland
3138: North Pacific Montane Grassland	Grassland	Grassland
3152: California Montane Riparian Systems	Riparian	Woodland/Riparian
3155: North American Warm Desert Riparian Forest and Woodland	Riparian	Woodland/Riparian
3163: Pacific Coastal Marsh Systems	Riparian	Woodland/Riparian
3181: Introduced Upland Vegetation-Annual Grassland	Grassland	Grassland
3182: Introduced Upland Vegetation-Perennial Grassland and Forbland	Grassland	Grassland
3183: Introduced Upland Vegetation-Annual and Biennial Forbland	Grassland	Grassland
3184: California Annual Grassland	Grassland	Grassland
3258: North American Warm Desert Riparian Herbaceous	Riparian	Woodland/Riparian
3292: Open water	Natural barren	Natural barren/Scrub
3294: Barren	Natural barren	Natural barren/Scrub
3295: Quarries-Strip Mines-Gravel Pits	Urban	Urban/Agriculture
3296: Developed-Low Intensity	Urban	Urban/Agriculture
3297: Developed-Medium Intensity	Urban	Urban/Agriculture
3298: Developed-High Intensity	Urban	Urban/Agriculture
3299: Developed-Roads	Urban	Urban/Agriculture
3900: Western Cool Temperate Urban Deciduous Forest	Urban	Urban/Agriculture
3901: Western Cool Temperate Urban Evergreen Forest	Urban	Urban/Agriculture
3902: Western Cool Temperate Urban Mixed Forest	Urban	Urban/Agriculture
3903: Western Cool Temperate Urban Herbaceous	Urban	Urban/Agriculture
3904: Western Cool Temperate Urban Shrubland	Urban	Urban/Agriculture
3910: Western Warm Temperate Urban Deciduous Forest	Urban	Urban/Agriculture
3911: Western Warm Temperate Urban Evergreen Forest	Urban	Urban/Agriculture
3912: Western Warm Temperate Urban Mixed Forest	Urban	Urban/Agriculture
3913: Western Warm Temperate Urban Herbaceous	Urban	Urban/Agriculture
3914: Western Warm Temperate Urban Shrubland	Urban	Urban/Agriculture
3921: Western Cool Temperate Developed Ruderal Evergreen Forest	Agriculture	Urban/Agriculture
3922: Western Cool Temperate Developed Ruderal Mixed Forest	Agriculture	Urban/Agriculture
3923: Western Cool Temperate Developed Ruderal Shrubland	Agriculture	Urban/Agriculture
3924: Western Cool Temperate Developed Ruderal Grassland	Agriculture	Urban/Agriculture
3926: Western Warm Temperate Developed Ruderal Evergreen Forest	Agriculture	Urban/Agriculture
3927: Western Warm Temperate Developed Ruderal Mixed Forest	Agriculture	Urban/Agriculture
3928: Western Warm Temperate Developed Ruderal Shrubland	Agriculture	Urban/Agriculture
3929: Western Warm Temperate Developed Ruderal Grassland	Agriculture	Urban/Agriculture
3946: Western Warm Temperate Undeveloped Ruderal Evergreen Forest	Agriculture	Urban/Agriculture

3947: Western Warm Temperate Undeveloped Ruderal Mixed Forest	Agriculture	Urban/Agriculture
3948: Western Warm Temperate Undeveloped Ruderal Shrubland	Agriculture	Urban/Agriculture
3949: Western Warm Temperate Undeveloped Ruderal Grassland	Agriculture	Urban/Agriculture
3960: Western Cool Temperate Orchard	Agriculture	Urban/Agriculture
3964: Western Cool Temperate Row Crop	Agriculture	Urban/Agriculture
3965: Western Cool Temperate Close Grown Crop	Agriculture	Urban/Agriculture
3966: Western Cool Temperate Fallow/Idle Cropland	Agriculture	Urban/Agriculture
3968: Western Cool Temperate Wheat	Agriculture	Urban/Agriculture
3980: Western Warm Temperate Orchard	Agriculture	Urban/Agriculture
3984: Western Warm Temperate Row Crop	Agriculture	Urban/Agriculture
3985: Western Warm Temperate Close Grown Crop	Agriculture	Urban/Agriculture
3986: Western Warm Temperate Fallow/Idle Cropland	Agriculture	Urban/Agriculture
3987: Western Warm Temperate Pasture and Hayland	Agriculture	Urban/Agriculture
3988: Western Warm Temperate Wheat	Agriculture	Urban/Agriculture

Appendix C. Characteristic scale of variables for each geospatial layer representation.

Scales were determined by creating univariate Path Selection Function models with each layer representation and examining AICc values for a layer representation across scales. The model and associated scale with the lowest AICc value was considered the characteristic scale of selection. These scales were then used in the multiple regression models for the 2,000 landscape definitions. Ten scales were evaluated ranging from 500m to 7,500m.

				Characteristic Scale (m)							
Geospatial layer	**Thematic Resolution**	**Spatial Grain**	**Cont-inuous**	**Class 1**	**Class 2**	**Class 3**	**Class 4**	**Class 5**	**Class 6**	**Class 7**	**Class 8**
County roads	2 classes	30m		7,500	7,500						
County roads	2 classes	60m		7,500	7,500						
County roads	2 classes	120m		7,500	7,500						
County roads	2 classes	180m		6,500	7,500						
County roads	2 classes	240m		6,500	7,500						
County roads	3 classes	30m		7,500	7,500	7,500					
County roads	3 classes	60m		7,500	7,500	7,500					
County roads	3 classes	120m		3,000	7,500	7,500					
County roads	3 classes	180m		6,500	7,500	7,500					
County roads	3 classes	240m		6,500	7,500	7,500					
County roads	4 classes	30m		7,500	7,500	500	500				
County roads	4 classes	60m		7,500	7,500	7,500	1,500				
County roads	4 classes	120m		3,000	7,500	7,500	2,000				
County roads	4 classes	180m		6,500	7,500	7,500	500				
County roads	4 classes	240m		6,500	7,500	7,500	2,000				
OSM roads	2 classes	30m		7,500	7,500						
OSM roads	2 classes	60m		7,500	7,500						
OSM roads	2 classes	120m		6,500	7,500						
OSM roads	2 classes	180m		6,500	7,500						
OSM roads	2 classes	240m		6,500	7,500						
OSM roads	3 classes	30m		7,500	7,500	7,500					
OSM roads	3 classes	60m		7,500	7,500	7,500					
OSM roads	3 classes	120m		7,500	7,500	7,500					
OSM roads	3 classes	180m		7,500	7,500	7,500					
OSM roads	3 classes	240m		7,500	7,500	7,500					
OSM roads	4 classes	30m		7,500	7,500	7,500	500				
OSM roads	4 classes	60m		7,500	7,500	7,500	1,500				
OSM roads	4 classes	120		3,000	7,500	7,500	2,000				
OSM roads	4 classes	180		6,500	6,500	6,500	500				
OSM roads	4 classes	240m		6,500	6,500	6,500	2,000				
CalVeg Land Cover	5 classes	30m		1,500	3,500	500	2,000	7,500			
CalVeg Land Cover	5 classes	60m		500	3,500	1,500	500	6,500			
CalVeg Land Cover	5 classes	120m		500	7,500	2,000	500	6,500			
CalVeg Land Cover	5 classes	180m		500	7,500	1,500	500	6,500			
CalVeg Land Cover	5 classes	240m		2,000	6,000	2,000	500	6,500			
CalVeg Land Cover	8 classes	30m		500	3,000	7,500	500	7,500	7,500	7,500	7,500

						Characteristic Scale (m)					
Geospatial layer	**Thematic Resolution**	**Spatial Grain**	**Cont-inuous**	**Class 1**	**Class 2**	**Class 3**	**Class 4**	**Class 5**	**Class 6**	**Class 7**	**Class 8**
CalVeg Land Cover	8 classes	60m		500	500	7,500	1,500	7,500	2,000	7,500	3,000
CalVeg Land Cover	8 classes	120m		500	500	7,500	2,000	7,500	500	7,500	5,500
CalVeg Land Cover	8 classes	180m		500	2,000	7,500	500	6,500	500	6,500	6,000
CalVeg Land Cover	8 classes	240m		2,000	1,500	7,500	2,000	6,500	500	7,500	6,000
LandFire Land Cover	5 classes	30m		1,500	3,500	1,500	1,500	7,500			
LandFire Land Cover	5 classes	60m		500	7,500	1,500	2,000	7,500			
LandFire Land Cover	5 classes	120m		500	7,500	7,500	500	6,500			
LandFire Land Cover	5 classes	180m		500	7,500	7,500	500	7,500			
LandFire Land Cover	5 classes	240m		500	7,500	2,000	7,500	6,500			
LandFire Land Cover	8 classes	30m		1,500	3,500	500	500	7,500	1,500	7,500	6,500
LandFire Land Cover	8 classes	60m		500	500	7,500	2,000	5,500	1,500	7,500	6,500
LandFire Land Cover	8 classes	120m		500	500	3,500	7,500	2,000	2,000	7,500	6,500
LandFire Land Cover	8 classes	180m		2,000	1,500	7,500	7,500	7,500	500	7,500	6,000
LandFire Land Cover	8 classes	240m		500	1,500	7,500	7,500	5,500	7,500	7,500	6,000
NLCD Land Cover	5 classes	30m		3,000	3,500	7,500	500	7,500			
NLCD Land Cover	5 classes	60m		3,000	3,500	7,500	7,500	7,500			
NLCD Land Cover	5 classes	120m		6,500	3,500	7,500	7,500	7,500			
NLCD Land Cover	5 classes	180m		500	4,500	7,500	6,500	7,500			
NLCD Land Cover	5 classes	240m		6,500	4,500	7,500	6,500	6,500			
NLCD Land Cover	8 classes	30m		3,000	2,000	500	7,500	7,500	7,500	7,500	500
NLCD Land Cover	8 classes	60m		3,000	1,500	3,500	7,500	7,500	1,500	7,500	5,500
NLCD Land Cover	8 classes	120m		6,500	1,500	3,500	7,500	7,500	7,500	7,500	3,500
NLCD Land Cover	8 classes	180m		500	1,500	4,500	7,500	7,500	7,500	7,500	3,500
NLCD Land Cover	8 classes	240m		6,500	1,500	3,000	7,500	7,500	7,500	6,500	3,500
NLCD Percent Impervious Surface	Continuous	30m	7,500								
NLCD Percent Impervious Surface	Continuous	60m	7,500								
NLCD Percent Impervious Surface	Continuous	120m	7,500								
NLCD Percent Impervious Surface	Continuous	180m	7,500								

Geospatial layer	Thematic Resolution	Spatial Grain	Cont-inuous	Characteristic Scale (m) Class 1	Class 2	Class 3	Class 4	Class 5	Class 6	Class 7	Class 8
NLCD Percent Impervious Surface	Continuous	240m	7,500								
NLCD Percent Impervious Surface	3 classes	30m		7,500	7,500	7,500					
NLCD Percent Impervious Surface	3 classes	60m		7,500	7,500	7,500					
NLCD Percent Impervious Surface	3 classes	120m		7,500	7,500	7,500					
NLCD Percent Impervious Surface	3 classes	180m		7,500	7,500	7,500					
NLCD Percent Impervious Surface	3 classes	240m		7,500	7,500	7,500					
NLCD Percent Impervious Surface	4 classes	30m		7,500	7,500	7,500	7,500				
NLCD Percent Impervious Surface	4 classes	60m		7,500	7,500	7,500	7,500				
NLCD Percent Impervious Surface	4 classes	120m		7,500	7,500	7,500	7,500				
NLCD Percent Impervious Surface	4 classes	240m		7,500	7,500	7,500	7,500				
NLCD Percent Impervious Surface	5 classes	30m		7,500	7,500	7,500	7,500	7,500			
NLCD Percent Impervious Surface	5 classes	60m		7,500	7,500	7,500	7,500	7,500			
NLCD Percent Impervious Surface	5 classes	120m		7,500	7,500	7,500	7,500	7,500			
NLCD Percent Impervious Surface	5 classes	180m		7,500	7,500	7,500	7,500	7,500			
NLCD Percent Impervious Surface	5 classes	240m		7,500	7,500	7,500	7,500	7,500			
LandFire Percent Vegetative Cover	Continuous	30m	3,500								

			Characteristic Scale (m)								
Geospatial layer	**Thematic Resolution**	**Spatial Grain**	**Cont-inuous**	**Class 1**	**Class 2**	**Class 3**	**Class 4**	**Class 5**	**Class 6**	**Class 7**	**Class 8**
LandFire Percent Vegetative Cover	Continuous	60m	3,500								
LandFire Percent Vegetative Cover	Continuous	120m	3,500								
LandFire Percent Vegetative Cover	Continuous	180m	3,500								
LandFire Percent Vegetative Cover	Continuous	240m	3,500								
LandFire Percent Vegetative Cover	3 classes	30m		3,500	7,500	3,500					
LandFire Percent Vegetative Cover	3 classes	60m		7,500	7,500	3,500					
LandFire Percent Vegetative Cover	3 classes	120m		7,500	7,500	3,500					
LandFire Percent Vegetative Cover	3 classes	240m		7,500	2,000	7,500					
LandFire Percent Vegetative Cover	4 classes	30m		3,500	3,000	7,500	3,500				
LandFire Percent Vegetative Cover	4 classes	60m		3,500	6,500	6,500	3,500				
LandFire Percent Vegetative Cover	4 classes	120m		7,500	500	1,500	7,500				
LandFire Percent Vegetative Cover	4 classes	180m		7,500	3,500	1,500	7,500				
LandFire Percent Vegetative Cover	4 classes	240m		7,500	7,500	1,500	7,500				
LandFire Percent Vegetative Cover	5 classes	30m		3,500	3,000	7,500	7,500	3,500			
LandFire Percent Vegetative Cover	5 classes	60m		7,500	6,000	7,500	7,500	3,500			
LandFire Percent Vegetative Cover	5 classes	120m		7,500	500	1,500	2,000	3,500			

Geospatial layer	Thematic Resolution	Spatial Grain	Cont-inuous	Characteristic Scale (m) Class 1	Class 2	Class 3	Class 4	Class 5	Class 6	Class 7	Class 8
LandFire Percent Vegetative Cover	5 classes	180m		7,500	3,500	1,500	1,500	6,000			
LandFire Percent Vegetative Cover	5 classes	240m		7,500	7,500	1,500	500	6,000			
Landsat Percent Vegetative Cover	Continuous	30m	500								
Landsat Percent Vegetative Cover	Continuous	60m	500								
Landsat Percent Vegetative Cover	Continuous	120m	500								
Landsat Percent Vegetative Cover	Continuous	240m	3,500								
Landsat Percent Vegetative Cover	3 classes	30m		500	7,500	3,500					
Landsat Percent Vegetative Cover	3 classes	60m		500	6,500	500					
Landsat Percent Vegetative Cover	3 classes	120m		6,500	6,500	2,000					
Landsat Percent Vegetative Cover	3 classes	180m		6,500	6,500	7,500					
Landsat Percent Vegetative Cover	3 classes	240m		6,500	6,500	7,500					
Landsat Percent Vegetative Cover	4 classes	30m		500	7,500	500	500				
Landsat Percent Vegetative Cover	4 classes	60m		6,500	7,500	3,500	6,500				
Landsat Percent Vegetative Cover	4 classes	120m		6,500	7,500	500	6,500				
Landsat Percent Vegetative Cover	4 classes	180m		6,500	7,500	500	6,500				
Landsat Percent Vegetative Cover	4 classes	240m		6,500	7,500	500	6,500				

Geospatial layer	Thematic Resolution	Spatial Grain	Cont-inuous	Characteristic Scale (m) Class 1	Class 2	Class 3	Class 4	Class 5	Class 6	Class 7	Class 8
Landsat Percent Vegetative Cover	5 classes	30m		500	7,500	500	3,500	6,500			
Landsat Percent Vegetative Cover	5 classes	60m		6,500	7,500	6,500	500	6,500			
Landsat Percent Vegetative Cover	5 classes	120m		6,500	7,500	500	2,000	6,500			
Landsat Percent Vegetative Cover	5 classes	240m		7,500	7,500	3,500	500	4,500			
NLCD Percent Vegetative Cover	Continuous	30m	6,500								
NLCD Percent Vegetative Cover	Continuous	60m	6,500								
NLCD Percent Vegetative Cover	Continuous	120m	6,500								
NLCD Percent Vegetative Cover	Continuous	180m	6,500								
NLCD Percent Vegetative Cover	Continuous	240m	6,500								
NLCD Percent Vegetative Cover	3 classes	30m		6,500	6,500	6,500					
NLCD Percent Vegetative Cover	3 classes	60m		6,500	6,500	6,500					
NLCD Percent Vegetative Cover	3 classes	120m		6,500	6,500	6,500					
NLCD Percent Vegetative Cover	3 classes	180m		500	500	6,500					
NLCD Percent Vegetative Cover	3 classes	240m		2,000	2,000	6,500					
NLCD Percent Vegetative Cover	4 classes	30m		6,500	6,500	6,500	6,500				
NLCD Percent Vegetative Cover	4 classes	60m		6,500	6,500	6,500	6,500				

				Characteristic Scale (m)							
Geospatial layer	**Thematic Resolution**	**Spatial Grain**	**Conti-nuous**	**Class 1**	**Class 2**	**Class 3**	**Class 4**	**Class 5**	**Class 6**	**Class 7**	**Class 8**
NLCD Percent Vegetative Cover	4 classes	120m		6,500	6,500	6,500	6,500				
NLCD Percent Vegetative Cover	4 classes	240m		4,500	1,500	4,500	6,500				
NLCD Percent Vegetative Cover	5 classes	30m		6,500	7,500	6,500	6,500	7,500			
NLCD Percent Vegetative Cover	5 classes	60m		6,500	6,500	6,500	6,500	1,500			
NLCD Percent Vegetative Cover	5 classes	120m		6,500	6,500	6,500	6,500	7,500			
NLCD Percent Vegetative Cover	5 classes	180m		4,500	6,500	4,500	6,500	7,500			
NLCD Percent Vegetative Cover	5 classes	240m		6,500	6,500	6,500	6,500	7,500			
Elevation	Continuous	30m	1,500								
Elevation	Continuous	60m	3,000								
Elevation	Continuous	120m	3,000								
Elevation	Continuous	180m	3,500								
Elevation	Continuous	240m	3,500								
Elevation	3 classes	30m		4,500	4,500	1,500					
Elevation	3 classes	60m		4,500	4,500	500					
Elevation	3 classes	120m		4,500	4,500	2,000					
Elevation	3 classes	180m		4,500	4,500	500					
Elevation	3 classes	240m		4,500	4,500	500					
Elevation	4 classes	30m		2,000	1,500	7,500	1,500				
Elevation	4 classes	60m		2,000	2,000	7,500	1,500				
Elevation	4 classes	120m		3,000	3,000	7,500	1,500				
Elevation	4 classes	180m		3,000	500	7,500	1,500				
Elevation	4 classes	240m		500	500	7,500	4,500				
Elevation	5 classes	30m		2,000	1,500	6,500	1,500	5,500			
Elevation	5 classes	60m		2,000	2,000	6,500	4,500	5,500			
Elevation	5 classes	120m		3,000	3,000	6,500	500	6,000			
Elevation	5 classes	180m		3,000	500	6,500	500	7,500			
Elevation	5 classes	240m		3,500	7,500	6,500	1,500	7,500			
Percent Slope	Continuous	30m	1,500								
Percent Slope	Continuous	60m	1,500								
Percent Slope	Continuous	120m	1,500								
Percent Slope	Continuous	180m	3,000								
Percent Slope	Continuous	240m	500								
Percent Slope	3 classes	30m		1,500	500	1,500					
Percent Slope	3 classes	60m		1,500	500	1,500					
Percent Slope	3 classes	120m		1,500	7,500	6,500					
Percent Slope	3 classes	180m		7,500	7,500	6,500					
Percent Slope	3 classes	240m		7,500	7,500	7,500					
Percent Slope	4 classes	30m		1,500	7,500	1,500	1,500				
Percent Slope	4 classes	120m		2,000	7,500	1,500	7,500				
Percent Slope	4 classes	180m		2,000	7,500	500	7,500				
Percent Slope	4 classes	240m		7,500	7,500	3,500	7,500				
Percent Slope	5 classes	30m		1,500	7,500	1,500	1,500	6,500			
Percent Slope	5 classes	60m		1,500	7,500	2,000	1,500	7,500			
Percent Slope	5 classes	120m		2,000	1,500	7,500	1,500	7,500			

Percent Slope	5 classes	180m		2,000	500	6,500	6,500	7,500			

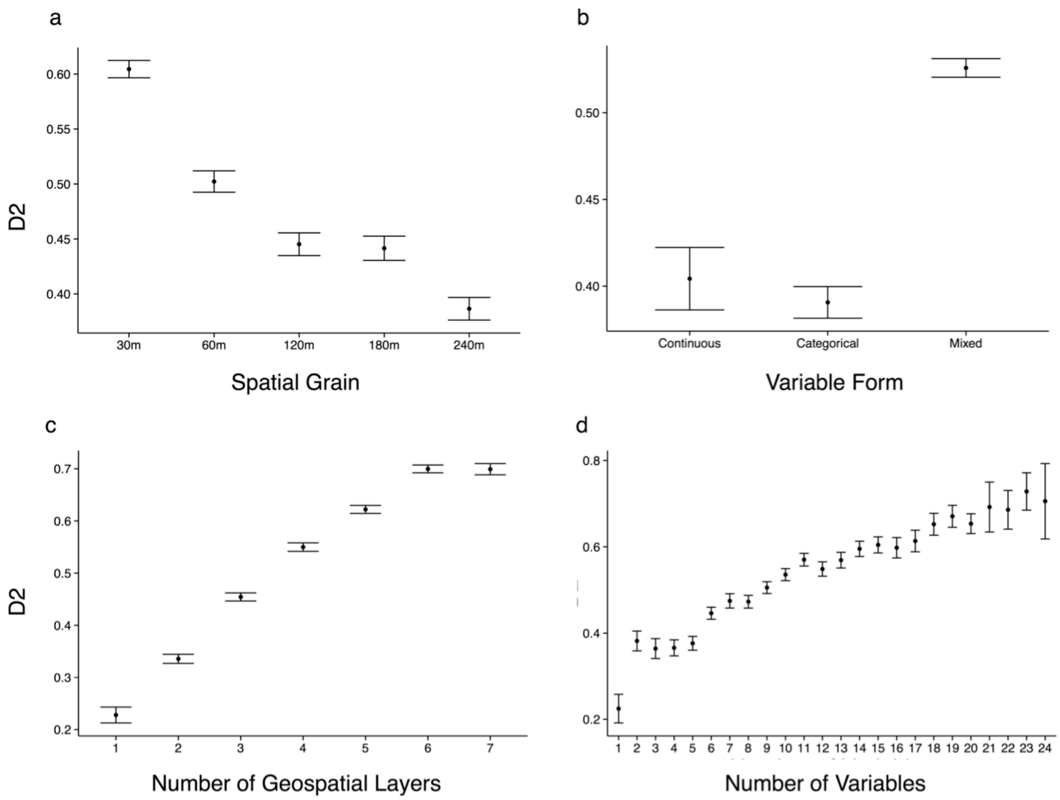
						Characteristic Scale (m)					
Geospatial layer	**Thematic Resolution**	**Spatial Grain**	**Conti-nuous**	**Class 1**	**Class 2**	**Class 3**	**Class 4**	**Class 5**	**Class 6**	**Class 7**	**Class 8**
Percent Slope	5 classes	240m		7,500	500	6,500	7,500	7,500			
Terrain Ruggedness	Continuous	30m	7,500								
Terrain Ruggedness	Continuous	60m	7,500								
Terrain Ruggedness	Continuous	120m	7,500								
Terrain Ruggedness	Continuous	180m	7,500								
Terrain Ruggedness	Continuous	240m	7,500								
Terrain Ruggedness	3 classes	30m		1,500	500	7,500					
Terrain Ruggedness	3 classes	60m		500	500	7,500					
Terrain Ruggedness	3 classes	120m		1,500	1,500	7,500					
Terrain Ruggedness	3 classes	180m		500	500	6,500					
Terrain Ruggedness	3 classes	240m		500	500	7,500					
Terrain Ruggedness	4 classes	30m		500	7,500	7,500	7,500				
Terrain Ruggedness	4 classes	60m		500	500	7,500	7,500				
Terrain Ruggedness	4 classes	120m		500	6,500	7,500	7,500				
Terrain Ruggedness	4 classes	180m		500	6,500	7,500	7,500				
Terrain Ruggedness	4 classes	240m		3,000	6,500	6,500	2,000				
Terrain Ruggedness	5 classes	30m		500	7,500	500	7,500	7,500			
Terrain Ruggedness	5 classes	60m		500	7,500	500	7,500	7,500			
Terrain Ruggedness	5 classes	120m		500	7,500	1,500	6,500	7,500			
Terrain Ruggedness	5 classes	180m		500	6,500	500	7,500	6,500			
Terrain Ruggedness	5 classes	240m		6,500	7,500	3,000	7,500	2,000			

Appendix D. Likelihood Ratio Test Results.

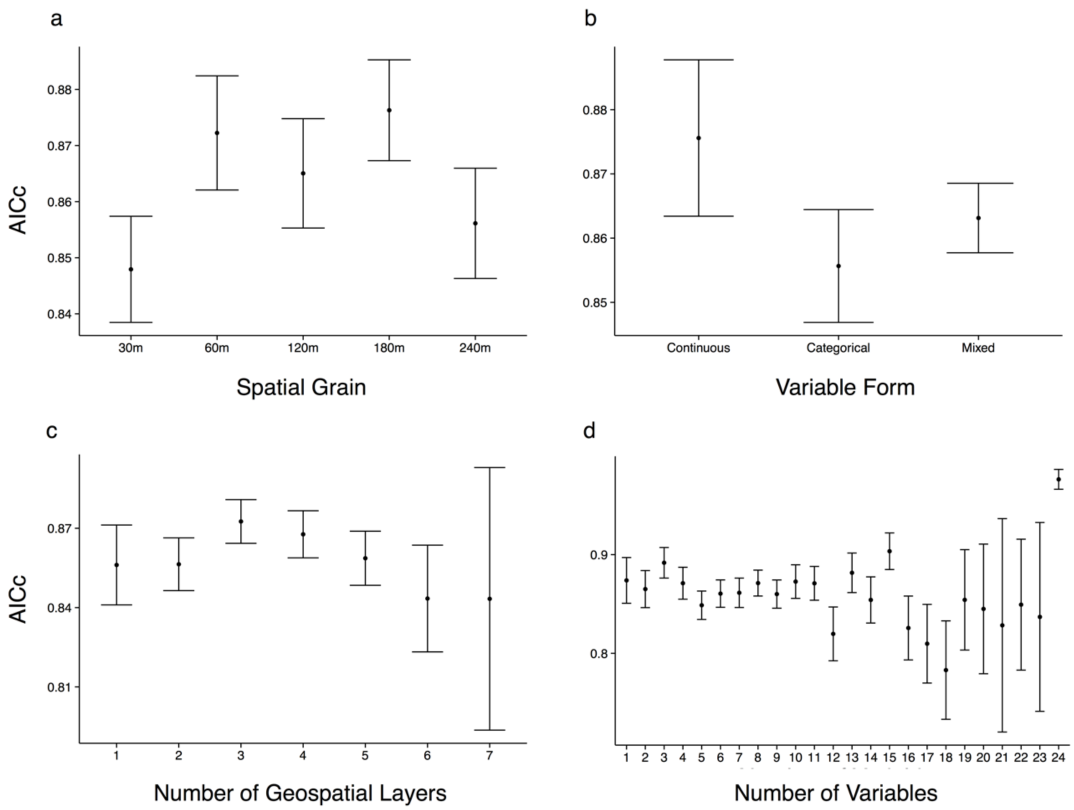
AICc, D2, and CCC for the 2,000 landscape definitions were modeled as a function of four landscape definition options (1) spatial grain (30m, 60m, 120m, 180m, 240m), (2) number of layers used in the model (1-7), (3) number of variables (1-24), and (4) whether the variables were all represented continuously, all represented categorically, or whether a mix of continuous or categorical representations were present. Likelihood Ratio Tests were performed comparing the full model with each of these definition options left out in turn.

AICc				**D2**				**CCC**			
Grain Size				***Grain Size***				***Grain Size***			
df	LL	X^2	p	df	LL	X^2	p	df	LL	X^2	p
40	-10690			40	1072			40	582.5		
36	-10957	534.2	<2.2e-16	36	812	519.5	<2.2e-16	36	579.7	5.7	0.226
No. of Layers				***No. of Layers***				***No. of Layers***			
#df	LL	X^2	p	#df	LL	X^2	p	#df	LL	X^2	p
40	-10690			40	1072			40	582.5		
34	-10919	456.7	<2.2e-16	34	853	437.8	<2.2e-16	34	581.2	2.7	0.841
Var Form				***Var Form***				***Var Form***			
#df	LL	X^2	p	#df	LL	X^2	p	#df	LL	X^2	p
40	-10690			40	1072			40	582.5		
38	-10691	1.26	0.534	38	1071	1.8	0.411	38	582.4	0.3	0.88
No. of Vars				***No. of Vars***				***No. of Vars***			
#df	LL	X^2	p	#df	LL	X^2	p	#df	LL	X^2	p
40	-10690			40	1072			40	582.5		
14	-10701	22.1	6.84E-01	14	1051	42.8	2.05E-02	14	571.7	21.7	0.06

Appendix E. Mean and standard error in model percent deviance explained as a function of spatial grain, variable form, number of geospatial layers, and number of variables in a landscape definition associated with modeling puma movement in southern California.



Appendix F. Mean and standard error in the concordance correlation coefficient as a function of spatial grain, variable form, number of geospatial layers, and number of variables in a landscape definition associated with modeling puma movement in southern California.



Appendix G. To predict probability of movement / conductance surfaces, we selected landscape definitions across the model performance continuum at the 0th, 25th, 50th, 75th and 100th percentile of AICc values. Model results for these five landscape definitions are provided below.

Top model (Mod 3993; AICc = 66.6). All layers had a spatial resolution of 30m.

Geospatial Layer	Thematic Resolution	Class	Coefficient
OSM Roads	2 class	1	-530.0
		2	-494.8
Elevation	4 class	1	18.3
		3	2.0
		4	-8.9
Terrain Ruggedness	3 class	1	-13.3
		2	-5.7
		3	-21.7
Percent Slope	continuous	-	-0.5

25th percentile of AICc Model (Mod 569; AICc =161.2). All layers had a spatial resolution of 30m.

Geospatial Layer	Thematic Resolution	Class	Coefficient
Elevation	3 class	1	-530.0
		3	-494.8
LandFire Percent Vegetative Cover	Continuous	-	0.3
Percent Impervious Surface	Continuous	-	-1.0

50th percentile of AICc Model (Mod 2700; AICc =219.1). All layers had a spatial resolution of 60m.

Geospatial Layer	Thematic Resolution	Class	Coefficient
LandFire Land Cover Type	8 class	1	8.3
		2	5.1
		3	2.4
		4	2.8
		6	-2.7
		7	-14.0
		8	23.9
Elevation	Continuous	-	-0.01
Terrain Ruggedness	Continuous	-	-62.4
NLCD Percent Vegetative Cover	4 class	1	-11.4
		2	4.1
		4	66.1

75th percentile of AICc Model (Mod 5845; AICc =288.5). All layers had a spatial resolution of 30m.

Geospatial Layer	Thematic Resolution	Class	Coefficient
Percent slope	Continuous	-	-0.4
Terrain Ruggedness	Continuous	-	58.0

100th percentile of AICc Model (Mod 4963; AICc =424.8). All layers had a spatial resolution of 180m.

Geospatial Layer	Thematic Resolution	Class	Coefficient
NLCD percent vegetative cover	4 class	1	6.5
		2	7.4

References

Addicott JF, Aho JM, Antolin MF, Padilla DK, Richardson JS, Soluk DA (1987) Ecological neighborhoods: scaling environmental patterns. Oikos 49: 340-346

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (Eds.), Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary. pp. 267–281

Alexander SM, Logan TB, Paquet PC (2006) Spatio-temporal co-occurrence of cougars (Felis concolor), wolves (Canis lupus) and their prey during winter: a comparison of two analytical methods. Journal of Biogeography 33: 2001–2012

Allen ML, Elbroch LM, Casady DS, Wittmer HU (2014) Seasonal variation in the feeding ecology of pumas (*Puma concolor*) in northern California. Canadian Journal of Zoology. 92: 397–403

Beier P (1995) Dispersal of juvenile cougars in fragmented habitat. Journal of Wildlife Management 59: 228-237

Beier P, Brost B (2010) Use of land facets to plan for climate change: conserving the arenas, not the actors. Conservation Biology 24: 701-710

Broennimann O, Petitpierre B, Randin C, Engler R, Di Cola Va, Breiner F, D'Amen M, Pellissier L, Pottier J, Pio D, Garcia Mateo R, Hordijk W, Dubuis A, Scherrer D, Salamin N, Guisan A (2015) Spatial Ecology Miscellaneous Methods. R Package available from: http://www.unil.ch/ecospat/home/menuinst/tools--data/tools.html

Burdett CL, Crooks KR, Theobald DM, Wilson KR, Boydston EE, et al. (2010) Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere 1: 4

Burnham KP, Anderson DR (2002) Model selection and mul- timodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York. ISBN 978-0-387- 22456-5

Burrough P A, Wilson JP, van Gaans PFM, Hansen AJ (2001) Fuzzy k-means classification of topo-climatic data as an aid to forest mapping in the Greater Yellowstone Area, USA. Landscape Ecology 16:523-546

Chust G, Pretus JL, Ducrot D, Ventura D (2004) Scale dependency of insect assemblages in response to landscape pattern. Lanscape Ecology 19: 41-57

Cushman SA, Evans JS, McGarigal K, Kiesecker JM (2010a) Toward Gleasonian Landscape Ecology: From Communities to Species, From Patches to Pixels. Res. Pap. RMRS-RP-84. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 12 p

Cushman SA, Gutzweiler K, Evans JS, McGarigal K (2010b) The gradient paradigm: A conceptual and analytical framework of landscape ecology. In Cushman SA, Huettmann F (Eds.) Spatial Complexity, Informatics, and Wildlife Conservation. Springer, New York. pp 83-110

Cushman SA, Landguth EL (2010a) Scale dependent inference in landscape genetics. Landscape Ecology 25: 967-979

Cushman SA, Landguth EL (2010b) Spurious correlations and inference in landscape genetics. Molecular Ecology 19: 3592-5602

Cushman SA, Lewis JS (2010) Movement behavior explains genetic differentiation in American black bears. Landscape Ecology 25:1613–1625

Cushman SA, Lewis JS, Landguth EL (2014) Why did the bear cross the road? Comparing the Performance of Multiple Resistance Surfaces and Connectivity Modeling Methods. Diversity 6: 844-854

Cushman SA, McGarigal K, McKelvey K, Vojta CD, Reagan CM (2013) Landscape analysis for habitat monitoring. In Rowland MM, Vojta CD (tech. eds.) A technical guide for monitoring wildlife habitat. Gen. Tech. Rep. WO-89. Washington, DC: U.S. Department of Agriculture, Forest Service: 6-1 – 6-18.

Dickson BG, Beier P (2007) Quantifying the influence of topographic position on cougar (*Puma concolor*) movement in southern California, USA. Journal of Zoology 271:270–277

Dickson BG, Jenness JS, Beier P (2005) Influence of vegetation, topography, and roads on cougar movement in southern California. Journal of Wildlife Management 69:264–276

Elliot NB, Cushman SA, Macdonald DW, Loveridge AJ (2014) The devil is in the dispersers: predictions of landscape connectivity change with demography. Journal of Applied Ecology 51: 1169-1178

Ernest HB, Vickers TW, Morrison SA, Buchalski MR, Boyce WM (2014) Fractured genetic connectivity threatens a southern California puma (Puma concolor) population. PLoS ONE 9(10):e107985. doi:10.1371/journal.pone. 0107985

European Environmental Agency (2010) CORINE (Coordination of information on the environment). The European Topic Centre on Land Use and Spatial Information. Available at: http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster#tab-gis-data

Forman, R.T.T. 1995 Land Mosaics: The Ecology of Landscapes and Regions. Cambridge University Press, Cambridge.

Gottschalk TK, Aue B, Hotes S, Ekschmitt K (2011) Influence of grain size on species-habitat models. Ecological Modelling 18: 3403-3412

Gray M, Wilmers CC, Reed SE, Merenlender AM. 2016. Landscape feature-based permeability models relate to puma occurrence. Landscape and Urban Planning 147: 50-58

Guisan A, Graham CH, Elith J, Huettmann F, NCEAS Species Distribution Modelling Group (2007) Sensitivity of predictive species distribution models to change in grain size. Diversity and Distributions 13: 332-340

Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. Bioscience 54: 227–233

Holmes BR, Laundré JW (2006) Use of open, edge and forest areas by pumas Puma concolor in winter: are pumas foraging optimally? Wildlife Biology, 12:201-209

Jenks GF (1967) The Data Model Concept in Statistical Mapping. International Yearbook of Cartography 7: 186–190

Jenness J (2013) DEM Surface Tools. Jenness Enterprises. Available at: http://www.jennessent.com/arcgis/surface_area.htm

Jin S, Yang L, Danielson P, Homer C, Fry J, Xian G (2013) A comprehensive change detection method for updating the National Land Cover Database to circa 2011. *Remote Sensing of Environment*, 132: 159 – 175. Downloaded from the national map viewer: http://viewer.nationalmap.gov/viewer/ on August 24, 2014

Johnson CJ, Nielsen SE, Merrill EH, Mcdonald TL, Boyce MS (2006) Resource selection functions based on use-avail- ability data: theoretic motivation and evaluation methods. Journal of Wildlife Management 70:347–357

Karl JW, Heglund PJ, Garton EO, Scott JM, Wright NM, Hutto RL (2000) Sensitivity of Species Habitat-Relationship Model Performance to Factors of Scale. Ecological Applications 10: 1690-1705

Kissling WD, Fernandez N, Paruelo JM (2009) Spatial risk assessment of livestock exposure to pumas in Patagonia, Argentina. Ecography 32: 807-817

Krishnamurthy R, Cushman SA, Sarkar MS, Malviya M, Naveeen M, Johnson JA, Sen S (2016) Multi-scale prediction of landscape resistance for tiger dispersal in central India. Landscape Ecology: DOI 10.1007/s10980-016-0363-0

Johnson D (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71

LandFire (2012a) Existing Vegetation Cover. U.S. Department of the Interior, Geological Survey. Downloaded from: http://www.landfire.gov/viewer/ on Aug 21 2014

LandFire (2012b) Existing Vegetation Type. U.S. Department of the Interior, Geological Survey. Downloaded from: http://www.landfire.gov/viewer/ on Aug 21 2014

Lawler JJ, O'Connor RJ , Hunsaker CT , Jones KB , Loveland TR, White D (2004) The effects of habitat resolution on models of avian diversity and distributions: a comparison of two land-cover classifications. Landscape Ecology 19: 515-530

Lewis JS, Rachlow JL, Garton EO, Vierling LA (2007) Effects of habitat on GPS collar performance: using data screening to reduce location error. Journal of Applied Ecology 44:663–671

Lin LI (1989) A concordance correlation coefficient to evaluate reproducibility. Biometrics 1:255–268

MacArthur R, Recher H, Cody M (1966) On the relation between habitat selection and species diversity. The American Naturalist 100: 319-332

Mateo Sánchez MC, Cushman SA, Saura S (2014) Scale dependence in habitat selection: the case of the endangered brown bear (Ursus arctos) in the Cantabrian Range (NW Spain). International Journal of Geographic Information Science 28: 1531-1546

McGarigal K, Cushman SA (2005) The gradient concept of landscape structure. In Wiens J, Moss M. (eds) Issues and perspectives in landscape ecology. Cambridge University Press, Cambridge. pp 112–119

McGarigal K., Wan HY, Zeller KA, Timm BC, Cushman SA (*2016*) Multi-scale habitat modeling: A review and outlook. Landscape Ecology: DOI*:10.1007/s10980-016-0374-x*

McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724

McRae BH, Shah VB, Mohapatra TK (2013) Circuitscape 4 user guide. The Nature Conservancy. http://www.circuitscape. org. Accessed 19 May 2015

Meyer CB, and Thuiller W (2006) Accuracy of resource selection functions across spatial scales. Diversity and Distributions 12:288–297

Orange County Transportation Authority (2011) Master plan of arterial highways. Orange County Transportation Authority, Orange, California. Accessed from http://www.octa.net/Plans-and-Programs/GIS-Data/GIS-Data-Download/ on Sept 18, 2014

Riverside County Geographic Information Systems (2013) County Static Data. Riverside County Innovation Center, Riverside CA. Accessed from: http://gis.rivcoit.org/GISData.aspx on Aug 24, 2014.

San Bernadino (2014) San Bernadino county centerlines. Downloaded from: http://maps.sanbag.ca.gov/website/Transportation_data.htm on Sept 18, 2014

SanGIS (2014) All roads shape file. SanGIS/SANDAG Data Warehouse. San Diego Geographic Information Source - JPA/San Diego Association of Governments

(SANDAG). Accessed from <http://www.sangis.org/Download_GIS_Data.htm> on July 20, 2014

Seoane J, Bustamente J, Diaz-Delgado R (2004) Are existing vegetation maps adequate to predict bird distributions? Ecological Modelling 175: 137-149

Sexton, J. O., Song, X.-P., Feng, M., Noojipady, P., Anand, A., Huang, C., Kim, D.-H., Collins, K.M., Channan, S., DiMiceli, C., Townshend, J.R.G. (2013). Global, 30-m resolution continuous fields of tree cover: Landsat-based rescaling of MODIS Vegetation Continuous Fields with lidar-based estimates of error. International Journal of Digital Earth, 130321031236007. doi:10.1080/17538947.2013.786146.

Thompson CM, McGarigal K (2002) The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York (USA). Landscape Ecology 17: 569-586.

Tobalske C (2002) Effects of spatial scale on the predictive ability of habitat models for the green woodpecker in Switzerland. In: Scott JM, Heglund PJ, Samson F, Haufler J, Morrison M, Raphael M, Wall B (Eds.), Predicting Species Occurrences: Issues of Accuracy and Scale. Island Press, Covelo, California. pp. 197–204

USDA Forest Service (2014) CalVeg: FSSDE.Eveg- Tile47A_02_v2. Pacific Southwest Region Remote Sensing Lab, McClellan

U.S. Geological Survey (2009) National Elevation Dataset. U.S.G.S. Sioux Falls, SD. Downloaded from: http://viewer.nationalmap.gov/viewer/ on Aug 20, 2014

Venier LA, Pearce J, McKee JE, McKenney DW, Niemi GJ (2004) Climate and satellite-derived land cover for predicting breeding bird distribution in the Great Lakes Basin. Journal of Biogeography 31:315-331

Vickers TW, Sanchez JN, Johnson CK, Morrison SA, Botta R, Smith T, Cohen BS, Huber PR, Ernest HB, Boyce WM (2015) Survival and mortality of pumas (Puma concolor) in a fragmented, urbanizing landscape. PlosONE. doi:10. 1371/journal.pone.0131490

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385– 397

Wilmers CC, Wang Y, Nickel B, Houghtaling P, Shakeri Y, Allen ML, Kermish-Wells J, Yovovich V, Williams T (2013) Scale dependent behavioral responses to human development by a large predator, the puma. PLoS ONE. doi:10.1371/journal.pone.0060590

Wu J (2004) Effects of changing scale on landscape pattern analysis: scaling relations. Landscape Ecology 19: 125-138

Zeller KA, McGarigal K, Beier P, Cushman SA, Vickers TW, Boyce WM (2014) Sensitivity of landscape resistance estimates based on point selection functions to scale and behavioral state: pumas as a case study. *Landscape Ecology* 29: 541-557

Zeller KA, McGarigal K, Beier P, Cushman SA, Vickers TW, Boyce WM (2015) Using step and path selection functions for estimating resistance to movement: pumas as a case study. *Landscape Ecology.* DOI: 10.1007/s10980-015-0301-6

BIBLIOGRAPHY

Addicott JF, Aho JM, Antolin MF, Padilla DL, Richardson JS, Soluk DA (1987) Ecological neighborhoods: scaling environmental patterns. Oikos 49:340–346

Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E (2003) The application of 'least- cost' modeling as a functional landscape model. Landsc Urban Plan 64:233–247

Agresti A (2002) Categorical data analysis, 2nd edn. Wiley, Hoboken, p 419

Akaike H (1973) Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (Eds.), Second International Symposium on Information Theory. Akademiai Kiado, Budapest, Hungary. pp. 267–281

Alexander SM, Logan TB, Paquet PC (2006) Spatio-temporal co-occurrence of cougars (Felis concolor), wolves (Canis lupus) and their prey during winter: a comparison of two analytical methods. Journal of Biogeography 33: 2001–2012

Allen ML, Elbroch LM, Casady DS, Wittmer HU (2014) Seasonal variation in the feeding ecology of pumas (*Puma concolor*) in northern California. Canadian Journal of Zoology. 92: 397–403

Bartelt PE, Klaver RW, Porter WP (2010) Modeling amphibian energetics, habitat suitability, and movements of western toads, Anaxyrus (= Bufo) boreas, across present and future landscapes. Ecol Model 221:2675–2686

Bates D, Maechler M, Bolker B (2013) Linear mixed-effects models using S4 classes. (R package). http://cran.r-project. org/web/packages/lme4/index.html. Accessed 20 April 2013

Beazley K, Smandych L, Snaith T, MacKinnon F, Austen-Smith P Jr, Dunker P (2005) Biodiversity considerations in conservation system planning: map-based approach for Nova Scotia, Canada. Ecol Appl 15:2192–2208

Beier P (1995) Dispersal of juvenile cougars in fragmented habitat. Journal of Wildlife Management 59: 228-237

Beier P, Brost B (2010) Use of land facets to plan for climate change: conserving the arenas, not the actors. Conservation Biology 24: 701-710

Beier P, Majka DR, Spencer WD (2008) Forks in the road: choices in procedures for designing wildland linkages. Conserv Biol 22:836–851

Beier P, Majka DR, Newell SL (2009) Uncertainty analysis of least-cost modeling for designing wildlife linkages. Ecol Appl 19:2067–2077

Boyce MS (2006) Scale for resource selection functions. Divers Distrib 12:269–276

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA (2002) Evaluating resource selection functions. Ecol Model 157:281–300

Braunisch V, Segelbacher G, Hirzel AH (2010) Modelling functional landscape connectivity from genetic population structure: a new spatially explicit approach. Mol Ecol 19:3664–3678

Broennimann O, Petitpierre B, Randin C, Engler R, Di Cola Va, Breiner F, D'Amen M, Pellissier L, Pottier J, Pio D, Garcia Mateo R, Hordijk W, Dubuis A, Scherrer D, Salamin N, Guisan A (2015) Spatial Ecology Miscellaneous Methods. R Package available from: http://www.unil.ch/ecospat/home/menuinst/tools--data/tools.html

Broquet T, Ray N, Petit E, Fryxell JM, Burel F (2009) Genetic isolation by distance and landscape connectivity in the American marten (Martes americana). Landscape Ecol 21:877–889

Brown DD, LaPoint S, Kays R, Heidrich W, Kummeth F, Wilelski M (2012) Accelerometer-informed GPS telemetry: reducing the trade-off between resolution and longevity. Wildl Soc Bull 36:139–146

Burdett CL, Crooks KR, Theobald DM, Wilson KR, Boydston EE, Lyren LM, Fisher RN, Vickers TW, Morrison SA, Boyce WM (2010) Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere 1: Article 4, p 1–21

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York. ISBN 978-0-387- 22456-5

Burrough P A, Wilson JP, van Gaans PFM, Hansen AJ (2001) Fuzzy k-means classification of topo-climatic data as an aid to forest mapping in the Greater Yellowstone Area, USA. Landscape Ecology 16:523-546

California Department of Fish and Game (1988) A guide to wildlife habitats of California. In Mayer KE, Laudenslayer WF Jr (eds) State of California Resources Agency. Department of Fish and Game, Sacramento, p 166. http:// www.dfg.ca.gov/biogeodata/cwhr/wildlife_habitats.asp# Tree. Accessed 29 Jan 2013

Chardon JP, Adriaensen F, Matthysen E (2003) Incorporating landscape elements into a connectivity measure: a case study for the Speckled wood butterfly (Pararge aegeria L.). Landscape Ecol 18:561–573

Chetkiewicz C-LB, Boyce MS (2009) Use of resource selection functions to identify conservation corridors. J Appl Ecol 46:1036–1047

Chust G, Pretus JL, Ducrot D, Ventura D (2004) Scale dependency of insect assemblages in response to landscape pattern. Lanscape Ecology 19: 41-57

Clark RW, Brown WS, Stechert R, Zamudio KR (2008) Integrating individual behavior and landscape genetics: the population structure of timber rattlesnake hibernacula. Mol Ecol 17:719–730

Clevenger AP, Wierzchowski J, Chruszcz B, Gunson K (2002) GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. Conserv Biol 16:503–514

Compton BW, McGarigal K, Cushman SA, Gamble LR (2007) A resistant-kernel model of connectivity for amphibians that breed in vernal pools. Conserv Biol 21:788–799

Compton BW, Rhymer JM, McCollough M (2002) Habitat selection by wood turtles (Clemmys insculpta): an application of paired logistic regression. Ecology 83:833–843

Coulon A, Cosson JF, Angibault JM, Cargnelutti B, Galan M, Morellet N, Petit E, Aulagnier S, Hewison AJM (2004) Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual-based approach. Mol Ecol 13:2841–2850 Cushman SA (2010) Animal movement data: GPS telemetry, autocorrelation and the need for path-level analysis. In: Cushman SA, Huettmann F (eds) Spatial complexity, informatics, and wildlife conservation. Springer, New York, pp 131–149

Coulon A, Morellet N, Goulard A, Cargnelutti B, Angibault JM, Hewison AJM (2008) Inferring the effects of landscape structure on roe deer (Capreolus capreolus) movements using a step selection function. Landscape Ecol 23:603–614

Crooks KR, Sanjayan M (2006) Connectivity conservation: maintaining connections for nature. In: Crooks KR, Sanjayan M (eds) Connectivity conservation. Cambridge University Press, Cambridge, p 1

Cushman SA, Chase M, Griffin C (2010) Mapping landscape resistance to identify corridors and barriers for elephant movement in South Africa. In: Cushman SA, Huettmann (eds) Spatial complexity, informatics, and wildlife conservation. Springer, Japan, pp 349–367. ISBN 978-4-431- 87770-7

Cushman SA, Evans JS, McGarigal K, Kiesecker JM (2010a) Toward Gleasonian Landscape Ecology: From Communities to Species, From Patches to Pixels. Res. Pap. RMRS-RP-84. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 12 p

Cushman SA, Gutzweiler K, Evans JS, McGarigal K (2010) The gradient paradigm: a conceptual and analytical framework for landscape ecology. In: Cushman SA, Huettmann F (eds) Spatial complexity, informatics, and wildlife conservation. Springer, New York, pp 83–108

Cushman SA, Landguth EL (2010) Scale dependent inference in landscape genetics. Landscape Ecology 25: 967-979

Cushman SA, Landguth EL (2010) Spurious correlations and inference in landscape genetics. Mol Ecol 19:3592–3602

Cushman SA, Lewis JS (2010) Movement behavior explains genetic differentiation in American black bears. Landscape Ecol 25:1613–1625

Cushman SA, Lewis JS (2010) Movement behavior explains genetic differentiation in American black bears. Landscape Ecol 25:1613–1625

Cushman SA, Lewis JS, Landguth EL (2014) Why did the bear cross the road? Comparing the performance of multiple resistance surfaces and connectivity modeling methods. Diversity 6:844–854

Cushman SA, McGarigal K, McKelvey K, Vojta CD, Reagan CM (2013) Landscape analysis for habitat monitoring. In Rowland MM, Vojta CD (tech. eds.) A technical guide for monitoring wildlife habitat. Gen. Tech. Rep. WO-89. Washington, DC: U.S. Department of Agriculture, Forest Service: 6-1 – 6-18.

Cushman SA, McKelvey KS, Hayden J, Schwartz MK (2006) Gene-flow in complex landscapes: testing multiple hypotheses with causal modeling. Am Nat 168:486–499

Cushman SA, McRae B, Adriaensen F, Beier P, Shirley M, Zeller K (2013) Biological corridors and connectivity. In: Macdonald DW, Willis KJ (eds) Key topics in conservation biology 2. Wiley-Blackwell, Hoboken, pp 384–404

Dalziel BD, Morales JM, Fryxell JM (2008) Fitting probability distributions to animal movement trajectories: using artificial neural networks to link distance, resources, and memory. Am Nat 172:248–258

DeCesare NJ, Hebblewhite M, Schmiegelow F, Hervieux D, McDermid GJ, Neufeld L, Bradley M, Whittington J, Smith KG, Morgantini LE, Wheatley M, Musiani M (2012) Transcending scale dependence in identifying habitat with resource selection functions. Ecol Appl 22:1068–1083

Desrochers A, Be´lisle M, Morand-Ferron J (2011) Integrating GIS and homing experiments to study avian movement costs. Landscape Ecol 26:47–58

Dickson BG, Beier P (2002) Home-range and habitat selection by adult cougars in southern California. J Wildl Manag 66:1235–1245

Dickson BG, Beier P (2007) Quantifying the influence of topographic position on cougar (Puma concolor) movement in southern California, USA. J Zool 271:270–277

Dickson BG, Jenness JS, Beier P (2005) Influence of vegetation, topography, and roads on cougar movement in southern California. J Wildl Manag 69:264–276

Dormann CF, McPherson JM, Araújo MB, Bivand R, Bollinger J, Carl G, Davies RG, Hirzel A, Jetz W, Kissling WD, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Shröder B, Schurr FM, Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609–628

Elliot NB, Cushman SA, Macdonald DW, Loveridge AJ (2014) The devil is in the dispersers: predictions of landscape connectivity change with demography. J Appl Ecol. doi:10. 1111/1365-2664.12282

Emaresi G, Pellet J, Dubey S, Hirzel AH, Fumagalli L (2011) Landscape genetics of the Alpine newt (Mesotriton alpestris) inferred from a strip-based approach. Conserv Genet 12:41–50

Epps CW, Wehausen JD, Bleich VC, Torres SG, Brashares JS (2007) Optimizing dispersal and corridor models using landscape genetics. J Appl Ecol 44:714–724

Epps CW, Mutayoba BM, Gwin L, Brashares JS (2011) An empirical evaluation of the African elephant as a focal species for connectivity planning in East Africa. Divers Distrib 17:603–612

Ernest HB, Vickers TW, Morrison SA, Buchalski MR, Boyce WM (2014) Fractured genetic connectivity threatens a southern California puma (Puma concolor) population. PLoS ONE 9(10):e107985. doi:10.1371/journal.pone. 0107985

Estrada EG, Alva JAV (2011) Package gPdtest: bootstrap goodness-of-fit test for the generalized Pareto distribution. http://cran.r-project.org/web/packages/gPdtest/index.html. Accessed 11 Feb 2015

Estrada-Pena A (2003) The relationships between habitat topology, critical scales of connectivity and tick abundance Ixodes ricinus in a heterogeneous landscape in northern Spain. Ecography 26:661–671

European Environmental Agency (2010) CORINE (Coordination of information on the environment). The European Topic Centre on Land Use and Spatial Information. Available at: http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster#tab-gis-data

Ferreras P (2001) Landscape structure and asymmetrical inter- patch connectivity in a metapopulation of the endangered Iberian lynx. Biol Conserv 100:125–136

Flamm RO, Weigle BL, Wright IE, Ross M, Aglietti S (2005) Estimation of manatee (Trichechus manatus latirostris) places and movement corridors using telemetry data. Ecol Appl 15:1415–1426

Foltete JC, Berthier K, Cosson JF (2008) Cost distance defined by a topological function of landscape. Ecol Model 210:104–114

Foody GM (2002) Status of land cover classification accuracy assessment. Remote Sens Environ 80:185–201

Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330

Forman, R.T.T. 1995 Land Mosaics: The Ecology of Landscapes and Regions. Cambridge University Press, Cambridge.

Frair JL, Fieberg J, Hebblewhite M, Cagnacci F, DeCesare NJ, Pedrotti L (2010) Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Phil Trans R Soc B 365:2187–2200

Freeman RC, Bell KP (2011) Conservation versus cluster subdivisions and implications for habitat connectivity. Landsc Urban Plan 101:30–42

Fritz H, Said S, Weimerskirch H (2003) Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. Proc R Soc Lond B 270:1143–1148

Gottschalk TK, Aue B, Hotes S, Ekschmitt K (2011) Influence of grain size on species-habitat models. Ecological Modelling 18: 3403-3412

Graham CH (2001) Factors influencing movement patterns of keel-billed toucans in a fragmented tropical landscape in southern Mexico. Conserv Biol 15:1789–1798

Gray M, Wilmers CC, Reed SE, Merenlender AM. 2016. Landscape feature-based permeability models relate to puma occurrence. Landscape and Urban Planning 147: 50-58

Guisan A, Graham CH, Elith J, Huettmann F, NCEAS Species Distribution Modelling Group (2007) Sensitivity of predictive species distribution models to change in grain size. Diversity and Distributions 13: 332-340

Hawkins BA, Diniz-Filho JAF, Bini LM, De Marco P, Blackburn TM (2007) Red herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology. Ecography 30:375–384

Holland JD, Bert DG, Fahrig L (2004) Determining the spatial scale of species' response to habitat. Bioscience 54: 227–233

Holmes BR, Laundré JW (2006) Use of open, edge and forest areas by pumas Puma concolor in winter: are pumas foraging optimally? Wildlife Biology, 12:201-209

ISI Web of Knowledge Thomson Reuters (2011) Web of Science. Retrieved June 16, 2011 from http://pcs.isi knowledge.com

Janin A, Le´na JP, Ray N, Delacourt C, Allemand P, Joly P (2009) Assessing landscape connectivity with calibrated cost-distance modelling: predicting common toad distribution in a context of spreading agriculture. J Appl Ecol 46:833–841

Jaquiery J, Broquet T, Hirzel AH, Yearsley J, Perrin N (2011) Inferring landscape effects on dispersal from genetic distances: how far can we go? Mol Ecol 20:692–705

Jenks GF (1967) The Data Model Concept in Statistical Mapping. International Yearbook of Cartography 7: 186–190

Jenness J (2013) DEM Surface Tools. Jenness Enterprises. Available at: http://www.jennessent.com/arcgis/surface_area.htm

Jin S, Yang L, Danielson P, Homer C, Fry J, Xian G (2013) A comprehensive change detection method for updating the National Land Cover Database to circa 2011. *Remote Sensing of Environment*, 132: 159 – 175. Downloaded from the national map viewer: http://viewer.nationalmap.gov/viewer/ on August 24, 2014

Johnson CJ, Gillingham MP (2004) Mapping uncertainty: sensitivity of wildlife habitat ratings to expert opinion. J Appl Ecol 41:1032–1041

Johnson CJ, Nielsen SE, Merrill EH, McDonald TL, Boyce MS (2006) Resource selection functions based on use-availability data: theoretic motivation and evaluation methods. J Wildl Manag 70:347–357

Johnson D (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71

Joly K (2005) The effects of sampling regime on the analysis of movements of overwintering female caribou in east-central Alaska. Rangifer 25:67–74

Karl JW, Heglund PJ, Garton EO, Scott JM, Wright NM, Hutto RL (2000) Sensitivity of Species Habitat-Relationship Model Performance to Factors of Scale. Ecological Applications 10: 1690-1705

Kautz R, Kawula R, Hoctor T, Comiskey J, Jansen D, Jennings D, Kasbohm J, Mazzzotti F, McBride R, Richardson L, Root K (2006) How much is enough? Landscape-scale conservation for the Florida panther. Biol Conserv 130:118–133

Kertson BN, Spencer RD, Marzluff JM, Hepinstall-Cymerman J, Grue CE (2011) Cougar space use and movements in the wildland-urban landscape of western Washington. Ecol Appl 21:2866–2881

Kindall JL, VanManen FT (2007) Identifying habitat linkages for American black bears in North Carolina, USA. J Wildl Manag 71:487–495

Kissling WD, Fernandez N, Paruelo JM (2009) Spatial risk assessment of livestock exposure to pumas in Patagonia, Argentina. Ecography 32: 807-817

Klug PE, Wisely SM, With KA (2011) Population genetic structure and landscape connectivity of the Eastern Yellowbelly Racer (Coluber constrictor flaviventris) in the contiguous tallgrass prairie of northeastern Kansas, USA. Landscape Ecol 26:281–294

Koen EL, Garroway CJ, Wilson PJ, Bowman J (2010) The effect of map boundary on estimates of landscape resistance to animal movement. PLoS ONE 5:1–8

Koscinsky D, Yates AG, Handford P, Lougheed SC (2009) Effects of landscape and history on diversification of a montane, stream-breeding amphibian. J Biogeogr 36:255–265

Krishnamurthy R, Cushman SA, Sarkar MS, Malviya M, Naveeen M, Johnson JA, Sen S (2016) Multi-scale prediction of landscape resistance for tiger dispersal in central India. Landscape Ecology: DOI 10.1007/s10980-016-0363-0

Kuemmerle T, Perzanowski K, Resit Akcakaya H, Beaudry F, Van Deelen TR, Parnikoza I, Khoyetskyy P, Waller DM, Radeloff VC (2011) Cost-effectiveness of strategies to establish a European bison metapopulation in the Carpathians. J Appl Ecol 48:317–329

Kuroe M, Yamaguchi N, Kadoya T, Miyashita T (2011) Matrix heterogeneity affects population size of the harvest mice: Bayesian estimation of matrix resistance and model validation. Oikos 120:271–279

Lawler JJ, O'Connor RJ , Hunsaker CT , Jones KB , Loveland TR, White D (2004) The effects of habitat resolution on models of avian diversity and distributions: a comparison of two land-cover classifications. Landscape Ecology 19: 515-530

Lewis JS, Rachlow JL, Garton EO, Vierling LA (2007) Effects of habitat on GPS collar performance: using data screening to reduce location error. Journal of Applied Ecology 44:663–671

Lin LI (1989) A concordance correlation coefficient to evaluate reproducibility. Biometrics 1:255–268

Laiolo P, Tella JL (2006) Landscape bioacoustics allow detection of the effects of habitat patchiness on population structure. Ecology 87:1203–1214

LandFire (2012a) Existing Vegetation Cover. U.S. Department of the Interior, Geological Survey. Downloaded from: http://www.landfire.gov/viewer/ on Aug 21 2014

LandFire (2012b) Existing Vegetation Type. U.S. Department of the Interior, Geological Survey. Downloaded from: http://www.landfire.gov/viewer/ on Aug 21 2014

LaRue MA, Nielsen CK (2008) Modelling potential dispersal corridors for cougars in Midwestern North America using least-cost path methods. Ecol Model 212:372–381

Landguth EL, Cushman SA, Schwartz MK, McKelvey KS, Murphy M, Luikart G (2010) Quantifying the lag time to detect barriers in landscape genetics. Mol Ecol 19:4179–4191

Laundre JW, Hernandez L (2003) Winter hunting habitat of pumas Puma concolor in northwestern Utah and southern Idaho, USA. Wildl Biol 9:123–129

Laundre JW, Loxterman J(2007) Impact of edge habitat on summer home range size in female pumas. Am Midl Nat 157:221–229

Legendre P (1993) Spatial autocorrelation—trouble or new paradigm? Ecology 74:1659–1673

Levin SA (1992) The problem of pattern and scale in ecology: the Robert H MacArthur Award lecture. Ecology 73: 1943–1967

Lewis JS, Rachlow JL, Garton EO, Vierling LA (2007) Effects of habitat on GPS collar performance: using data screening to reduce location error. J Appl Ecol 44:663–671

Lin LI (1989) A concordance correlation coefficient to evaluate reproducibility. Biometrics 1:255–268

Loveland TR, Reed BC, Brown JF, Ohlen DO, Zhu Z, Yang L, Merchant JW (2000) Development of a global land cover characteristics database and IGBP DISCover from 1 km AVHRR data. Int J Remote Sens 21:1303–1330 Magle SB, Theobald DM, Crooks KR (2009) A comparison of metrics predicting landscape connectivity for a highly interactive species along an urban gradient in Colorado, USA. Landscape Ecol 24:267–280

Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. Trends Ecol Evol 18:189–197

Manly BF, McDonald LL, Thomas DL, Mcdonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies, 2nd edn. Kluwer Academic Publishers, Dordrecht

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2010) Resource selection by animals: statistical design and analysis for field studies, 2nd edn. Kluwer, Amsterdam

Martin AE, Fahrig L (2012) Measuring and selecting scales of effect for landscape predictors in species-habitat models. Ecol Appl 22:2277–2292

MacArthur R, Recher H, Cody M (1966) On the relation between habitat selection and species diversity. The American Naturalist 100: 319-332

Mateo Sánchez MC, Cushman SA, Saura S (2014) Scale dependence in habitat selection: the case of the endangered brown bear (Ursus arctos) in the Cantabrian Range (NW Spain). International Journal of Geographic Information Science 28: 1531-1546

McGarigal K, Cushman SA (2005) The gradient concept of landscape structure. In: Wiens J, Moss M (eds) Issues and perspectives in landscape ecology. Cambridge University Press, Cambridge, pp 112–119

McGarigal K., Wan HY, Zeller KA, Timm BC, Cushman SA (*2016*) Multi-scale habitat modeling: A review and outlook. Landscape Ecology: DOI*:*10.1007/s10980-016-0374-x

McRae BH (2006) Isolation by resistance. Evolution 60:1551–1561 McRae BH, Beier P (2007) Circuit theory predicts gene flow in plant and animal populations. Proc Nat Acad Sci 104:19885–19890

McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724

McRae BH, Shah VB, Mohapatra TK (2013) Circuitscape 4 user guide. The Nature Conservancy. http://www.circuitscape. org. Accessed 19 May 2015

Meyer CB, Thuiller W (2006) Accuracy of resource selection functions across spatial scales. Divers Distrib 12:288–297 Morales JM, Haydon DT, Frair J, Holsinger KE, Fyxell JM (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. Ecology 85:2436–2445

Michels E, Cottenie K, Neys L, DeGelas K, Coppin P, DeMeester L (2001) Geographical and genetic distances among zooplankton populations in a set of interconnected ponds: a plea for using GIS modelling of the effective geographical distance. Mol Ecol 10:1929–1938

Mills KJ, Patterson BR, Murray DL (2006) Effects of variable sampling frequencies on GPS transmitter efficiency and estimated wolf home range size and movement distance. Wildl Soc Bull 34:1463–1469

Murphy MA, Dezzani R, Pilliod DS, Storfer A (2010) Landscape genetics of high mountain frog metapopulations. Mol Ecol 19:3634–3649

Newby JR (2011) Puma dispersal ecology in the central Rocky Mountains. Master's thesis, University of Montana, Missoula, MT, pp 1–111

Nichol JE, Wong MS, Corlett R, Nichol DW (2010) Assessing avian habitat fragmentation in urban areas of Hong Kong (Kowloon) at high spatial resolution using spectral unmixing. Landsc Urban Plan 95:54–60

Norththrup JM, Hooten MB, Anderson CR Jr, Wittemyer G (2013) Practical guidance on characterizing availability in resource selection functions under a use-availability design. Ecology 94:1456–1463

O'Brien D, Manseau M, Fall A, Fortin MJ (2006) Testing the importance of spatial configuration of winter habitat for woodland caribou: an application of graph theory. Biol Conserv 130:70–83

Orange County Transportation Authority (2011) Master plan of arterial highways. Orange County Transportation Authority, Orange, California. Accessed from http://www.octa.net/Plans-and-Programs/GIS-Data/GIS-Data-Download/ on Sept 18, 2014

Pearce JL, Cherry K, Drielsma M, Ferrier S, Whish G (2001) Incorporating expert opinion and fine-scale vegetation mapping into statistical models of faunal distribution. J Appl Ecol 38:412–424

Pinto N, Keitt TH (2009) Beyond the least-cost path: evaluating corridor redundancy using a graph-theoretic approach. Landscape Ecol 24:253–266

Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J (2008) State-space models of individual animal movement. Trends Ecol Evol 23:87–94

Potts JR, Mokross K, Stouffer PC, Lewis MA (2014) Step selection techniques uncover the environmental predictors of space use patterns in flocks of Amazonian birds. Ecol Evol 24:4578–4588

Pullinger MG, Johnson CJ (2010) Maintaining or restoring connectivity of modified landscapes: evaluating the least- cost path model with multiple sources of ecological information. Landscape Ecol 25:1547–1560

R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/. Accessed 15 May 2013

Reding DM, Cushman SA, Gosselink TE, Clark WR (2013) Linking movement behavior and fine-scale genetic structure to model landscape connectivity for bobcats (Lynx rufus). Landscape Ecol 28:471–486

Rabinowitz A, Zeller KA (2010) A range-wide model of landscape connectivity and conservation for the jaguar, Panthera onca. Biol Conserv 143:939–945

Rae C, Rothley K, Dragicevic S (2007) Implications of error and uncertainty for an environmental planning scenario: a sensitivity analysis of GIS-based variables in reserve design. Landsc Urban Plan 79:210–217

Rayfield B, Fortin MJ, Fall A (2010) The sensitivity of least-cost habitat graphs to relative cost surface values. Landscape Ecol 25:519–532

Rettie WJ, McLoughlin PD (1999) Overcoming radio telemetry bias is habitat-selection studies. Can J Zool 77:1175–1184

Richard Y, Armstrong DP (2010) Cost distance modeling of landscape connectivity and gap-crossing ability using radio-tracking data. J Appl Ecol 47:603–610

Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. Am Nat 158:87–99

Riverside County Geographic Information Systems (2013) County Static Data. Riverside County Innovation Center, Riverside CA. Accessed from: http://gis.rivcoit.org/GISData.aspx on Aug 24, 2014.

Roever CL, Boyce MS, Stenhouse GB (2010) Grizzly bear movements relative to roads: application of step selection functions. Ecography 33:1113–1122

Ruth TK, Buotte PC, Quigley HB (2010) Comparing ground telemetry and global positioning system methods to determine cougar kill rates. J Wildl Manag 74:1122–1133

Saaty TL (1980) The analytic hierarchy process. McGraw-Hill, New York

San Bernadino (2014) San Bernadino county centerlines. Downloaded from: http://maps.sanbag.ca.gov/website/Transportation_data.htm on Sept 18, 2014

SanGIS (2014) All roads shape file. SanGIS/SANDAG Data Warehouse. San Diego Geographic Information Source - JPA/San Diego Association of Governments (SANDAG). Accessed from <http://www.sangis.org/Download_GIS_Data.htm> on July 20, 2014

Savage WK, Fremier AK, Shaffer HB (2010) Landscape genetics of alpine Sierra Nevada salamanders reveal extreme population subdivision in space and time. Mol Ecol 19:3301–3314

Sawyer SC, Epps CW, Brashares JS (2011) Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? J Appl Ecol 48:668–678

Schwartz MK, Copeland JP, Anderson NJ, Squires JR, Inman RM, McKelvey KS, Pilgrim KL, Waits LP, Cushman SA (2009) Wolverine gene flow across a narrow climatic niche. Ecology 90:3222–3232

Seoane J, Bustamente J, Diaz-Delgado R (2004) Are existing vegetation maps adequate to predict bird distributions? Ecological Modelling 175: 137-149

Seoane J, Bustamente J, Diaz-Delgado R (2005) Effect of expert opinion on the predictive ability of environmental models of bird distribution. Conserv Biol 19:512–522

Sexton, J. O., Song, X.-P., Feng, M., Noojipady, P., Anand, A., Huang, C., Kim, D.-H., Collins, K.M., Channan, S., DiMiceli, C., Townshend, J.R.G. (2013). Global, 30-m resolution continuous fields of tree cover: Landsat-based rescaling of MODIS Vegetation Continuous Fields with lidar-based estimates of error. International Journal of Digital Earth, 130321031236007. doi:10.1080/17538947.2013.786146.

Shirk AJ, Wallin DO, Cushman SA, Rica CG, Warheit KI (2010) Inferring landscape effects on gene flow: a new model selection framework. Mol Ecol 19:3603– 3619

Short Bull RA, Cushman SA, Mace R, Chilton T, Kendall KC, Landguth EL, Schwartz MK, McKelvey K, Allendorf FW, Luikart G (2011) Why replication is so important in landscape genetics: American black bear in the Rocky Mountains. Mol Ecol 20:1092–1107

Singleton PH, Gaines WL, Lehmkuhl JF (2002) Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least- cost corridor assessment. Research Paper PNW-RP-549. U.S. Forest Service Pacific Northwest Research Station, Portland, OR

Spear SF, Balkenhol N, Fortin MJ, McRae BH, Scribner K (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Mol Ecol 19:3576–3591

Squires JR, DeCesare NJ, Olson LE, Kolbe JA, Hebblewhite M, Parks SA (2013) Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. Biol Conserv 157:187–195

Stevens VM, Verkenne C, Vandewoestijne S, Wesselingh RA, Baguette M (2006) Gene flow and functional connectivity in the natterjack toad. Mol Ecol 15:2333–2344

Sutcliffe OL, Bakkestuen V, Fry G, Stabbetorp OE (2003) Modelling the benefits of farmland restoration: methodology and application to butterfly movement. Landsc Urban Plan 63:15–31

Sweanor LL, Logan KA, Bauer JW, Millsap B, Boyce WM (2008) Puma and human spatial and temporal use of a popular California state park. J Wildl Manag 72:1076–1084

Thatcher CA, VanManen FT, Clark JD (2009) A habitat assessment for Florida panther population expansion into central Florida. J Mammal 90:918–925

Thompson CM, McGarigal K (2002) The influence of research scale on bald eagle habitat selection along the lower Hudson River, New York. Landscape Ecol 17:569–586

Thurfjell H, Ciuti S, Boyce MS (2014) Applications of step- selection functions in ecology and conservation. Mov Ecol 2:4

Tobalske C (2002) Effects of spatial scale on the predictive ability of habitat models for the green woodpecker in Switzerland. In: Scott JM, Heglund PJ, Samson F, Haufler J, Morrison M, Raphael M, Wall B (Eds.), Predicting Species Occurrences: Issues of Accuracy and Scale. Island Press, Covelo, California. pp. 197–204

USDA Forest Service (2007) CalVeg: FSSDE.Eveg- Tile47A_02_v2. Pacific Southwest Region Remote Sensing Lab, McClellan

U.S. Geological Survey (2009) National Elevation Dataset. U.S.G.S. Sioux Falls, SD. Downloaded from: http://viewer.nationalmap.gov/viewer/ on Aug 20, 2014

Van Beest FM, Van Moorter B, Milner JM (2012) Temperature- mediated habitat use and selection by a heat-sensitive northern ungulate. Anim Behav 84:723–735

Venier LA, Pearce J, McKee JE, McKenney DW, Niemi GJ (2004) Climate and satellite-derived land cover for predicting breeding bird distribution in the Great Lakes Basin. Journal of Biogeography 31:315-331

Vickers TW, Sanchez JN, Johnson CK, Morrison SA, Botta R, Smith T, Cohen BS, Huber PR, Ernest HB, Boyce WM (2015) Survival and mortality of pumas (Puma concolor) in a fragmented, urbanizing landscape. PlosONE. doi:10. 1371/journal.pone.0131490

Vignieri SN (2005) Streams over mountains: influence of riparian connectivity on gene flow in the Pacific jumping mouse (Zapus trinotatus). Mol Ecol 14:1925–1937

Wang YH, Yang KC, Bridgman CL, Lin LK (2008) Habitat suitability modelling to correlate gene flow with landscape connectivity. Landscape Ecol 23:989–1000

Wang IJ, Savage WK, Shaffer B (2009) Landscape genetics and least-cost path analysis reveal unexpected dispersal routes in the California tiger salamander (Ambystoma californiense). Mol Ecol 18:1365–1374

Wasserman TN, Cushman SA, Schwartz MK, Wallin DO (2010) Spatial scaling and multi-model inference in landscape genetics: Martes Americana in northern Idaho. Landscape Ecol 25:1601–1612

Watts K, Eycott AE, Handley P, Ray D, Humphrey JW, Quine CP (2010) Targeting and evaluating biodiversity conservation action within fragmented landscapes: an approach based on generic focal species and least-cost networks. Landscape Ecol 25:1305–1318

Wheatley M (2010) Domains of scale in forest-landscape metrics: implications for species-habitat modeling. Acta Oecol 36:259–267

Wheatley M, Johnson C (2009) Factors limiting our understanding of ecological scale. Ecol Complex 6:150–159

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385–397

Wilmers CC, Wang Y, Nickel B, Houghtaling P, Shakeri Y, Allen ML, Kermish-Wells J, Yovovich V, Williams T (2013) Scale dependent behavioral responses to human development by a large predator, the puma. PLoS ONE 8:e60590. doi:10.1371/journal.pone.0060590

Worton BJ (1995) A convex hull-based estimator of home-range size. Biometrics 51:1206–1215

Wu J (2004) Effects of changing scale on landscape pattern analysis: scaling relations. Landscape Ecology 19: 125-138

Zeller KA, McGarigal K, Beier P, Cushman SA, Vickers TW, Boyce WM (2014) Sensitivity of landscape resistance estimates based on point selection functions to scale and behavioral state: pumas as a case study. Landscape Ecol 29:541–557

Zeller KA, McGarigal K, Beier P, Cushman SA, Vickers TW, Boyce WM (2015) Using step and path selection functions for estimating resistance to movement: pumas as a case study. *Landscape Ecology.* DOI: 10.1007/s10980-015-0301-6

Zeller KA, McGarigal K, Whiteley AR (2012) Estimating landscape resistance to movement: a review. Landscape Ecol 27:777–797

Zimmermann F, Breitenmoser U (2007) Potential distribution and population size of the Eurasian lynx Lynx lynx in the Jura Mountains and possible corridors to adjacent ranges. Wildl Biol 13:406–416