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RESEARCH ARTICLE

Movement behavior explains genetic differentiation in American black bears

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Abstract Individual-based landscape genetic analyses provide empirically based models of gene flow. It would be valuable to verify the predictions of these models using independent data of a different type. Analyses using different data sources that produce consistent results provide strong support for the generality of the findings. Mating and dispersal movements are the mechanisms through which gene flow operates in animal populations. The best means to verify landscape genetic predictions would be to use movement data to independently predict landscape resistance. We used path-level, conditional logistic regression to predict landscape resistance for American black bear (*Ursus americanus*) in a landscape in which previous work predicted population connectivity using individual-based landscape genetics. We found consistent landscape factors influence genetic differentiation and movement path selection, with strong similarities between the predicted landscape resistance surfaces. Genetic differentiation in American black bear is driven by spring movement (mating and dispersal) in relation to residential development, roads, elevation and forest cover. Given the limited periods of the year when gene flow events primarily occur, models of landscape connectivity should carefully consider temporal changes in functional landscape resistance.

Keywords Movement behavior · Path-level analysis · Connectivity · Landscape genetics · Black bear · *Ursus americanus*

Introduction

Landscape genetic research is providing increasingly sophisticated methods to infer the influences of landscape structure on population connectivity. Individual-based analyses predicting the genetic differences among all pairs of sampled organisms based on the cost distances between them as functions of multiple landscape resistance hypotheses provide a particularly useful approach (e.g. Coulon et al. 2004; Cushman et al. 2006). Recent work has refined and extended these approaches by incorporating multiscale modeling and improved model selection approaches (Shirk et al. 2010; Wasserman et al. 2010). Simulation modeling has shown that individual based landscape genetic inference of landscape

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resistance to gene flow provides high power to identify the landscape factors driving genetic differentiation and reject incorrect but correlated alternative models (Cushman and Landguth 2010b). Individual-based landscape genetic approaches also appear relatively robust to variation in the grain and extent of analysis (Cushman and Landguth 2010b).

Simulation analysis, however, also indicated high sensitivity to incorrect specification of the landscape resistance model (Cushman and Landguth 2010a). Incorrect specification of the landscape variables included in the resistance model and the thematic resolution at which they are represented can distort the apparent relationships between landscape patterns and gene flow. Given the sensitivity of landscape genetics to incorrect specification and thematic content, it would be valuable to compare analyses using multiple methods and independent data sets. Two different analyses based on different kinds of data that produce a consistent result provide strong support for the findings. Mating and dispersal movement behavior are the mechanisms through which gene flow operates in animal populations. Using movement data to independently predict landscape resistance should provide a valuable means to verify the robustness of landscape genetic predictions.

There has been little research to date comparing predictions of landscape connectivity provided by landscape genetics with predictions from movement behavior. Recently, Shanahan et al. (2010) sought to determine whether individual-level movement characteristics are a mechanistic driver of genetic differentiation of closely related bird species across a complex landscape. Their analysis was based on evaluating a priori models that predict genetic relatedness patterns based on how species with different life-history traits are expected to respond to habitat boundaries. Their analysis, however, did not use actual data on observed movement of individual birds to verify the predictions of landscape genetic models. Coulon et al. (2004, 2006) showed that genetic structure (i.e., individual-based genetic distances) and actual movement paths are not explained by the same variables in roe deer. Extending this work, Coulon et al. (2008) used a conditional logistic regression approach to predict effects of landscape features on Roe deer movement paths in a study area where previous landscape genetic work had shown correlation between landcover and gene flow. Their study is the first to explicitly link behavioral mechanisms to observed genetic substructure. Direct linkages between genetic differentiation and organism behavior are important to understand population differentiation in spatially complex environments.

In this article we present a direct linkage of the behavior of individual organisms with observed genetic structure across a complex landscape. We predict that as organisms move through spatially complex landscapes, they respond to multiple ecological attributes, expressing movement paths that minimize fitness costs. Until recently, it was not possible to obtain precise records of movement paths over extended periods of time to associate movement behavior with landscapes structure. However, this has changed dramatically with the advent of Global Positioning System (GPS) telemetry technology (e.g. Osborn and Parker 2003). GPS telemetry data provides spatially precise records of the movement paths of individual animals at a temporal sampling rate that allows direct assessment of the influences of landscape features on movement paths. This enables the development of species-specific landscape resistance models in which the resistance of any location, or pixel, in a landscape is a function of multiple landscape features measured at one or several scales. Fortin et al. (2005) is the first published example of using GPS data in a step selection function to predict relationship between landscape features and movement path selection. More recently, Coulon et al. (2008) used a step selection function to predict movement of roe deer in relation to landscape variables.

This study differs from previous work in that it focuses at the path-level rather than the step level. It uses a path-level spatial randomization method to assess the effects of multiple landscape features on movement path selection (e.g. Cushman et al. 2010a, b). The path-level randomization approach provides a robust means to compare the landscape features an animal encounters in its utilized path with those that would be encountered in a large sample of available paths of identical length and topology. By holding length and topology constant and randomizing location in the landscape, the approach avoids pseudoreplication and autocorrelation of observations, as may be an issue with analyses evaluating point data or sequential movement steps (Harris et al. 1990; Litvaitis et al. 1994; Cushman 2010).

The objectives of this study were to use path-level analysis of movement (Cushman et al. 2010a) and case–control logistic regression (Hegel et al. 2009) to predict selection of movement paths by American black bears (*Ursus americanus*) as a function of elevation, roads, human development and forest canopy, and then to evaluate the degree to which resistance models derived from movement data verify a resistance model previously identified through landscape genetics (Cushman et al. 2006). Case–control logistic regression provides an important advance over previous approaches based on factorial analysis of alternative resistance models (e.g. Cushman et al. 2010a), as it provides a robust way to estimate variable coefficients and rank alternative hypotheses with Akaike's Information Criteria (AIC; Burnham and Anderson 2002). We had three specific hypotheses. First, we hypothesized that black bear movement behavior in the part of the year in which breeding and dispersal occur is more strongly related to genetic differentation than movement behavior during other parts of the year when dispersal is less common. Second, we hypothesized that movement behavior of black bears during the breeding and dispersal season is a function of the same landscape factors identified in the landscape genetic analysis. Third, we hypothesized that the predicted resistance map produced by the movement modeling during the breeding and dispersal season is highly correlated with the resistance map produced from the landscape genetic analysis, and that the resistance map produced during other times of the year would have lower correlation with the landscape genetic resistance model.

Materials and methods

Study area

The study area consists of approximately 1,500 km^2 in the Purcell Mountains of north Idaho, USA (Fig. 1). Landownership consisted on US Forest Service (Idaho Panhandle National Forest), state, private timber lands, and private residences. The topography is mountainous, with steep ridges, narrow valleys and many cliffs and cirques at the highest elevations. Elevation ranges from approximately 700 to 2,400 m. The Kootenai River bounds the study area on the west, separating the Selkirk Mountains on the west from the Purcell Mountains on the east with a 5–8 km wide unforested, agricultural valley. The

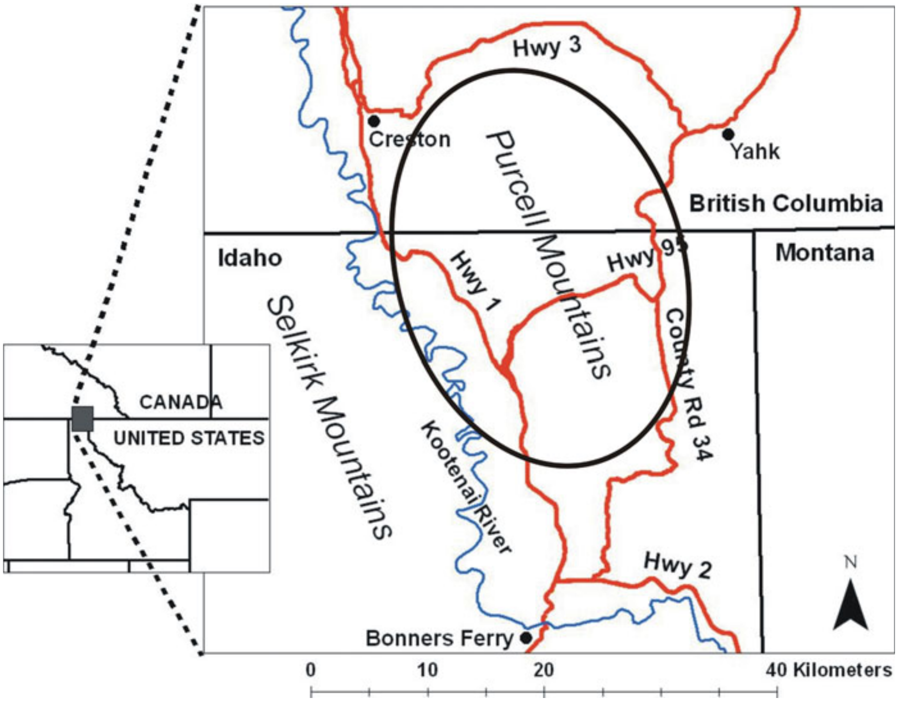

Fig. 1 Study area where analyses of gene flow (Cushman et al. 2006) and movement patterns of black bears were evaluated in northern Idaho, USA, and southern British Columbia, Canada. The *black ellipse traces* the approximate extent of the movement paths of the collared bears included in the study

area is heavily forested, with *Abies lasiocarpa* (subalpine fir) and *Picea engelmannii* (Engelmann spruce) codominant above 1,300 m, and a diverse mixed conifer forest dominating below 1,300 m. For further description of the vegetation in the study area, see Lewis (2007). This study area is the portion of the Cushman et al. (2006) study area that lies to the east of the Kootenai River.

Previous landscape genetic analysis

Cushman et al. (2006) used non-invasive genetic sampling, least cost path modeling and causal modeling with partial Mantel tests to evaluate 110 hypotheses concerning landscape resistance effects on genetic differentiation on American black bears in the study area. The goal was to determine the relative support for isolation by distance and barriers in comparison to isolation by gradients of landscape resistance. In addition, there are many possible alternative models for landscape effects on population connectivity of this species. A priori, we proposed elevation, roads, topographical slope, land-use and land-cover as factors hypothesized to affect gene flow in this species. In addition, each of these factors could influence bear gene flow in a number of potential ways. Therefore, we constructed a factorial of multiple levels of each of these factors, totaling 108 alternative landscape resistance hypotheses (Cushman et al. 2006).

We used the ArcGIS to produce cost distance matrices that correspond to each of the 110 alternative models (108 landscape models, isolation by distance, and isolation by the Kootenai River barrier). The cost distance matrices corresponding to each landscape resistance hypotheses were created using the COSTDISTANCE function (ESRI 2005). This entailed creating cost matrices reflecting the least-cost distance from the location at which each bear's DNA sample was recorded to every other bear's location across each of the 108 resistance surfaces. We next identified which of the seven models had the strongest support. All 110 resistance hypotheses were significantly related to the pattern of genetic difference among bears. After partialling out the relationship with Euclidean distance, 10 landscape resistance models were still significant. These models indicate that gene flow in this population is influenced predominantly by landscape-resistance gradients with no significant independent relationships with the Kootenai River barrier or geographical distance.

Ranking the 10 significant partial models by the Monte Carlo permuted *P*-value provided a means to determine which hypotheses have the greatest support and to identify the combination of landscape factors most related to the genetic structure of this population. The 10 significant partial models were all concentrated in one small area of a four-dimensional factorial space (roads, elevation, forest cover, slope), indicating a unimodal peak of support. Within this small area of concentration, the best-supported models were associated with minimum resistance to movement at middle elevations, high resistance of nonforested habitat to movement, no relationship with slope, and equivocal support for the different levels of road resistance. The goal was to determine the relative support for isolation by putative movement barriers, geographical distance, roads, landcover, and topographical slope, and to identify the combination of factors that had the most support as the causal driver of genetic differentiation for black bears. The results indicated that gene flow of black bears is facilitated by high forest cover at middle elevations, with avoidance of non-forest, agriculture and residential development and equivocal response to crossing roads. The landscape resistance model produced by Cushman et al. (2006) was used in this study for comparison with the landscape resistance model identified through path-level analysis of bear movement data.

Black bear telemetry data

Bears were trapped from June to mid-August in 2004–2006 using Aldrich foot snares (Johnson and Pelton 1980) and immobilized with a Telazol/Xylazine combination and reversed Xylazine with either Yohimbine or Tolazoline. Lotek 3300L GPS collars with cotton spacers were fitted on all bears >35 kg. Collars were programmed to record a location every 20 min from April (den emergence) to November (den entrance) and information was stored on the collar, providing consistent fine scale movement data with high fix rates and small location errors (Lewis 2007). Each winter (2005–2007), we visited bear dens to retrieve and replace GPS collars. During winter den work, black bears were immobilized with a Ketamine/Xylazine combination. If we could not visit a den during winter, the collar's remote drop-off mechanism released the collar from the animal the following summer. These methods were approved by the University of Idaho Animal Care and Use Committee (Protocol 2005-27).

For this analysis, we used location data from 2 years, 2005 and 2006, given the few bears monitored during 2004 and 2007. We divided the year of bear activity into two periods, early and late seasons. Early season was defined as the time between den emergence from hibernation until July 15, and late season was defined from July 16 until bears return to hibernation. The year was divided into two parts because of important differences in food resources, differences in traversibility of the landscape due to spring snow pack, and behavioral differences between early and late season. Early season coincides with the breeding season of black bears and is the season in which juvenile bears leave their mothers and disperse. Temporal activity patterns also differed between the early and late seasons (Lewis 2007).

Several bears were monitored for both years. To avoid bias, we included each individual only from the season year (2005 or 2006) in which it had the largest number recorded GPS locations. We only included paths that contained at least 250 individual points in a given season (early or late). This resulted in a total 19 bears included in the early season analysis (five from 2005; 14 from 2006) and 20 bears in the late-season analysis (seven from 2005; 13 from 2006). In the early season analysis there were three males and two females from 2005, and 11 males and three females in 2006. In the late season analysis there were one female and six males in 2005, and three females and 10 males in 2006.

Path-level analysis

Our movement analysis was based on contrasting the frequency that the utilized movement path crosses various landscape features with the frequency at which these features would be crossed in a large sample of available movement paths of the same length and topology. Our analysis tests alternative hypotheses of landscape resistance against the movement paths selected by individual bears. First, the movement path utilized by each bear in each season was created by converting the series of sequential point locations for each bear in each season into a line in ARCINFO (ESRI 2005). Second, 199 available paths with identical topology were created by randomly shifting and rotating the utilized path. The available paths were randomly shifted a distance between 0 and 20 km in latitude and longitude, and randomly rotated between 0 and 360°.

A priori selection of variables

We a priori proposed four landscape features that we believed to influence black bear movement and which would enable an independent test of the resistance model identified in Cushman et al. (2006). These landscape features included: (1) canopy closure, (2) density of houses and other buildings, (3) roads, including secondary forest roads, paved county roads, and highways, and (4) elevation.

Scaling of landscape resistance factors

The functional form and scale at which each landscape feature was represented in analysis may have large impacts on the strength of relationships with black bear movement (Wiens 1989; Cushman et al. 2010b; Cushman and Landguth 2010b). We investigated the relationships between movement path selection and the four independent variables across a range of functional forms and spatial scales. Correctly representing the thematic resolution and form of the functional relationship between each landscape feature and genetic structure is essential to identifying the correct pattern process relationship (e.g. Cushman and Landguth 2010b; Shirk et al. 2010; Wasserman et al. 2010). Least cost path modeling can be used to evaluate how resistance of landscape elements influences animal movement (e.g. Cushman et al. 2010a).

Resistance due to canopy cover was evaluated over five different levels that included power functions of 0.2, 0.4, 0.6, 1.5, 2.0 power. Landscape resistance predicted by these power functions ranges from strongly convex to strongly concave (Figure S1). Landscape resistance due to elevation was modeled as a Gaussian function, on the expectation that black bears should show a unimodal optimum in movement ability with respect to elevation (e.g. Cushman et al. 2006). The form of the Gaussian function was defined on the basis of the optimum elevation and the standard deviation (Figure S2). The optimum elevation was assigned a minimum resistance of 1 and the maximum resistance of 10. The three elevation models consisted of Gaussian functions with minimum resistance at 500, 1,000, and 1,500 m, with standard deviation of 500 m. These are the same three elevation models as evaluated in Cushman et al. (2006). Three levels of resistance due to roads were considered and represented as categorical functions (Figure S3). These three road resistance layers varied the relative resistance of secondary forest roads, paved secondary county roads, and state highways (Table 1). All non-road pixels were given a resistance of 1. We evaluated ten landscape resistance layers due to density of houses and other buildings (Figure S4). These were created by placing a unimodal resistant kernel (e.g. Compton et al. 2007) of varying width over each building summing the kernels into a resistance surface. The ten scales corresponded to kernel widths of 100–1,000 m by 100 m steps. The maximum resistance on these maps was scaled to 10 with a minimum resistance of 1.

Conditional logistic regression

We utilized logistic regression in a case–control form as it is ideally suited to the task of mathematically discriminating ecological differences between utilized and available movement paths. In this analysis we have a matched case–control design with one utilized path matched with 199 available paths. In such circumstances conditional logistic-regression is an appropriate modeling approach (Manly et al. 2002; Fortin et al. 2005; Coulon et al. 2008; Hegel et al.

Table 1 Description of the different forms of each variable evaluated in the univariate-scaling analysis

Variable	Description
Roads	
R2_5_10	Resistance 2 forest roads, 5 county roads, 10 highways, 1 elsewhere
R5_15_45	Resistance 5 forest roads, 15 county roads, 45 highways, 1 elsewhere
R5_20_80	Resistance 5 forest roads, 20 county roads, 80 highways, 1 elsewhere
Canopy cover	
C0.2	Resistance canopy cover to the 0.2 power
C0.4	Resistance canopy cover to the 0.4 power
C0.6	Resistance canopy cover to the 0.6 power
C1.5	Resistance canopy cover to the 1.5 power
C2	Resistance canopy cover to the 2.0 power
Elevation	
E500	Resistance inverse Guassian function of elevation, minimum value of 1 at 500 m, increasing to maximum of 10 with 1,000 m standard deviation
E1000	Resistance inverse Guassian function of elevation, minimum value of 1 at 1,000 m, increasing to maximum of 10 with 1,000 m standard deviation
E1500	Resistance inverse Guassian function of elevation, minimum value of 1 at 1,500 m, increasing to maximum of 10 with 1,000 m standard deviation
Development	
D100	Resistance kernel density of human structures with 100 mm kernel radius
D200	Resistance kernel density of human structures with 200 m kernel radius
D300	Resistance kernel density of human structures with 300 m kernel radius
D400	Resistance kernel density of human structures with 400 m kernel radius
D500	Resistance kernel density of human structures with 500 m kernel radius
D600	Resistance kernel density of human structures with 600 m kernel radius
D700	Resistance kernel density of human structures with 700 m kernel radius
D800	Resistance kernel density of human structures with 800 m kernel radius
D900	Resistance kernel density of human structures with 900 m kernel radius
D1000	Resistance kernel density of human structures with 1,000 m kernel radius

2009). Conditional logistic regression models use data in which a used (presence) location is specifically matched to a number of unused, or available, locations to create a group (stratum), and results of the model are conditional upon each group. These approaches have been used to deal with situations in which habitat availability changes during the course of a study (Arthur et al. 1996), and to deal with potential temporal autocorrelation arising from data collected from GPS radio-telemetry data (Johnson et al. 2004). This approach is particularly useful when there is a lack of independence in the data, such as in GPS radio-telemetry data (Fortin et al. 2005; Coulon et al. 2008). Interpretation of model coefficients is the same as for ordinary logistic regression, yet may be viewed as more reliable given that the natural clustering in the data is accounted for (Hegel et al. 2009). There is no intercept estimated since the model is conditioned on each stratum.

We conducted the logistic regression in two steps. First we conducted a univariate scaling analysis (e.g. Thompson and McGarigal 2002) to identify which of the several alternative forms of each landscape variable had the strongest relationship with selected bear paths. To produce the independent variables for the logistic regression analysis, we computed the mean value of all pixels the utilized and available paths traversed for each predictor variable. We ranked the various forms of each landscape variable by the chi-square p-value on the likelihood ratio produced by a univariate logistic regression model between utilized and available paths.

In the second step, we proposed a suite of candidate models constructed from combinations of the predictor variables, with each predictor variable represented at the scale identified as the most supported one in the first step. As we had no a priori biological reason to exclude any particular variable combination, we evaluated all 15 combinations of the four independent variables (Table 2). We ranked these models by AICc values (AIC corrected for small sample size; Burnham and Anderson 2002) and used model averaging across all candidate models based on AICc weights to produce a final model with associated parameter estimates (Burnham and Anderson 2002). We produced a resistance map from this model by calculating $b1v1 + b2v2 + \cdots + bnvn$, where bi is the coefficient for variable vi.

Table 2 Description of the 15 candidate models evaluated for both early and late season, AICc values, ΔAICc, and Akaike model weights (*w*)

Model acronym	Model description	Early season			Late season		
		AICc	ΔAICc	*w*	AICc	ΔAICc	*w*
C	Canopy cover to the 0.2 power	226.44	47.33	0.00	268.62	5.41	0.02
D	Kernel density of human structures, 100 m kernel radius	214.43	35.32	0.00	266.71	3.50	0.06
E	Inverse Gaussian function of elevation: mean 1,000, 1,000 m SD early season; mean 1,500, 1,000 m SD late season	213.65	34.54	0.00	269.40	6.19	0.02
R	Resistance to crossing roads	222.76	43.65	0.00	263.21	0.00	0.35
RE	Roads and elevation	194.64	15.53	0.00	264.83	1.61	0.16
DE	Human structures and elevation	179.11	0.00	0.43	269.17	5.95	0.02
CE	Canopy cover and elevation	213.02	33.91	0.00	271.10	7.88	0.01
DR	Human structures and roads	216.80	37.69	0.00	265.57	2.35	0.11
CR	Canopy cover and roads	225.22	46.11	0.00	265.65	2.43	0.10
CD	Canopy cover and human structures	216.78	37.67	0.00	269.09	5.87	0.02
CRE	Canopy cover, roads and elevation	197.16	18.05	0.00	267.47	4.26	0.04
CDR	Canopy cover, human structures and roads	219.55	40.44	0.00	268.25	5.04	0.03
CDE	Canopy cover, human structures and elevation	181.20	2.09	0.15	271.68	8.47	0.01
DRE	Human structures, roads and elevation	179.85	0.74	0.30	267.20	3.99	0.05
CDRE	Canopy cover, human structures, roads and elevation	181.80	2.69	0.11	270.29	7.07	0.01

Similarity of the results based on behavioral data with those from landscape genetic analysis

We evaluated the similarity between the resistance model predicted by the conditional path-level logistic regression analysis with that produced in the Cushman et al. (2006) landscape genetic analysis in three ways. First, we compared the variables included in the two models. Second, we compared the signs of the variable coefficients in the path model with the direction of the relationship in the landscape genetic analysis. Third we correlated the resistance surface produced from landscape genetics with that predicted by logistic regression.

Results

Univariate scaling

Ranking across power transformations indicated highest support for landscape resistance as a function of canopy closure to the 0.2 power in both early and late seasons (Figure S5). Ranking across resistant kernel widths resulted in highest support for landscape resistance as function of density of human structures based on a 100 m radius resistant kernel (Figure S6). The 100 m radius kernel was the most supported kernel in both seasons. Ranking across road classifications revealed highest support for landscape resistance as a function of roads in which resistance is 5 for crossing forest roads, 20 for crossing county roads and 80 for crossing highways (Figure S7). This suggests that forest roads are relatively more easily crossed than county roads and highways present very high resistance to movement. This was the most supported roads resistance model in both early and late seasons. Ranking the three elevation models showed highest support for landscape resistance in the early season as an inverse Gaussian function of elevation with minimum value of 1 at 1,000 m and increasing resistance with a 1,000 m standard deviation (Figure S8). In the late season there was little difference in support for the different elevation models, with marginally higher support for the 1,500 m model.

Multi-variate model

We calculated AICc weights and performed model averaging to produce final landscape resistance models for the early and the late season. For the early season, elevation and human development exhibited the greatest importance, with 95% confidence intervals of variable coefficients not overlapping 0, and roads and canopy closure being less important (Tables 2, 3). In comparison to the early season model, results for the late season indicated that roads were the most important factor influencing bear movement, with 95% confidence intervals of variable coefficients not overlapping 0, and canopy closure, human development, and elevation explaining bear movement to a lesser degree (Table 3).

Comparison of resistance surfaces

The resistance model produced by landscape genetics (Cushman et al. 2006) and the resistance model produced by logistic regression based on early season bear paths included the same environmental features

Table 3 Final parameter estimates and AIC importance values for canopy closure, development, roads, and elevation during early and late seasons used in analyses of black bear movement paths in the Purcell Mountains of Idaho, USA

Variable	Early season			Late season		
	Parameter	AIC importance		Parameter	AIC importance	
	Estimate	SE	Value	Estimate	SE	Value
Canopy closure	−0.25	0.45	0.27	−0.05	0.27	0.24
Development	−471.07	149.1	1.00	−9.22	21.64	0.30
Roads	−0.97	1.13	0.41	−1.68	0.80	0.85
Elevation	−1.58	0.40	1.00	0.04	0.08	0.30

AIC importance value for a variable provides a measure of relative importance among the variables evaluated across models, given equal representation across all a priori models

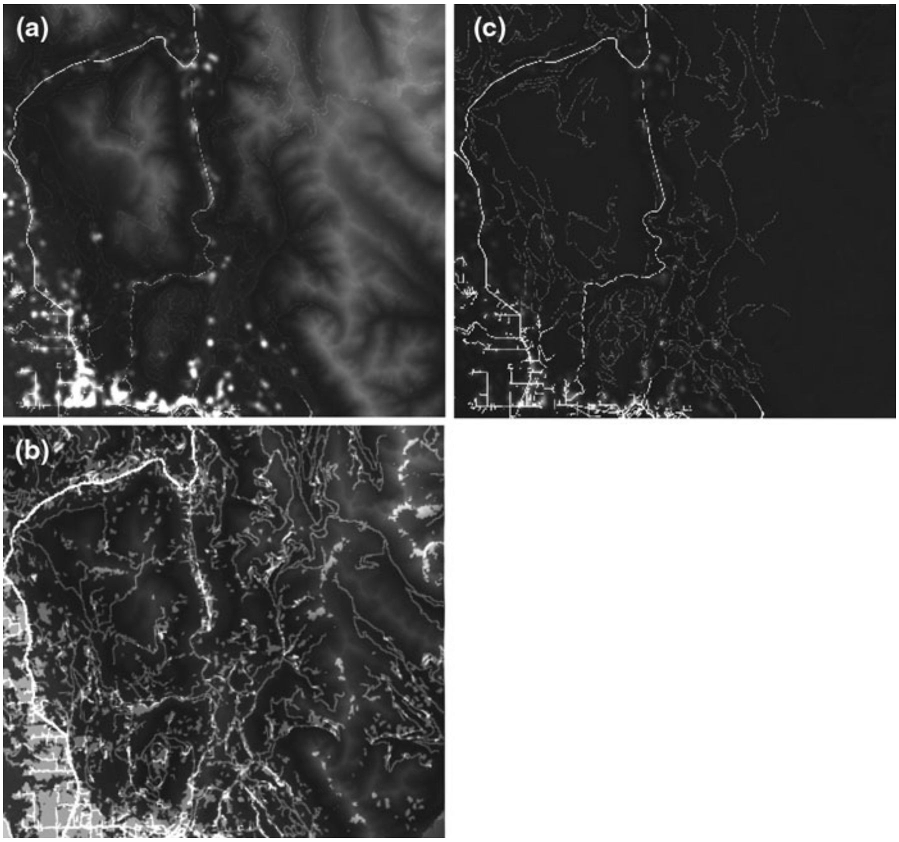

Fig. 2 Resistance maps produced by **a** early season (spring), **b** resistance map produced from landscape genetic analyses by Cushman et al. (2006) and **c** late season (summer) movement path analysis

with the same qualitative relationship (i.e. sign of variable coefficients; Table 3). In contrast, the late season model was dominated by the effect of roads (Table 3) and had a qualitatively different relationship with elevation than the early season model. The resistance maps produced from the averaged models of early and late season movement are shown in Fig. 2, in comparison with the resistance model produced by landscape genetics.

There was high spatial correlation between the early season movement model and the resistance model derived from landscape genetics (Table 4). The correlations between the late season model and the genetics-based model and between the early and late season models are much lower (Table 4). Using partial correlation we evaluated if the relationship between the early season model and genetic-based resistance models by partialling out the correlation with the late season model model, and vice versa. The relationship between the early season and genetic-based resistance models was unaffected by partialling out the late season model, while the correlation between the late season and genetic-based resistance models became negative partialling out the early season model. This shows strong similarity between early season movement and landscape genetic resistance models and no support of independent relationship between late season movement and genetics-

Table 4 Simple (upper triangle) and partial (lower triangle) Spearman correlations between resistance values in three resistance maps (Fig. 2)

	Genetic	Early	Late
Genetic	–	0.410	0.131
Early	0.4018	–	0.5020
Late	−0.0980	0.5010	–

Genetic resistance map from Cushman et al. (2006); *Early* resistance map early season movement paths of black bears; *Late* resistance from late season movement paths of black bears based models after accounting for the early season model. The resistance map derived from early season bear movement behavior and that derived from patterns of genetic differentiation provide similar understandings of landscape resistance to black bear movement.

Discussion

Comparison of resistance models produced by landscape genetics and movement data

Our major goal was to evaluate how well movement behavior of black bears could explain genetic differentiation as a function of landscape resistance. We used independently developed landscape resistance maps from landscape genetics on genetic distance among pairs of bears distributed across the landscape (Cushman et al. 2006) and analysis of black bear movement data. The predictor variables in both analyses are landscape resistance as functions of elevation, roads, human development and forest cover. We included the same suite of predictor variables to determine if models produced from the two data sources were comparable in terms of variable participation and direction of relationship. We hypothesized that behavior during the breeding and dispersal season is the mechanism driving genetic differentiation.

Our results indicated high similarity between the resistance surface predicted by landscape genetics and that produced from the early season path-level analysis. The two models included the same variables with the same qualitative relationship to movement resistance and produced highly correlated resistance maps. In contrast, the late season model was quite different from that of Cushman et al. (2006). Roads were the driving factor in late season, with less support for other variables.

There were some differences between the early season movement model and the landscape genetics model. The models differed in terms of the relative importance of roads and forest cover. The effect of roads appeared to be larger in the movement model, while the effect of forest cover was larger in the landscape genetics model. We hypothesize that the relatively small effect of forest cover in the movement model is largely due to the differences in the spatial extent of the two analyses. The Cushman et al. (2006) analysis modeled gene flow among 146 bears distributed between the Selkirk and Purcell Mountains. That analysis included least cost dispersal distances between many bears separated by the 5–8 km wide Kootenai river valley. In contrast, the analysis reported here was limited to the spatial extent of available GPS locations in Purcell Mountains, which included less area of agricultural and other non-forest types than the Cushman et al. (2006) study area. Thus, the observation of relatively small forest effect in the movement model analysis may be due to the fact that the study area used in the movement analysis was dominated by continuous forest: forest cover may not be highly limiting to bear movement within this geographical scope. This may not mean that forest cover is less important for movement path selection than for gene flow. Rather, the differences in the availability of landscape features within the two study areas leads to different degrees to which a landscape variable influences genetic differentiation and movement path selection. Other research in the study area demonstrated that on both fine and broad scales, black bears avoid agricultural areas, although bears would occasionally cross these non-forested landscape features (Lewis 2007).

Path-level analysis identifies scale of response to multiple landscape variables

Our scaling analysis enabled us to identify the functional scale at which each environmental variable was most related to the selection of movement paths by black bears. Across both seasons, the form of the canopy cover variable most strongly related to bear movement paths was a function of canopy cover to the 0.2 power. This created a highly convex response curve with landscape resistance decreasing rapidly as canopy cover increases from zero. This suggests a non-linear relationship in which bear movement is inhibited by open-land conditions, but that even low levels of canopy cover provide quality movement habitat for bears. Human development was highly related to bear movement paths across all kernel widths tested. This indicated a strong and consistent avoidance of human developments including houses and other structures. In both early and late seasons the strongest relationship was found at a 100 m kernel radius. This result showed avoidance of human structures at all scales, with increasing avoidance as proximity increases. This is similar to what Cushman et al. (2010a) found for elephant avoidance of human development in southern Africa using a similar path-level analysis. In both early and late season models, the road resistance layer with the highest contrast between highways and forest roads was the most supported, indicating that paved secondary roads offer four times as much resistance to crossing as gravel forest roads, and that highways offer a 16 times higher resistance than forest roads and a four times higher resistance than secondary roads. Thus, there was much stronger avoidance of crossing highways than of forest roads. These results are consistent with other studies reporting that bears are more likely to avoid highways than secondary roads (Brody and Pelton 1989; Beringer et al. 1990). While bears have been shown to avoid areas near highways in the Purcell Mountains (Lewis 2007), bears in this study did cross Highway 95 multiple times and selected areas with specific habitat features for highway crossing (Lewis 2007).

Differences between early and late season movement behavior of black bears in relation to landscape features

There are several potential explanations for the differences between early and late season movement models. First, in spring, deep snow restricts access to areas above 1,300–1,500 m, which probably restricts bears to an elevational belt centered at about 1,000 m. This concentration of bears at lower elevations also forces bears into proximity to the highest density of human development in the study area. Thus, human development enters the early season model because human development is a landscape feature prominent at the elevational zone bears are restricted to in the early season.

In the late season model, bears have access to all elevations after spring snowpack has melted. This enables them to utilize habitat at all elevations. Also, the primary summer food resource for bears is thin-leaf huckleberry (*Vaccinium membranosa*), which is concentrated at elevations from approximately 1,300 to 2,000 m. It is likely that bears select movement paths in summer to maximize availability of forage and minimize their risk of associated with road crossing. Bears in the study area selected for habitat in late summer and fall associated with huckleberry shrubs (Lewis 2007). Human development was not a significant predictor of summer movement as there is little human development in the study area above 1,000 m. Other research evaluating black bear occurrence reported that bears avoid human development during this season, although the relationship in late summer/fall was weaker than the spring/early summer season (Lewis 2007).

Implications for landscape connectivity

We believe that the early season resistance model is the appropriate resistance surface for comparison with the gene flow model produced by Cushman et al. (2006). This is because spring is the season when bears mate and juveniles disperse. Across North America, there are similarities among black bear populations regarding the characteristics of dispersal events by sub-adults. Family break-up of females and their associated 1.5 year old sub-adults occurs between May and July (Rogers 1977; Reynolds and Beecham 1980; Clevenger and Pelton 1990; Schwartz and Franzmann 1992) and dispersal events are observed from June to September (Lee and Vaughan 2003. Black bear mating occurs primarily between May and July (Reynolds and Beecham 1980; Clevenger and Pelton 1990). Therefore, the seasonal movement model that coincides with the timing of these events is likely to provide the best mechanistic explanation for gene flow. This has several implications. First, given seasonal changes in landscape resistance and the limited periods of the year when gene flow events primarily occur, models of landscape connectivity should carefully consider temporal changes in landscape resistance. A connectivity model built over the entire year or for summer only would reach entirely different conclusions about the factors limiting bear movement than a spring model. Also, it is interesting to note that if genetic differentiation is mainly driven by early season movement, the effects of landscape structure on population connectivity are likely larger than would be surmised from the overall relationship between bear movement and landscape features across the year. For instance, bear paths are highly constrained by limited access to high elevation habitat in spring and by avoidance of human development and roads. This suggests that road density and residential development may have a larger effect on bear population connectivity that would be surmised from the overall pattern of roads and development in the landscape. This has important conservation implications and suggests that even landscapes with large amounts of undeveloped forest land could suffer from negative fragmentation effects if there is extensive human development in low elevation habitat that bears utilize during breeding and dispersal.

Comparison with related research

Coulon et al. (2008), using a movement path analysis similar to that used here, found that roe deer movements were influenced by all landscape features they evaluated, but not always in the predicted direction. Their results suggested that roe deer tend to avoid buildings, roads, valley bottoms and possibly the more wooded areas. However, Coulon et al. (2004, 2006) found that genetic differentiation in the roe deer population is related to landscape resistance, such that in a fragmented woodland area roe deer dispersal is strongly linked to wooded structures and hence that gene flow within the roe deer population is influenced by the connectivity of the patches of woodland across the landscape. This is an example showing that movement behavior may not always explain genetic patterns. In contrast, our results were fully consistent with our hypothesized relationship between early season movement and genetic differentiation. Our movement model for the early season was heuristically identical to that produced by the landscape genetic analysis (Cushman et al. 2006), including the same variables with the same direction of relationship. This suggests that for black bear in the northern Rocky Mountains there is a close linkage between movement behavior and genetic differentiation driven by mating and dispersal in the early season landscape.

Scope and direction of future work

Different bear groups (e.g., sex, age class, social status) may also demonstrate varying patterns of movement and gene flow, as has been shown for patterns of habitat selection (Lewis et al. 2007) To ensure that results were comparable between the landscape genetic and movement models, bears were grouped for analyses. Future work could focus on how different bear groups respond to landscape resistance. Also, it would be interesting to repeat the movement modeling study over a larger extent that captures the same degree of landscape structure as the Cushman et al. (2006) study, which included a much larger extent and a wider range of landscape conditions. Some of the differences we see in the relative importance of forest cover versus roads and human development is likely due to the differences in the composition and configuration of the two study areas.

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References

Arthur SM, Manly BFJ, McDonald LL, Garner GW (1996) Assessing habitat selection when availability changes. Ecology 77:215–227

Beringer JJ, Seibert SG, Pelton MR (1990) Incidence of road crossing by black bears on Pisgah National Forest, North Carolina. Int Conf Bear Res Manag 8:85–92

Brody AJ, Pelton MR (1989) Effects of roads on black bear movements in western North Carolina. Wildl Soc Bull 17:5–10

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

Clevenger AP, Pelton MR (1990) Pre and post breakup movements and space use of black bear family groups in Cherokee national forest, Tennessee. Int Conf Bear Res Manag 8:289–295

Compton B, McGarigal K, Cushman SA, Gamble L (2007) A resistant kernel model of connectivity for vernal pool breeding amphibians. 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

Coulon A, Guillot G, Cosson JF, Angibault JMA, Aulagnier S, Cargnelutti B, Galan M, Hewison AJM (2006) Genetic structure is influenced by landscape features: empirical evidence from a roe deer population. Mol Ecol 15: 1669–1679

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

Cushman SA (2010) Animal movement data: GPS telemetry, autocorrelation and the need for path-level analysis. In: Cushman SA, Huettman F (eds) Spatial complexity, informatics and wildlife conservation. Springer, Tokyo, pp 131–150

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

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

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

Cushman SA, Chase MJ, Griffin C (2010a) Mapping landscape resistance to identify corridors and barriers for elephant movement in southern Africa. In: Cushman SA, Huettman F (eds) Spatial complexity, informatics and wildlife conservation. Springer, Tokyo, pp 349–368

Cushman SA, McGarial K, Gutzwiller K, Evans J (2010b) The gradient paradigm: a conceptual and analytical framework for landscape ecology. In: Cushman SA, Huettman F (eds) Spatial complexity, informatics and wildlife conservation. Springer, Tokyo, pp 83–110

ESRI (2005) ARCGIS. Environmental Systems Research Incorporated, Redlands, CA

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

Harris RB, Fancy SG, Douglas DC et al (1990) Tracking wildlife by satellite: current systems and performance. (Tech. Report 30). US Fish and Wildlife Service

Hegel TM, Cushman SA, Huettmann F (2009) Current state of the art for statistical modelling of species distributions. In: Cushman SA, Huettman F (eds) Spatial complexity informatics and wildlife conservation. Springer, Tokyo, pp 273–312

Johnson KG, Pelton MR (1980) Prebaiting and snaring techniques for black bears. Wildl Soc Bull 8:46–54

Johnson CJ, Seip DR, Boyce MS (2004) A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple scales. J Appl Ecol 41:238–251

Lee DJ, Vaughan MR (2003) Dispersal movements by subadult American black bears in Virginia. Ursus 14:162–170

Lewis JS (2007) The effects of human influences on black bear habitat selection and movement patterns within a highway corridor. Thesis, University of Idaho, Moscow

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

Litvaitis JA, Titus K, Anderson EM (1994) Measuring vertebrate use of terrestrial habits and foods. In Bookhout TA (ed) Research and management techniques for wildlife and habitats. The Wildlife Society, Bethesda, MD, pp 254–270

Manly BFJ, McDonald LL, Thomas D (2002) Resource selection by animals: statistical design and analysis for field studies. Kluwer, Boston

Osborn FV, Parker GE (2003) Towards an integrated approach for reducing the conflict between elephants and people: a review of current research. Oryx 3:1–5

Reynolds DG, Beecham J (1980) Home range activities and reproduction of black bears in west-central Idaho. Int Conf Bear Res Manag 4:181–190

Rogers LL (1977) Social relationships, movements, and population dynamics of black bears in northeastern Minnesota. PhD thesis, University of Minnesota, Minneapolis

Schwartz CC, Franzmann AW (1992) Dispersal and survival of subadult black bears from the Kenai Peninsula, Alaska. J Wildl Manag 56:426–431

Shanahan DF, Possingham HP, Riginos C (2010) Models based on individual level movement predict spatial patterns of genetic relatedness for two Australian forest birds. Landscape Ecol. doi:10.1007/s10980-010-9542-6

Shirk A, Wallin DO, Cushman SA, Rice RC, Warheit C (2010) Inferring landscape effects on gene flow: a new multi-scale model selection framework. Mol Ecol 19:3603–3619

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

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. doi:10.1007/s10980-010-9525-7

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