

Empirical estimation of dispersal resistance surfaces: a case study with red-cockaded woodpeckers

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Abstract Persistence of wildlife populations depends on the degree to which landscape features facilitate animal movements between isolated habitat patches. Due to limited data availability, the effect of landscape features on animal dispersal is typically estimated using expert opinion. With sufficient data, however, resistance surfaces can be estimated empirically. After modeling suitable prospecting habitat using an extensive dataset from the federally endangered red-cockaded woodpecker (*Picoides borealis*), we used data from over 800 prospecting events from 34 radio-tagged birds to identify the best relationship between habitat suitability and resistance surfaces. Our results demonstrated that juvenile female *P. borealis* prospecting for new territories beyond

their natal territories preferred to traverse through forests with tall canopy and minimal midstory vegetation. The non-linear relationship between habitat suitability and resistance surfaces was the most biologically relevant transformation, which in turn identified the specific forest composition that promoted and inhibited prospecting and dispersal behavior. These results corresponded with over 60 % of dispersal events from an independent dataset of short-distance dispersal events. This new understanding of *P. borealis* prospecting behavior will help to identify areas necessary for maintaining habitat connectivity and to implement effective management strategies. Our approach also provides a framework to not only estimate and evaluate resistance surfaces based on species-specific responses to intervening landscape features, but also addresses an often-neglected step, selecting a biologically relevant function to transform habitat suitability model into a resistance surface.

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Introduction

Human activities have drastically altered the spatial configuration of ecosystems, often with negative consequences for the genetic diversity, persistence, and connectivity of wildlife populations (Fahrig and Merriam 1994). To mitigate these negative effects, in particular the fragmenting of wildlife habitat, land managers often attempt to maintain connections or reconnect populations existing in geographically distinct habitats or conservation areas (Beier et al. 2008). However, to properly design and implement this strategy, it is necessary to account for how environmental characteristics facilitate or impede animal movements between habitats. An increasingly common approach for providing this information is to construct raster-based maps, typically known as resistance surfaces, that depict friction values indicating how various natural- and human-modified land-covers influence movement for a particular species (Adriaensen et al. 2003).

Under ideal circumstances, resistance surfaces can account for the appropriate level of environmental detail, as well as how animal movement behavior responds to environmental variation, thus quantifying how the movement behaviors of a given species vary through the different environmental conditions encountered in the landscape (Zeller et al. 2012). The ability to obtain detailed data about the movements of individual organisms has been greatly increased by technological advances in radio-telemetry and remotely sensed data, substantially improving the reliability of habitat suitability models and our understanding of animal movement and dispersal (Hall et al. 1997; Manly et al. 2002). Conservation planners are now routinely employing resistance surfaces based on such data to model habitat connectivity (Chetkiewicz and Boyce 2009). With sufficient data, this approach can effectively capture the interplay between landscape structure and movement behavior, and thus can be used to estimate habitat connectivity and animal dispersal.

The major challenge in constructing a resistance surface is the estimation of friction values that accurately depict the effect of different environments on animal movement (Adriaensen et al. 2003).

Due to the time, cost, and logistical difficulties of collecting data on animal movement behaviors in different habitat types, conservation planners often develop friction values from expert opinion (Schultz and Crone 2001; Beier et al. 2009). In many cases, as an alternative to this, habitat suitability models have been used to derive friction values for a resistance surface (Zeller et al. 2012). There is little guidance for determining the proper function for transforming habitat suitability maps into resistance surfaces (Schultz and Crone 2001; Schadt et al. 2002; Beier et al. 2008, 2009).

Most studies that employ this method use a single function to transform habitat suitability values into friction values, and typically do not justify the selection of the specific function used (Ferreras 2001; Singleton et al. 2004; Sun et al. 2007; Richard-Zawacki 2009; Richard and Armstrong 2010). However, different functions may yield different resistance surfaces, and can affect connectivity estimates, resulting in uncertainty in model results if unexamined assumptions are made about this relationship (Beier et al. 2008). Two recent and otherwise comprehensive reviews describing resistance surface modeling discuss the benefits of using habitat suitability models to generate resistance surfaces, but do not mention the role that the transformation function plays in the final modeling results (Sawyer et al. 2011; Zeller et al. 2012).

In this paper we demonstrate the effect that the choice of transformation function has on resulting resistance surface using movement data for the red-cockaded woodpecker (*Picoides borealis*), an ideal model-species for analyzing animal movements through complex landscapes. *Picoides borealis* are endemic to mature pine forests, particularly longleaf pine (*Pinus palustris*), in the southeastern US (Conner et al. 2001). Longleaf pine forest is now highly fragmented and reduced to less than 3 % of its original extent due to timber harvesting, fire suppression, and development (Frost 2006). This has impacted *P. borealis* connectivity by introducing a wide range of land-cover types that alter prospecting and dispersing movement behavior. *P. borealis* has been intensively studied through several long-term monitoring programs since its listing as a federally endangered species in 1970 (U.S. Department of the Interior 1970). As a result, its habitat requirements, social behavior, population biology, and dispersal behavior are well understood (Daniels and Walters 2000; Costa and

Daniels 2004; Kesler et al. 2010). *Picoides borealis* is capable of relatively long dispersal events (over 30 km) from their natal territory to their initial breeding territory in their first year (Walters 1990; Kesler et al. 2010). Prior to dispersal, juveniles exhibit prospecting behavior, consisting of forays from their natal territory searching for and evaluating potential breeding territories (Clobert et al. 2001; Pasinelli and Walters 2002).

Despite numerous *P. borealis* studies, little is known about how natural and human-modified landscape features influence *P. borealis* prospecting and dispersal movements. A goal of this study was to empirically evaluate how environmental conditions, estimated with remotely sensed data, are associated with prospecting movement behavior. A resulting model of prospecting habitat was then transformed into a resistance surface. Since there is no consensus on how to select the appropriate transformation function, we compared a wide spectrum of relationships between *P. borealis* prospecting habitat suitability and resistance surfaces. Our empirically estimated resistance surface was independently evaluated with a separate dataset of dispersal events to assess how habitat connectivity estimated in this way corresponds to actual connectivity as reflected in actual dispersal events.

Materials and methods

Study species

Picoides borealis are territorial, cooperative breeders (Walters 1990), in which a single-family group defends a home territory. Cavities for nesting and roosting are excavated in living pines, and each group member has its own roost cavity (Walters et al. 1988). Thus territories include a set of cavity trees. Home ranges are slightly larger than territories due to occasional excursions into neighboring territories and undefended areas. In our study area group home ranges average 0.84 km² (0.56–1.28 km², Walters et al. 2002). Many juvenile males remain in their natal territories for several years and help care for subsequent offspring (Walters et al. 1988, 1990; Haig et al. 1994). In contrast, most juvenile females disperse from their natal territory to their initial breeding territory in their first year.

Female natal dispersal distances exhibit a right-skewed distribution, with most birds dispersing less than

3.5 km and a small proportion dispersing as far as 31 km (Walters 1990; Kesler et al. 2010). Previous mark-recapture studies (e.g., Pasinelli and Walters 2002) and, more recently detailed radio-telemetry data (Kesler et al. 2010), have demonstrated that *P. borealis* acquire information from multiple territories by performing extensive exploratory or prospecting forays from their natal territory, during which they search for and evaluate potential breeding territories prior to their final dispersal event (Clobert et al. 2001; Norris and Stutchbury 2001; Forsman et al. 2002; Gillies and St. Clair 2008).

Study site

The Sandhills ecoregion of North Carolina (Griffith et al. 2007) features rolling topography and deep, fluvial, sandy soils interdigitated with alluvial clays in bottomlands (Peet 2006). The region historically was dominated by fire-dependent longleaf pine woodlands, with low stem density, partially open canopy, a minimal hardwood midstory, and dense herbaceous understory vegetation (Provencher et al. 2001; Frost 2006). Most of these woodlands have been replaced by cropland, pasture, and mixed woodland (Griffith et al. 2007), and the forests that remain consist primarily of mixed-pine [longleaf, loblolly (*P. taeda*), shortleaf (*P. echinata*), and pond pine (*P. serotina*)] in second-growth forest with varying amounts of hardwood understory and midstory (Griffith et al. 2007).

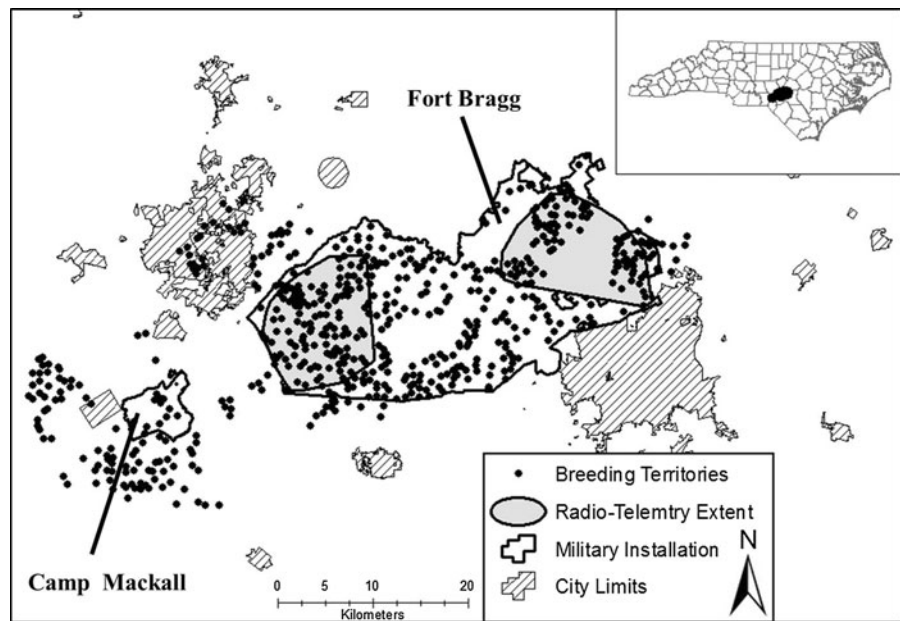
This study was conducted within a 2,388 km² area within the Sandhills ecoregion centered on two U.S. Army installations, Fort Bragg and Camp Mackall (79°12'W 35°7'N, Fig. 1). The largest tracts of longleaf pine forest within the study area are on these two sites (Britcher and Patten 2004), which also harbor greater than 70 % ($n = 437$) of the 604 established *P. borealis* territories within the study region (Fig. 1). These military bases are surrounded by a complex matrix of landscapes that may impede dispersal of *P. borealis* between on-base and off-base habitats.

Animal detection data

Breeding territories and dispersal events

Picoides borealis have been the subject of a long-term nest-monitoring and banding data collection project administered by the Sandhills Ecological Institute and the Endangered Species Branch of the Department of

Fig. 1 The study area extent with the centers of red-cockaded woodpecker (*Picoides borealis*) territories and military installation boundaries. The two grey-filled solid-lined polygons illustrate the spatial coverage of radio telemetry data collection (2006 = west, 2007 = east)



Natural Resources on Ft. Bragg. Juvenile and adult *P. borealis* within active breeding territories have been marked with a unique combination of bands following established protocols (Walters et al. 1988) and monitored each breeding season. Thus, the identity and family relationships of all juvenile females, as well as those of the birds on all the territories to which they dispersed, are known. To define the location of these breeding territories for the analyses conducted in this work, the geographic coordinates for the cavity trees within a territory have been averaged to estimate territory centers (Kesler et al. 2010).

Radio telemetry

Thirty-four juvenile female *P. borealis* (2006 $n = 18$ and 2007 $n = 16$) still residing in their natal territories were captured in their roosting cavities and fitted with a 1.4 g transmitter glued to the base of 2 tail feathers (BD-2, Holohil Systems Ltd., ON, Canada). These birds were tracked for the life of their radio transmitters (~ 9 weeks) on the western and eastern portion of Fort Bragg. Radio-tagged woodpeckers were located daily at least every 30 min during 4-h tracking sessions.

Radio-tagged birds that explored beyond the boundary of their natal territory but returned before sunset to roost with their natal group were considered

foraging (Kesler et al. 2010). If radio-tagged birds were not observed in their natal territory, they were located within the study area using a vehicle-mounted omnidirectional antenna. Upon locating the general area of a radio-tagged individual, we proceeded on foot using a handheld, 3-element Yagi directional antenna (Wildlife Materials, Inc., Carbondale, IL, USA) and a receiver (R-1000, Communication Specialist, Inc. Orange, CA, USA) to record the foraging individual's Universal Transverse Mercator (UTM) coordinate using a hand-held Garmin® global positioning system unit (GPS; Olathe, KS, USA).

Telemetry data were summarized to determine the number of days each bird visited each particular territory (frequency of territory visits). A territory visit was confirmed by observing intra-species interactions during extra-territorial movements. For example, prospecting individuals frequently interacted aggressively with the family groups and inspected cavities at the territories they visited. In the absence of observed intra-species interactions, the territory a radio-tagged bird visited was defined as the closest territory within 500 m of the bird's GPS location. Foray distances were approximated using the linear distance between the centers of the natal and the visited territories. Each individual's prospecting range was defined as the maximum foray distance traveled from the home territory.

Environmental variables

Forest structural attributes (vegetation height characteristics and percent cover) expected to influence *P. borealis* movements were estimated using discrete-return, airborne light detection and range (LiDAR) data collected during leaf-off canopy conditions (31 December 2000 and 18 February 2001). The ground spacing between LiDAR postings ranged from 2 to 2.25 m, the flight altitude ranged from 914 to 1,676 m, and the elevation calibration ranged from 9 to 12 cm elevation root mean square error. The raw LiDAR data containing three-dimensional coordinates of laser hits were converted with Fusion software (McGaughey 2008) to a 30 × 30 m resolution raster. The 30 m cell size was selected to correspond with the lower range of observed *P. borealis* direct flight distance between trees (30–50 m, J.R. Walters, personal observation). There were an average of 289 LiDAR samples per 30 m cell (SE = 0.13). A bare-earth digital elevation model (DEM) was derived from these data by the North Carolina Floodplain Mapping Program (www.floodmaps.nc.gov) prior to our analysis. Heights from LiDAR points to the ground were calculated relative to this DEM to derive seven forest structure variables: (1–2) Maximum and median vegetation heights; (3–6) percent cover at four height classes (1–8, 8–13, 13–20, and >20 m); and (7) the skewness of vegetation heights (a measure of overall forest structure) (Smart et al. 2012).

Prospecting habitat suitability map

A generalized linear mixed modeling (GLMM) approach was used to estimate suitable prospecting habitat with the seven variables representing LiDAR-derived forest structure found at *P. borealis* prospecting locations. For each recorded prospecting location, two additional random locations within the bird's prospecting range were sampled to represent available habitat. We included a term for individual in the GLMM models as a random effect to address concerns of autocorrelation within radio-tagged individuals. We assessed multi-collinearity among explanatory variables using the variance inflation ratio (VIF) for each variable using the DAAG package in R (Version 2.14.1, R Development Core Team 2010). When VIF exceeds 10, a variable is considered to have high multi-collinearity (Ott and Longnecker 2001).

All LiDAR-derived variables had VIF values below this threshold (<2).

All possible models ($n = 256$) based on the seven LiDAR-derived variables were constructed to predict suitable prospecting habitat. Model selection was based on Akaike's Information Criterion adjusted for small sample sizes (AICc; Burnham and Anderson 2002), and models were ranked using the difference in AICc score (ΔAICc) relative to the model with the minimum (best) AICc score. The relative importance value of each variable was calculated by summing the weight (ω_i) of all the models where the variable of interest was included. AICc weights near one indicate strong relative importance for a particular variable in relation to other models (Burnham and Anderson 2002). Model averaging was also used to calculate the coefficient and standard error for each forest structure variable across all possible models (Burnham and Anderson 2002). The GLMM model-averaged coefficients (β) were used to create a habitat suitability surface, where probability values near one indicate the most suitable habitat conditions and values near zero indicate the least suitable habitat.

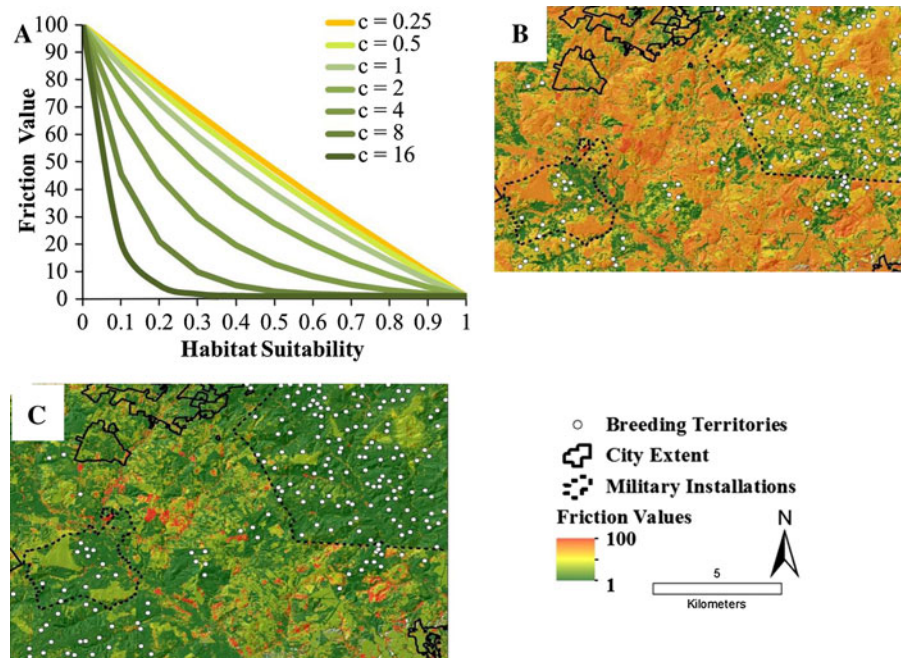
Resistance surface and friction-weighted distance

Linear or negative exponential functions are most commonly used for transforming habitat suitability models into resistance surfaces (Zeller et al. 2012). The linear function ($f = 1 - h$) assumes a steady increase in friction values, f , as habitat suitability, h , declines. In contrast, negative exponential functions ($f = h^{-1}$) assume a gradual change in friction values with suitability when suitability values are relatively high (>0.5), but a drastic increase in friction values as habitat suitability declines beyond the mid range. Rather than simply assuming that one of these forms is correct, we employed a function (Eq. 1) that asymptotically approaches both of these extremes depending on the value of a single rescaling parameter, c . Thus, the function covers a full spectrum of relationships not typically considered when relating habitat suitability values and friction values.

$$f = 100 - 99 \frac{1 - \exp(-ch)}{1 - \exp(-c)} \quad (1)$$

We employed seven different values for c , ranging from 0.25 to 16 (Fig. 2). As c increases, f approaches a negative exponential function of h . As c decreases, the

Fig. 2 Seven curves used to transform habitat suitability values into friction values (*top left*) and a sample of the resistance surfaces corresponding to a nearly linear ($c = 0.25$, *top right*) and a highly non-linear transformation ($c = 16$, *bottom left*)



relationship approaches that of a linear function. Based on Eq. 1, friction values could be assigned to landscape features in the range from 1 to 100, with $f = 1$ representing the lowest friction values and $f = 100$ representing the highest friction.

For each resistance surface, friction-weighted distance, also referred to as cumulative cost, can be calculated for any path between two points in the landscape by summing friction values along a path. The least cost path is the single path associated with the minimum friction-weighted distance between a source and destination (Adriaensen et al. 2003). For the highest-possible quality habitat (i.e., $f = 1$) the friction-weighted distance is equivalent to Euclidean distance, and the cost of movement is minimized. Note that this approach does not assume that birds will necessarily travel along the least cost path between territories, but rather it provides a quantitative metric describing the relative cost-distance between territories.

Discrete-choice analysis

Studies that evaluate a species' prospecting behavior in relation to resource availability, such as food and nesting sites, usually assume that all resources in the study area are equally available to all individuals in the population

regardless of the species' dispersal ability (Manly et al. 2002; Selonen and Hanski 2006). However, each juvenile emerging from its natal site is surrounded by a unique set of environmental features that potentially influence prospecting behavior. To account for variation in surrounding environmental features, discrete-choice analysis was used, in which the choice set for each individual was defined as all territories within 6 km, the 95th percentile of the observed foray distance from natal sites (Kesler et al. 2010).

Friction-weighted distance from an individual's natal territory to every other territory within the 6 km range was compared for each function (i.e., the seven values of c) relating habitat suitability to friction. Radio-tagged *P. borealis* visited territories within their prospecting range either never, once, or multiple times. The frequency of territory visits observed during prospecting using radio telemetry was used as the response variable for the discrete-choice models. For each model, the likelihood of a bird visiting a territory within its prospecting range was estimated, and the best predictive model was selected based on AICc and the model's weight of evidence (ω_i ; Burnham and Anderson 2002). All discrete-choice modeling was conducted with the Cox PH model within the Survival package in R (Version 2.14.1, R Development Core Team 2010).

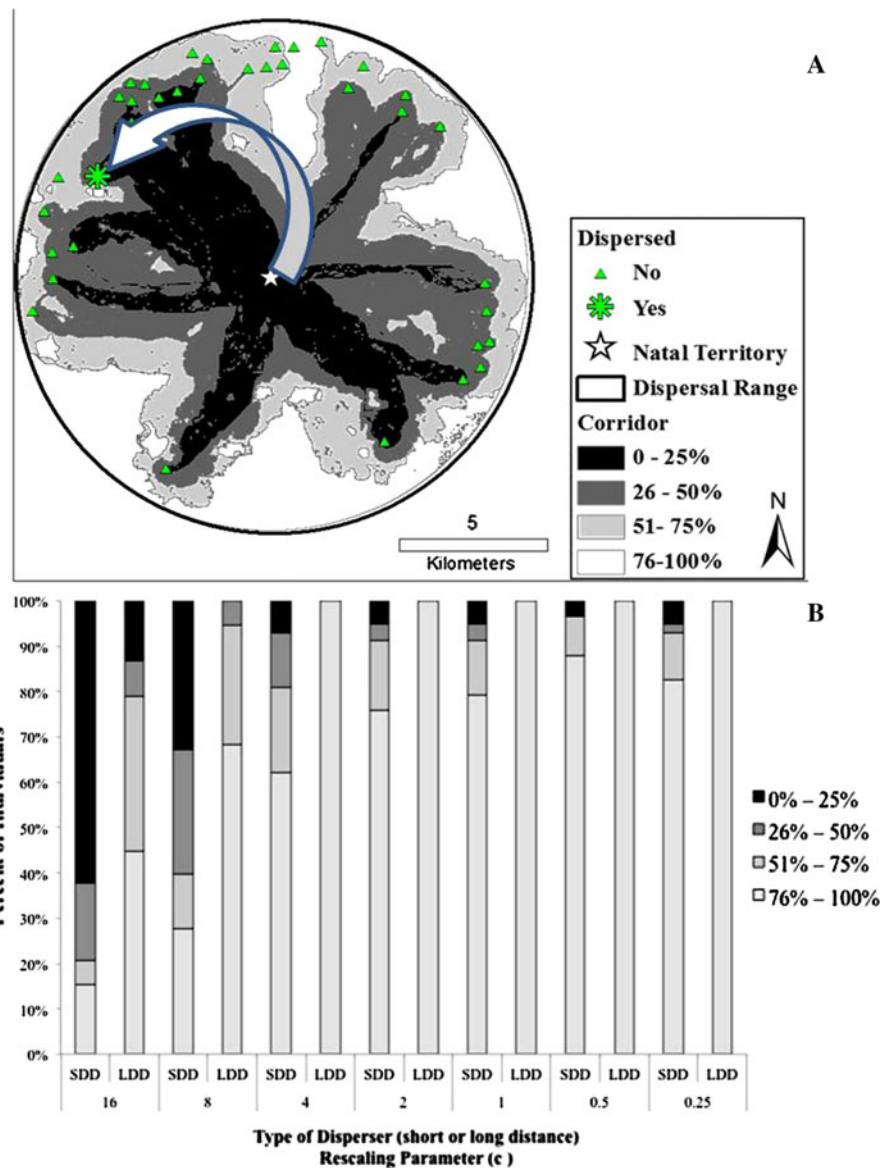
Evaluating resistance surface models

We compared the fit of each resistance-surface model to an independent dataset of recorded dispersals of juvenile females born in 2005 ($n = 53$) and 2006 ($n = 32$) throughout the study area. For each dispersal event in this dataset, all territories with similar geographic distance from their natal territory were selected as potential breeding territories available during dispersal (Fig. 3a). A least-cost corridor model was constructed for each resistance surface. For each dispersal event in this dataset, the friction-weighted

distances were calculated to and from every cell between the natal territory and all potential breeding territories. The friction-weighted distances for both directions were then added together to create a single raster representing the relative ease of dispersing from the natal site to all potential breeding territories.

Corridor values, or the sum of friction-weighted distance to and from natal and potential breeding sites, varied considerably for each dispersal event. Therefore, the distribution of corridor values among potential breeding sites was used as a basis for evaluating the success of each resistance surface. This

Fig. 3 An example of a juvenile female red-cockaded woodpecker (*Picoides borealis*) dispersing to a breeding territory within the least-cost corridor derived from the top-ranked resistance surface (a). The percentage of short-distance (SDD) and long-distance (LDD) dispersers that settled into territories within four corridor widths, determined by least-cost percentiles from a resistance surface for each rescaling parameter (b)



was done by segmenting the distribution of each individual's corridor values into quantiles. In general, the most difficult corridors to traverse (76–100 % quantile) will be located near the perimeter of the dispersal range, while the center of the dispersal range typically contains the lowest 25th percentile cells, and thus the least-cost corridor from the natal territory to a potential destination territory (Fig. 3a). When the observed bird dispersed to a territory within the corridor containing the lowest 25th percentile of friction-weighted distances (i.e., least-cost corridor, Fig. 3a), the resistance surface closely matches observed dispersal events. Since *P. borealis* dispersal distance distribution is skewed, we assessed if short-distance disperser's response to the environment differently than long-distance disperser's, using 6 km as the threshold value to differentiate between short- and long-distance. The overall performance of each resistance model was evaluated for short- and long-distance dispersers by calculating the percentage of individuals that dispersed to territories within each of the 25 % least-cost corridor.

Results

Radio telemetry

Radio tracking in 2006 and 2007 returned an average of 40 (SE = 4) and 121 (SE = 25) locations per individual, respectively. When tracked individuals were not traveling with family group members and traveled beyond their natal territory, locations were

defined as prospecting movements. These locations comprised the majority of observed locations in the study (68.1 % in 2006 and 78.2 % in 2007). Prospecting birds conducted 282 and 533 territory visits in 2006 and 2007, respectively. The number of visits a prospecting bird conducted ranged from 1 to 23 territories per female, and approximately half of the individuals visited a non-natal territory multiple times. The maximum prospecting range from a natal site was 8.9 km ($\bar{X} = 3.5$ km, SE = 0.3).

Prospecting habitat suitability

Six LiDAR-derived forest structure variables had high relative importance values ($\omega_i > 0.90$) for estimating *P. borealis* prospecting habitat (see Table 1). The only variable with relatively low importance was skewness of vegetation heights ($\omega_i = 0.19$). No single model had overwhelming evidence of support (Table S1), that is AICc $\omega_i > 0.9$. Therefore, model averaging based on ω_i of all possible models was appropriate to estimate parameters (Burnham and Anderson 2002).

According to the multi-model inference coefficient estimates, *P. borealis* prospecting habitat was associated with forested areas containing low percentage vegetation cover in the mid-story (1–8 m), low median vegetation heights, and high percentage vegetation cover in the 8–20 m height classes (Table 1). Although *P. borealis* were located in areas with the tallest vegetation, they were less likely to prospect in areas with high percentage of cover over 20 m tall compared to random areas within their prospecting range.

Table 1 The generalized linear mixed model average coefficient (β) estimates, standard errors, and relative importance of each LiDAR-derived forest structure variable used to construct the prospecting habitat suitability model

Parameter	β	SE	95 % confidence interval	Relative importance
Intercept	-1.364	0.117	-1.597 to -1.140	
Cover (1–8 m)	-0.024	0.002	-0.029 to -0.020	1.000
Cover (8–13 m)	0.032	0.004	0.025 to 0.040	1.000
Cover (13–20 m)	0.011	0.003	0.004 to 0.017	0.941
Cover (>20 m)	-0.033	0.007	-0.046 to -0.019	1.000
Maximum vegetation height (m)	0.049	0.007	0.035 to 0.063	1.000
Median vegetation height (m)	-0.079	0.015	-0.109 to -0.049	1.000
Skewness vegetation height	-0.022	0.032	-0.091 to 0.036	0.196

Multi-model inference was used via model averaging from all possible model combinations of seven variables based on models ranked by AIC and adjusted for small sample size

Discrete-choice analysis

A discrete-choice analysis was implemented with the number of days a radio-tagged bird visited and revisited each territory to determine which resistance surface best represented prospecting behavior. Euclidean distance was a very poor predictor of prospecting behavior (Table 2). The top-ranked discrete-choice model had the largest rescaling constant ($c = 16$, Table 2; Fig. 2) suggesting that the relationship between forest structure and the friction values on a resistance surface was best represented with a non-linear function, closely resembling a negative exponential function. This model also suggested that within the prospecting range (6 km), there is a negative relationship between probability of visiting a territory and friction-weighted distance ($\beta = -5.32 \times 10^{-4}$, $SE = 2.47 \times 10^{-5}$, $P < 0.001$). That is, territories with greater friction-weighted distances from the natal site were less likely to be visited multiple times during forays.

The best performing transformation function (i.e., $c = 16$) suggests that the subtle differences in high or intermediate quality habitat (i.e., $h > 0.4$) do not strongly influence prospecting movements, as within this range friction values remain close to one (Fig. 2). When h is greater than 0.4, the forest has less than 20 % mid-story cover (1–8 m), moderate (over 15 %) vegetation cover over 8 m tall, and maximum tree

height of >17 m. However, the variation in poor quality habitat ($h = 0.1$ –0.3) did have a strong effect on prospecting ($f = 2$ –21). Extremely poor quality habitat ($h < 0.1$), which contains over 70 % mid-story cover (1–8 m), minimal vegetation cover above 8 m in height, and few trees taller than 10 m, acts as a substantial barrier for prospecting *P. borealis*.

Evaluating resistance surface models

Even when available destination territories were located at similar Euclidean distances from the natal territory, the top-ranked resistance surface ($c = 16$) explained dispersal events better than all the other transformation functions (Fig. 3b). This resistance surface closely fit the actual dispersal destinations for short-distance dispersers, with over 60 % of this group of birds selecting a territory within the 25th percentile least-cost corridor. In contrast, long-distance dispersers exhibited a distinctly different pattern, with only 13 % of these individuals selecting a territory within the 25th percentile least-cost corridor (Fig. 3b). For comparison, the second-ranked resistance surface ($c = 1$) predicted less than 10 % of the dispersal events, all of which were short-distance dispersers.

Discussion

Our ability to accurately predict animal movements has been significantly improved by replacing uniform landscapes with a resistance surface that accounts for species movement behavior among complex landscape features (Verbeylen et al. 2003; Magle et al. 2009; Richard and Armstrong 2010, our study). Once environmental features presumed to enhance species movements are identified, the habitat suitability surface can be transformed into a resistance surface to highlight locations where environmental and landscape features are expected to impede movement (Beier et al. 2008; Zeller et al. 2012). Here, movement data collected during prospecting events were used to obtain insight into suitable prospecting habitat. Our results showed that juvenile female *P. borealis* locations collected during extra-territorial forays were strongly dependent upon six out of the seven LiDAR-derived forest structure variables (Table 1). Since there is no clear consensus on the “correct” function to

Table 2 Ranking of prospecting behavior discrete-choice models in relation to habitat suitability models constructed with varying friction values

Rank	Rescaling constants	AICc ^a	Delta ^b	Wt ^c
1	16	5,584.61	0.00	1.0000
2	1	5,606.91	22.29	0.0000
3	2	5,607.23	22.62	0.0000
4	0.5	5,608.72	24.11	0.0000
5	0.25	5,609.28	24.67	0.0000
6	4	5,614.74	30.13	0.0000
7	8	5,614.99	30.38	0.0000
8	Euclidean	5,620.01	35.39	0.0000

^a Akaike’s Information Criterion adjusted for small sample size

^b Difference between AICc value of the current model and the value for the most parsimonious model

^c Relative likelihood of the model given the data and set of candidate models (model weights sum to 1.0)

transform habitat suitability into friction values, we offer a simple functional form that spans the behavior of commonly used transformation functions (i.e., linear and negative exponential functions) to provide clearer understanding about how suitable prospecting habitat translates into movement capacity for a resistance surface model.

Applications to *Picoides borealis* conservation

The complex suite of environmental features that comprise *P. borealis* habitat is typically described using expensive, labor intensive in situ measurements of the environment at small spatial scales (<1 h) within close proximity of breeding and foraging sites (Conner et al. 2002; Rudolph et al. 2002; Walters et al. 2002; Wood et al. 2008). This derives in part from the logistical difficulties of collecting detailed forest structure data in a geographically extensive area. Here we capitalized on a partnership with the North Carolina Floodplain Mapping Program to extrapolate vegetation structure metrics throughout an entire region. This information allowed us to quantify how prospecting birds react to a wide variety of detailed vegetation structure in novel environments.

Our results suggest that prospecting juvenile female *P. borealis* rely strongly on forest structure characteristics to guide their movements beyond their natal territory. Although our results mostly reflect selection among the pine stands that dominated the landscape, they are also affected by the other habitat types present as we did not distinguish habitat types in our analyses. Other habitat types present include open areas, young pine plantations and various types of riparian habitat. *P. borealis* prefer open, mature pine stands with sparse midstory vegetation and rich ground cover for both foraging and nesting (USFWS 2003). Even though *P. borealis* rarely interact with vegetation below 8 m (Hooper and Lennartz 1981, A. Trainor, personal observation), prospecting birds, like foraging and nesting birds, avoided forested areas with dense mid-story cover (Table 1). In contrast, forest stands with high percent cover between 8 and 13 m were positively associated with prospecting habitat. Such areas likely are either pine stands that are younger and denser than preferred for foraging, or riparian vegetation along small streams. Thus our results suggest that *P. borealis* are capable of traveling through lower quality foraging habitat when searching for potential

breeding territories. Surprisingly, prospecting locations were negatively associated with canopy cover >20 m tall (Table 1). However, this observation could be an artifact resulting from the limited amount of canopy exceeding 20 m in the region, possibly including bottomland hardwood forest along major drainages. Less than 25 % of the study area has canopy cover taller 20 m. Moreover, these small patches of tall trees have <15 % total cover from vegetation.

In the absence of longleaf pine trees greater than 60 years old and taller than 20 m, *P. borealis* may use longleaf pine trees between 30 and 60 years old, which usually range from 13 to 20 m tall (Platt et al. 1988; U. S. Fish and Wildlife Service 2003). The strong positive relationship between prospecting locations and vegetation cover in the 13 to 20 m height range supports our assertion that prospecting birds will travel through pine stands younger than those they prefer for foraging.

In addition to identifying specific forest structure metrics that influence movement, our results showed that *P. borealis* have a flexible dispersal capacity. This finding is reflected in the highly non-linear ($c = 16$) relationship between prospecting habitat quality and resistance surface providing a better fit over other possible relationships. Examining this nonlinear relationship in detail showed a specific threshold ($h = 0.15$) where *P. borealis* seem to divide their environment into two categories, (1) traversable forest containing low mid-story cover of <20 %, >12 % canopy cover, and trees >17 m and (2) movement barriers composed of dense mid-story with >70 % cover, minimal canopy cover >8 m, and very few short trees <10 m. Note that open areas and young pine plantations would fall into the second category. Therefore, despite *P. borealis*'s ability to fly long distances (Walters 1990; Kesler et al. 2010) and cope with a wide range of environments, territories beyond open deforested areas or remaining forests with encroaching hardwood midstory are likely inaccessible to young *P. borealis* prospecting for their initial breeding site. Furthermore, rapid growth of urban and agriculture land-use practices will restrict *P. borealis* exploratory movements, thus further reducing the population's overall connectivity.

Land in the southeastern United States is often managed for conservation of *P. borealis* populations. Our approach, and the resulting maps of prospecting-habitat suitability and dispersal resistance, can be used

by managers to prevent future land-use changes from negatively impacting habitat connectivity for *P. borealis*. To increase the reliability of our resistance surface, we evaluated the model with an independent dataset of capture-mark-recapture dispersal events. The best resistance surface correctly predicted more than 60 % of the short distance dispersals (1 to 6 km), but only 13 % of the long-distance dispersals (Fig. 3b). These results demonstrate the complexity of *P. borealis* dispersal behavior, and suggest that short-distance dispersal is strongly guided by forest structure, but long-distance dispersal may be inherently less sensitive to intervening landscapes.

Previously, Kesler et al. (2010) reported that *P. borealis* long-distance dispersal involves ‘jumping’ behavior distinct from that of short-distance dispersers or forays. It is also possible that the environmental cues affecting long-distance movements were not represented in our resistance surfaces. In either case, further research is required to fully understand these rarely observed long-distance dispersal events, since this behavior is critical for connecting populations in naturally heterogeneous or fragmented environments (Trakhtenbrot et al. 2005). In light of these results, caution should be applied when using a single resistance surface to reflect an entire population’s dispersal behavior.

Transforming suitable habitat to resistance surface

Little attention has been devoted to selecting the appropriate mathematical function to transform habitat suitability maps into resistance surfaces (Beier et al. 2008). Moreover, the nature of this relationship has rarely been documented with detailed movement data. We took advantage of a well-studied species with an extensive set of movement data to develop a general method for exploring relationships between habitat suitability and resistance surfaces. When multiple functions were compared to observed movements, the most highly non-linear relationship greatly outperformed all other functions.

This insight has implications for conservation and management efforts that rely on a single transformation function. For instance, a linear function (1—habitat suitability) is the most common function used to create a resistance surface (Zeller et al. 2012), likely due to its straightforward calculation. However, if a linear function were used here without evaluation,

the resulting resistance surface would underestimate the ability of *P. borealis* to traverse heterogeneous landscapes, and thus underestimate the population’s connectivity.

Conclusion

Selecting the optimal (i.e., the most biologically relevant) functional form is necessary to accurately create resistance surfaces from habitat suitability models, and thus to enable conservation planners to generate appropriate strategic conservation actions. As movement behavior becomes increasingly available for a wider range of taxonomic groups, our approach can easily be expanded to evaluate the best transformation from habitat suitability to resistance surfaces. Moreover, the modeling approach applied here may substantially reduce a significant source of uncertainty when quantifying species movement capacity through complex landscapes. A moderately non-linear or linear relationship may be a more appropriate transformation for a habitat suitability model into a resistance surface for species that have restricted movement capacity and/or for species that are sensitive to subtle changes when traversing the landscape. Ideally, future studies should justify the relationship between habitat suitability models and resistance surfaces.

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