The Journal of Wildlife Management 79(2):220–234; 2015; DOI: 10.1002/jwmg.829

Research Article

Cost-Distance Analysis of Mesopredators as a Tool for Avian Habitat Restoration on a Naturally Fragmented Landscape

JOHN H. PORTER, *Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22904, USA*
RAYMOND D. DUESER, *Department of Wildland Resources, Utah State University, Logan, UT 84322, USA*
NANCY D. MONCRIEF,[1] *Virginia Museum of Natural History, Martinsville, VA 24112, USA*

ABSTRACT Removal of mammalian mesopredators is a strategy frequently applied to problems of conservation management, such as protection of rare or endangered species. Effectiveness of predator removal is often dependent on the ease with which additional predators can immigrate into the removal area. We applied cost-distance analysis, coupled to a sensitivity analysis, and least-cost path analysis to raccoons (*Procyon lotor*) and red foxes (*Vulpes vulpes*) on the Virginia barrier islands to determine the landscape resistance (i.e., difficulty) for mesopredators to reach individual islands from both mainland and island sources, to assess the relative role of mainland versus island populations as sources of immigrants to unoccupied (or depopulated) islands, and to formulate strategies that focus management efforts on a few key predator sources. The minimum energetic resistances to immigration varied over 3 orders of magnitude, making some islands better targets for removal efforts than others. Additionally, because of differences in the distribution of resident populations on the islands, resistance to immigration to a typical island is at least 3 times less for raccoons than for red foxes. Landscape resistance to red fox immigration is typically lower from the mainland, whereas for raccoons inter-island movements are typically less costly. Empirical data from long-term field studies of raccoons and red foxes in this system support the resistance structure identified. Overwater transits made by marked and resighted raccoons all were relatively short and relatively low-cost. Similarly, islands that were recolonized following the removal of raccoons and red foxes all were characterized by very low resistance values. These results are used to identify specific islands for which predator removal efforts are most likely to be successful in aiding the recovery of beach-nesting and colonial waterbirds in this system. A similar approach may be applied in any landscape where there are distinct differences in the costs of traversing different elements of the landscape. © 2015 The Wildlife Society.

KEY WORDS connectivity, cost-distance analysis, landscape permeability, landscape resistance, least-cost path analysis, predator management, *Procyon lotor*, raccoon, red fox, *Vulpes vulpes*.

Increased abundances and expanding geographic ranges of mammalian mesopredators in recent decades have seriously complicated the conservation and management of ecosystems around the world (Prugh et al. 2009, Carey et al. 2012). Rare species (Goodrich and Buskirk 1995) and species on islands (Burger and Gochfeld 1994, Courchamp et al. 2003, Brooke et al. 2007) are particularly susceptible to the detrimental effects of mesopredators. Examples include the extinctions of birds from Pacific islands caused by introduction of mammalian predators (Blackburn et al. 2004, 2005), the impact of snakes on birds on Guam (Savidge 1987, Wiles et al. 2003), and changes in plant communities caused by introduction of the arctic fox (*Alopex lagopus*; Croll et al. 2005). Most often the predator is an exotic species, introduced to the region (Baxter et al. 2008), but even native predators that have co-evolved with their prey can have significant impacts when there are changes in their abundance or distribution (Martin et al. 2010). Furthermore, overabundant mesopredators often have comparable effects in fragmented habitats on mainland areas (Beasley et al. 2013). The management of mesopredators has thus become a critical issue for conservation and restoration (Coté and Sutherland 1997, Crooks and Soulé 1999).

Although a variety of non-lethal methods have been developed for reducing predation effects on species of conservation concern (Goodrich and Buskirk 1995, Jiménez and Conover 2001, Courchamp et al. 2003), direct control by predator trapping and removal remains a frequently used approach to predation management (Reynolds and Tapper 1996, Hecht and Nickerson 1999, Lavers et al. 2010). There is a growing emphasis on developing strategies designed to enhance the efficiency and effectiveness of mesopredator management on extensive landscapes (Sinclair et al. 1998, Harding et al. 2001, Martin et al. 2010, Peery and Henry 2010, Robinson et al. 2013). These studies confirm that

Received: 11 September 2013; Accepted: 4 November 2014
Published: 3 January 2015

[1] *E-mail: nancy.moncrief@vmnh.virginia.gov*

taking a formal approach to predation management is likely to pay dividends in terms of efficiency and efficacy, particularly when reliable data on predator abundance and demography are available. Unfortunately, such data usually are not available. In these cases, an approach that focuses on the underlying landscape and simple estimates of predator occurrence may be a useful approach to designing a predation management strategy.

Martin et al. (2010) applied a multi-factorial structured decision-making process centered on models of predator and prey population dynamics to evaluate how control of raccoons (*Procyon lotor*) might promote the conservation of a declining population of the American oystercatcher (*Haematopus palliatus*) on the Outer Banks islands along the central coast of North Carolina (USA). Similarly, Brooke et al. (2007) prioritized removals of invasive species (including predators) from islands of various sizes using measures of area-weighted financial cost and potential conservation benefit. However, neither of these studies incorporated treatment of landscape relationships that might affect the rate of predator reinvasion.

More recently, Harris et al. (2012) proposed a method for prioritizing islands for invasive rodent eradication, with an emphasis on reinvasion risk and conservation value. They proposed that eradication efforts be planned in a metapopulation context, taking into account the likelihood of both human-mediated and natural reinvasion. They envisioned as an eradication unit a group of adjacent islands separated from one another by less than the maximum natural dispersal distance of the target invasive species but surrounded by a wider buffer of open water. Eradication efforts would be focused on units in which the individual islands are considered eradicable and which are relatively immune to anthropogenic reinvasion. Potential eradication units are then evaluated and ranked for their conservation value, a measure of the conservation gain to be realized in the event of a successful eradication. Harris et al. (2012) envision cases in which the conservation value is high and the risk of reinvasion is either high or unknown. This method uses distances beyond which reinvasion is assumed to rarely occur. We build on the work of Harris et al. (2012) by extending beyond simple distance measures to quantify the relative landscape-imposed cost of reaching different islands.

Extensive use of space by the predator can seriously restrict the efficacy of a removal program (Mosnier et al. 2008). Removal is most likely to be successful in situations where the opportunity for immigration is low (Hartman and Eastman 1999, Barton and Roth 2007, Rosatte et al. 2007). When possible, removals should be targeted at areas with naturally occurring barriers to immigration (Brooke et al. 2007, Zalewski et al. 2009, Harris et al. 2012). The water surrounding islands constitutes such a natural barrier, but even for islands the potential effectiveness of predator removals is highly variable, dictated largely by relative isolation and the degree to which removals disrupt in situ recruitment (Courchamp et al. 2003). Isolation is relatively easy to define for offshore or oceanic islands, based on Euclidean distance alone (Harris et al. 2012). Isolation is more difficult to quantify for near-shore and estuarine islands embedded in an extensive matrix of salt marshes, tidal flats, and lagoons.

One approach to assessing proximity and accessibility on a complex landscape is cost-distance analysis, also called "least-cost modelling" (Adriaensen et al. 2003) or "cost-distance modelling" (Graham 2001), in which the minimum cumulative cost of moving from a source location to a destination is calculated based on the resistance of each cell of a geographical information system (GIS) raster. Resistance may reflect substrate or habitat preferences of animals, physiological costs, reductions in survival, or an integration of all 3 (Zeller et al. 2012). Estimates of resistance for raster cells associated with specific land cover classes can be based on expert opinion, genetic relatedness, and observed movements (Spear et al. 2010, Zeller et al. 2012). If costs for all land cover types are equal, cost-distance analysis yields a measure of simple Euclidean distance, which may be sufficient when landscapes are either uniform and undifferentiated with respect to transit costs or when they are configured so that migrants infrequently cross land cover boundaries.

The data required for cost-distance analysis (i.e., land cover data, estimates of resistance for different landscape elements, and identification of populated sources) often are more readily available than the detailed abundance and demographic data required for some other approaches. Cost-distance analysis can be extended to include least-cost path analysis, which designates a specific, hypothetical path that minimizes the cost of transit (Zeller et al. 2012), and may be used to identify likely sources of immigrants. Cost-distance analysis has been applied in conservation studies to identify barriers to gene flow (Lada et al. 2008, Murtskhvaladze et al. 2010, Reding et al. 2013, Zielinski et al. 2013, Guarnizo and Cannatella 2014), identify sites for reintroductions (Kramer-Schadt et al. 2004, Thatcher et al. 2006), mitigate the negative effects of habitat fragmentation (Zimmermann and Breitenmoser 2007, Leoniak et al. 2012, Carroll et al. 2013, Squires et al. 2013), identify areas of high conservation value (Kautz et al. 2006, Beier et al. 2008, Hebblewhite et al. 2012), and support biodiversity adaptation to climate change (Howard and Schlesinger 2013, Wasserman et al. 2013). Whereas these applications aimed to promote the movement and continuity of the focal species across the landscape, Gonzales and Gergel (2007) and Zalewski et al. (2009) used cost-distance analysis to devise a strategy for disrupting the spread of invasive species.

We extended this latter application to reduce conflicts between over-abundant native mesopredators and species of conservation concern on the 1,000-km^2 naturally fragmented landscape of the Virginia barrier islands (USA). These islands provide critical nesting habitat for 27 species of beach-nesting and colonial waterbirds, many of which have declined in recent decades (Williams et al. 1990, 2007). Concurrently, there has been an expansion in both the number of individuals and the number of islands occupied by mammalian mesopredators, particularly raccoons and red foxes (*Vulpes vulpes*, hereafter foxes; Erwin et al. 2001, Brinker et al. 2007). Mesopredator increase in this area is a consequence of the decline in hunting and trapping associated with the demise of waterfowl hunting clubs on the islands (Graham 1976*a, b*) and the increase in abundance of mesopredators on the mainland. Keiŝs (2001) reported that the number of nesting waterbird colonies remaining on the islands is inversely related to the occurrence of raccoons and foxes. After observing an increase of otherwise suitable nesting habitat in recent decades, Wilson et al. (2007) concluded that factors other than habitat availability, including nest predation by mammals, are probably responsible for the recent decline of beach-nesting birds. Erwin and Beck (2007) and Erwin et al. (2007) emphasized the importance of predation management as part of any attempt to restore nesting habitat for waterbirds in the mid-Atlantic region.

We used cost-distance analysis to help identify likely sources of raccoon and fox immigrants on the islands. Our objective was to identify locations having both minimal potential for reoccupation by predators following removal and high conservation value for beach-nesting and colonial waterbirds. To this end, we applied cost-distance analysis to 1) estimate landscape resistance that needs to be overcome for a raccoon or fox to travel to any given island from both mainland and island sources, assuming that relative physiological costs of swimming versus terrestrial locomotion would serve as a measure of landscape resistance; 2) assess the relative role of mainland and island populations as sources of immigrants to unoccupied (or depopulated) islands; 3) compare the results of cost-distance analysis with empirical data from field studies of raccoon movement to assess the degree of conformity between theoretical and actual movement patterns on the islands; 4) test the rates of raccoon and red fox immigration to islands having different minimum-cost values and from which these species had been removed; and 5) identify high priority source locations to target for predator monitoring and removal efforts.

STUDY AREA

The study area included the mainland of the southern Delmarva Peninsula and the barrier and marsh islands that extend approximately 150 km along the seaward margin of the Peninsula (Fig. 1). The islands are separated from the mainland and from one another by marshes, marsh islands, and open bays that connect to the Atlantic Ocean through deep inlets (Oertel et al. 1989, Hayden et al. 1991). The islands range from 1 m to 10 m in elevation, and vary from 14 ha to 9,344 ha in area. Vegetation composition varies from emergent sandbars to low-lying marsh, to grassland with extensive overwash zones, to shrub thickets, and finally to mature forests on elevated islands (McCaffrey and Dueser 1990). As measured from the National Oceanic and Atmospheric Administration (NOAA) Coastal-Change Analysis Program (C-CAP) land cover data layers for the lower Delmarva Peninsula (Virginia and Maryland) for the year 2005 (http://www.csc.noaa.gov/digitalcoast/data/ccapregional), the distance between nearest-neighbor islands averages 0.81 km (SE = 0.16), and the distance between adjacent islands that are separated by deep, swift-running inlets averages 0.52 km (SE = 0.08). The average island distance from the mainland is 5.84 km (SE = 0.75; range: 0.35–12.9 km).

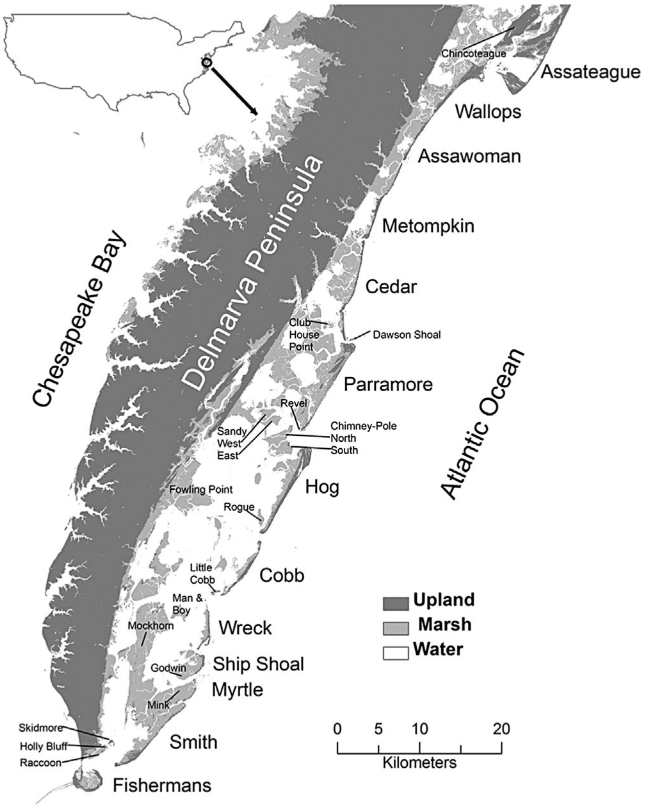

Figure 1. The 31 island and marsh surfaces of the Virginia barrier island complex used in this study.

The study area included 31 marsh and island surfaces in our analyses (Fig. 1), each of which had a history of nesting by beach-nesting and colonial waterbirds (Williams et al. 1990, 2007). Assateague, Chincoteague, Fishermans, and Wallops islands are connected to the mainland by highway bridges. All other surfaces are accessible only by crossing open water. Several islands have been occupied by humans sporadically, but have been essentially deserted since a series of severe storms in the early 1930s (Barnes and Truitt 1997). The islands are held in public ownership by the United States Fish and Wildlife Service (USFWS, Chincoteague and Eastern Shore of Virginia National Wildlife Refuges), the Commonwealth of Virginia (Wreck Island Natural Area and Mockhorn Island Wildlife Management Area), or are owned by The Nature Conservancy. The Nature Conservancy holdings comprise the Virginia Coast Reserve, a National Science Foundation Long-term Ecological Research site, a Man and the Biosphere Reserve, and a Western Hemisphere International Shorebird Reserve Network site (Badger 1991, 1997).

METHODS

Cost-Distance Analysis

Cost-distance analysis is a means of incorporating the influence of landscape heterogeneity on potential animal movements. It requires that the landscape be characterized in a meaningful way with respect to movements (Schadt et al. 2002, Kautz et al. 2006), that appropriate landscape resistance values be assigned, and that sources be properly identified (Zeller et al. 2012). A raster resistance surface contains the resistance value (i.e., cost of traversing) for each raster cell (Graham 2001). Resistance may also be referred to as friction or impedance. Resistance may be estimated based on expert opinion or physiological energy expenditure, or it may be inferred from occurrence, observed movements, or genetic relatedness (Spear et al. 2010, Zeller et al. 2012). To create a resistance surface, we started with the NOAA C-CAP land-cover data layers for the lower Delmarva Peninsula (Virginia and Maryland) for the year 2005. We simplified the classification from 23 cover classes to 3 classes: upland, salt marsh, and water (Table 1). The layer had 30-m pixel resolution, and classification accuracies >90% for water and salt marshes (layer metadata). Each class represented a distinct habitat relative to the mobility of raccoons and foxes (Dueser et al. 2013).

We estimated resistance values based on the relative energetic cost of traversing a distance of 1 km for each cover class. Our values were based on published estimates for the relative cost of mammalian locomotion, with the same values used for both raccoons and foxes (see Supplementary Materials on file with http://onlinelibrary.wiley.com). We set costs at 1 for traversing 1 km of upland, 4 for traversing 1 km of water, and 2 for traversing salt-marsh.

We defined the mainland source region as all the upland contiguous with the Delmarva Peninsula. Similarly, we defined an island source as the upland portion of an island (i.e., any area higher in elevation than tidal marsh) that supported a year-round population of the focal species. For raccoons, we used prior reports (Paradiso and Handley 1965, Dueser et al. 1979, Hanlon et al. 1989) and extensive field investigations between 1998 and 2007 (Keišs 2001, Martin 2007, Dueser et al. 2013; B. R. Truitt, The Nature Conservancy, personal communication) to identify 11 source islands (Table 2). Each source island had woody habitat and a source of fresh water, both of which are positively correlated with raccoon population density and their temporal stability in fragmented landscapes (Beasley et al. 2011). For foxes, we used prior reports (Paradiso and Handley 1965, Krim et al. 1990, Brittingham 1993) and observations and/or records from trapping of adults with kits during the years 1998–2010 (R. D. Dueser, Utah State University, and N. D. Moncrief, Virginia Museum of Natural History, unpublished data; B. R. Truitt, personal communication) to identify 4 source islands (Table 3), each of which was also a raccoon source.

We established destination points on the upland of each island on the north, south, and middle, thus excluding isolated areas of upland surrounded by marsh (e.g., hummocks). We added 1 to 3 additional destination points adjacent to islands lacking a North-South orientation. We calculated the minimum cost of reaching a destination island as the minimum net resistance between the source and any 1 of these destination points. Calculation of the minimum costs for inter-island migration required multiple cost-distance analyses. One analysis calculated the minimum costs for moving from any of the islands that we identified as potential sources to each of the non-source islands. We then conducted a separate analysis for each source island, with the target island removed from the source pool and calculating the cost of moving to that island from any of the remaining source islands.

Table 1. Land-cover classes of the Virginia barrier islands in 2005, as designated by the Coastal-Change Analysis Program (C-CAP) and simplified for use in this study. Cost of travel and percentage of total island area are indicated for each C-CAP cover class except water.

C-CAP Land-cover class	Simplified cover class	Percent of island area	Cost of travel
High Intensity Developed	Upland	0.10	1
Medium Intensity Developed	”	0.41	1
Low Intensity Developed	”	0.96	1
Open Spaces Developed	”	0.93	1
Cultivated Land	”	0.09	1
Pasture/Hay	”	0.00	1
Grassland	”	0.74	1
Deciduous Forest	”	0.67	1
Evergreen Forest	”	2.11	1
Mixed Forest	”	0.65	1
Scrub/Shrub	”	2.45	1
Palustrine Forested Wetland	”	6.33	1
Palustrine Scrub/Shrub Wetland	”	1.07	1
Estuarine Forested Wetland	”	0.04	1
Estuarine Scrub/Shrub Wetland	”	0.55	1
Unconsolidated Shore	”	5.03	1
Bare Land	”	12.29	1
Background	Water	0.17	4
Water	”		4
Palustrine Aquatic Bed	”	0.01	4
Estuarine Aquatic Bed	”	0.00	4
Palustrine Emergent Wetland	Marsh	1.25	2
Estuarine Emergent Wetland	”	64.13	2

Table 2. Minimum-cost sources for raccoons on the Virginia barrier islands and comparison of cost ratio between mainland and island sources. The minimum-cost source is the island (or the mainland) used as a source that had the lowest cost of transit. A high mainland:island cost ratio indicates that costs of traveling from a source island are much lower than the cost of traveling from the mainland. A high island:mainland cost ratio indicates that travel cost from a source island is much higher than the cost of traveling from the mainland. Ratios <1.0 are not shown. Asterisks denote source islands.

Island	Minimum-cost source	Cost ratio mainland:island	Cost ratio island:mainland
Assateague*	Chincoteague	1.3	
Assawoman	Wallops	134.2	
Cedar*	Parramore	3.5	
Chimney Pole North	Revel	7.6	
Chimney Pole South	Hog	6.3	
Chincoteague*	Wallops	10.2	
Club House Point	Cedar	3.2	
Cobb	Hog	10.6	
Dawson Shoals	Cedar	42.2	
Fishermans*	Mainland		11.8
Fowling Point	Mainland		14.6
Godwin	Smith	2.8	
Hog*	Parramore	2.7	
Holly Bluff	Skidmore	1.1	
Little Cobb	Hog	2.4	
Man and Boy	Mockhorn	3.4	
Metompkin	Cedar	1.3	
Mink	Smith	7.2	
Mockhorn*	Smith	1.1	
Myrtle	Smith	262.5	
Parramore*	Revel	99.4	
Raccoon	Mainland		2.2
Revel*	Parramore	42.8	
Rogue	Hog	30.9	
Sandy East	Revel	1.9	
Sandy West	Mainland		1.1
Ship Shoal	Smith	4.5	
Skidmore*	Mainland		2.2
Smith*	Mockhorn	1.7	
Wallops*	Chincoteague	1.3	
Wreck	Smith	2.5	

For our cost-distance analysis, we used the ArcGIS (Environmental Systems Research Institute, Inc., Redlands, CA) CostPath tool to calculate minimum-cost values as the minimum accumulated cost (i.e., total resistance encountered) required to reach the least costly of the 3 or more destination locations on each island. To aid in distinguishing between sources, we mapped specific least-cost paths using the ArcGIS Shortest Path tool. Because of skewed distributions, we used SPSS 20.0 and 22.0 (SPSS, Inc., Chicago, IL) nonparametric tests (Spearman's rho and Kolmogorov–Smirnov) to analyze minimum costs for rank correlations and differences in distributions, respectively.

To test the sensitivity of our results to the selection of particular resistance values, we repeated the mainland-to-island analysis using resistance values for upland, marsh, and water of 1, 1.5, and 3, and 1, 4, and 8, respectively. This provided a test of the influence of extremely low and extremely high resistances based on measurements of energy expenditures for swimming versus walking (see Supplementary Materials). Finally, we repeated the mainland-to-island analysis using a constant value of 1 for all land cover types to calculate the Euclidean distance between a mainland source and each island destination. We compared analyses with different suites of resistance values using Spearman's rho and a graphical examination of linearity.

Evidence from Field Studies

We examined the validity of our results from cost-distance and least-cost path analyses using data from 2 independent field studies of overwater movement by mesopredators in this system. First, Dueser et al. (2013) documented overwater movement by 25 resighted raccoons (out of 335 marked animals) during 8 years of fieldwork (1999–2007) on 9 Virginia barrier islands and 9 sites on the adjacent Delmarva Peninsula mainland. For each observed instance of overwater movement reported by Dueser et al. (2013), we estimated the minimum cost between the first point of observation (source) and last point of observation (destination). Despite the extensive effort expended to obtain these field data, the low number of direct observations of overwater movement precluded standard statistical analysis. Nevertheless, we were able to predict (based on cost-distance analysis results) that all observed movements would have relatively low minimum costs.

Next, we tested the validity of the results of our cost-distance and least-cost path analyses using field evidence of overwater movement in the form of immigration by unmarked raccoons ($n = 62$ individuals) and foxes ($n = 46$) during 10 years (2001–2010) of removal trapping on 5 non-source islands (Assawoman, Metompkin, Wreck, Ship Shoal, and Myrtle). These low-lying, frequently-flooded islands had limited fresh water or shelter for mesopredators but offered excellent nesting habitat for beach-nesting and

Table 3. Minimum-cost sources for red foxes on the Virginia barrier islands and comparison of cost ratio between mainland and island sources. The minimum-cost source is the island (or the mainland) used as a source that had the lowest cost of transit. A high mainland:island cost ratio indicates that costs of traveling from a source island are much lower than the cost of traveling from the mainland. A high island:mainland cost ratio indicates that travel cost from a source island is much higher than the cost of traveling from the mainland. Ratios <1.0 are not shown. Asterisks denote source islands.

Island	Minimum-cost source	Cost ratio mainland:island	Cost ratio island:mainland
Assateague*	Chincoteague	1.3	
Assawoman	Wallops	121.7	
Cedar	Parramore	3.4	
Chimney Pole North	Parramore	5.9	
Chimney Pole South	Parramore	2.6	
Chincoteague*	Wallops	10.2	
Club House Point	Parramore	1.6	
Cobb	Parramore	1.5	
Dawson Shoals	Parramore	12.1	
Fishermans	Mainland		43.7
Fowling Point	Mainland		16.2
Godwin	Mainland		1.7
Hog	Parramore	2.7	
Holly Bluff	Mainland		48.1
Little Cobb	Mainland		1.1
Man and Boy	Mainland		2.7
Metompkin	Mainland		2.1
Mink	Mainland		2.2
Mockhorn	Mainland		8.5
Myrtle	Mainland		2.5
Parramore*	Mainland		2.1
Raccoon	Mainland		79.9
Revel	Parramore	43.9	
Rogue	Parramore	1.6	
Sandy East	Parramore	1.2	
Sandy West	Mainland		1.5
Ship Shoal	Mainland		1.8
Skidmore	Mainland		25.2
Smith	Mainland		5.7
Wallops*	Chincoteague	1.3	
Wreck	Mainland		1.3

colonial waterbirds (Wilson et al. 2007). The Nature Conservancy, the USFWS, and the Virginia Department of Game and Inland Fisheries initiated fieldwork on these 5 islands in 2001, with the intention of removing all raccoons and foxes annually; track and sign surveys preceded use of traps, snares, and shooting by Wildlife Services personnel of the United States Department of Agriculture. We classified as recent immigrants all animals captured on these islands during 2002–2010 (B. R. Truitt, personal communication; A. L. Wilke, The Nature Conservancy, personal communication). We predicted that the number of immigrants, following removals, would be greater for islands with low minimum costs relative to those with high minimum costs. We used a 1-tailed Spearman's rho to test for the predicted negative rank correlations between minimum costs from island and mainland sources and number of recent immigrants.

RESULTS

Mainland-to-Island Movement Costs

To calculate the relative cost of travel from the mainland to each of the destination islands, we used a single cost-distance analysis for both raccoons and foxes because the mainland serves as a potential source for both species. The median cost of reaching an island from the mainland was 12.00 (i.e., equivalent to 12 km of upland travel, 6 km of travel through marsh, or 3 km of swimming). Nineteen of the islands required >10 cost units, and of those 9 had costs >20. We found wide variation, ranging from <1 cost unit for Assateague, Fishermans, and Raccoon islands, each of which is separated from the mainland by only a narrow tidal channel, to >30 for Rogue, Cobb, and Little Cobb islands, which are separated from both the mainland and lagoonal marshes by a wide expanse of open water (Fig. 2A). The progression in costs to reach the islands from the mainland followed a relatively smooth, increasing curve from least costly to most costly, with no abrupt transitions and no obvious outliers (Fig. 2A).

Least-cost paths tended to incorporate marsh bridges between the mainland and barrier islands, rather than crossing large areas of open water (Fig. 3A). Exceptions included Cobb, Rogue, Little Cobb, Wreck, and Godwin islands, all of which entailed crossing an uninterrupted stretch of water between 2.4 km and 5.5 km in width. Although the mainland was the ultimate source, least-cost paths often crossed intermediate bridge islands. Mockhorn Island was particularly important in this regard. Least-cost paths for 6 islands used Mockhorn as an intermediate step on their way from the mainland.

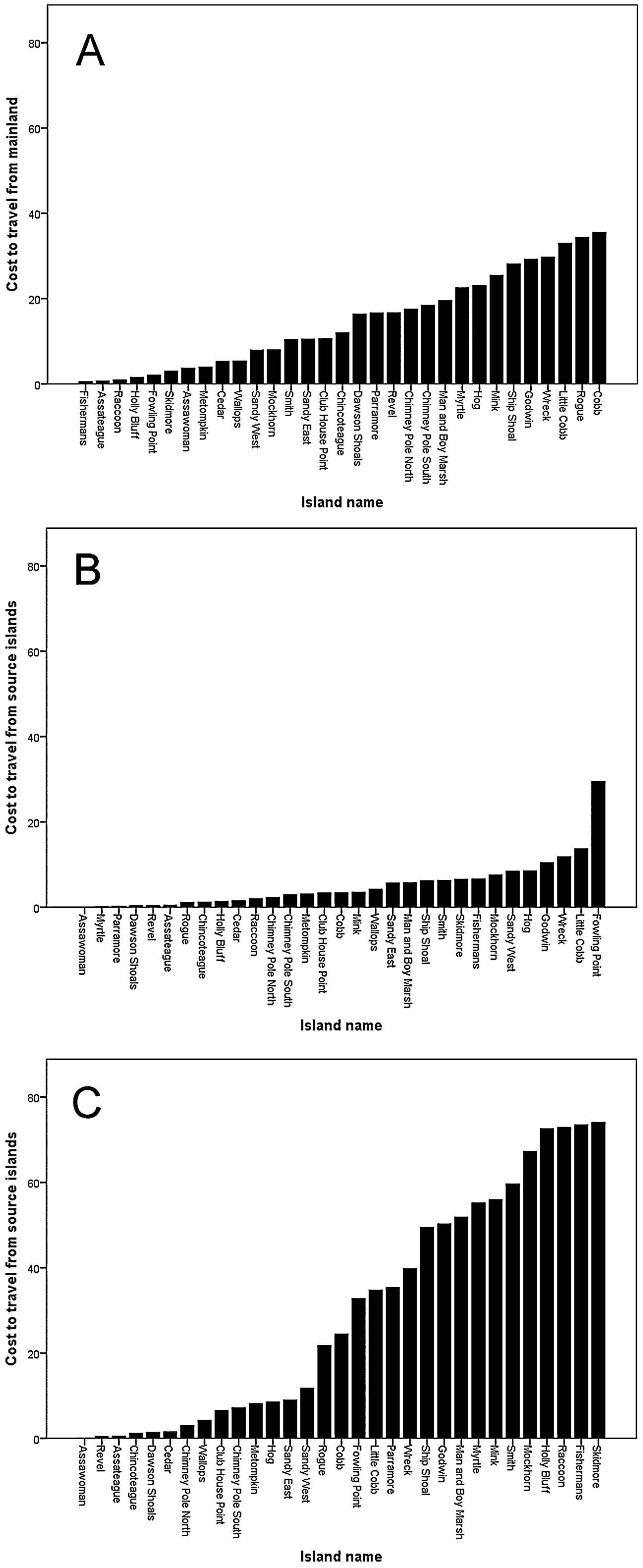

Figure 2. Comparison of minimum costs for raccoons and red foxes on the Virginia barrier islands to each of the 31 destination surfaces from the mainland (A), from the source islands for raccoons (B), and from the source islands for red foxes (C).

When we repeated the mainland-source analysis using different resistance values, we found strong linear relationships between the minimum costs of the islands with the original (intermediate) resistances and those with the more extreme values, both high and low (Fig. 4). Although the slopes of the lines inevitably differ when different total weights are used, the strong linear relationships show that the ranking of islands by minimum cost remains largely unaltered. Pairwise correlations between the minimum costs using different sets of resistance values were always high (all 3 pairwise correlations had Spearman's rho >0.99, $P \leq 0.001$).

When we set all resistances to 1 to obtain an estimate of Euclidean (straight line) distances, there was a perceptible loss of linearity at minimum costs >20 when the curve flattens out (Fig. 4). Eight islands that had nearly identical Euclidean distances (9.8–10.73 km) exhibited widely varying minimum costs (22.5–34.33 cost units), indicating that both distance and resistance surfaces play a role in determining the minimum costs on this landscape.

Inter-Island Movement Costs for Raccoons

The median cost of raccoon immigration to an island from another island was 3.36, versus 12.00 for movement from the mainland. Only 4 islands (Fowling Point Marsh, Godwin, Little Cobb, and Wreck) required >10 cost units for inter-island immigration (Fig. 2B), as opposed to 19 islands for mainland immigration. A Kolmogorov–Smirnov test indicated significant differences in the cost distributions for island and mainland raccoon sources ($P \leq 0.01$; Figs. 2A and B). Minimum costs of inter-island movements for raccoons exhibited an uneven distribution, with Fowling Point as a conspicuous outlier (Fig. 2B). Whereas least-cost paths from the mainland frequently overlapped (typically along lagoonal marshes), inter-island paths tended to be widely separated, primarily running between the northern and southern tips of the islands (Fig. 3B).

When we considered the island and mainland sources together, island-to-island movements, rather than mainland-to-island movements, had the lowest costs. The median cost for travel from a lowest-resistance source (either mainland or island) was 2.80. For 26 islands, the most cost-effective raccoon source was another island (island: mainland cost ratio <1.00; Table 2); 6 islands had at least a 30-fold higher cost associated with movement from the mainland rather than from an island source. The mainland: island and island:mainland ratios were approximately equal for 8 islands (both ratios <2.00). The mainland was the most cost-effective source for only 5 islands (Table 2). Smith was an especially important source island, serving as the minimum-cost source for 6 additional islands, only 1 of which was itself also a source (Table 2).

Inter-Island Movement Costs for Foxes

The median cost of immigration to an island from a source island was 24.44 units. Eighteen of the islands required >10 cost units for foxes (Fig. 2C). The distribution of inter-island costs for foxes (Fig. 2C) reflected generally higher costs than for mainland-to-island movements (Fig. 2A) and was less

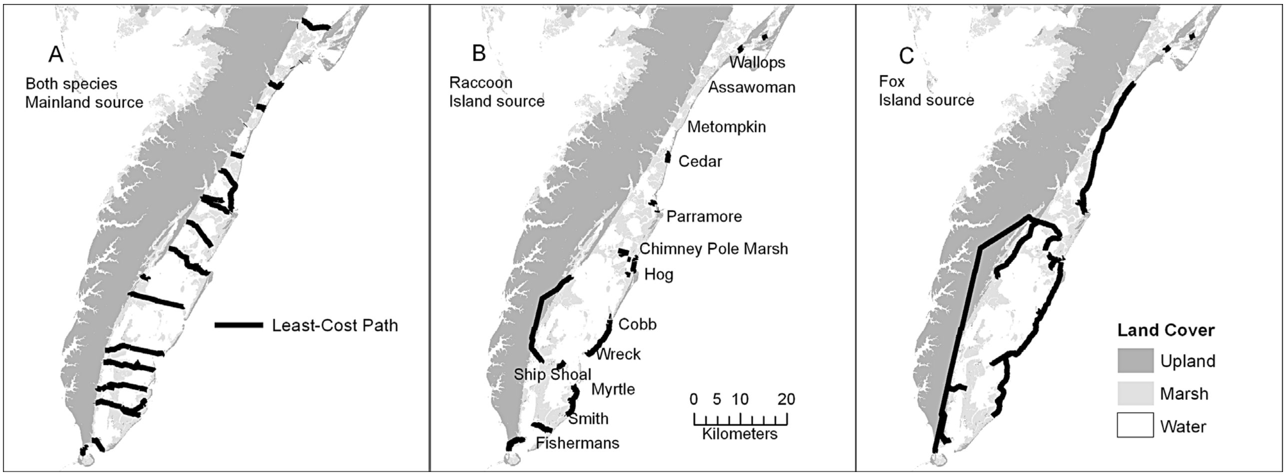

Figure 3. Least-cost travel pathways for raccoons and red foxes on the Virginia barrier islands to each of the 31 destination surfaces from the mainland (A), from the source islands for raccoons (B), and from the source islands for red foxes (C).

evenly distributed, with roughly half the islands having extremely high costs relative to travel from the mainland. A Kolmogorov–Smirnov test indicated a significant difference between the cost distributions for mainland and island sources ($P \leq 0.009$). When we used the source with the minimum cost (either island or mainland), the median cost of travel for foxes was 7.18 units, nearly 3 times the equivalent cost for raccoons. Similar to the inter-island paths for raccoons, least-cost paths for foxes ran primarily between the northern and southern tips of the islands, but unlike raccoons, ran along the islands as well (Fig. 3C). Parramore served as the source for all islands south of Metompkin, and for 5 of the southern islands the mainland was used as a bridge.

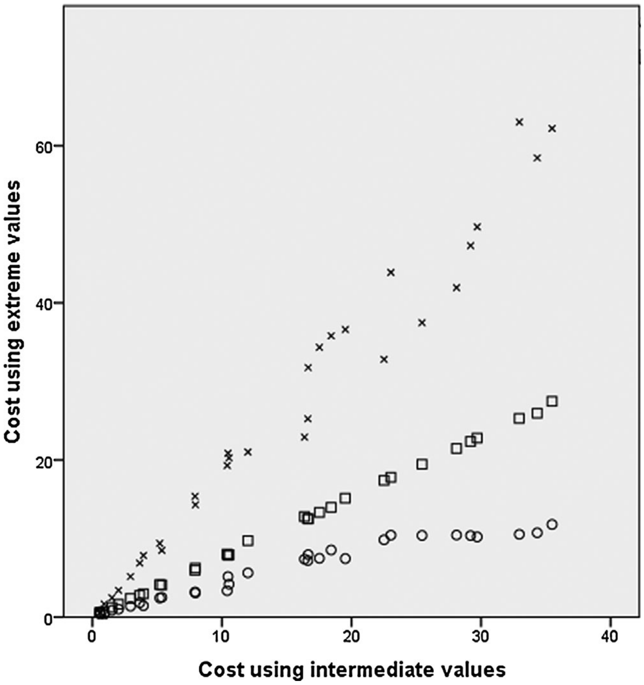

Figure 4. Comparison of intermediate and extreme minimum-cost estimates for raccoons and red foxes on the Virginia barrier islands to reach each of the 31 destination surfaces from the mainland. Each line represents a comparison between an intermediate set of travel costs for upland, marsh, and water (1, 2, and 4, respectively) and 1 of 3 more extreme sets of values: extremely low (1, 1.5, and 3; open squares), extremely high (1, 4, and 8; ×), and all equal (1, 1, and 1; open circles). The latter values provide an estimate of Euclidean distance between the mainland and the destination.

Mainland-to-island movements typically had the lowest costs for foxes. For 17 islands, the most cost-effective fox source was the mainland (mainland:island cost ratio <1.00; Table 3). The mainland:island and island:mainland costs were approximately equal for 11 islands (both ratios <2.00; Table 3). An island was the most cost-effective source for 14 islands. Of the source islands, only Parramore, which was the clear minimum-cost source for 10 islands (all island: mainland ratios <1.00), served as the source for more than 2 islands (Table 3).

Costs of transit for raccoons and foxes were correlated, but not strongly so. Minimum costs for inter-island movements were positively correlated (Spearman's rho $= 0.441$, $P \leq 0.013$) as was minimum cost regardless of source (Spearman's rho $= 0.660$, $P \leq 0.001$). Despite the high level of statistical significance, there was little predictive power in the relationship, with less than 44% of the variance in relative ranks explained.

Comparison with Evidence from Field Studies

We used data from 2 independent field studies of overwater movement by mesopredators in this system to examine the validity of our cost-distance and least-cost path analyses. The first study reported directly observed movements of raccoons that were either marked-and-released at the point of capture or that were translocated across open water and released on the upland of an adjacent island (Dueser et al. 2013). Overwater movement was observed for only 3 of 303 (1%) individuals marked and released at the point of capture, precluding statistical analysis of these movements. Nevertheless, these 3 individuals made 4 overwater crossings, all over relatively short straight-line distances between capture locations (0.2 km to 0.5 km) with low minimum costs between islands (0.06–1.51). Dueser et al. (2013) also reported that 22 of 32 translocated raccoons (69%) subsequently moved across open water within 2 to 385 days of translocation. Again, all travel was over relatively short distances between capture locations (0.5 km to 3.5 km) with low minimum costs between islands (0.39–2.02). Both groups of animals crossed relatively narrow, slow-flowing channels. None of the 335 marked raccoons were observed to cross a tidal inlet (Dueser et al. 2013).

The second field study provided indirect evidence of overwater movement by unmarked raccoons and foxes in the form of immigration by individuals of both species following removal trapping on 5 non-source islands (Assawoman, Metompkin, Wreck, Ship Shoal, and Myrtle). Removal trapping of raccoons resulted in the capture of 0 to 14 animals per island in any given year during 2001–2010 (Table 4; B. R. Truitt, unpublished data; D. J. Allaben, United States Department of Agriculture, personal communication). No raccoons were removed (or detected in track surveys) on Ship Shoal or Wreck during 2001–2010 (Table 4; R. D. Dueser and N. D. Moncrief, unpublished data; B. R. Truitt, personal communication), although tracks had been observed in previous years (1998–2000 R. D. Dueser and N. D. Moncrief, unpublished data). As expected, for raccoons there was a strongly negative rank correlation between minimum costs from the mainland and the overall immigration rate (Spearman's rho $= -0.975$, $P \leq 0.002$, 1-tailed). We observed the same pattern when we used the lowest cost source (either mainland or island; Spearman's rho $= -0.872$, $P \leq 0.027$, 1-tailed).

Removal trapping of foxes on Assawoman, Metompkin, Wreck, Ship Shoal, and Myrtle islands resulted in capture of 0 to 10 animals per island in any given year during 2001–2010 (Table 4). Although foxes were detected on only 2 of the 5 islands during this period, the minimum cost values for these 2 islands were a tenth of the value of the islands with no detections (Table 4). The rank correlation between minimum cost and number of recent immigrants was the same for the mainland and the lowest-cost source (Spearman's rho $= -0.894$, $P \leq 0.020$, 1-tailed).

DISCUSSION

Cost-distance analysis provides a formal approach for using landscape-level information to plan predation management on extensive, highly fragmented landscapes, extending the distance threshold approach of Harris et al. (2012). Although our results refer specifically to the landscape of the Virginia barrier islands, we believe cost-distance analysis may apply more broadly to extensive, highly fragmented landscapes elsewhere. In the case of the islands, we observed wide variation in the relative difficulty of reaching different islands, from 0.03 cost units for movements across a narrow channel between Wallops and Assawoman islands, to 32.95 cost units to move from the mainland across >5 km of open water to Little Cobb Island (Fig. 2).

The overall costs of immigration differed between species because of the disparity in both the number of source islands (11 for raccoons vs. only 4 for foxes) and the distribution of source islands (there is no southern island source for foxes). Raccoons had lower overall movement costs (median 2.80), and islands served as the primary minimum-cost source of raccoons (Table 2). Conversely, fox movement costs were approximately 3 times higher (median 7.18), and the mainland served as the primary minimum-cost source of foxes (Table 3). These findings suggest that, in this system, foxes might be more effectively removed than raccoons. They also suggest that removals of island raccoons might have both direct effects (i.e., reduction of abundance) and indirect effects (i.e., reduction in number of sources).

Cost-Distance Analysis

Successful application of cost-distance analysis requires characterization of the landscape in ways that are meaningful to the species of interest (Schadt et al. 2002, Kautz et al. 2006), assignment of appropriate resistances for different land cover elements (Spear et al. 2010, Zeller et al. 2012), and accurate identification of source regions. For our study, we used a high-quality land cover layer and a very coarse landscape categorization, where crossing different classes demands extremely different modes of locomotion

Table 4. Number of raccoons (R) and red foxes (F) removed from each of 5 non-source Virginia barrier islands during the period 2001–2010. MC is minimum cost of movement to the island.

	Assawoman		Metompkin		Wreck		Ship Shoal		Myrtle	
Year	R	F	R	F	R	F	R	F	R	F
2001	2	10	1	2	0	0	0	0	0	0
2002	1	3	0	1	0	0	0	0	3	0
2003	2	4	0	1	0	0	0	0	2	0
2004	0	8	3	2	0	0	0	0	0	0
2005	0	0	2	0	0	0	0	0	0	0
2006	0	0	1	0	0	0	0	0	0	0
2007	7	6	2	3	0	0	0	0	0	0
2008	0	0	14	1	0	0	0	0	0	0
2009	10	3	5	0	0	0	0	0	0	0
2010	6	2	1	0	0	0	0	0	0	0
Mean (SE) 2002–2010	2.9 (1.26)	2.9 (0.94)	3.1 (1.46)	0.9 (0.35)	0.0	0.0	0.0	0.0	0.6 (0.38)	0.0
MC from mainland	3.65	3.65	3.94	3.94	29.70	29.70	28.11	28.11	22.51	22.51
MC from island	0.03	0.03	3.09	8.13	11.80	39.81	6.19	49.47	0.09	55.18
MC island source	Wallops	Wallops	Cedar	Wallops	Smith	Parramore	Smith	Parramore	Smith	Parramore

(e.g., walking vs. swimming). If additional information had been available for the relative resistances for different types of upland (e.g., forest vs. grassland), the analysis could have been further refined. We assigned resistances based on published values of energetic costs for terrestrial mammals (see Supplementary Materials), and we tested the sensitivity of our results to the selection of particular resistance values. Finally, we assigned source regions based on long-term field observations by a diverse group of researchers.

Several empirical studies generally similar to ours (i.e., cost-distance analysis based on univariate data with a small number [2–10] of land cover categories) subjected their cost-distance analysis results to some type of sensitivity (uncertainty) analysis (Graham 2001, Schadt et al. 2002, Chardon et al. 2003, Verbeylen et al. 2003, Kautz et al. 2006). Both the test procedures and the results of these analyses were idiosyncratic in nature, but all suggested that data-driven resistance estimates produce relatively stable cost–distance estimates. In a modeling study, Rayfield et al. (2010) used 3 classes, which they labeled as hospitable (similar to our upland), hospitable matrix (similar to our marsh), and non-hospitable matrix (similar to our water), and tested the effect of using different resistance values across landscapes that differed in fragmentation and proportion of hospitable area. They found that only changes in relative costs between hospitable matrix and non-hospitable matrix of greater than 1 order of magnitude caused major changes in the results of least-cost path analysis.

We tested the sensitivity of our results to the assignment of resistance values by using extremely low (water 3 times as costly as land) and extremely high (water 8 times as costly as land) resistances. We found strong linear relationships between the minimum costs obtained for each island (Fig. 4). Although there were unavoidable uncertainties in our process for assigning energetically based resistance values, each of the values we chose was appropriate based on published, biologically grounded estimates for mammalian costs of locomotion (see Supplementary Materials). Therefore we assert that our results, although not exact, are not disproportionately dictated by the specific resistance values we used.

Much of the pattern of connectivity between sources and destinations would have been apparent based on distance measures alone, as shown by the linear relationship between Euclidean distance (all resistances = 1) and our cost-distance analysis results for islands with mainland-to-island distances of less than 9 km (Fig. 3). However, for 9 islands with mainland-to-island distances of 9 km or greater, our cost-distance analysis provided differentiation that was not predicted based on distance alone. This result is not surprising given that cost-distance analysis incorporates both spatial (Euclidean distance) and landscape (resistance surface) components. When the landscape between source and destination is relatively uniform, minimum costs will simply mirror Euclidean distance. However, in circumstances where intervening landscapes are heterogeneous and complex, cost-distance analysis will differ from Euclidean distance. In using cost-distance analysis to plan predator management campaigns, it is unimportant whether distance or resistance components are dominating, except to the degree that there may be a larger amount of uncertainty associated with the estimation of resistance values than of distances. As we showed, cost-distance analysis can be used to estimate Euclidean distance by the simple expedient of setting all resistance values to 1. Regardless of whether distance alone or cost-distance analysis is used, information about the landscape relationships of sources and destinations can help inform decisions about where to focus management efforts in the absence of detailed population data. We concur with Etherington and Holland (2013) that minimum cost rather than the length of the least-cost path, is more appropriate in a predator management context.

Performance of Cost-Distance Analysis

Although there is an extensive and growing literature that reports methods for modeling movement of animals (Koen et al. 2012, Zeller et al. 2012), relatively few studies have used empirical data to assess systematically the predictions of these models (reviewed by Rayfield et al. 2010, Spear et al. 2010, Sawyer et al. 2011). In the absence of directly tracking the lifetime movements of individuals on the islands, we were left with 2 proxy tests of the performance of cost-distance analysis. In the first test, we compared the minimum costs for moving between pairs of surfaces with the observed frequency of movements by marked animals and the overwater distances between these surfaces. Dueser et al. (2013) observed overwater movement by only 1% of 303 raccoons that were released at the point of capture. In contrast, 69% of 32 translocated individuals were observed to move across open water, suggesting that overwater transit is more a function of motivation than simple mobility. Nonetheless, all overwater movements of marked animals involved crossing relatively narrow (≤ 0.5 km), slow-flowing tidal channels; none involved crossing a swift-running tidal inlet, and none were mainland-to-island. Combined with the frequent observation of marked raccoons moving >1 km per day on upland areas (Dueser et al. 2013), these observations validated our assignment of a low resistance value to upland and a high resistance value to open water. Also, as predicted by cost-distance analysis, all observed movements by marked animals overcame only a relatively small total resistance (minimum costs ≤ 2.02).

Our second test of using cost-distance analysis to predict movement used rates of immigration by unmarked animals to 5 non-source islands where removal trapping was conducted 2002–2010 (Table 4). The 2 islands that had the lowest estimated cost (Assawoman and Metompkin) experienced persistent immigration. In contrast, the islands with high estimated costs (Wreck, Ship Shoal, and Myrtle) experienced little or no immigration following removals. This result supported our contention that cost-distance analysis can be used as a predictor of subsequent immigration into locations where animals were removed.

Enhancing Predator Management

When considered together, information on travel costs and sources provide insights into the structure of likely movements by mesopredators in this system. For raccoons, 3 main findings are evident (Fig. 5). First, the mainland serves as the

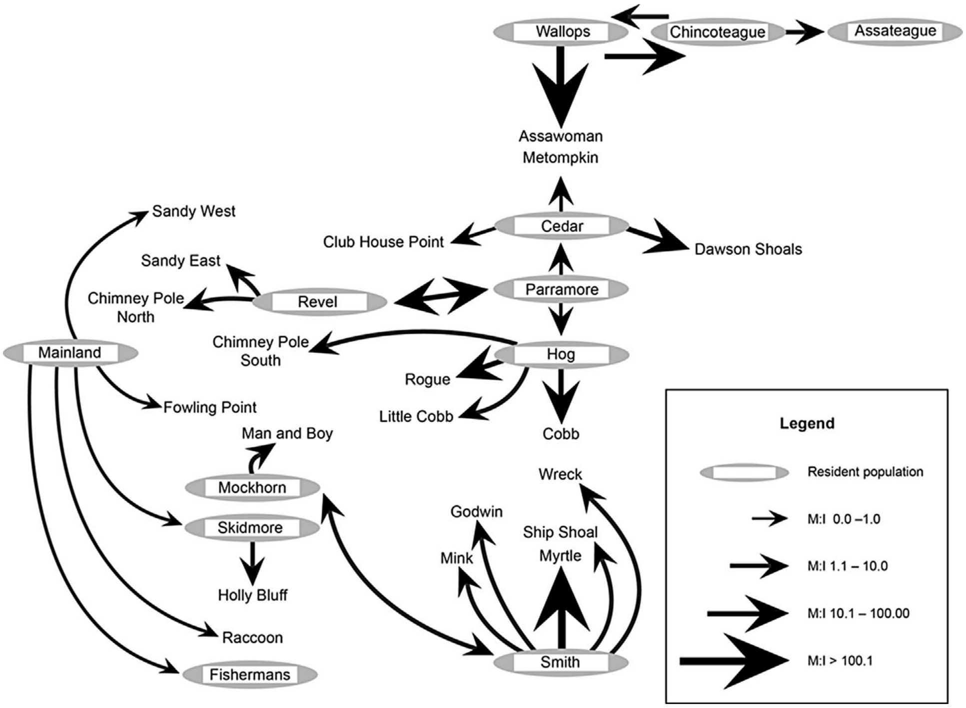

Figure 5. Schematic representation of the minimum-cost network for raccoons on the Virginia barrier islands. Arrows connect each island with its most cost-efficient source. M:I is mainland:island cost ratio. A high mainland:island cost ratio indicates that costs of traveling from a source island are much lower than the cost of traveling from the mainland.

most cost-effective source for only 5 destinations, all located relatively close to the mainland. It is not the most cost-effective source for any of the more-distant islands. Cost effectiveness for island sources is typically 10–100 times higher than for the mainland. Second, there are essentially 3 sectors in the island complex, centered on Chincoteague in the north, Parramore in the middle, and Smith in the south. Each of these sectors includes multiple (2–4) sources, and some of these sources are reciprocal (e.g., Parramore and Revel), but there is no apparent connection between sectors. Finally, several of the non-source islands (e.g., Ship Shoal and Wreck) are relatively distant from their apparent source island (Fig. 1). In contrast to raccoons, the mainland serves as the most cost-effective source of foxes for 17 islands, even including the most distant ones (Fig. 6). Again, cost effectiveness for island sources is typically 10–100 times that for mainland. For foxes, there are only 2 sectors in the island complex, centered on Chincoteague in the north and Parramore in the middle. The northern sector includes 3 source islands, whereas the middle sector includes only 1 (Parramore).

The observed patterns of connectivity suggest 2 approaches to predator management on the islands depending on the overall objectives and the funding available. Periodic, relatively less-expensive monitoring and removals timed to precede the avian nesting season would enhance the availability of nesting locations for birds on the relatively small, low-lying non-source islands Myrtle, Ship Shoal, and Wreck, all of which are relatively remote from the mainland ($22.51 \leq$ minimum cost ≤ 29.70), but relatively accessible from Smith ($0.09 \leq$ minimum cost ≤ 11.80). The same might apply to Assawoman and Metompkin, although both of these islands are relatively accessible from both the mainland and another island ($0.03 \leq$ minimum cost ≤ 3.09). This is essentially the approach that was taken by managers during 2001–2010, and as predicted by the cost-distance analysis, monitoring and periodic removals have been more effective on Myrtle, Ship Shoal, and Wreck than on Assawoman and Metompkin (Table 4).

Alternatively, wholesale eradication of mesopredators on the relatively large, elevated source islands might ultimately decrease the number of animals available for immigration to non-source islands, thereby enhancing availability of avian nesting habitat on both the source and non-source islands. The complete removal of raccoons and foxes from Parramore, Revel, and Smith would greatly increase the costs of immigration to at least 10 non-source islands. This approach has been tried with mixed results, perhaps because of insufficient funding for removals (B. R. Truitt, personal communication). Following the removal of 23 foxes from Parramore during 2002–2010, surveys and trapping in 2011–2014 indicated that foxes have been eliminated from this island (R. D. Dueser and N. D. Moncrief, unpublished data; B. R. Truitt, personal communication). On the other hand, even though 1033 raccoons were removed from Parramore, Revel, and Smith (2002–2010), these 3 islands still support robust resident populations of raccoons (B. R. Truitt, unpublished data; D.J. Allaben, personal communication), and these islands still have the potential to serve as sources of raccoons.

The approach adopted for identifying locations for predator management will depend on the overall set of

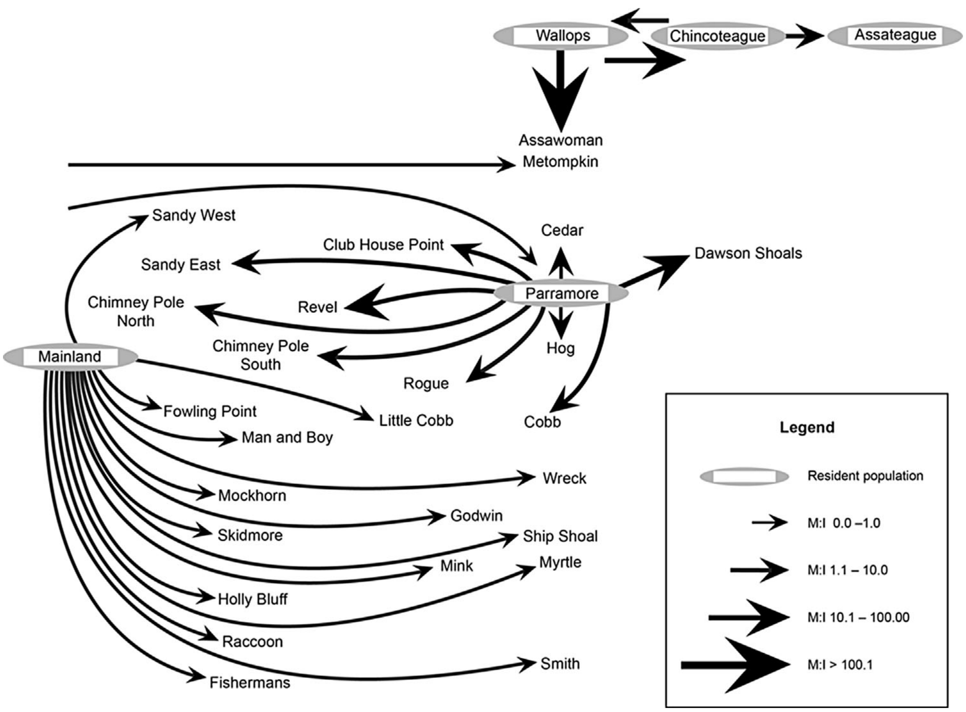

Figure 6. Schematic representation of the minimum-cost network for red foxes on the Virginia barrier islands. Arrows connect each island with its most cost-efficient source. M:I is mainland:island cost ratio. A high mainland:island cost ratio indicates that costs of traveling from a source island are much lower than the cost of traveling from the mainland.

management objectives, the empirical information available, and the resources available for implementing the management on the ground (Martin et al. 2010). One appealing aspect of cost-distance analysis is that it can provide insights into optimizing effectiveness of predator management while requiring only modest data resources. Land-cover maps are widely available, identification of source locations requires only modest population surveys, and even rough estimates of energetic costs of travel can yield valuable insights into probable sources of predators. When additional data are available, they can be combined with results of cost-distance and least-cost path analyses to provide additional insights and quantitative, as well as qualitative results. For example, if there are sufficient data on observed movements, the cost-distance models can be used to estimate the costs of those observed movements, forming the basis for calculating the probability that particular movements will occur. Such probabilities could then be coupled with information on population density for source regions to provide quantitative estimates of the amount of immigration expected.

MANAGEMENT IMPLICATIONS

There is an urgent need for a robust strategy for allocating the available funds for the restoration of island species (Brooke et al. 2007). Harris et al. (2012) proposed a method for prioritizing islands for invasive rodent eradication, with an emphasis on reinvasion risk and conservation value. They envision cases in which the conservation value is high and the risk of reinvasion is either high or unknown. Such cases might require the implementation of a monitoring system as a safeguard against uncontrolled reinvasion, similar to what we have proposed for the Virginia barrier islands. Cost-distance analysis can be a powerful tool for designing a predation management strategy on a fragmented landscape. In the simplest cases, such analysis might be no more useful than simply studying a map and contemplating the possible pathways that predators might take to cross a landscape. In other instances, however, in which there are multiple possible alternative routes to a high priority conservation area, or in which there are gaps in the areas available or accessible for management, cost-distance analysis may be a valuable tool for identifying efficient management scenarios. On the Virginia barrier islands, we were able to quantify the widely varying costs associated with immigration of raccoons and foxes to islands. The likely minimum-cost source for raccoons on most islands was another island, but the likely minimum-cost source for foxes was the mainland. We used this information to identify 2 options for predator control efforts aimed at promoting successful nesting by beach-nesting and colonial waterbirds on the islands: periodic predator removals from non-source islands that have high costs (and thus low immigration rates) and predator eradication on islands that serve as a persistent source of immigrants to other islands. Given the resources available, the former approach has been more successful so far; the latter approach has proven effective for foxes on Parramore Island. We suggest that cost-distance analysis may be a useful tool for planning predator management in any landscape where there are distinct differences in the costs of traversing different elements of the landscape.

ACKNOWLEDGMENTS

We thank B. R. Truitt, R. K. Rose, and 2 anonymous reviewers for constructive reviews of an early draft of this manuscript. We appreciate the contributions of all our collaborators on the Virginia barrier islands, particularly D. J. Allaben, R. A. Ayers, R. Boettcher, P. P. Denmon, D. P. Field, K. Holcomb, O. Keišs, J. D. Martin, S. M. Rice, B. R. Truitt, and A. L. Wilke. This work was funded (in part) by the Virginia Coastal Zone Management Program at the Department of Environmental Quality through grants NA67OZ0360-01, FY 1996, Task 25; NA77OZ0204-01, FY 1997, Task 1.4; NA87OZ0253-01, FY 1998, Task 1.8; NA97OZ0181-01, FY 1999, Task 1.5; NA17OZ2355-01, FY 2002, Task 12.07; NA03NOS4190104, FY 2003, Task 12.10; NA05NOS4191180, FY 2005, Task 9.06; and NA06NOS4190241, FY 2006, Task 10.06 of the National Oceanic and Atmospheric Administration (NOAA), Office of Ocean and Coastal Resource Management, Under the Coastal Zone Management Act of 1972, as amended. Views expressed herein are those of the authors and do not necessarily reflect views of NOAA or any of its subagencies. This work also was supported by funding from NSF grants DEB-0621014 and DEB-1237733 to the University of Virginia, the Berryman Institute for Wildlife Damage Management, and the National Fish and Wildlife Foundation in cooperation with the Disney Company. This is a contribution from the Virginia Coast Reserve Long-Term Ecological Research Program.

LITERATURE CITED

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

Badger, C. J. 1991. Reserve joins shorebird network. The Islands: The Virginia Coast Reserve. Spring 1991:6.

Badger, C. J. 1997. A generation of coastal conservation. The Islands: The Virginia Coast Reserve. Special Edition.

Barnes, B. M., and B. R. Truitt. 1997. Seashore chronicles: three centuries of the Virginia barrier islands, University Press of Virginia, Charlottesville, USA.

Barton, B. T., and J. D. Roth. 2007. Raccoon removal on sea turtle nesting beaches. Journal of Wildlife Management 71:1234–1237.

Baxter, P. W. J., J. L. Sabo, C. Wilcox, M. A. McCarthy, and H. P. Possingham. 2008. Cost-effective suppression and eradication of invasive predators. Conservation Biology 22:89–98.

Beasley, J. C., Z. H. Olson, G. Dharmarajan, T. S. I. I. Eagan, and O. E. Rhodes, Jr. 2011. Spatio-temporal variation in the demographic attributes of a generalist mesopredator. Landscape Ecology 26:937–950.

Beasley, J. C., Z. H. Olson, W. S. Beatty, G. Dharmarajan, and O. E. Rhodes, Jr. 2013. Effects of culling on mesopredator population dynamics. PLos ONE 8:e58982.

Beier, P., D. R. Majka, and W. D. Spencer. 2008. Forks in the road: choices in procedures for designing wildland linkages. Conservation Biology 22:836–851.

Blackburn, T. M., P. Cassey, R. P. Duncan, K. L. Evans, and K. J. Gaston. 2004. Avian extinction and mammalian introductions on oceanic islands. Science 305:1955–1958.

Blackburn, T. M., O. L. Petchey, P. Cassey, and K. J. Gaston. 2005. Functional diversity of mammalian predators and extinction in island birds. Ecology 86:2916–2923.

Brinker, D. F., J. M. McCann, B. Williams, and B. D. Watts. 2007. Colonial-nesting seabirds in the Chesapeake Bay Region: where have we been and where are we going? Waterbirds 30:93–104.

Brittingham, C. D. 1993. Establishment of home range by juvenile barrier island red fox (Vulpes vulpes) after dispersal. Thesis, University of Maryland Eastern Shore, Princess Anne, USA.

Brooke, M. L., G. M. Hilton, and T. L. F. Martins. 2007. Prioritizing the world's islands for vertebrate-eradication programmes. Animal Conservation 10:380–390.

Burger, J., and M. Gochfeld. 1994. Predation and effects of humans on island-nesting seabirds. Pages 39–67 *in* D. N. Nettleship, J. Burger, and M. Gochfeld editors. Seabirds on islands: threats, case studies and action plans. BirdLife Conservation Series No. 1, BirdLife International, Cambridge, England.

Carey, M. P., B. L. Sanderson, K. A. Barnes, and J. D. Olden. 2012. Native invaders – challenges for science, management, policy and society. Frontiers in Ecology and Environment 10:373–381.

Carroll, C., R. J. Fredrickson, and R. C. Lacy. 2013. Developing metapopulation connectivity criteria from genetic and habitat data to recover the endangered Mexican wolf. Conservation Biology 28: 76–86.

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.

Coté, I. M., and W. J. Sutherland. 1997. The effectiveness of removing predators to protect bird populations. Conservation Biology 11: 395–405.

Courchamp, F., J.-L. Chapuis, and M. Pascal. 2003. Mammal invaders on islands: impact, control and control impact. Biological Reviews 78: 347–383.

Croll, D. A., J. L. Maron, J. A. Estes, E. M. Danner, and G. V. Byrd. 2005. Introduced predators transform subarctic islands from grassland to tundra. Science 307:1959–1961.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Dueser, R. D., W. C. Brown, G. S. Hogue, C. McCaffrey, S. A. McCuskey, and G. J. Hennessey. 1979. Mammals on the Virginia barrier islands. Journal of Mammalogy 60:425–429.

Dueser, R. D., N. D. Moncrief, O. Keišs, J. D. Martin, J. H. Porter, and B. R. Truitt. 2013. Overwater movement of raccoons (*Procyon lotor*) in a naturally fragmented coastal landscape. Northeastern Naturalist 20:511–528.

Erwin, R. M., and R. A. Beck. 2007. Restoration of waterbird habitats in Chesapeake Bay: great expectations or *Sisyphus* revisited? Waterbirds 30:163–176.

Erwin, R. M., J. Miller, and J. G. Reese. 2007. Poplar Island environmental restoration project: challenges in waterbird restoration on an island in Chesapeake Bay. Ecological Restoration 25:256–262.

Erwin, R. M., B. R. Truitt, and J. E. Jiménez. 2001. Ground-nesting waterbirds and mammalian carnivores in the Virginia barrier island region: running out of options. Journal of Coastal Research 17:292–296.

Etherington, T. R., and E. P. Holland. 2013. Least-cost path length versus accumulated-cost as connectivity measures. Landscape Ecology 28: 1223–1229.

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.

Goodrich, J. M., and S. W. Buskirk. 1995. Control of abundant native vertebrates for conservation of endangered species. Conservation Biology 9:1357–1364.

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.

Graham, M. A. 1976*a*. The Virginia barrier islands: a brief history. The Nature Conservancy News 26:18–22.

Graham, M. A. 1976*b*. Land use history: a study of man's influence on Virginia's barrier islands. Pages 1–86 *in* R. D. Dueser, M. A. Graham, G. J. Hennessy, C. McCaffrey, A. W. Niederoda, T. W. Rice, and B. Williams, editors. Virginia coast reserve study, ecosystem description. The Nature Conservancy, Arlington, Virginia, USA.

Guarnizo, C. E., and D. C. Cannatella. 2014. Geographic determinants of gene flow in two sister species of tropical Andean frogs. Journal of Heredity 105:216–225.

Hanlon, C. A., D. E. Hays, A. N. Hamir, D. E. Snyder, S. Jenkins, C. P. Hable, and C. E. Rupprecht. 1989. Proposed field evaluation of a rabies recombinant vaccine for raccoons (*Procyon lotor*): site selection, target species characteristics, and placebo baiting trials. Journal of Wildlife Diseases 25:555–567.

Harding, E. K., D. F. Doak, and J. D. Albertson. 2001. Evaluating the effectiveness of predator control: the non-native red fox as a case study. Conservation Biology 15:1114–1122.

Harris, D. B., S. D. Gregory, L. S. Bull, and F. Courchamp. 2012. Island prioritization for invasive rodent eradications with an emphasis on reinvasion risk. Biological Invasions 14:1251–1263.

Hartman, L. H., and D. S. Eastman. 1999. Distribution of introduced raccoons *Procyon lotor* on the Queen Charlotte Islands: implications for burrow-nesting seabirds. Biological Conservation 88:1–13.

Hayden, B. P., R. D. Dueser, J. T. Callahan, and H. H. Shugart. 1991. Long-term research at the Virginia coast reserve: modeling a highly dynamic environment. BioScience 41:310–318.

Hebblewhite, M., F. Zimmermann, Z. Li, D. G. Miquelle, M. Zhang, H. Sun, Z. Wu, F. Mörschel, L. Sheng, A. Purekhovsky, Z. Chunquan, and N. Pettorelli. 2012. Is there a future for Amur tigers in a restored tiger conservation landscape in Northeast China? Animal Conservation 15:579–592.

Hecht, A., and P. R. Nickerson. 1999. The need for predator management in conservation of some vulnerable species. Endangered Species Update 16:114–118.

Howard, T. G., and M. D. Schlesinger. 2013. Wildlife habitat connectivity in the changing climate of New York 's Hudson Valley. Annals of the New York Academy of Sciences 1298:103–119.

Jiménez, J. E., and M. R. Conover. 2001. Ecological approaches to reduce predation on ground-nesting gamebirds and their nests. Wildlife Society Bulletin 29:62–69.

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

Keišs, O. 2001. Mammalian predator distribution and abundance on the Virginia barrier islands in relation to breeding habits of colonial birds. Thesis, Utah State University, Logan, USA.

Koen, E. L., J. Bowman, and A. A. Walpole. 2012. The effect of cost surface parameterization on landscape resistance estimates. Molecular Ecology Resources 12:686–696.

Kramer-Schadt, S., E. Revilla, T. Wiegand, and U. Breitenmoser. 2004. Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of European lynx. Journal of Applied Ecology 41:711–723.

Krim, P. M., T. L. Bashore, and G. L. Kirkland, Jr. 1990. Den site characteristics and food habits of the red fox (*Vulpes vulpes*) on Assateague Island, Maryland. Virginia Journal of Science 41:340–351.

Lada, H., J. R. Thomson, R. Mac Nally, and A. C. Taylor. 2008. Impacts of a massive landscape change on a carnivorous marsupial in southeastern Australia: inferences from a landscape genetics analysis. Journal of Applied Ecology 45:1732–1741.

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 Modeling 212:372–381.

Lavers, J. L., C. Wilcox, and C. J. Donlan. 2010. Bird demographic responses to predator removal programs. Biological Invasions 12:3839–3859.

Leoniak, G., S. Barnum, J. L. Atwood, K. Rinehart, and M. Elbroch. 2012. Testing GIS generated least-cost path predictions for *Martes pennanti* (Fisher) and its application for identifying mammalian road-crossings in northern New Hampshire. Northeastern Naturalist 19:147–156.

Martin, J., A. F. O'Connell, W. L. Kendall, M. C. Runge, T. R. Simons, A. H. Waldstein, S. A. Schulte, S. J. Converse, G. W. Smith, T. Pinion, M. Rikard, and E. F. Zipkin. 2010. Optimal control of native predators. Biological Conservation 143:1751–1758.

Martin, J. D. 2007. A test of conditioned food aversion to control raccoon predation on the eggs of ground-nesting shorebird species on the barrier islands of Virginia. Thesis, Utah State University, Logan, USA.

McCaffrey, C. A., and R. D. Dueser. 1990. Plant associations of the Virginia barrier islands. Virginia Journal of Science 41:282–299.

Mosnier, A., D. Boisjoly, R. Courtois, and J.-P. Ouellet. 2008. Extensive predator space use can limit the efficacy of a control program. Journal of Wildlife Management 72:483–491.

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

Oertel, G. F., M. S. Kearney, S. P. Leatherman, and H. J. Woo. 1989. Anatomy of a barrier platform: outer barrier lagoon, Southern Delmarva Peninsula, Virginia. Marine Geology 88:303–318.

Paradiso, J., and C. O. Handley, Jr. 1965. Checklist of mammals of Assateague Island. Chesapeake Science 6:167–177.

Peery, M. Z., and R. W. Henry. 2010. Recovering marbled murrelets via corvid management: a population viability analysis. Biological Conservation 143:2414–2424.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. BioScience 59:779–791.

Rayfield, B., M.-J. Fortin, and A. Fall. 2010. The sensitivity of least-cost habitat graphs to relative cost surface values. Landscape Ecology 25:519–532.

Reding, D. M., S. A. Cushman, T. E. Gosselink, and W. R. Clark. 2013. Linking movement behavior and fine-scale genetic structure to model landscape connectivity for bobcats (*Lynx rufus*). Landscape Ecology 28:471–486.

Reynolds, J. C., and S. C. Tapper. 1996. Control of mammalian predators in game management and conservation. Mammal Review 26:127–155.

Robinson, O. J., N. H. Fefferman, and J. L. Lockwood. 2013. How to effectively manage invasive predators to protect their native prey. Biological Conservation 165:146–153.

Rosatte, R., K. Sobey, D. Donovan, M. Allan, L. Bruce, T. Buchanan, and C. Davies. 2007. Raccoon density and movements after population reduction to control rabies. Journal of Wildlife Management 71:2373–2378.

Savidge, J. A. 1987. Extinction of an island forest avifauna by an introduced snake. Ecology 68:660–668.

Sawyer, S. C., C. W. Epps, and J. S. Brashares. 2011. Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? Journal of Applied Ecology 48:668–678.

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

Sinclair, A. R. E., R. P. Pech, C. R. Dickman, D. Hik, P. Mahon, and A. E. Newsome. 1998. Predicting effects of predation on conservation of endangered prey. Conservation Biology 12:564–575.

Spear, S. F., N. Balkenhol, M.-J. Fortin, B. H. McRae, and K. Scribner. 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Molecular Ecology 19:3576–3591.

Squires, J. R., N. J. DeCesare, L. E. Olson, J. A. Kolbe, M. Hebblewhite, and S. A. Parks. 2013. Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. Biological Conservation 157:187–195.

Thatcher, C. A., F. T. Van Manen, and J. D. Clark. 2006. Identifying suitable sites for Florida panther reintroduction. Journal of Wildlife Management 70:752–763.

Verbeylen, G., L. De Bruyn, 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.

Wasserman, T. N., S. A. Cushman, J. S. Littell, A. J. Shirk, and E. L. Landguth. 2013. Population connectivity and genetic diversity of American marten (*Martes americana*) in the United States northern Rocky Mountains in a climate change context. Conservation Genetics 14:529–541.

Wiles, G. J., J. Bart, R. E. Beck, Jr. , and C. F. Aguon. 2003. Impacts of the brown tree snake: patterns of decline and species persistence in Guam's avifauna. Conservation Biology 17:1350–1360.

Williams, B., R. A. Beck, B. Akers, and J. W. Via. 1990. Longitudinal surveys of the beach-nesting and colonial waterbirds of the Virginia barrier islands. Virginia Journal of Science 41:381–388.

Williams, B., D. F. Brinker, and B. D. Watts. 2007. The status of colonial nesting wading bird populations within the Chesapeake Bay and Atlantic barrier island-lagoon system. Waterbirds 30:82–92.

Wilson, M. D., B. D. Watts, and J. E. LeClerc. 2007. Assessing habitat stability for disturbance-prone species by evaluating landscape dynamics along the Virginia barrier islands. Center for Conservation Biology Technical Report Series CCBTR-07±06, College of William and Mary, Williamsburg, Virginia.

Zalewski, A., S. B. Piertney, 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.

Zeller, K. A., K. McGarigal, and A. R. Whiteley. 2012. Estimating landscape resistance to movement: a review. Landscape Ecology 27:777–797.

Zielinski, W. J., F. V. Schlexer, S. A. Parks, K. L. Pilgrim, and M. K. Schwartz. 2013. Small geographic range but not panmictic: how forests structure the endangered Point Arena mountain beaver (*Aplodontia rufa nigra*). Conservation Genetics 14:369–383.

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.

Associate Editor: Amy Kuenzi.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Supplementary Materials

6 September 2014

Porter, J.H., R. D. Dueser, and N. D. Moncrief.

Cost-Distance Analysis of Mesopredators as a Tool for Avian Habitat Restoration on a Naturally Fragmented Landscape.

Journal of Wildlife Management.

APPENDIX S1.

Details on estimation of resistance values

The biggest challenge for calculating resistance surfaces is assignment of resistance values (Spear et al. 2010). The preferred method for parameterizing resistance surfaces is field data, such as that obtained with mark-recapture, radio telemetry, and track surveys (Spear et al. 2010). If there is extensive information on observed movements, resistances can be estimated directly (Richard and Armstrong 2010, Desrochers et al. 2011). However, for many organisms, it is quite difficult to obtain field data that are adequate for estimating resistance surfaces (Spear et al. 2010). Spear et al. (2010) report only 8 publications that used some type of non-genetic field data to independently inform resistance assignment. We are aware of only two additional studies (Pullinger and Johnson 2010; Leoniak et al. 2012) that do so, despite the extensive and growing literature that reports methods for modeling movement of animals (Zeller et al. 2012).

In our study system of raccoons (*Procyon lotor*) and red foxes (*Vulpes vulpes*, hereafter foxes) on the Virginia barrier islands, we were unable to obtain statistically robust field data in order to directly estimate resistances. We documented overwater movement by only 25 marked and resighted raccoons (out of 335), despite extensive expenditures of time and money during 8 years of targeted fieldwork (1999-2007) on 9 islands and 9 sites on the adjacent mainland (Dueser et al. 2013). All of the movements were relatively short distances between capture locations (0.2 to 3.5 km) separated by relatively narrow, slow-flowing channels, and none of the 335 marked raccoons were observed to cross a tidal inlet (Dueser et al. 2013). Thus, we do not have sufficient empirical data for this system to estimate resistances. Nevertheless, raccoons and foxes are present (at least transiently) on islands (e.g., Cobb, Wreck) that are surrounded by considerable amounts of open water (R. D. Dueser and N. D. Moncrief, unpublished data; B. R. Truitt, personal communication), indicating that these animals are capable of overwater movements over longer distances than we were able to document using our methods of direct observation.

In the absence of empirical data from field studies for estimation of resistance, we used data for the metabolic energy cost expended by an individual while traversing different habitat types, as recommended by Sawyer et al. (2011). We suggest that this is the most straightforward cost metric in systems such as ours, where terrestrial organisms are moving through open water between source and destination upland/island surfaces. The matrix (water) is a discrete barrier that surrounds the suitable habitat (island). Water is used only temporarily while moving between habitable landscape features because it is unsuitable habitat for long periods for terrestrial animals. Most importantly, animals spend different amounts of energy to move through water versus on land.

Unfortunately there is no detailed information available on the energetic cost of habitat-specific locomotion for raccoons and foxes. Therefore, we used measures of energy expenditure based on the costs of locomotion for other cursorial quadrupedal mammals, using data for all species for which energetic costs have been measured for both terrestrial and aquatic locomotion (Table S1). Fish and Baudinette (1999) and Williams et al. (2002) have shown that the relative cost of running and swimming for a species correlates with that animal's degree of locomotor specialization. Terrestrial mammals are relatively poor swimmers because they lack complete streamlining of the body, they use inefficient drag-based paddle propulsion, and they swim at the surface, which creates increased energy loss as a result of wave drag (Fish et al., 2001). For most species, movements are relatively more difficult in water because water is 800 times denser and 60 times more viscous than air (Williams et al. 2002).

These differences are reflected in the relative cost of locomotion for the terrestrial and semi-aquatic species in Table S1. When considering the pair of rodent species (Norway rat and Australian water rat), the cost of transport for swimming versus terrestrial locomotion is higher for Norway rats (Taylor et al. 1970, Benthem et al. 1994) which are considered to be terrestrial, in comparison to the semi-aquatic Australian water rat (Fish and Baudinette 1999). The American mink is the only species of carnivore for which data are available for cost of transport both on land and in water. Therefore, we used the mink values (swimming costs about 3 times more energy than running; Williams 1983a,b) to estimate values for raccoons and foxes, which are also carnivores. However, mink are considered to be semi-aquatic, and their cost of swimming versus running is likely to be lower than the swimming-versus-running costs of foxes and raccoons.

Extrapolating from the mink values, we estimated that the cost of transport for swimming by foxes and raccoons is at least 4 times the cost of walking by these species. We arbitrarily assigned an energy cost (resistance) of 1 for walking across one kilometer of upland (i.e., 0.001 cost unit = 1 meter of upland travel), and we assigned a resistance of 4 times that of land for swimming across one kilometer of water. We found no studies of the relative metabolic energy cost for terrestrial mammals to traverse salt marshes, which have a dual character depending on the tidal stage, being land during low tide and water during high tide. We therefore assigned an intermediate relative energetic cost of 2 resistance units to cross one kilometer of marsh.

In order to facilitate comparisons, and because of their similarities in locomotor adaptations, we used the same resistances for raccoons and foxes. Although they both occur on coastal islands (Hartman and Eastman 1999; Abbott 2000), there is a paucity of information about locomotion costs and overwater movement for these species. Extensive reviews of the behavior, ecology, and management of raccoons (Gehrt 2003) and foxes (Cypher 2003) include general statements about movement of individuals but lack references to specific information on locomotor behavior and metabolism, either on land or in water. In the absence of such information, we chose to use the most parsimonious approach: we assigned the same resistances for both species. Our reasoning was as follows: both species are terrestrial quadrupeds with relatively long legs, long bushy tails, and seasonally heavy fur. Neither has webbed feet or other adaptations associated with an aquatic or semi-aquatic lifestyle. Both raccoons and foxes swim by paddle propulsion using combinations of forefeet, hindfeet or all 4 feet in movements that are modifications of a terrestrial gait (Fish 1994). This swimming mode is associated with slow surface swimming and precise maneuverability (Fish 1994), and it is of low performance efficiency compared to the swimming behavior of fully aquatic mammals (Williams 1999, Fish 1996, Santori et al. 2008). As a result, large differences in cost of transport have been reported in comparisons between terrestrial and aquatic mammals (Fish 1996, Fish 2000), but there are no data for direct comparisons between raccoons and foxes. In sum, any species differences in locomotion costs that we might propose for this analysis would be highly speculative.

Literature Cited for Supplementary Materials

Abbott, I. 2000. Improving the conservation of threatened and rare mammal species through translocation to islands: case study Western Australia. Biological Conservation 93:195–201.

Benthem, L., J. W. Bolhuis, J. van der Leest, A. B. Steffens, J. P. Zock, and W. G. Zijlstra. 1994. Methods for measurement of energy expenditure and substrate concentrations in swimming rats. Physiology & Behavior 56:151–159.

Cypher, B.L. 2003. *Vulpes* species, *Urocyon* species, and *Alopex lagopus*. Pages 511–546 *in* G. A. Feldhamer, B. C. Thompson, and J.A. Chapman, editors. Wild mammals of North America: biology management and conservation, second edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

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

DiPrampero, P.E. 1986. The energy cost of human locomotion on land and in water. International Journal of Sports Medicine 7:55–72.

Dueser, R. D., N D. Moncrief, O. Keišs, J. D. Martin, J. H. Porter, and B. R. Truitt. 2013. Overwater movement of raccoons (*Procyon lotor*) in a naturally fragmented coastal landscape. Northeastern Naturalist 20:511–528.

Fish, F. E. 1994. Influence of hydrodynamic design and propulsive mode on mammalian swimming energetics. Australian Journal of Zoology 42:79–101.

Fish, F.E. 1996. Transitions from drag-based to lift-based propulsion in mammalian swimming. American Zoology 36:628–641.

Fish, F.E. 2000. Biomechanics and energetics in aquatic and semiaquatic mammals: platypus to whale. Physiological and Biochemical Zoology 73:683–698.

Fish, F. E., and R. V. Baudinette. 1999. Energetics of locomotion by the Australian water rat (*Hydromys chrysogaster*): a comparison of swimming and running in a semi-aquatic mammal. Journal of Experimental Biology 202:353–363.

Fish, F.E., P. B. Frappell, R. V. Baudinette, and P. M. Macfarlane. 2001. Energetics of terrestrial locomotion of the platypus *Ornithorhynchus anatinus*. The Journal of Experimental Biology 204:797–803.

Gehrt, S.D. 2003. Raccoon, *Procyon lotor*, and allies. Pages 611–634 *in* G. A. Feldhamer, B. C. Thompson, and J.A. Chapman, editors. Wild mammals of North America: biology management and conservation, second edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Hartman, L. H. and D. S. Eastman. 1999. Distribution of introduced raccoons *Procyon lotor* on the Queen Charlotte Islands: implications for burrow-nesting seabirds. Biological Conservation 88:1–13.

Holmér, I., and P.-O. Astrand. 1972. Swimming training and maximal oxygen uptake. Journal of Applied Physiology 33:510–513.

Leoniak, G., S. Barnum, J. L. Atwood, K. Rinehart, and M. Elbroch. 2012. Testing GIS generated least-cost path predictions for *Martes pennanti* (Fisher) and its application for identifying mammalian road-crossings in northern New Hampshire. Northeastern Naturalist 19:147–156.

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.

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.

Santori, R.T., M. V. Vieira, O. Rocha-Barbosa, J. A. Magnan-Neto, and N. Gobbi. 2008. Water absorption of the fur and swimming behavior of semiaquatic and terrestrial Oryzomine rodents. Journal of Mammalogy 89:1152–1161.

Sawyer, S. C., Epps, C. W., and Brashares, J. S. 2011. Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? Journal of Applied Ecology 48:668-678.

Spear, S.F., N. Balkenhol, M.-J. Fortin, B.H. McRae and K. Scribner. 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Molecular Ecology 19:3576-3591.

Taylor, C.R., K. Schmidt-Nielsen, and J.L. Raab. 1970. Scaling of the energetic cost of running to body size in mammals. American Journal of Physiology 219:1104–1107.

Williams, T. M. 1983a. Locomotion in the North American mink, a semi-aquatic mammal. I. Swimming energetics and body drag. Journal of Experimental Biology 103:155–168.

Williams, T. M. 1983b. Locomotion in the North American mink, a semi-aquatic mammal. II. The effect of an elongate body on running energetics and gait patterns. Journal of Experimental Biology 105:283–295.

Williams, T.M. 1999. The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. Philosophical Transactions of the Royal Society of London 354:193–201.

Williams, T. M., M. Ben-David, S. Noren, M. Rutishauser, K. McDonald, and W. Heyward. 2002. Running energetics of the North American river otter: do short legs necessarily reduce efficiency on land? Comparative Biochemistry and Physiology, Part A 133:203–212.

Zeller, K. A., K. McGarigal, and A. R. Whiteley. 2012. Estimating landscape resistance to movement: a review. Landscape Ecology 27:777–797.

Table S1. Values for cost of transport for terrestrial locomotion versus swimming for 5 species of mammals.

Taxon	Locomotor Specialization	Mammalian Order	Relative Cost of Transport	References
Platypus *Ornithorhyncus anatinus*	Semi-aquatic	Monotremata	terrestrial locomotion is 2.1 times swimming	Fish et al. 2001
Human *Homo sapiens*	Terrestrial	Primates	swimming is 3.9 times terrestrial locomotion	Holmer and Astrand 1972, DiPrampero 1986
Norway rat *Rattus norvegicus*	Terrestrial	Rodentia	swimming is 1.8 times terrestrial locomotion	Taylor et al. 1970, Benthem et al. 1994
Australian water rat *Hydromys chrysogaster*	Semi-aquatic	Rodentia	swimming is 1.25 times terrestrial locomotion	Fish and Baudinette 1999
American mink *Mustela vison*	Semi-aquatic	Carnivora	swimming is 2.7 times terrestrial locomotion	Williams 1983a, 1983b