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Research Paper

Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements

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HIGHLIGHTS

- We studied movements of kinkajous, a neotropical, arboreal mammal species.
- Kinkajous are tightly linked to forest in the home range.
- During dispersal and mating movements, they readily crossed unsuitable habitat.
- Tolerance for unsuitable habitat during dispersal seems common.
- This may make planning corridors for mobile species more flexible.

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ABSTRACT

Resistance values based on habitat suitability are frequently the basis for modeling landscape connectivity and designing wildlife corridors to facilitate dispersal movements. However, animals may use the landscape differently during dispersal movements than in the home range. We hypothesized that (1) habitat features that are avoided within an animal's home range offer little resistance to animals during natal or breeding dispersal and more specifically that (2) resistance to dispersal is a negative exponential function of habitat suitability within the home range. To test these hypotheses, we used field movement data of kinkajous (*Potos flavus*), a neotropical, arboreal mammal, to parameterize alternative resistance surfaces based on home range resource use, home range movement data, parent-offspring locations, and breeding pair locations. We used correlation analysis to compare performance of these surfaces. Our results suggest that kinkajous perceive the fragmented landscape as more connected during dispersal than while in the home range. Although kinkajous are tightly linked to forest during movements in the home range, farms and pastures did not pose higher resistance to dispersal movements than forests. Similar tolerance for low-quality habitat has now been observed in dispersal movements of several wildlife species. A negative exponential relationship between habitat suitability and resistance characterizes landscape connectivity perception of mobile species during dispersal movements. If mobile animals can readily traverse habitat of lower quality, large fractions of the landscape may offer low resistance, allowing greater flexibility in where a corridor is located.

1. Introduction

Landscape connectivity reflects the ability of wildlife to move through a landscape (Taylor, Fahrig, Henein, & Merriam, 1993). Maintaining or re-establishing landscape connectivity in the face of increasing anthropogenic habitat loss and fragmentation is critical for protecting biodiversity and viable wildlife populations, and for allowing wildlife species to shift their ranges in response to climate changes (Hilty, Lidicker, & Merenlender, 2012). Wildlife corridors, defined as "a swath of land intended to allow passage by a particular wildlife species between two or more wildland areas" (Beier, Majka, & Spencer, 2008), are an important tool for maintaining connectivity between protected areas (Crooks & Sanjayan, 2006). For more

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sedentary species (corridor dwellers – Beier et al., 2008), corridors must meet all life-history needs, because they require multiple generations to move through a corridor to the next protected area. But for more mobile species, corridors are mostly intended to facilitate natal and breeding dispersal movements.

Natal dispersal is defined as movement of an animal from the area where it is born to another area where it joins, or attempts to join, the local breeding population (Ronce, 2007). Natal dispersal is critical for genetic diversity, demographic viability of metapopulations, recolonization, and range shifts (Trakhtenbrot, Nathan, Perry, & Richardson, 2005). Breeding dispersal movements by established adults to find breeding partners also help to maintain genetic diversity, and reduce risk of breeding with close relatives (Clobert, Wolff, Nichols, Danchin, & Dhondt, 2001).

To identify the path between two locations most conducive to movement, least-cost models are commonly used (Sawyer, Epps, & Brashares, 2011). These models are based on resistance surfaces, which are raster grids that contain information on the degree to which each grid cell facilitates or impedes movement of the study organism (Spear, Balkenhol, Fortin, McRae, & Scribner, 2010). Resistance values for input into corridor design are usually based on knowledge of habitat suitability. They are most frequently estimated by experts familiar with the focal species' habitat use, or inferred from analysis of movements in the home range (Zeller, McGarigal, & Whiteley, 2012).

For corridor design, it is important that the input-resistance layer of the least-cost path analysis reflects how much each landscape feature affects natal and breeding dispersal movement. It is also important that corridor design can be accomplished rapidly and inexpensively. Therefore, if resistance surfaces from habitat suitability studies are equivalent to resistance surfaces from natal and breeding dispersal movements, they would be appropriate for corridor design. However, animals may use the landscape differently during home range, natal and breeding dispersal movements (e.g., Elliot, Cushman, Macdonald, & Loveridge, 2014). Several recent studies indicate that during long-distance movements animals might be able to move through areas that would be classified as moderately suitable in the home range (e.g., Gaston et al., 2016; Keeley, Beier, & Gagnon, 2016; Mateo-Sanchez et al., 2015; Trainor, Walters, Morris, Sexton, & Moody, 2013). To account for this, connectivity analyses can be based on different behavioral states (e.g., resource use, movement behavior) which results in different connectivity patterns (Abrahms et al., 2016; Blazquez-Cabrera et al., 2016; Zeller et al., 2014). Based on these results, Abrahms et al. (2016) and Blazquez-Cabrera et al. (2016) recommend that corridors should be designed based on resistance maps that were informed by movement behavior. An alternative approach to account for differences in landscape use between specific movement behavior and resource use behavior in the home range is to derive resistance values from habitat suitability values transformed into resistance with a negative exponential function (Fig. 1, Keeley et al., 2016; Trainor et al., 2013).

In this study, we test the similarity between connectivity maps parameterized by models that do not take natal or breeding dispersal movements into account and those that do. Our model system are kinkajous (*Potos flavus*, Procyonidae) in a landscape in Costa Rica that is fragmented into many small patches of forest and non-forest. We hypothesized that (1) landscape connectivity will be greater for natal and breeding dispersal movements than for home range movements because the animals will be more willing to move through habitat of medium to low suitability; (2) resistance to dispersal is a negative exponential function of habitat suitability within the home range (Trainor et al., 2013); and, (3) connectivity modeled from movement (home range movement steps and dispersal movements) will be more similar than connectivity modeled from animal locations in the home range. Comparison of these connectivity maps gives us a better understanding of how kinkajous perceive the landscape during different life stages.

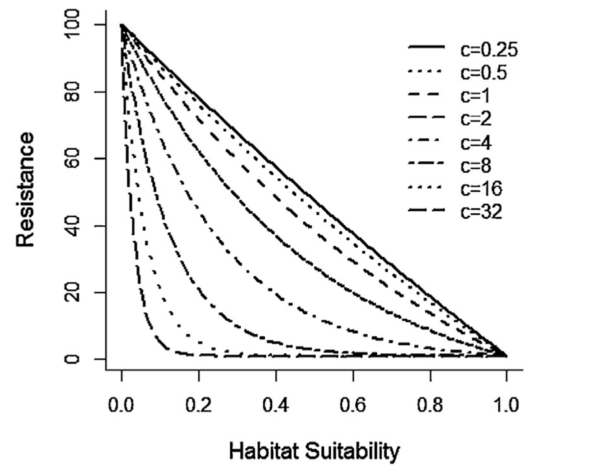

Fig. 1. Eight curves used to transform habitat suitability values into resistance values. The curves are based on the transformation function R = 100–99 * ((1 – exp(-c*H))/(1–exp(-c))), where R is resistance, H is suitability, and the factor c determines the shape of the curves.

2. Methods

2.1. Study system: area and focal species

We conducted our study in the Caribbean lowland region of northeastern Costa Rica. The dominant natural vegetation type is wet tropical lowland forest (Savage, 2002). The area receives about 4 m of rain annually and has a mean annual temperature of 25 °C (Sanford, Paaby, Luvall, & Phillips, 1994). Once comprised of almost continuous rainforest, the landscape is now characterized by a mosaic of rainforest remnants of varying sizes, reforested areas, pasture, agriculture, and urban areas (Fagan et al., 2013). Our study focused on the kinkajou, a species of the order Carnivora (Procyonidae). They are medium sized (2.0–3.5 kg), nocturnal, arboreal, mostly frugivorous mammals, and common in Neotropical forests (Ford & Hoffmann, 1988).

2.2. Landscape variables

Habitat selection has not been quantitatively studied in kinkajous. To characterize kinkajou habitat in our landscape, we created a set of raster variables. All layers were in the WGS84 coordinate system, projected with the Universal Transverse Mercator (UTM) system, and had a grid cell size of 30 by 30 m. We reclassified a land cover map created by Fagan et al. (2013) into four classes: native forest (mature lowland forest, mature swamp forest), reforestation (with both native and exotic species), cropland, and pasture. Roads and human settlements were a minor component in the study area and therefore not included. Because kinkajous might prefer or avoid edge habitat, we generated two edge-related variables, namely distance to the nearest forest edge for each cell within forest, and distance to the nearest forest edge for all non-forested cells.

2.3. Movement data

We radio-collared kinkajous captured with Tomahawk traps (32 × 32 × 102 cm) baited with banana and tied to branches in the tree canopy. We restrained captured kinkajous in holding cones (Koprowski, 2002) that obviated sedatives while we attached store-on-board GPS collars (Quantum 4000E Mini Collar, Telemetry Solutions, California). Collars weighed 55 g, which is 2.8% of the