

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.

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1. Introduction

Landscape connectivity reflects the ability of wildlife to move through a landscape (Taylor, Fahrig, Henein, & Merriam, 1993).

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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

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

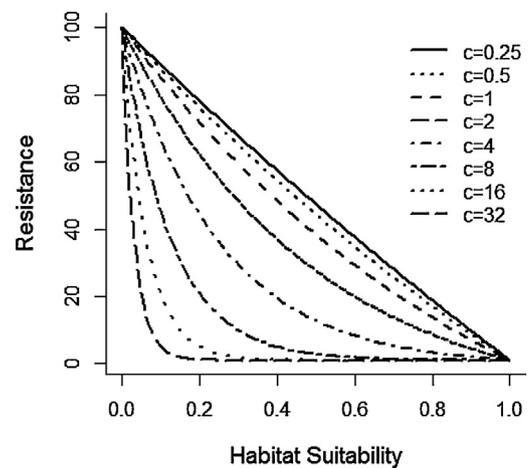


Fig. 1. Eight curves used to transform habitat suitability values into resistance values. The curves are based on the transformation function $R = 100 - 99 * ((1 - \exp(-c * H)) / (1 - \exp(-c)))$, where R is resistance, H is suitability, and the factor c determines the shape of the curves.

connectivity maps gives us a better understanding of how kinkajous perceive the landscape during different life stages.

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

smallest kinkajou we collared (1.95 kg). This is less than the 5–10% of body mass recommended as upper limit for collar weight (Wilson et al., 1996). Collars were programmed to record the animal's location every 20 min between 18:00 and 6:00 h (sunset in Costa Rica is at about 17:30, sunrise at 5:30 every day). GPS error was ± 12 m (*pers. observation*). We monitored the approximate location of the collared animals daily using the VHF transmitter built into each GPS collar. To retrieve the collars, we either recaptured the animal or, if the animal had become trap shy, waited until a weak link, consisting of two 28-gauge steel wire strands coated with a corrosive and encased in a rubber sleeve, broke, causing the collar to fall off prior to the end of the transmitter battery life. We released the animals at the capture site to document movement within the home range. We released two kinkajous about 4 km (the expected median dispersal distance; Bowman, Jaeger, & Fahrig, 2002) from the capture site to observe use of a likely unfamiliar landscape during homing movement.

Between March and August 2012, we fitted 16 kinkajou females with GPS collars and released 14 of them in the home range. We retrieved 11 collars and lost 5. The devised weak link built into the collars worked well and ensured that collars would not remain indefinitely on animals that had become trap-shy. All animal handling followed Northern Arizona University Institutional Animal Care and Use Committee protocol 10-004. From the GPS collar data set, we removed two-dimensional fixes with a PDOP >5 to avoid locations with large errors (Lewis, Rachlow, Garton, & Vierling, 2007).

2.4. Estimating habitat suitability from locations within the home range

We estimated habitat suitability with resource selection functions (RSFs). We reduced the GPS collar data sets to resemble VHF telemetry study data sets by randomly selecting one location between 4:00 and 6:00 h and one location between 21:00 and 23:00 per kinkajou per day. The time windows reflect times of assumed peak activity that were temporally far enough apart to minimize dependence between successive locations. We calculated RSFs by comparing used to available habitat in a paired, or conditional, logistic regression framework to quantify selection for each habitat attribute (Compton, Rhymer, & McCollough, 2002; Zeller et al., 2016). In a paired framework, the resulting resistance estimates reflect a pixel's resistance relative to the surrounding, whereas in an unpaired framework the resistance estimates reflect overall resistance of the different landscape variables (Zeller et al., 2016). Used habitat was characterized by values of habitat variables in grid cells with GPS fixes. Following Zeller et al. (2014), to characterize available habitat, we first fit a generalized Pareto distribution to the straight-line distances between consecutive GPS points using the POT package (Ribatet, 2012). At each location, we then placed a Pareto kernel, and truncated this kernel at the smaller of the 97.5 percentile of the Pareto distribution or the maximum observed movement distance. Finally, we calculated the proportion of each land cover type and the mean distance to edge, where each cell in the Pareto kernel was inversely weighted by the distance to the observed location to account for probability of use (Zeller et al., 2014).

We explored different scales of resource selection by considering different spatial availability scales. To do so we calculated 4 Pareto kernels, corresponding to 20-min, 40-min, 60-min, and 80-min intervals between consecutive fixes. We calculated the difference between used and available for each variable (i.e. proportion of each land cover type and the mean distance to edge), and set the response variable equal to one for each GPS location. We then conducted a two-step conditional logistic regression (Zeller et al., 2014). In the first step, we conducted a univariate scaling analy-

sis for each variable at each scale. In this conditional mixed-effects logistic regression (lmer function in the lme4 package, v. 0.999999-2; Bates, Maechler, Bolker, & Walker, 2014), we included individual kinkajous as a random effect. We retained the scale with the lowest AIC ranking for the second step.

In the second step, we created a multi-scale model by using the best spatial scale for each habitat covariate (identified in step one). Because many of our paired mixed effects models using individual animals as the random effect failed to converge, we used generalized linear models, but retained the paired framework (glm function in R, R Core Team, 2014). To select the best model, we conducted an automated model selection using the glmulti package in R (Calcagno & de Mazancourt, 2010). This package builds all possible unique models involving the candidate variables. We selected the best model based on the AICc value (AIC corrected for small sample size; Burnham & Anderson, 2002). There were no other well-supported models, i.e., the second-best models had delta AIC values ≥ 4 .

2.5. Estimating habitat suitability from movement steps within the home range

To estimate habitat suitability from movement steps in the home range we applied step selection functions (SSFs). We defined a step as the straight-line path between two consecutive GPS fixes. We only included steps with the minimum GPS fix acquisition intervals (20 min). To focus on movement behavior, we excluded steps shorter than 20 m 1065 steps remained in the analysis. To characterize the used habitat, we calculated the proportion of each land cover and the mean of the continuous variables within a 30-m buffer on each side of the segment. To characterize the available habitat, we calculated these same proportions and means within a Pareto kernel centered on the starting point of each step. We generated the Pareto kernel the same way as in the RSF calculations (Zeller et al., 2014, 2016), but only for the 20-min scale to avoid losing movement path information. We used the differences between used and available habitat values as predictor variables. In this specification, the response variable is 1 and there is no model intercept (Agresti, 2002; Zeller et al., 2016).

2.6. Obtaining genetic samples

We took a tissue sample in the form of an ear snip from the kinkajous we captured in live traps. We treated the small wound with antibiotic salve (Neosporin®). We stored the tissue samples in RNAlater™ (Ambion®, Austin, Texas).

To find parent-offspring and mother-father pairs we needed to collect genetic samples from a large part of the population. To collect genetic samples more efficiently than through trapping we devised a hair snare for kinkajous (Fig. 2). It consisted of a hooked stick about 1 m long that supported protruding thinner sticks wrapped in plastic packing tape (Scotch™, St. Paul, Minnesota) with the sticky side out. The snare was securely mounted in the canopy. With their prehensile tails holding on to a tree's branch, the kinkajous climbed down the stick to reach the two bananas (1 ripe, 1 unripe) at the bottom of the snare, leaving some hairs on the sticky tape. They ate the ripe banana and bit into the unripe banana. The bite marks were an indication of whether a kinkajou or a different species had eaten the ripe banana. We also learned to identify kinkajou hairs by their color, thickness, shape, and length. We pulled the hairs off the tape with tweezers and stored them in small paper envelopes. Desiccant in the enclosed, cooled storage area ensured suitable storage conditions. We replaced all tape after the bananas had been eaten. When first deploying the hair snares, we set motion-activated trail cameras (Bushnell®, Overland Park, Kansas) to document which species visited the snares and how they



Fig. 2. Hair snare trap developed for collecting genetic samples from kinkajous (*Potos flavus*).

behavior. Because kinkajous usually removed the bait by eating the entire ripe banana, we analyzed all hairs from one hair snare as one sample.

Using this method, we systematically sampled 34 forest remnants in our study area. We hung hair snares about 100 m apart along transects at the forest edge and along trails in the interior. We checked the snares every second day to prevent DNA from deteriorating in the hot, humid tropical climate. We left the snares up until a kinkajou had left hairs or for one week, whatever was shorter.

2.7. Genetic analysis

We used the QIAamp[®] DNA Investigator Kit (Qiagen Inc., Valencia, California) and manufacturer protocols to extract DNA from hair and tissue. Because several of the microsatellites developed for kinkajous (Kays, Gittleman, & Wayne, 2000) did not amplify or were monomorphic in our study area, we applied high-throughput sequencing. We designed 34 marker pairs for regions about 300 bp long within kinkajou genes posted on GenBank (<http://www.ncbi.nlm.nih.gov/genbank>; Table S-1) and tested them for self-complementarity, self-dimer and cross-dimer formation in FastPCR (Kalendar, Lee, & Schulman, 2011). To verify that the non-invasively collected hair samples were from kinkajous, we included primers to the mitochondrial cytochrome b region, which is commonly used for determining phylogenetic relationships between organisms within families and genera (e.g., Agnarsson, Zambrana-Torrel, Flores-Saldana, & May-Collado, 2011). Using the NCBI Basic Local Alignment Search Tool (BLAST, <http://blast.ncbi.nlm.nih.gov/Blast.cgi>) we confirmed that the hair samples were from kinkajous. We also included primers to the sex-linked amelogenin gene, to determine the gender of the non-invasively collected samples (Pfeiffer & Brenig, 2005). We visualized the sequenced amelogenin reads of each sample in Tablet (Milne et al., 2013).

We amplified the 34 loci in 5 multiplex reactions using the polymerase chain reaction (PCR). PCR reactions contained 0.02 U/ μ L 2G Fast Polymerase (KAPA Biosystems), 200 μ M dNTPs, 1 \times 2G Buffer A, 3.0 mM MgCl₂, 50 nM of each primer, 6% glycerol (v/v), and 1 μ L DNA template. We amplified all samples under the following conditions: 95 °C for 2 min, 35 cycles at 95 °C for 30 s, 55 °C for 30 s, and 72 °C for 2 min. All reactions for each sample were combined into a single well (3 μ L per reaction), cleaned up, and prepared for sequencing on an Illumina MiSeq desktop sequencer (San Diego, California) following a new protocol (Andrew Krohn, unpublished manuscript). We sequenced 310 samples.

2.8. DNA variant detection

To detect single nucleotide polymorphisms (SNPs) and insertions or deletions of bases in the DNA (INDELs) we applied a series of bioinformatic steps to the Illumina output. We removed reads with a mapping quality <30, trimmed off the adapters, and barcode-demultiplexed our samples with ea-utils (Aronesty, 2011). We mapped the reads to the reference sequences with BWA (Li & Durbin, 2009). We used SAMtools (Li et al., 2009) and Picard-tools (<http://picard.sourceforge.net>, last accessed April 1, 2015) to sort, merge, index, and validate the output files.

We applied GATK (McKenna et al., 2010) INDEL realignment and duplicate removal, and performed SNP and INDEL discovery across all samples simultaneously using standard hard filtering parameters according to GATK Best Practices recommendations (Van der Auwera et al., 2013). We only retained samples for which >70% of the SNPs and INDELs were called.

2.9. Parentage analysis

Based on the SNP and INDEL information we reconstructed the pedigree of the sampled kinkajous using the R-package MasterBayes (Hadfield, Richardson, & Burke, 2006). MasterBayes uses a Bayesian approach that incorporates both phenotype and genotype information to determine the most likely pedigree (Hadfield et al., 2006). Other advantages of this program include (1) that it can integrate multiple genotypes of single individuals and use the information to estimate genotyping error, and (2) that there is no need to set the proportion of the population for which genotypes could be obtained. We included the spatial coordinates of the capture locations as phenotype information in the parentage analysis. MasterBayes used this information to take the Euclidean distance between parents and the distance between mother and offspring into account. Because we could not determine the individual's age from the hair snare samples, we relaxed the restriction that potential parents do not appear in the set of potential offspring. Parents are assigned to offspring via Gibbs sampling (Heller, 2009). For each offspring, the Gibbs sampler generates candidate parents, conditional on the pool of available parents, but also takes into account the possibility of unsampled animals. The probability of an animal being an offspring's candidate parent is calculated for every animal in the sample. The actual candidate mother and father are then assigned according to highest probability (Heller, 2009). We ran the model in MasterBayes for 250,000 iterations with a burn-in of 50,000 iterations and a thinning interval of 100. We only accepted parents that were assigned at the 80% confidence level (Edelman, 2014; Waser & Hadfield, 2011).

2.10. Estimating resistance from natal and breeding dispersal movements

Applying a new approach by Graves, Chandler, Royle, Beier, and Kendall (2014), we used the locations of mother and offspring of a mother-father-offspring triad, or locations of a pair of parents

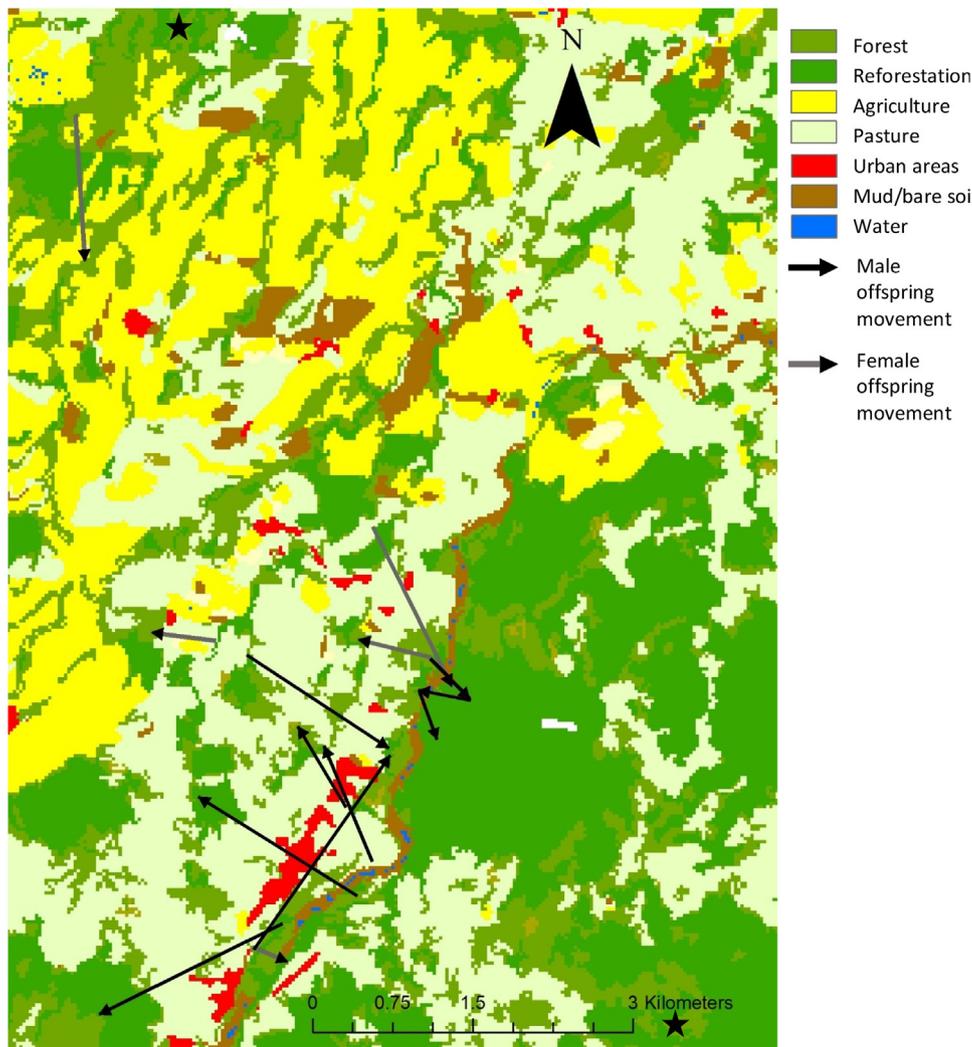


Fig. 3. Locations of mothers and offspring. The arrows indicate the direction of movement from the mother's home range to the location where we detected the offspring. Solid arrow: male offspring; dashed arrow: female offspring. The black stars indicate the two focal nodes used to examine correlations between current flow under various pairs of models (Figs. 5 and 6).

from triads in which the fathers were not in the same patch as the mothers, as the termini (start or end points) of natal or breeding dispersal movements, respectively. We considered an offspring to have dispersed if it was located in a different forest patch than the mother or in the same forest but on the other side of a large river or >2 km away. We estimated resistance of environmental features (e.g. native forest, non-forested land) to movement by calculating the ratio of the probability of moving from the start point to the actual endpoint, to the sum of weighted probabilities of moving from the start point to all other possible endpoints (i.e. all pixels) on the landscape. We based the probability calculations on least-cost distances. When estimating resistance from parent-offspring pairs, the probabilities of moving to all other possible endpoints was weighted by a Gaussian function, reflecting the distribution of observed dispersal distances: few animals dispersed short distances, most animals dispersed intermediate distances, and few animals dispersed long distances. When estimating resistance from mother-father pairs, the probabilities were weighted by a negative exponential function to reflect the distribution of distances between mothers and fathers. We obtained resistance coefficients by minimizing the log-likelihood of this multinomial probability mass function. The significance threshold for resistance values was set at 0.05. We conducted these calculations in R (R Core Team,

2014), following the code provided by Graves et al. (2014) in the Supplementary material.

To allow comparison of resistance values from RSF, SSF, natal and breeding dispersal models, we transformed the habitat suitability z-values obtained from the RSF and SSF models into resistance values using a linear function, and scaled them to 0–1. We also scaled the habitat resistance z-values obtained from the natal and breeding dispersal models to 0–1.

2.11. Resistance and current surfaces

To produce resistance surfaces (Fig. S-1a and b) we used the raw coefficients (suitability values) from the best resource and step selection models (not the transformed z-values). The suitability value of each cell was calculated as

$$S = \beta_1 * v_1 + \beta_2 * v_2 + \dots + \beta_n * v_n \quad (1)$$

where S is the suitability and β_i is the coefficient for the variable v_i .

We rescaled the suitability map to a range of 0–1. Values near one indicate the most suitable habitat conditions and values near zero indicate the least suitable habitat. To transform suitability values into resistance values we used eight curves based on the

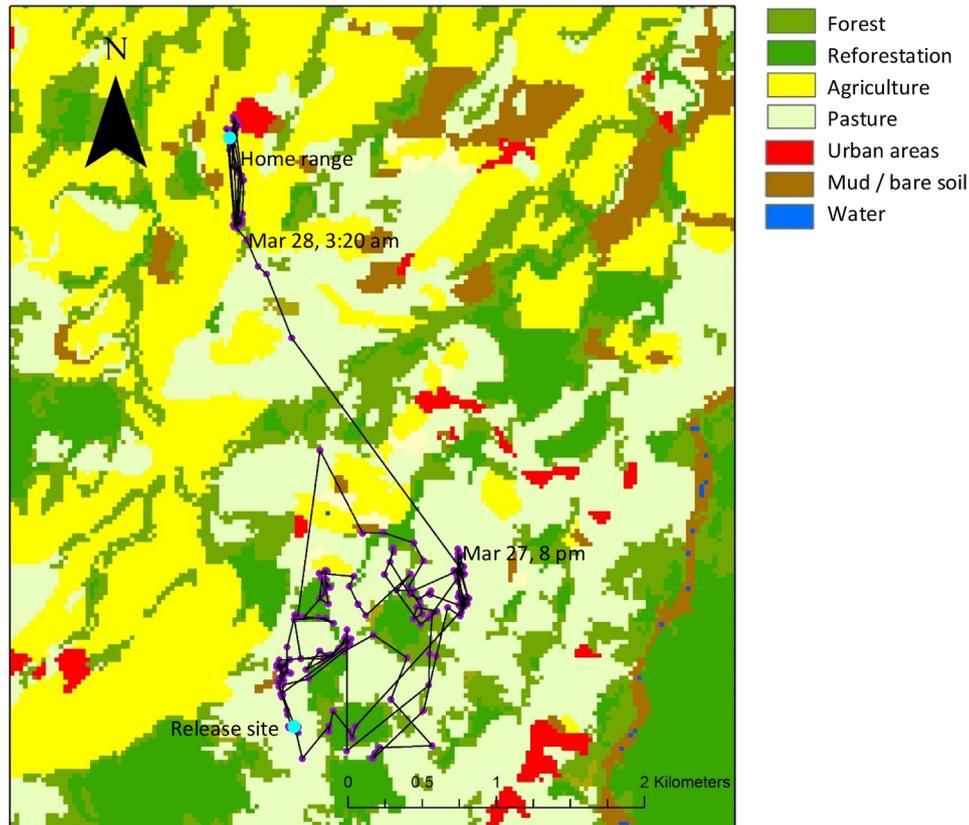


Fig. 4. Movement path of a female kinkajou translocated 4 km from the capture location.

transformation function (2) to define the relationship between suitability and resistance (Trainor et al., 2013).

$$100 - 99 * ((1 - \exp(-c * h)) / (1 - \exp(-c))) \quad (2)$$

where h is the suitability matrix and $c = 0.25, 0.5, 1, 2, 4, 8, 16$ or 32 . For each of the 8 transformations, resistance = 1 when suitability = 1 and resistance = 100 when suitability = 0. At $c = 0.25$ the relationship is nearly linear, but as c increases, resistance values become an increasingly nonlinear negative exponential function of suitability

Table 1

Univariate selection coefficients (β) as a function of scale (minutes between radio-locations) for kinkajous in northeastern Costa Rica. The scale with the lowest AIC ranking was retained for the full model.

Variable	scale	β	SE(β)	z value	Pr > z)	Log Likelihood	AIC	Delta AIC	Akaike weights
native forest	80	2.552	0.25	10.215	0	-239	483	0	1.00
	60	2.662	0.352	7.572	0	-253	510	28	0.00
	40	2.73	0.475	5.754	0	-264	533	50	0.00
	20	2.986	0.852	3.504	0	-281	565	83	0.00
reforestation	80	-0.025	0.759	-0.033	0.974	-310	624	0	0.88
	60	-0.183	0.754	-0.243	0.808	-312	628	4	0.12
	20	-0.507	0.295	-1.72	0.085	-319	642	17	0.00
	40	-0.218	0.245	-0.891	0.373	-320	644	19	0.00
agriculture	80	-5.589	11.659	-0.479	0.632	-183	472	0	1.00
	60	-5.585	9.226	-0.605	0.545	-253	511	38	0.00
	40	-6.712	7.009	-0.958	0.338	-299	601	129	0.00
	20	1.354	1.914	0.707	0.479	-316	635	163	0.00
pasture	80	-3.806	0.314	-12.101	0	-215	434	0	1.00
	60	-3.887	0.364	-10.692	0	-241	486	52	0.00
	40	-3.85	0.4	-9.618	0	-258	520	87	0.00
	20	-3.763	0.498	-7.559	0	-285	573	140	0.00
distance to open	80	0.066	0.012	5.399	0	-190	385	0	1.00
	60	0.076	0.013	5.94	0	-203	410	25	0.00
	40	0.086	0.015	5.717	0	-218	439	54	0.00
	20	0.108	0.021	5.04	0	-246	496	111	0.00
distance to forest	80	-0.062	0.005	-12.627	0	-135	273	0	1.00
	60	-0.093	0.008	-11.982	0	-148	301	28	0.00
	40	-0.125	0.011	-11.162	0	-167	338	65	0.00
	20	-0.175	0.017	-10.026	0	-212	429	156	0.00

(Fig. 1). To test a null model, we also created a flat surface in which the resistance of every cell is 1.

To produce resistance surfaces (Fig. S-1c) from the resistance coefficients estimated from natal and breeding dispersal movements we calculated the resistance value of each cell as

$$R = \beta_1 * v_1 + \beta_2 * v_2 + \dots + \beta_n * v_n \tag{3}$$

where R is the resistance and β_i is the coefficient for the variable v_i .

To explore the agreement between movement probabilities expected under the resistance estimates derived from resource and step selection models and those from natal and breeding dispersal movements, we calculated Pearson correlation coefficients between current maps produced by CircuitScape (McRae & Shah, 2009; Nowakowski, Veiman-Echeverria, Kurz, & Donnelly, 2015). CircuitScape is based on electronic circuit theory and predicts areas of high flow (high movement probability) between a pair of focal nodes (source and ground of an electric current). The current maps represent hypotheses about movement probabilities along different paths as a function of landscape structure and the relative resistance of different landscape features. Because we are interested in comparing the relative amount of movement expected in each cell using each model, we compared the current maps, not the raw resistance maps. We calculated flow (relative amount of predicted movement) between a pair of focal nodes located in forest patches in the north and south of the study landscape (Fig. 3). To exclude areas of uniformly low movement probability that were located behind the focal nodes from the analysis, we correlated only the center parts of the landscape (areas >1 km from any edge of the map).

We expected high agreement (i.e. strong correlations) between current maps informed by natal and breeding dispersal and current maps informed by habitat suitability transformed to resistance with a negative exponential function ($c = 2-32$). We expected lower agreement between current maps informed by natal and breeding dispersal and current maps informed by a linear transformation ($c = 0.25$) of habitat suitability to resistance, as well as between natal and breeding dispersal current maps and the null model maps.

3. Results

3.1. Habitat suitability

The GPS collars remained on the animals an average of 14 days (SD=6, range: 5–26) and recorded a total of 3215 fixes (median = 196, range = 37–676). Minimum convex polygon home range sizes of 10 collared females were on average 15.9 ha (SD = 7.77, range: 4–25.6 ha), after removing an outlier caused by low fix-rate (Fig. S-2, Table S-2). We lost the collar of one of the translocated kinkajous. The collar of the other female kinkajou that we released 4 km away from the capture site recorded 328 fixes over 18 days, when we captured her back in her home range. She spent 14 days moving among multiple forest patches in an area of

153 ha and then, in one night, moved 2.7 km back to her home range (Fig. 4).

The Pareto kernel distances in the resource selection functions varied from 170 to 588 m (Table S-3). We assessed resource selection at the 20–80 min GPS acquisition intervals. In univariate analyses, the strongest response to each variable occurred at the coarsest scale (80-min/588-m, Table 1). Although a stronger response might occur at scales longer than 80 min, we did not test the 120 min scale because the Pareto kernel distance decreased as the interval increased from 80 min to 120 min (due to animals reversing direction at the edges of small forest patches). In the best multivariate RSF and the best SSF model, kinkajous preferred native forest and reforestation sites, and avoided pasture and even more so agricultural areas (Table 2). They responded positively to distance to non-forest, meaning they avoided the forest edge when inside forest. Similarly, they responded negatively to distance to forest, meaning that when in pasture or agricultural areas, they tended to stay close to forests.

All radio-tagged female kinkajous (10) stayed within a single forest patch during the entire 5–26 days of observation. Three individuals undertook 1–4 short excursions (mean = 2.3; mean distance 523 m, SD = 177 m) to trees at the edge of a village or within a pasture. About 97.8% of GPS locations were in natural or regenerating forest, 1.45% in pasture, and 0.5% in farmland.

3.2. Mother-offspring and mother-father pairs

Kinkajous visiting the hair snares usually wrapped their prehensile tail around the branch at the top of the snare stick and hung down to reach the bananas, in the process touching the sticky tape with their bellies. Other species observed at the hair snares were Central American woolly opossums (*Caluromys derbianus*), variegated squirrels (*Sciurus variegatoides*), and capuchin monkeys (*Cebus capucinus*). We placed 491 hair snares and obtained 241 hair samples that we classified as kinkajou (49% success rate). We also collected 69 tissue or hair samples from kinkajous captured in live traps. Samples were obtained from 32 of the 34 forest remnants we sampled. All the hair samples that we visually classified as kinkajous were genetically confirmed to be kinkajou. The sex-linked amelogenin gene had five SNPs that were homozygous in females and heterozygous in males.

Filtering at Q30, we detected 201 SNPs and 8 INDELS in 25 loci. The mean depth per site for SNPs (i.e., the average number of times a nucleotide is read during the sequencing process) was 99.34 (SD = 75.4). The mean depth per site for INDELS was 108.5 (SD = 89.96).

In 218 of the 310 samples over 70% of the SNPs and INDELS were called. We collected duplicate samples for 9 individuals. Of the 209 remaining samples, 94 were males and 115 females. We detected 45 mother-father-offspring triads, 2 mother-offspring dyads and 3 father-offspring dyads with a probability >0.8. The mean distance between mothers and fathers was 1538 m (SD = 1266; range: 31–6876 m). In twenty-nine of the 45 mother-father-offspring tri-

Table 2
Estimates of coefficients for the best resource selection model (based on animal locations) and of the best step selection model (based on movements within the home range) for kinkajous in northeastern Costa Rica. Estimates significantly <0 indicate avoidance or unsuitability. Estimates significantly >0 indicate selection or suitability. The z-value = coefficient/SE.

habitat variable	Best scale	RSF				SSF			
		Estimate	Std. Error	z value	Pr > z	Estimate	Std. Error	z value	Pr > z
native forest	80 min	6.24	2.26	2.76	0.006	9.65	1.38	6.99	<0.001
reforestation	80 min	5.58	2.12	2.64	0.008	8.18	1.24	6.61	<0.001
agriculture	80 min	-12.77	1.96	-6.53	<0.001	-11.87	1.51	-7.85	<0.001
pasture	80 min	-5.46	1.84	-2.97	0.003	-3.89	1.14	-3.40	0.0007
dist. to open	80 min	0.02	0.01	1.47	0.142	0.01	0.01	0.95	0.34
dist. to forest	80 min	-0.05	0.01	-5.88	<0.001	-0.08	0.01	-9.05	<0.001

Table 3

Resistance coefficients of land cover types estimated from locations of parent-offspring pairs and mother-father pairs for kinkajous in northeastern Costa Rica. Low values indicate low resistance to movement. High values indicate high resistance to movement. The z-value = coefficient/SE.

	Parent-Offspring Pairs (n = 15)				Mother-Father Pairs (n = 29)			
	Estimate	Std. Error	z value	p value	Estimate	Std. Error	z value	p value
native forest	0.82	0.33	2.48	0.013	1.37	0.27	5.10	<0.001
reforestation	0.7	0.33	2.12	0.034	0.94	0.27	3.48	<0.001
not forested	1.24	0.31	4.00	<0.001	1.61	0.36	4.50	<0.001
distance to open	0.56	0.25	2.24	0.025	1.29	0.64	2.04	0.041
distance to forest	0.11	0.20	0.55	0.582	-0.14	0.17	-0.83	0.407

Table 4

Comparison of resistance values estimated from resource and step selection models, and natal and breeding dispersal models for kinkajous in northeastern Costa Rica. Z-values of RSF and SSF models were transformed from suitability to resistance using a linear function. All values were scaled to 0–1.

	RSF	SSF		natal dispersal	breeding dispersal
native forest	0.24	0.00	native forest	0.56	1.00
reforestation	0.25	0.02	reforestation	0.50	0.73
agriculture	0.83	0.92	non-forested	0.81	0.90
pasture	0.59	0.62			
dist. to open	0.32	0.35	dist. to open	0.52	0.48
dist. to forest	0.78	1.00	dist. to forest	0.23	0.00

ads the fathers were not in the same patch as the mothers (mean distance between mothers and fathers: 1887 m; SD = 1350; range: 441–6876 m). We found 15 offspring (7 females and 8 males) that had likely dispersed from the natal home range (Fig. 3). The mean dispersal distance was 1157 m (SD = 583; range: 350–2189 m).

Based on the mother-offspring pair locations, forests and reforested areas posed some resistance to movement. Resistance of non-forested areas was slightly higher (Table 3). Based on mother-father locations, forests posed higher resistance than reforested areas. We combined pasture and agricultural areas as non-forested areas to increase signal strength with small sample size. Dispersers in forests showed no preference for forest interior or forest edge and dispersers in non-forest showed no preference for being close to forested pixels. However, animals in their home ranges avoided pixels far from the forest (Table 4). Also, forests have higher resistance for natal and breeding dispersal movements than for home range resource use and movements (Table 4).

3.3. Agreement between current maps

Agreement between current maps was generally high (correlation coefficient >0.9). Landscape connectivity was greater for dispersal movements than for home range movements (Fig. 6). Agreement was higher between natal and breeding dispersal current maps and maps informed by habitat suitability transformed to resistance with a negative exponential function than between natal and breeding dispersal current maps and current maps informed by a linear transformation of habitat suitability to resistance (Figs. 5 and 6, S-3). The SSF results were not more highly correlated with the natal and breeding dispersal results than the RSF results (Fig. 5), indicating that connectivity modeled from movement steps in the home range does not differ from connectivity modeled from random locations in the home range. The natal and breeding dispersal current maps were most strongly correlated with the null model current maps, indicating that natal and breeding dispersal current surfaces are essentially flat resistance surfaces (Fig. 5).

4. Discussion

The results of our RSF and SSF home range analyses clearly indicate that kinkajous are forest specialists. The GPS-collared animals rarely left forest patches, preferred the interior of forest patches to

edges, and when in pastures or farmland tended to stay near the forest edge. Most individuals stayed within a single forest patch for the entire 5–26 days of monitoring. Our results are consistent with qualitative observations that kinkajous are forest mammals (Ford & Hoffmann, 1988). There are no quantitative observations for comparison.

Our results suggest that, as expected, kinkajous perceive the fragmented landscape as more connected during natal and breeding dispersal movements than while in the home range. Despite behaving like forest specialists within the home range, dispersed offspring as well as fathers usually occurred in different forest patches than the mother, indicating that the animals have crossed pastures or agricultural areas. Moreover, the amount of farm or pasture between forest patches did not affect the probability that a pair of patches would be the homes of a mother-father pair or a mother-offspring pair. Against our hypothesis, the natal and breeding dispersal current surfaces were essentially flat resistance surfaces, meaning that no landscape features posed differential resistance to kinkajou movement during natal and breeding dispersal movements. However, mother-father and mother-offspring pair locations only result from successful natal and breeding dispersal movements. We do not know the proportion of animals that have attempted movements but failed. The correlations between the dispersal movement and RSF/SSF current maps were high (>0.92). Nevertheless, they show different movement probabilities as a function of landscape structure (Fig. 5, Fig. S-3) and the relative resistance of different landscape features varies based on the underlying resistance maps. Therefore, we interpret the differences in correlations as biologically meaningful.

Although kinkajous apparently crossed agricultural areas and pastures successfully in our landscape, our study area had relatively small farms and pastures. In other studies, unsuitable landscape features affected connectivity when size of the unsuitable feature was highly variable and included some large unsuitable patches (Short Bull et al., 2011). We speculate that natal and breeding dispersal current maps would be most highly correlated with current maps derived from habitat suitability transformed into resistance using negative exponential functions in landscapes that have larger patches of non-habitat than the farms, pastures, and croplands in our landscape. A similar study in a landscape with more variable distances between forest remnants would be necessary to reveal the distances over which kinkajous are able to traverse non-forested areas during natal and breeding dispersal movements.

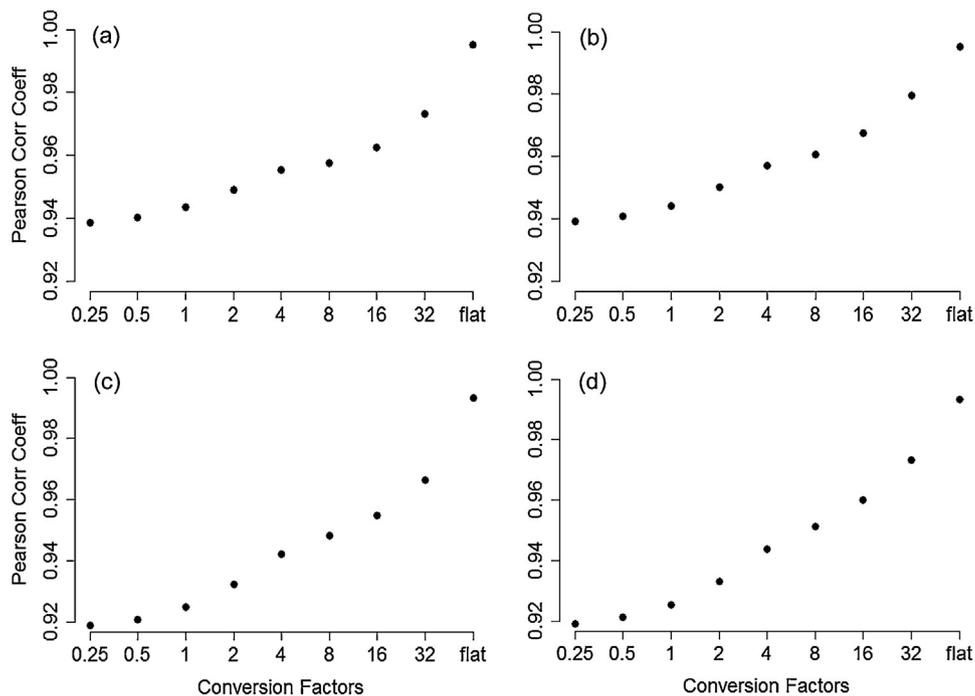


Fig. 5. Pearson correlation coefficients for correlations between current flow maps (i.e., maps reflecting relative probability of movement) based on natal dispersal movements and (a) resource selection or (b) step selection; and breeding dispersal movements and (c) resource selection or (d) step selection. Conversion factors specify the linear (0.25), or negative exponential (0.5–32) transformations, or a flat surface (where all cells have a value of 1) between habitat suitability and resistance.

Against our hypothesis, the current map correlations indicated that the SSF analysis and RSF analysis performed equally well in characterizing how kinkajous use the landscape while dispersing, perhaps because the collared kinkajous rarely left the forest patches while in the home range. In contrast, Zeller et al. (2014) found that SSFs for mountain lions (*Puma concolor*) indicated more tolerance of habitat features that were avoided in RSF analyses. Similarly, Abrahms et al. (2016) and Blazquez-Cabrera et al. (2016) found for African wild dogs (*Lycaon pictus*) and Iberian lynx (*Lynx pardinus*) respectively, that resistance estimates from movement behavior are more similar to resistance estimates from dispersal or exploratory movements than resistance estimates from general home range data.

Likewise, long-distance movements have been better predicted by habitat suitability transformed to resistance using negative exponential functions. Keeley et al. (2016) calculated costs of long-distance movements of desert bighorn sheep (*Ovis canadensis nelsoni*) in Arizona based on resistance surfaces generated by resource and step selection functions as well as expert opinion. The authors concluded that resistance to long-distance movement was best estimated by a negative exponential function of habitat suitability. Similarly, landscape resistance to exploratory movements of red-cockaded woodpeckers (*Picoides borealis*) in North Carolina was a strongly negative exponential function of habitat suitability (Trainor et al., 2013), and landscape genetic patterns of brown bears (*Ursus arctos*) in Spain were consistent with a negative exponential relationship between resistance and habitat suitability (Mateo-Sanchez et al., 2015). These studies did not test whether a flat surface would better reflect resistance to long-distance movement.

In addition to the studies cited above, resistance to natal and breeding dispersal movements or gene flow was less than expected based on habitat suitability for butterflies (*Junonia coenia* and *Euptoieta claudia*, Haddad & Tewksbury, 2005), American marten (*Martes americana*, Wasserman, Cushman, Schwartz, & Wallin, 2010), lions (*Panthera leo*, Elliot et al., 2014), and salaman-

ders (*Plethodon albagula*, Peterman, Connette, Semlitsch, & Eggert, 2014). Reding, Cushman, Gosselink, and Clark (2013) reported that bobcats (*Lynx rufus*) strongly preferred forest cover for within-home range movements but forest cover did not explain genetic structure. Although the authors speculated that the lack of genetic pattern was due to the region's fine-scaled forest fragmentation, we suggest that their resistance surface (a linear transformation of suitability estimated from within-home range movement) might not reflect resistance to natal and breeding dispersal movements. Like kinkajous, dispersing bobcats may readily traverse habitat of moderate to low suitability. We hypothesize that most mobile animals readily move through patches of moderately to highly unsuitable habitat during natal and breeding dispersal movements.

Although we are unaware of studies showing that resistance to dispersal is a linear function of habitat suitability in the home range (upper curve in Fig. 1), this linear relationship may hold for species with low dispersal ability (e.g. wingless orthopterans – Reinhardt, Köhler, Maas, & Detzel, 2005; amphibians – Cushman, 2006), and in species that do not readily cross habitat gaps (e.g. some understory birds in tropical forests – Lees & Peres, 2009). Such species may require continuous good-quality corridors.

We also hypothesize that there is a threshold size for unsuitable habitat patches such that animals will rarely or never cross patches larger than that threshold. If this hypothesis is correct, determining that threshold distance should be an important focus of corridor research. Although the answers will be species-specific, there may be general answers for suites of species. For example, Doerr, Barrett, and Doerr (2011) analyzed dispersal movements of five Australian woodland birds and found similar dispersal movement strategies, possibly shaped over evolutionary time by natural patterns of variability in the landscape.

Although genetic data give insight into natal and breeding dispersal movements, they are by definition biased towards successful events and will therefore underestimate resistance that arises from mortality in specific habitats. The fact that the translocated kinkajou waited 14 days before finally returning home in one

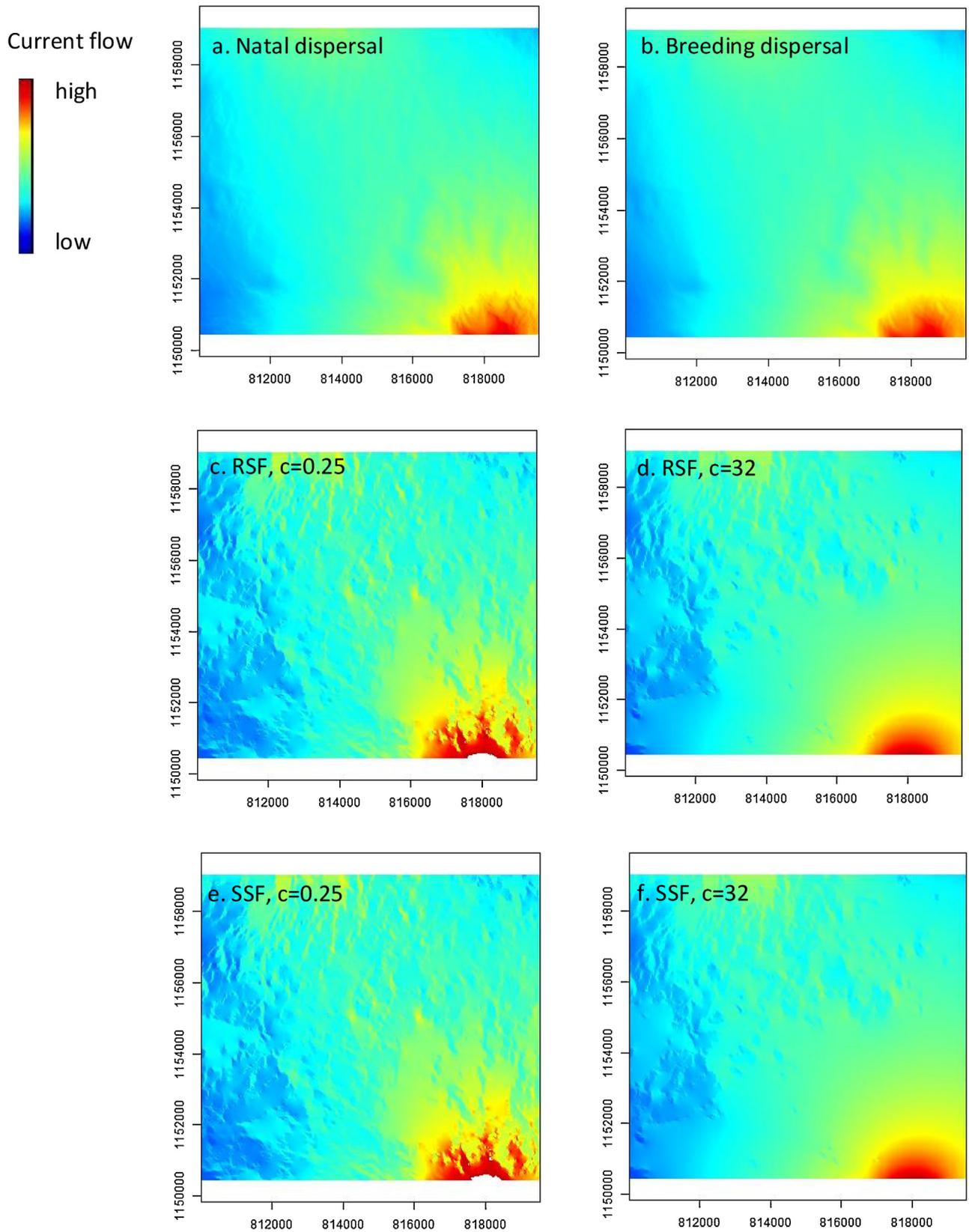


Fig. 6. Select current flow maps which represent hypotheses about movement probabilities along different paths as a function of landscape structure and the relative resistance of different landscape features. The top 2 panels show current flow based on resistance estimated from natal (a) and breeding (b) dispersal movement models. The 2 middle panels show current flow based on resource selection function (RSF) models, with habitat suitability translated into resistance with a linear relationship ($c = 0.25$; panel c) and a negative exponential relationship ($c = 32$; panel d). The 2 bottom panels represent current flow based on step selection function (SSF) models, with habitat suitability translated into resistance with a linear relationship ($c = 0.25$; panel e) and a negative exponential relationship ($c = 32$; panel f).

movement indicates that there may be risk involved in moving through pastures and agricultural areas. The avoidance of territorial conspecifics may have contributed to the tolerance of apparently unsuitable habitat by dispersing kinkajous. During homing movements of the adult kinkajou translocated away from her home range, the animal stayed in very small forest patches or at the edge of forests, which may indicate avoidance of territorial conspecifics (Fig. 4). Resistance estimates obtained from parent-offspring pairs compared to those obtained from adults (Table 4) suggests a shift consistent with avoidance of territorial conspecifics. Similarly, (Elliot et al., 2014) found that landscape resistance to movement differed among adult female, adult male, and dispersing juvenile male lions (*Panthera leo*). Adult males and females selected for grassland and shrubland and avoided woodland and areas with high anthropogenic risks. In contrast, dispersing males avoided grassland and shrubland, selected woodlands, and showed higher tolerance for areas with high anthropogenic risks, likely to avoid contact with territorial conspecifics. The negative exponential transformation will not account for the flipping of preference and avoidance between adults and dispersers. Thus, it is important to choose the correct demographic group to estimate resistance for connectivity modeling.

More research is necessary to better understand kinkajou social organization and spatial ecology in fragmented landscapes. Kays and Gittleman (2001) observed several social groups consisting of two adult males and one adult female and her offspring in a large continuous forest. One breeding female with her offspring was not part of such a social group. Both dominant and subordinate males copulated with group females. Kays and Gittleman (2001) observed one dispersal event in which a sub-adult female moved to a neighboring group. In a related genetic study, female kinkajous were less related to female neighbors than were male kinkajous to male neighbors, suggesting female-biased dispersal (Kays et al., 2000). Because most forest fragments in our study landscape were too small to support three adult kinkajous, social organization on our landscape probably differed from that observed by Kays and Gittleman (2001). The locations of mother-father-offspring triads suggest that kinkajous in our landscape moved considerable distances during the mating season. We genetically detected dispersal by seven females and eight males, indicating that dispersal may not be female biased in our fragmented landscape.

Because we assumed dispersal in kinkajous was female-biased (Kays et al., 2000), we outfitted only females with GPS collars. Thus, the home range resistance estimates reflect female behavior while the resistance estimates based on dispersal include males and females. Potentially, male kinkajous show less avoidance of non-forest land covers during home range movements than females, in which case landscape resistance values derived from home range and dispersal movements would be similar. Additional GPS tracking studies are needed to clarify differences in home range behavior between male and female kinkajous in fragmented landscapes.

The results of our RSF and SSF home range analyses clearly indicate that kinkajous are forest specialists. The GPS-collared animals rarely left forest patches, preferred the interior of forest patches to edges, and when in pastures or farmland tended to stay near the forest edge. Most individuals stayed within a single forest patch for the entire 5–26 days of monitoring.

Although many studies genetically identified parent-offspring pairs (e.g., Pinho, da Silva, Hrbek, Venticinque, & Farias, 2014), Graves et al. (2014) were the first to propose that landscape resistance could be inferred from locations of these pairs. We followed their new approach to estimate landscape resistance to dispersal from mother-offspring pairs. We also applied the approach to estimate landscape resistance to dispersal from locations of mother-father pairs. Based on simulations, Graves et al. (2014) suggested the “approach provides reasonable estimates even at

low samples sizes (25 dispersal events) [...]” Our results confirm the ability of the approach to make inferences from small sample sizes. Our resistance from 15 dispersal events were similar to the resistance estimated from the 29 mother-father pairs, and the confidence intervals (with the exception of ‘distance to forest’) were statistically significant. We believe this is a useful tool for directly estimating resistance at low cost from genetic data.

4.1. Limitations of the study

We encountered several challenges during this study. We lost five GPS collars and the data stored on them probably due to failure of the VHF units. In addition, the GPS-fix rate of some collars was low, despite kinkajous living in the canopy. Tests showed that inside tree cavities the collars were able to record the location. Humidity and technical problems may have caused these issues.

We had to discard a number of hair samples due to low quality resulting in low amplification rates. Kinkajou hair follicles are extremely small and therefore contain only small amounts of DNA. In addition, the hot, humid climate may have caused DNA to break down rapidly (Murphy, Kendall, Robinson, & Waits, 2007), even though we strived to minimize the time the hairs were exposed to the climate. Due to these quality issues and not sampling a closed population we likely missed numerous parent-offspring triads living in the study area.

5. Conclusions

Our study showed that during natal and breeding dispersal, kinkajous, a habitat specialist, can readily move through a matrix that strongly contrasts with suitable habitat. If, as we hypothesize, most mobile animals readily traverse habitat of moderate and low suitability for natal and breeding dispersal, planning for wildlife corridors would be more flexible than if resistance is assumed to be a linear function of habitat suitability in the home range. In this circumstance, corridor designers would no longer focus on “What is the location of the least-cost path?” Instead they would focus on identifying the major barriers to movement (roads, fences, canals, rail lines, intensely developed urban and industrial areas, noise and light pollution) and the major mortality factors in connective zones (road kill, conflict with humans and human property), and devising strategies to mitigate those barriers and mortality factors. Focal species for corridor design should include species with the lowest ability to cross gaps. Although observed movement paths are most convincing to many stakeholders and therefore are more likely to lead to action, we suggest that connectivity models based on resistance estimates from parent-offspring pairs, or from suitably transformed resource or step selection functions, can also perform quite well.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.landurbplan.2017.01.007>.

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