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Quantifying past and present connectivity illuminates a rapidly changing landscape for the African elephant

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Abstract

There is widespread concern about impacts of land-use change on connectivity among animal and plant populations, but those impacts are difficult to quantify. Moreover, lack of knowledge regarding ecosystems before fragmentation may obscure appropriate conservation targets. We use occurrence and population genetic data to contrast connectivity for a long-lived mega-herbivore over historical and contemporary time frames. We test whether (i) historical gene flow is predicted by persistent landscape features rather than human settlement, (ii) contemporary connectivity is most affected by human settlement and (iii) recent gene flow estimates show the effects of both factors. We used 16 microsatellite loci to estimate historical and recent gene flow among African elephant (*Loxodonta africana*) populations in seven protected areas in Tanzania, East Africa. We used historical gene flow (F_{ST} and G'_{ST}) to test and optimize models of historical landscape resistance to movement. We inferred contemporary landscape resistance from elephant resource selection, assessed via walking surveys across ~15 400 km^2 of protected and unprotected lands. We used assignment-based recent gene flow estimates to optimize and test the contemporary resistance model, and to test a combined historical and contemporary model. We detected striking changes in connectivity. Historical connectivity among elephant populations was strongly influenced by slope but not human settlement, whereas contemporary connectivity was influenced most by human settlement. Recent gene flow was strongly influenced by slope but was also correlated with contemporary resistance. Inferences across multiple timescales can better inform conservation efforts on large and complex landscapes, while mitigating the fundamental problem of shifting baselines in conservation.

Keywords: African elephant, corridor, gene flow, resistance surface, resource selection probability function

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Introduction

Habitat fragmentation is a major threat to biodiversity worldwide (Wilcox & Murphy 1985). Widespread recognition of one consequence of habitat fragmentation, loss of connectivity (dispersal and gene flow) among plant and animal populations, has led to growing interest in conserving or re-establishing corridors or multi-species linkages (Beier *et al.* 2008). Conservation efforts aimed at increasing connectivity between isolated populations (e.g. Soule *et al.* 1979; Newmark 1995, 1996, 2008) assume that such connectivity existed historically but has been reduced by recent and often striking

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changes in human land use. However, re-envisioning those lost connections has typically relied on anecdotal reports or guesswork. Assessing contemporary connectivity among populations is equally difficult, and such assessments are often undertaken only after significant land-use changes have occurred. Thus, the potential for a rapidly shifting baseline cannot be ignored (Gardner *et al.* 2009), especially when defining conservation targets for hard-to-study processes such as connectivity.

Attempts to better quantify connectivity by predicting potential movement or gene flow over large landscapes have relied increasingly on approaches that use resistance or cost surfaces based on predicted influences of different habitats on animal movement (Spear *et al.* 2010). Least-cost path (Adriaensen *et al.* 2003) or circuit-theoretic (McRae *et al.* 2008) methods are then used to measure effective distances between locations and predict likely movement paths (least-cost) or describe areas with higher predicted use (circuit-theory). Although such models are widely used as a conservation tool, confronting them with empirical data has proved challenging (Cushman & Lewis 2010; Sawyer *et al.* 2011).

Methods to derive resistance surfaces for connectivity models empirically are increasingly being explored—but each has limitations (Zeller *et al.* 2012). Resistance surfaces for contemporary landscapes can be estimated from location data that are used to generate resource selection function (RSF) or resource selection probability function (RSPF) models; resistance surfaces are then created by inverting habitat selection or use probabilities (e.g. Chetkiewicz & Boyce 2009). Path-based analyses of animal movement also can be subjected to use/availability analysis (Driezen *et al.* 2007; Zellmer & Knowles 2009; Cushman *et al.* 2010). However, approaches based on direct monitoring of animal locations may be constrained by financial and logistical limitations. Such data sets also may be influenced most by use within home ranges and definitions of habitat availability rather than dispersal or rare long-distance movements, and may offer little guidance for restoration in already-altered landscapes.

Population genetic data have been used to test and optimize resistance surfaces (Cushman *et al.* 2006; Epps *et al.* 2007; Shirk *et al.* 2010). However, genetic connectivity may be only indirectly related to demographic connectivity (Lowe & Allendorf 2010), and interpretation of population genetic structure is confounded by time: genetic drift is weak for species with large effective population sizes (N_e) and long generation times. Thus, although standard metrics of genetic distance (e.g. F_{ST}) among populations will be influenced by effects of recent landscape changes, the influence of historical landscapes may be much stronger (Balkenhol *et al.* 2009a). Individual-based analyses, where appropriate, and other metrics of genetic dissimilarity may be more sensitive to recent changes (Landguth *et al.* 2010). Population assignment tests (Paetkau *et al.* 1995) that estimate gene flow over more recent time periods (e.g. previous 1–2 generations, Faubet & Gaggiotti 2008; Wilson & Rannala 2003) also may offer new opportunities to estimate resistance on recent landscapes (e.g. Chiucchi & Gibbs 2010).

While each method for confronting connectivity (resistance) models with empirical data has limitations, using multiple methods may create new insights and strengthen inferences. Here, we combine field and genetic data to contrast the historical and current connectivity of a long-lived mega-herbivore in East Africa. Specifically, we examine gene flow and contemporary distribution of African elephants (*Loxodonta africana*) to infer changes in population connectivity among protected areas in Tanzania. African elephants are a conservation flagship species and a valued game animal in Tanzania, but are also increasingly involved in human–wildlife conflict. Tanzania's human population has increased from 5 million in 1931 (national census, Anonymous 1931) to an estimated 44 million in 2009 (Anonymous 2011), and this growth is associated with expanded settlements and more intensive agriculture in many rural areas. African elephants often avoid areas with high human activity (e.g. Blom *et al.* 2005; Cushman *et al.* 2010; Pittiglio *et al.* 2011), and elephant activity outside protected areas in central Tanzania is strongly correlated with species richness of other large mammals, suggesting that they could serve as focal species for connectivity conservation (Epps *et al.* 2011). African elephants have one of the longest generation times of any terrestrial mammal (25 years, Blanc 2008) and have large population sizes in many protected areas in Tanzania (Stoner *et al.* 2007), implying that effective population sizes (N_e) are large. Therefore, we predicted that population genetic structure of elephants in Tanzania would reflect historical patterns of dispersal (e.g. hundreds of years before present) more than recent landscape changes.

Here, we combine habitat use and population genetic data to assess (i) the degree of connectivity between elephant populations in protected areas and (ii) the extent to which these populations were connected by gene flow historically. First, we estimate genetic distance (F_{ST} and G'_{ST}) among core elephant populations in seven protected areas across central and southern Tanzania, optimize parameters for resistance models for the historical landscape based on genetic distance, and use simulated data to evaluate how rapidly F_{ST} would change after a decline in migration rates. Second, we estimate elephant resource selection from dung and track locations detected along walking transects

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(systematically conducted across a potential movement corridor), and transform the resource selection model to a resistance surface to represent contemporary connectivity. Third, we use assignment test-based estimates of gene flow on the recent landscape (within the last generation) to optimize the contemporary resistance model and test historical, contemporary and combined resistance models. Last, we compare resistance between historical and contemporary time frames to determine where recent human activity has most affected connectivity among elephant populations. We predicted that the (i) historical gene flow would reflect permanent landscape features but not current human activity, (ii) contemporary landscape resistance (inferred from RSPF modelling) also would reflect permanent landscape features but would be driven primarily by human activity, and (iii) recent gene flow estimates would be correlated with both the historical and contemporary resistance models.

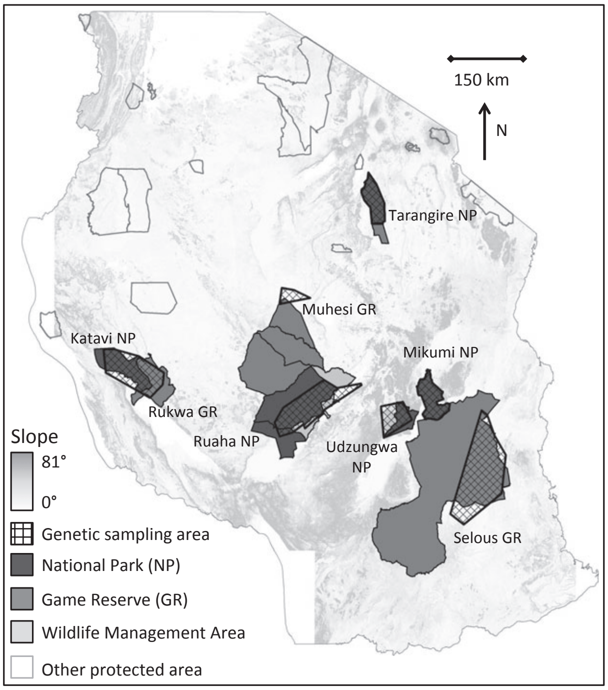

Fig. 1 Genetic sampling areas for elephant populations in central and southern Tanzania, with major protected areas (solid-coloured and named if included in the genetic sampling) and slope (excluding some areas along the western edge of the country). Genetic sampling area polygons were drawn around the maximum extent of the locations of genetic samples.

Methods

Genetic samples and genetic structure

We used DNA extracted from elephant dung samples collected within the last 13 years (Wasser *et al.* 2007, 2008) in seven major protected areas or protected area complexes in central and southern Tanzania (Fig. 1; hereafter, 'genetic study area'). We chose those areas because they represent major concentrations of elephants in a biologically complex and less-studied region of East Africa. Elephant populations are strongly concentrated in existing protected areas (see present distribution; Anonymous 2007); therefore, we used a population-based approach and sampled as widely as possible across each focal area. Because of the clustered nature of both the populations and the sampling, individual-based approaches that perform best with an even sample distribution appeared less appropriate. Sample sizes were ≥ 20 for all populations except Udzungwa Mountains national parks (NP; $n = 11$), where repeated sampling attempts generated few viable samples because of humid conditions and low elephant densities (Table 1). We genotyped dung samples at up to 16 microsatellite loci (see Appendix S1, Supporting information and Wasser *et al.* 2008, 2007); we included only samples successfully genotyped at ≥ 10 loci in subsequent analyses. We defined populations spatially using simple polygons drawn to enclose sampling locations within or near each protected area; we used the entire protected area if precise sample locations were not known (Fig. 1, Mikumi and Tarangire). Because some of those sampling areas were relatively large, creating the potential for a Modifiable Areal Unit Problem (Jelinski & Wu 1996), we evaluated F_{IS} for each population to determine whether there was evidence for substructure within those populations. We also split samples from two of the largest polygons and evaluated population pairwise F_{ST} values between those clusters. We tested for violations of Hardy–Weinberg equilibrium and linkage disequilibrium within populations and by locus using GENEPOP v4.0.10 (Rousset 2008), applying a Bonferroni correction for multiple comparisons across populations and loci. We estimated global F_{ST} for the full data set using GENEPOP (Rousset 2008).

Estimating historical gene flow

Although genetic structure reflects both long-term and recent patterns of gene flow, we interpreted population pairwise F_{ST} to be primarily an index of long-term (historical) patterns of gene flow (see Introduction). We estimated population pairwise F_{ST} using GENEPOP (Rousset 2008) and converted those values to Slatkin's linearized F_{ST} (Slatkin 1995). As an alternative to F_{ST}, we also estimated G'_{ST} (using SMOGD, Crawford 2010), because it may be more appropriate for highly variable microsatellite data (Hedrick 2005; but see Whitlock 2011). To evaluate the assumption that F_{ST} would largely reflect

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Table 1 Genetic sample size (n), observed (H_o) and expected (H_e) heterozygosity (estimated using ARLEQUIN v. 3.11), inbreeding coefficient (F_{IS}; estimated using Genepop), average number of alleles per locus, and corrected allelic richness for African elephant populations in seven protected areas in central and southern Tanzania

Sampling area[*]	n	H_o	H_e	F_{IS}	Average alleles/locus[†]	Average allelic richness (corrected for sample size)[‡]
Katavi National Park/Rukwa Game Reserve	30	0.62	0.62	−0.006	5.69	4.02
Mikumi National Park	62	0.67	0.64	−0.043	7.00	4.18
Ruaha National Park	29	0.66	0.63	−0.036	6.19	4.32
Muhesi Game Reserve	20	0.62	0.62	0.003	5.69	4.18
Selous Game Reserve	25	0.65	0.62	−0.042	5.13	3.86
Tarangire National Park	40	0.60	0.64	0.069	6.69	4.21
Udzungwa Mountains National Park	11	0.64	0.64	0.007	4.94	4.40

[*] Only portions of Ruaha National Park, Muhesi Game Reserve, Selous Game Reserve and Udzungwa Mountains National Park were sampled.

[†] Not corrected for differences in sample size.

[‡] We used FSTAT (Goudet 1995) to estimate corrected allelic richness by subsampling based on the smallest sample size.

genetic structure prior to the dramatic human population increases in the twentieth century, we simulated data to test rates of change in genetic structure (Appendix S2, Supporting information). We also attempted to estimate long-term migration rates among population pairs using coalescent approaches as implemented in MIGRATE (Beerli & Felsenstein 2001), but abandoned that approach because estimates never converged due to weak genetic structure (not shown).

Estimating recent gene flow using BIMR

We used assignment tests implemented in Program BIMR (Faubet & Gaggiotti 2008) to estimate recent migration rates (within the last generation) among protected areas. This approach performs best when migration rates are high but global F_{ST} values exceed 0.01 (Faubet & Gaggiotti 2008), and was identified as one of the best-performing methods to test hypotheses about the effect of landscape resistance and isolation by distance (IBD) on genetic structure (Balkenhol *et al.* 2009b). For each analysis, we used 10 replicate runs of the program (see Appendix S3, Supporting information) to estimate pairwise migration rates between population pairs; we averaged estimates to and from each population and across runs to generate a symmetrical matrix for correlation testing.

Field data on elephant distribution

We conducted walking transects to search for elephant dung and tracks across a ~15 400 km^2 area (hereafter, ‘field study area’) in central Tanzania bounded by Ruaha National Park to the west, Mikumi National Park to the east, and Udzungwa Mountains National Park to the south (Fig. 1, see Epps *et al.* 2011 for further details). We chose the field study area to investigate a potential link between elephant populations in the Selous–Mikumi complex and the Ruaha ecosystem (Jones *et al.* 2009). The study area included fully protected areas (the NP listed above), partially protected areas open to limited hunting or other extractive uses, and village lands and Game Controlled Areas (GCAs) where agriculture, extractive use of wildlife and forest resources, and human settlement (village lands) were either permitted or not typically deterred by enforcement (see Appendix S4, Supporting information).

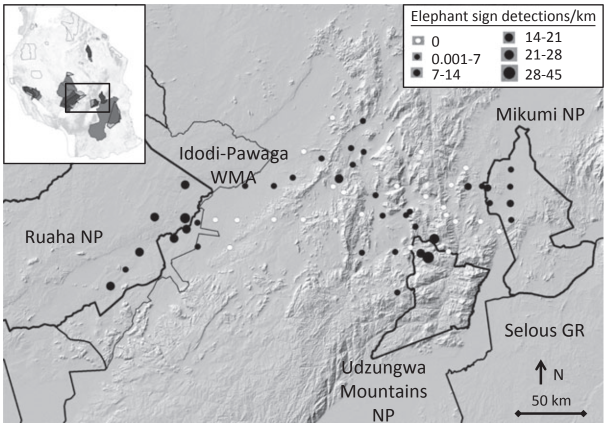

Fig. 2 Elephant detections per kilometre on walking transects conducted in 2006–2007 in the field study area in central Tanzania, with topographical relief depicted in grey shading; elephants were detected in some locations well outside of protected areas. Protected areas (NP, national parks; GR, game reserves; WMA, wildlife management area) are outlined in black.

We surveyed 61 unique walking transects (total length, 481 km; mean and SD, 7.9 ± 2.9 km) from September 2006 to February 2007 and from August to November 2007 (Fig. 2). We recorded a binary response

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(used/not used) for each 10-m interval of the surveyed transects if elephant dung or tracks were detected within ~2.5 m of the transect centre line (Appendix S4, Supporting information). We placed 50 of 61 transects according to a randomly determined, regular grid of points [with 10-min (~19 km) spacing in most areas, although 5- and 7-min grids were initially employed in some of the protected areas]; those transects were triangular, cross country, with vertices based on the preassigned starting location (e.g. Waltert *et al.* 2008). We surveyed the remaining 11 locations using opportunistic 'recce' style transects (Walsh & White 1999), where we travelled irregular routes to explore an area. We sampled at the end of the long wet season, through the dry season, and into the early wet season (Appendix S4, Supporting information; Epps *et al.* 2011). Thus, our surveying captured both wet- and dry-season activity patterns but did not clearly separate whether habitat selection varied across seasons.

Modelling historical gene flow based on landscape features

We evaluated whether genetic distances among elephant populations in central and southern Tanzania were correlated with distance or persistent landscape features. We used a Mantel-based model optimization framework (e.g. Epps *et al.* 2007) to determine optimal transformations for single variables, then developed and tested more complicated models using multiple regression on distance matrices (MDRM, Legendre *et al.* 1994; Lichstein 2007). We tested two basic hypotheses of isolation by landscape resistance (IBR) based on (i) slope, because elephants typically avoid steeper slopes (Wall *et al.* 2006) and (ii) distance to fresh water (lakes and rivers), which influences elephant movements (e.g. Cushman *et al.* 2010). We treated IBD (distances between sampling polygon edges) as the null hypothesis, and used a four-part approach: (i) for each landscape hypothesis, we generated a set of resistance models with progressively stronger resistance values based on power transformations of the primary resistance layer (e.g. slope^x; see Figs S1 and S2, Supporting information); (ii) for each resistance model, we used Program CIRCUITSCAPE (v.3.5.2, Shah & McRae 2008) to calculate cumulative resistance between all population pairs over all possible pathways on the underlying resistance surface (McRae *et al.* 2008); (iii) we used simple Mantel tests (Smouse *et al.* 1986) to evaluate the correlation of pairwise linearized F_{ST} and G'_{ST} estimates with the pairwise estimates of cumulative resistance from each resistance model (graphed in Figs S1 and S2, Supporting information); and (iv) for each landscape hypothesis, we evaluated whether any resistance model was more correlated with F_{ST} or G'_{ST} than the null hypothesis of IBD (geographic distance), and whether we saw a clear unimodal peak in the strength of correlations over the range of transformations tested (Shirk *et al.* 2010). If so, we used the transformation with the strongest correlation coefficient as the 'optimized' model in subsequent analyses. Although Mantel tests have been criticized for a variety of reasons including inflated type I error in the presence of spatial autocorrelation (Guillot & Rousset 2012), we did not rely on significance tests in the optimization process. Furthermore, Mantel tests are considered appropriate for exploratory analyses of relationships for distance-based measurements (Legendre & Fortin 2010).

After determining whether there was support for each landscape hypothesis (slope or water) as above, we used multiple regression of distance matrices (MRDM) (as implemented in Program R, *ecodist* package) to evaluate the performance of each optimized model. Balkenhol *et al.* (2009b) found that MRDM was the best-performing method for landscape genetic analysis of population data. We used 10 000 permutations to assess significance of each test. We assessed colinearity of predictor variables (Table S1, Supporting information) and plotted variables against genetic distance to examine linearity and determine whether transformation was necessary (Fig. S3, Supporting information). Next, we tested how the best-fitting resistance models from the optimization exercises predicted genetic distance as univariate models, then in multivariate models including geographic distance to test whether the resistance models performed better than geographic distance (based on effects tests for each variable). We used the final model from this process as our optimized historical resistance model.

Estimating the resource selection probability function model and contemporary resistance surface

Although data on elephant movement would be most appropriate for modelling contemporary resistance, collection of movement data across this landscape (e.g. by satellite telemetry) was not logistically feasible due to expense, low elephant population density in the corridor areas, and permitting constraints. Therefore, we employed a use vs. available study design to estimate resource selection by elephants. We defined used sites ($n = 2207$) by transect intervals wherein dung and tracks were detected (e.g. Pradhan & Wegge 2007) and available sites by each sampling interval ($n = 44\ 301$). Hence, both the used and available sites were equally constrained to the sampling transects in an approach consistent with Keim *et al.* (2011). For both used and available locations, we used a Geographic Information System (GIS; ARCGIS 10.1) to measure covariates (Table

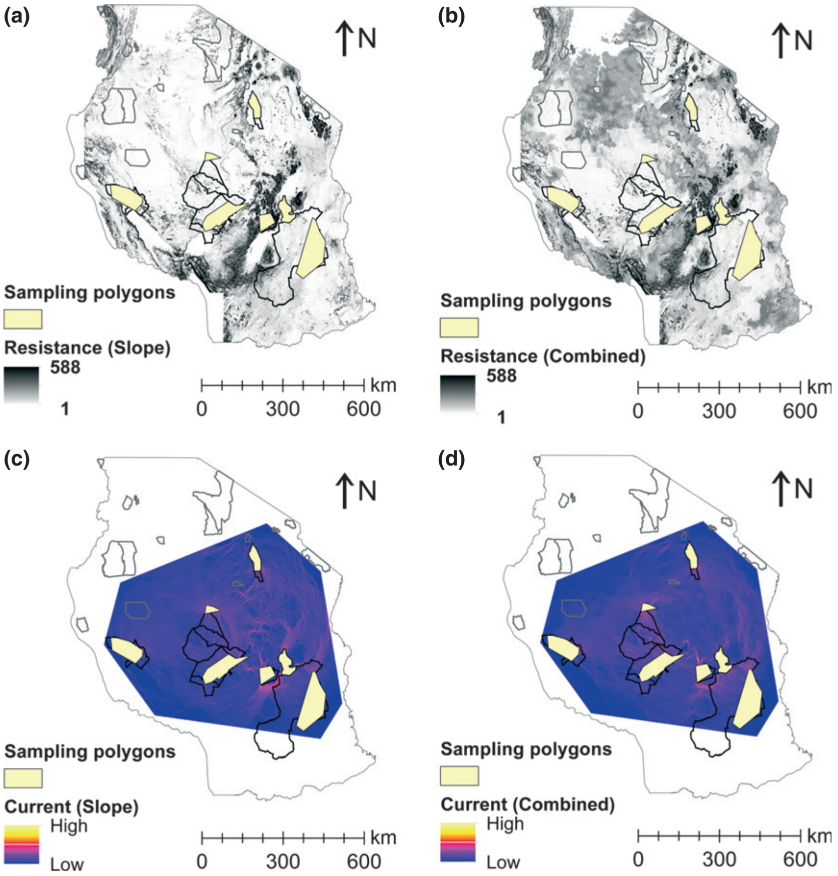

Fig. 3 Resistance models for elephant movement, including the 'historical' model (a) based on slope, and the 'combined' model (b) based on the combination of the historical model and a contemporary resistance model derived from a habitat selection model, with corresponding maps depicting flow of 'current' among genetic sampling areas based on the historical (c) and the combined (d) resistance models. Areas with higher current values have higher probability of movement through that location for a random walk between sample areas; warmer colours indicate 'bottlenecks' or areas through which movement would be forced. Protected areas are outlined in black and grey.

S2, Supporting information) relevant to our predictions that elephants would select protected areas and avoid areas with dense human settlement or agriculture (Epps *et al.* 2011), avoid steeper slopes (Wall *et al.* 2006), but select areas near water and with cooler aspects (south-facing in the Southern Hemisphere). Recognizing that different model forms should be considered to determine which model best fits the data (Rosner 1995), we considered two competing model forms as part of the model selection process: the exponential RSF and the logistic form of the RSPF (Lele & Keim 2006). We selected the model form and covariates that best fit the data in two steps (Table S3, Supporting information). First, we estimated resource selection using maximum likelihood methods and selected the model form and covariates that best fit the data using Schwarz Information Criteria (SIC, Schwarz 1978). We used SIC because that criterion appears better than AIC for determining relative importance of variables (Astrup *et al.* 2008; Raffalovich *et al.* 2008). Second, we examined the distribution and range of the predicted values for anomalies (e.g. maximum probabilities of selection near zero or a confined distribution of probability values).

We mapped the final resource selection model across the genetic study area. For landscape predictions, input variables were limited to the minimum and maximum values observed within the sampled distribution to prevent extrapolations beyond the limits of our data. Although we extended our model beyond the area from which it was developed (Figs 1–3), the field study area contained a heterogeneous mix of habitats and levels of human activity and thus should permit cautious extrapolation of the model elsewhere in Tanzania.

Although resistance surfaces (where higher values imply lower suitability for use or movement) have been generated from RSF or RSPF models (where higher values imply greater levels of habitat use) by simply inverting the resistance surface (e.g. Chetkiewicz & Boyce 2009),

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different models for scaling the resulting resistance surface warrant exploration. This is particularly true because animals might be more willing to travel through poor-quality habitat during rapid long-distance movements than during daily foraging. We created a basic resistance surface by inverting probabilities of selection from the RSPF model (1/RSPF) across the entire landscape for the genetic study, but then used recent gene flow estimates (Program BIMR, see above) to optimize the 1/RSPF model. We created models of increasingly lower resistance by transforming the 1/RSPF resistance model using power transformations ranging from 1 (no change) to 0.2 [$(1/\text{RSPF})^{1/5}$], and used CIRCUITSCAPE to calculate cumulative resistance among populations for each transformation. We used simple Mantel tests to determine which transformation was most strongly correlated with estimates of recent gene flow (Fig. S4, Supporting information), and used that optimized model [hereafter, the 'contemporary (RSPF)' resistance model] for further testing.

Testing and comparing models of historical and contemporary connectivity with recent gene flow

We predicted that genetic structure (historical gene flow) would be predicted by persistent landscape features (described earlier) but not human activity and that recent gene flow would be predicted by both persistent landscape features and human activity. We used MRDM to estimate whether recent gene flow estimates were predicted by cumulative resistance estimates from (i) the historical resistance model, (ii) the contemporary resistance model and (iii) a combined model, which used the highest value from the historical or contemporary models in each grid cell. By using the highest value, we assumed that resistance due to human activity (the primary driver of the combined model, see Results) would be additive to resistance from persistent landscape features that would affect gene flow in all time frames. Next, we used multivariate MRDM and the effects tests for each variable to evaluate our predictions that: (i) recent gene flow estimates would be predicted by contemporary resistance even after controlling for geographic distance by including it as a covariate, (ii) recent gene flow estimates would be predicted by both contemporary resistance and historical resistance and (iii) recent gene flow estimates would be predicted by the combined (historical plus contemporary) resistance model better than by the historical landscape model alone. Finally, we used MRDM to test our prediction that historical gene flow (F_{ST} and G'_{ST}) would not be predicted by the contemporary landscape resistance model.

As an additional test of the contemporary and historical resistance models, we evaluated posterior probabilities for competing explanatory models in Program BIMR. Matrices from each potentially explanatory model (e.g. geographic distance, or cumulative resistance) can be used by BIMR as priors for migration rate estimation; posterior probabilities are then estimated for each model and combinations of models allowing comparisons of model performance (Faubet & Gaggiotti 2008). First, we used BIMR to test the performance of the historical model in contrast to IBD and an empty model with no explanatory matrices, as a further test of the historical model's influence on recent gene flow. Next, we used BIMR to estimate the posterior probability of the historical model, the contemporary (RSPF) model, and both models simultaneously as separate variables (not combined). Lastly, we contrasted posterior probabilities of the combined (historical and present day) model and the historical model, but excluded simultaneous estimates for both models, because the combined model included the historical model. For each test, we evaluated average posterior probabilities across 10 replicate analytical runs, and also evaluated posterior probabilities for the run with the lowest Bayesian deviance for assignments (the most likely run, Faubet 2007).

Finally, we evaluated the ratio of cumulative resistance estimates from the combined resistance model to the historical model for each population pair. We used these ratios to rank pairwise comparisons and identify which pairs of sampling areas have experienced the greatest declines in connectivity.

Results

Genetic samples and structure

At the population level, no microsatellite loci exhibited significant linkage disequilibrium after Bonferroni correction for multiple comparisons (72 of 840 comparisons were significant at $P < 0.05$). Across all populations, no pairs of loci were in significant linkage disequilibrium after correction for multiple comparisons (14 of 120 were linked at $P < 0.05$). Tests by population and by locus exhibited no significant departure from Hardy–Weinberg equilibrium after correction for multiple comparisons. We observed very low F_{IS} values in the seven populations (Table 1), and F_{ST} values between sample clusters within the two largest polygons (Selous and Katavi-Rukwa) were among the lowest observed (0.004 and 0.005), suggesting that little genetic structure existed within the original polygons and thus they were ecologically defensible.

Historical and recent estimates of gene flow

African elephant populations among central and southern protected areas in Tanzania were at most weakly

Table 2 Slatkin's (1995) linearized F_{ST} values (above diagonal) and migration rates (percentage of genes derived from migrants within the last generation as estimated by BIMR (Faubet & Gaggiotti 2008), below diagonal), among African elephant populations in seven protected areas in Tanzania

	Katavi	Mikumi	Ruaha	Muhesi	Selous	Tarangire	Udzungwa
Katavi	—	0.022	0.004	0.004	0.040	0.012	0.016
Mikumi	0.00864	—	0.015	0.017	0.008	0.011	0.005
Ruaha	0.0836	0.0365	—	0	0.034	0.007	0.021
Muhesi	0.0210	0.0214	0.127	—	0.029	0.006	0.014
Selous	0.000124	0.205	0.00359	0.000409	—	0.020	0.022
Tarangire	0.00184	0.0150	0.0243	0.00423	0.000532	—	0.004
Udzungwa	0.000174	0.0621	0.00842	0.000574	4.53×10^{-8}	0.000608	—

differentiated with a global F_{ST} estimate of 0.014 and relatively similar estimates of genetic diversity (Table 1). Population pairwise linearized F_{ST} values among sampling polygons ranged from 0 to 0.04 (Table 2). Estimates of recent (BIMR *m*) gene flow among elephant populations showed considerable variation among different pairs of protected areas (Table 2; Fig. S5, Supporting information), but were relatively consistent across runs (data not shown). Both analyses suggested very weak genetic structure and high levels of gene flow among western protected areas (Ruaha, Muhesi and Katavi) as well as between Mikumi and Selous in the east, and moderate levels of gene flow across the field study area (Ruaha-Udzungwa-Mikumi; Table 2). Estimates of historical genetic structure suggested moderate connectivity of elephants in Tarangire with both western and eastern protected area clusters; recent gene flow estimates for those comparisons were moderate to weak (Table 2).

After simulating a 10-fold decrease in migration rates across all populations, for simulated populations and sample sizes representative of our study, at least four generations (100 years) were needed to detect a change in genetic structure (see Figs S2-1 and S2-2 in Appendix S2, Supporting information).

Resource selection function model and contemporary resistance surface

We detected elephants at 2207 locations on 38 of 61 transects. Elephant activity spanned nearly the entire field study area but was not ubiquitous (Fig. 2); although we did not separate wet- and dry-season data, we noted elephant activity far outside of protected areas in both seasons. The final RSPF model was in the form of the logistic RSPF (Table S3, Supporting information) and showed that the elephants selected protected areas, mid-range slope values and cooler aspects, but avoided areas with higher human population density, agriculture and greater distances to water (Table 3; Fig. S6, Supporting information). Human population density and protected area status had the strongest effects based on SIC (Table S3, Supporting information) and effect size (Table 3). The variables in the final model are consistent with other studies on elephant habitat use (Wall *et al.* 2006; Cushman *et al.* 2010; de Knegt *et al.* 2011), suggesting that our sampling and analytical design was appropriate for quantifying habitat use by elephants in this area.

Testing and comparing models of historical and recent gene flow with contemporary connectivity

We did not detect IBD in our indices of historical gene flow (Table 4). However, we detected strong isolation by resistance (IBR) from slope (Table 4), with the highest correlation at $(\text{slope})^{1.5}$, hereafter the 'historical (slope) model' (Fig. S1, Supporting information). A multivariate MRDM model including both slope and geographic distance performed no better than the model for slope alone, and the effects test did not support geographic distance (Table 4). Historical gene flow was not predicted by distance to water (Fig. S2, Supporting information) or the optimized contemporary resistance model (Table 4). Recent gene flow (square root transformed to improve linearity, Figs S7 and S8, Supporting information) likewise was not predicted by geographic distance but was strongly predicted by the historical (slope) resistance model (Table 4).

The untransformed 1/RSPF model was slightly less correlated with recent gene flow ($r = 0.47$, $P = 0.001$) than was the IBD model (Fig. S4, Supporting information). However, the cube root transformation of the 1/RSPF resistance model was much more strongly correlated with recent gene flow estimates ($r = -0.65$, $P < 0.0001$; Fig. S4, Supporting information): thus, the untransformed 1/RSPF model appeared to overestimate resistance. MRDM likewise supported the optimized (cube root) 1/RSPF resistance (hereafter, "contemporary [RSPF]") model but not IBD (Table 4). The multivariate MRDM models including both contemporary (RSPF) and historical (slope) resistance models supported both

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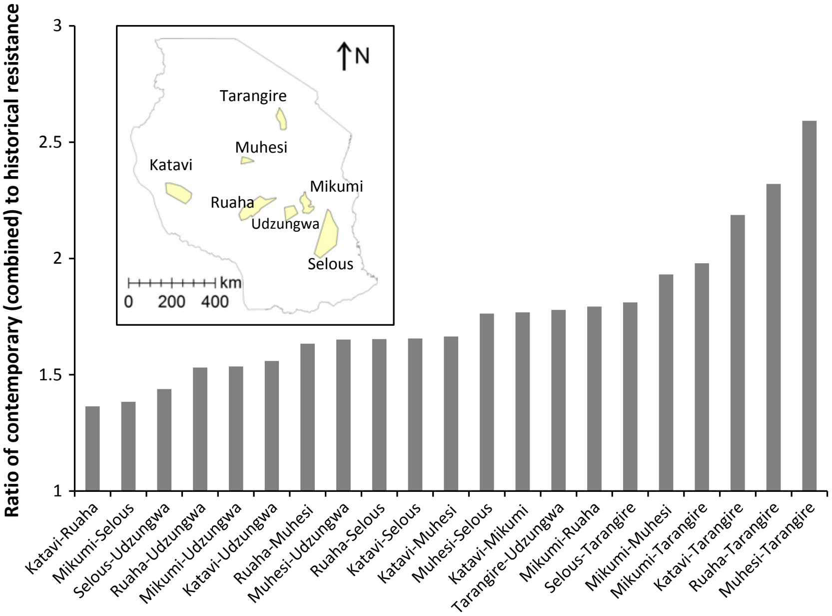

Fig. 4 Ratio of cumulative population pairwise resistance estimates (combined resistance model/historical resistance model) for seven elephant populations sampled in central and southern Tanzania (named in inset map of sampling polygons). Higher ratios indicate increased resistance in the contemporary compared to historical time frames. Pairwise comparisons including Tarangire National park had the greatest increase in resistance due to intense human activity in northeastern Tanzania.

variables but not geographic distance; R^2 values from univariate MRDM models suggested that the historical (slope) model explained more variation in recent gene flow than did the contemporary (RSPF) model (Table 4). Finally, the combined resistance model (based on maximum values for the historical and contemporary models) had the highest R^2 of any univariate MRDM model, and was the only variable supported in multivariate models including both slope and the combined model (Table 4). Many of these variables were strongly collinear (Table S1, Supporting information), but conclusions were consistent across analyses.

Conclusions from evaluating posterior probabilities of competing explanatory models for recent gene flow (in Program BIMR) were similar. The first test demonstrated that the historical (slope) model was strongly favoured over the IBD model (Table 5). In the second test that compared the historical (slope) model and the contemporary (RSPF) resistance model, migration rates were best explained by the historical (slope) model although the contemporary (RSPF) model had higher relative support than geographic distance in the previous analysis. However, the third test that contrasted posterior probabilities for the historical (slope) model and the combined resistance model indicated that the migration rates were best explained by the combined model across the majority of replicate runs: thus, recent gene flow reflected both the contemporary (largely driven by human activity) and historical (slope) estimates of resistance (Table 5).

The predicted patterns of gene flow shifted markedly from the historical to the combined model (Fig. 3). Resistance increased between all pairs of protected areas, but, by far, the largest increases occurred between Tarangire National Park and protected areas to the south due to the dense human settlement in northeastern Tanzania (Figs 3 and 4).

Table 3 Parameter estimates and significance tests for variables in the best-supported resource selection probability function (RSPF) model (based on model selection with Schwarz Information Criteria) for elephants in central Tanzania

Effect	Estimate	SE	z value	P (>|z|)
Intercept	−2.704	0.119	−22.633	<0.0001
Human population density*	−1.691	0.112	−15.084	<0.0001
Distance from water (km)†	−0.102	0.015	−6.877	<0.0001
Slope‡	12.929	1.348	9.594	<0.0001
(Slope)^2	−23.044	3.122	−7.382	<0.0001
Protected area status§	2.355	0.136	17.315	<0.0001
Agricultural areas¶	−1.829	0.195	−9.379	<0.0001
‘Aspect’**	0.280	0.073	3.833	0.0002

*Ward level, 2002 census; standardized about mean (11.304) and standard deviation (8.272).

†Estimated using AFRICOVER C. 1997 (FAO 2005).

‡Transformed and converted from degrees to radians as: sine ((slope * π)/180).

§Scored as ‘1’ if within a patrolled protected area (see Appendix S4); estimated using a corrected version of the World Database of Protected Areas (v. 2005).

¶Scored as ‘1’ if within agricultural areas identified by AFRICOVER C. 1997 (FAO 2005).

**Transformed and converted from degrees to radians as: sine (((Aspect + 225) * π)/180).

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Table 4 Tests of explanatory models for historical and recent gene flow among elephant populations in Tanzania using multiple regression of distance matrices (MRDM), conducted in Program R using the *ecodist* package. Scatterplots of the univariate relationships are presented in Figs S3, S7 and S8 (Supporting information). Variables that are supported by significant ($P < 0.05$) model F tests (univariate models) or effects tests (multivariate models) are indicated in bold

					Effects test for single variables in multivariate models	
Response	Model	Model R^2	Model F test	Significance of model F test	Variable	P value
Linearized F_{ST}	Geodis[*]	0.033	7.21	0.076	—	—
	Slope[†]	0.130	31.09	0.002	—	—
	RSPF[‡]	0.005	1.02	0.407	—	—
	Geodis + **Slope**	0.136	16.23	0.007	Geodis	0.481
					Slope	0.004
G'_{ST}	Geodis	0.040	8.66	0.077	—	—
	Slope	0.170	41.69	0.001	—	—
	RSPF	<0.001	<0.01	0.961	—	—
	Geodis + **Slope**	0.173	21.62	0.003	Geodis	0.499
					Slope	0.002
BIMR[§]	Geodis	0.037	8.00	0.078	—	—
	Slope	0.352	113.2	0.0001	—	—
	RSPF	0.188	48.07	0.0004	—	—
	Combo[¶]	0.464	179.8	0.0001	—	—
	Geodis + **Slope**	0.352	56.32	0.0001	Geodis	0.945
					Slope	0.0001
	Slope + **RSPF**	0.419	74.58	0.0001	Slope	0.0001
					RSPF	0.0016
	Slope + **RSPF** + Geodis	0.430	51.70	0.0002	Slope	0.0001
					RSPF	0.0012
					Geodis	0.2570
	Slope + **Combo**	0.465	89.79	0.0001	Slope	0.6699
					Combo	0.0008
	Slope + **Combo** + RSPF	0.465	59.79	0.0002	Slope	0.5651
					Combo	0.0162
					RSPF	0.6625

RSPF, resource selection probability function.

[*] Geographic distance.

[†] Optimized model used in all tests: (Slope)$^{1.5}$.

[‡] Optimized model used in all tests: (1/RSPF)$^{0.33}$.

[§] Square-root transformed to improve linearity (see Figs S7 and S8). Tests using the untransformed estimates showed identical conclusions about the relative importance of variables but slightly lower fits for the overall models (not shown).

[¶] Resistance model created using the highest value from the Slope$^{1.5}$ and (1/RSPF)$^{0.33}$ models for each grid cell.

Discussion

Historically, gene flow among most African elephant populations in central and southern Tanzania (Table 2, Fig. 3c) was high (as observed in Kenya, Okello *et al.* 2008). However, estimates of recent gene flow, field assessment of elephant activity among three central protected areas, and our model of contemporary landscape resistance based on habitat use suggested that connectivity is now threatened, if not absent, among some populations that were linked previously by relatively strong gene flow. Although topography was still the strongest determinant of recent gene flow, expanding human settlement has caused detectable changes in recent gene flow among protected areas in Tanzania. Landscape resistance has not increased evenly: among many protected areas, substantial potential for gene flow still remains, while other connections are likely severed at this time (Figs 3, 4 and S6, Supporting information).

Using multiple types of data to optimize resistance models allowed new inferences and improved model performance, although each type had limitations. For instance, while the contemporary resistance model (derived from location data) explained variation in recent gene flow, adding the historical model clearly improved model performance (combined model, Table 4). Moreover, the un-optimized contemporary (1/RSPF) model may have overstated the influence of

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Table 5 Posterior probabilities of explanatory models for pairwise estimates of recent gene flow (previous generation) among elephant populations in central and southern Tanzania, estimated using a Bayesian population assignment test (Program BIMR; Faubet & Gaggiotti 2008)

Test	Explanatory model(s)	Proportion of runs with highest posterior probability	Average posterior probability*
Historical vs. distance	None	0/10	0.05
	Distance	0/10	0.05
	Historical (slope)[†]	10/10	**0.63**
	Distance, Historical (slope)	0/10	0.25
Historical vs. contemporary	None	0/10	0.04
	Historical (slope)	10/10	**0.44**
	Contemporary (RSPF)[‡]	0/10	0.17
	Historical, Contemporary (RSPF)	0/10	0.24
Historical vs. combined	None	0/10	0.02[§]
	Historical (slope)	2/10	0.32
	Combined[¶]	8/10	**0.40**[§]

RSPF, resource selection probability function.

*The model favoured in the run with lowest Bayesian deviance is indicated in boldface for each test.

[†] Optimized model used in all tests: $(\mathrm{Slope})^{1.5}$.

[‡] Optimized model used in all tests: $(1/\mathrm{RSPF})^{0.33}$.

[§] Although the combined model was always favoured in >75% of the runs, in one of three replicate analyses (not shown), the null model was favoured in the single run with the lowest Bayesian deviance (but only in that run); we speculate that this may have resulted from strong colinearity between the slope and combined models.

[¶] Resistance model created by comparing the $\mathrm{Slope}^{1.5}$ and $(1/\mathrm{RSPF})^{0.33}$ models in the Geographic Information System and using the highest value from each overlapping pair of grid cells.

human activity on connectivity because it was based on habitat use rather than movement: elephants might better tolerate human activity when rapidly dispersing through an area vs. foraging. Using the recent gene flow estimates to optimize the contemporary model resulted in lower resistance estimates. Our data set only slightly exceeded the minimum genetic structure recommended for BIMR, and our sample sizes (Table 1; mean = 31) were lower than those tested by Faubet & Gaggiotti (2008, $n = 50$). Thus, although our recent gene flow estimates were consistent with the models developed from other data, individual estimates among population pairs should be interpreted with caution especially where sample sizes were low.

Our approach does not fully delineate different timescales. For instance, our indices of historical gene flow (F_{ST} and G'_{ST}) must have included some effects of recent landscape changes, particularly as the effects of past landscapes disappear more quickly for animals with long dispersal distances (Landguth *et al.* 2010). However, our finding that at least four generations (for elephants, 100 years) after a severe decline in gene flow would be needed to detect a change in genetic structure for these populations (simulated data, Appendix S2, Supporting information) supports our assumption that genetic structure of elephant populations in Tanzania largely reflects conditions prior to twentieth century human population explosion. Even our recent gene flow estimates may still reflect a time lag: because elephant generations overlap, the previous generation of living individuals would include animals alive within the last ~100 years. Our analysis was also complicated by strong colinearity among some competing models (such as the historical and combined modes). However, we believe that the combined model is most suitable for modelling gene flow on the current landscape (Fig. 3), because it incorporates empirical data on gene flow as well as the impacts of recent human activity.

The influence of human activity varied sharply over time. Although we observed high levels of elephant activity in some locations far outside protected areas (Fig. 2), contemporary elephant habitat selection and thus resistance was most strongly influenced by human activity (Table 3). As observed elsewhere (e.g. Douglas-Hamilton *et al.* 2005; Galanti *et al.* 2006; Wittemyer *et al.* 2007; Blake *et al.* 2008; Pittiglio *et al.* 2011), areas with higher human population density, outside protected areas, and within agricultural areas were strongly less selected by elephants (Table 3, Fig. S6, Supporting information), probably because of conflict with humans and high levels of illegal harvest in Tanzania (Wasser *et al.* 2009). Recent gene flow estimates were best predicted by slope but also were predicted by contemporary resistance and thus human activity (Table 4). However, variation in historical gene flow (F_{ST} or G'_{ST}) was not predicted by the contemporary resistance

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model (Table 4), further indicating that genetic structure still largely reflected the historical landscape.

The effect of persistent landscape features also varied across timescales and models, but had consistent elements. For instance, steep slopes impeded movement in historical, recent, and contemporary time frames (Tables 3–5). African elephants clearly use mountainous areas and can negotiate relatively steep slopes over short distances, but long-distance movement over steep terrain may be restricted by energetic limitations (Wall *et al.* 2006). However, the contemporary (habitat selection) model showed that elephants now select mid-range slopes (slope and its quadratic, Table 3), suggesting that the elephants are shifting to steeper habitats, perhaps because human settlement often occurs on lower slopes in river valleys. Other differences between historical and contemporary models likely resulted because elephants respond to different habitat elements at local vs. landscape scales (de Knegt *et al.* 2011). Distance to water did not affect historical gene flow (Fig. S2, Supporting information), perhaps because elephants are less closely tied to water during the wet season (personal observation), but elephants selected areas near water and cooler aspects in the best-supported RSPF model based on contemporary locations (Table 3). Thus, water availability and microsite characteristics affect fine- but not coarse-scale movements (de Knegt *et al.* 2011), again demonstrating that habitat use is a different process than gene flow.

The different scales and biological processes involved (e.g. dispersal and reproduction vs. daily foraging) necessitate caution when making comparisons across models. However, the strong effect of slope on movement as inferred from the genetic data highlights the utility of combining genetic analyses (which address connectivity in the sense of movement followed by breeding) with habitat-use models based on the occurrence data, because the latter may not fully reflect the influence of landscape on long-distance movements. Conversely, the addition of the habitat model highlighted the importance of human activity on the contemporary landscape and helped address the time lag inherent to genetic-based models. Thus, our study underscores the need for multiple lines of evidence when estimating connectivity (Cushman & Lewis 2010).

The connectivity of elephant populations in Tanzanian protected areas reflects a landscape in transition: elephants are still moving surprising distances outside protected areas (Fig. 2), even over steep terrain and near human settlements, but areas of dense human settlement and poaching threats have likely greatly reduced or eliminated many such movements (Figs 3 and 4). Movement corridors across the Ruaha-Udzungwa-Mikumi field study area (Fig. 2) appear highly threatened: local people described some routes that appear to have already been abandoned, while others fall near areas with rapid expansion of housing and agriculture (see Jones *et al.* 2009; Epps *et al.* 2011). Movements across the field study area may be the only remaining link between eastern/southern and northern/western populations of elephants in Tanzania (Fig. 3c,d). However, connectivity appears mostly intact among the park and game reserves of the Ruaha ecosystem and Katavi National Park to the west (Figs 1, 3, 4 and S6, Supporting information) as well as between Mikumi National Park and the Selous Game Reserve. Those populations also showed the highest connectivity in the past (Table 2; Fig. 3a,c).

Invoking the historical landscape involves much uncertainty, and we should not assume elephants moved without restriction until recent decades. Humans have been present in Tanzania for millennia, and it is clearly erroneous to envision existing protected areas as remnants of untouched wilderness: many had human settlement, agricultural or pastoral activity before people were removed during reserve establishment. Other areas may have reopened to elephants in the late 1960s during Tanzania's *Ujamaa*, a period of government-induced social change that included widespread resettlement and village consolidation. Furthermore, elephant hunting for ivory was widespread in the nineteenth century and even earlier, although the scale of elephant killing in Tanzania may have increased sharply in the late twentieth century (Wasser *et al.* 2009). However, elephants were known to occur across nearly the entire country in the nineteenth and early twentieth centuries (summarized by the Tanzania Mammal Atlas Project, Anonymous 2007), and recent human population size far exceeds past levels. While Kjekshus (1977) argued that settlement patterns prior to European colonization of the interior were more widespread and stable than is often assumed, he also stated 'we should immediately recognize that large parts of the country have never been vied for as areas of human exploitation' (p. 48). Thus, our findings strongly suggest that current patterns of human settlement are causing unprecedented changes in connectivity among elephant populations.

African elephants exemplify the challenges inherent to connectivity conservation. They are large and wide ranging, but increasingly restricted to protected areas due to conflict with humans. Loss of migration routes in other areas of East and Southern Africa has led to local overpopulation of elephants and caused habitat destruction (e.g. Amboseli NP and Kruger NP). For elephants, as for other species, we must ask whether it is worth investing the resources to preserve movement corridors among protected areas. In that context, understanding both long-term and contemporary patterns of

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movement or gene flow will help us prioritize based on high levels of previous connectivity, high threat to contemporary connectivity, or both.

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C.E. and J.B. designed the field study, C.E. carried out the field study with assistance from B.M. and J.B., S.W., B.M. and C.E. collected genetic samples; S.W. and B.M. generated the genetic data; J.K., C.E. and S.W. developed the RSPF model; C.E. designed and conducted connectivity and genetic analyses and C.E. led writing of the paper with assistance from all authors.

Data accessibility

Microsatellite data for elephants (Genepop file); elephant detections, random locations along transects and accompanying data for variables included in RSPF model; geographic distance matrix; cumulative resistance matrix (slope$^{1.5}$); cumulative resistance matrix (distance to water^{1}); cumulative resistance matrix [(1/RSPF)$^{0.33}$]; cumulative resistance matrix (combined model); slope GIS raster data (untransformed); distance to water GIS raster data (untransformed), RSPF model (not converted to resistance) as a GIS raster; GIS vector layer describing genetic sampling polygons: DRYAD entry doi:10.5061/dryad.q03 g2.

Supporting information

Additional supporting information may be found in the online version of this article.

Appendix S1 Detailed protocols for faecal genotyping.

Appendix S2 Simulated change in genetic structure after reduction in migration rates.

Appendix S3 Detailed settings for Program BIMR and CIRCUITSCAPE.

Appendix S4 Detailed description of field study area and protocol for walking transects.

Table S1 Correlation among explanatory variables.

Table S2 Labels and definitions for resource selection covariates.

Table S3 Candidate models for resource selection analyses.

Fig. S1 Optimization of the slope resistance model.

Fig. S2 Optimization of the distance to water resistance model.

Fig. S3 Scatterplots of genetic distance vs. explanatory variables.

Fig. S4 Optimization of the resource selection probability function resistance model.

Fig. S5 Recent migration rates vs. cumulative resistance values (combined model).

Fig. S6 Resource selection probability function (RSPF) model of elephant habitat use.

Fig. S7 Scatterplots of recent gene flow vs. explanatory variables.

Fig. S8 Scatterplots of recent gene flow (transformed) vs. explanatory variables.

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