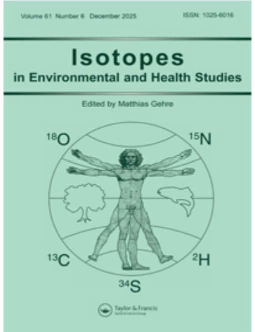

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Elephant range and population, strontium isotopes, and genetics combine to give local-scale specificity to ivory hotspot tracking*

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ABSTRACT
We use Sr isotopes to increase the precision of DNA-based origin estimates of wildlife products. Population information is used to develop Sr isotope Elephant Polygons that are overlaid onto the region of origin identified by DNA assignment to determine the sources of seized ivory samples. Our approach is cognizant of isotope mixing due to isotope turnover within animals and also of the large home range of elephants or other mobile species. Genetic information from 3 different law enforcement ivory seizures suggests a region of origin confined to Kenya and Tanzania in eastern Africa. We determine characteristic $^{87}Sr/^{86}Sr$ ratios for each of 25 different Elephant Polygons within this region using analyses of more the 600 known-origin reference samples. Using both the $^{87}Sr/^{86}Sr$ ratios of the seized ivory samples and elephant population estimates from individual Elephant Polygons we find that at least 75 % of the samples likely came from a single Elephant Polygon which includes the Tsavo National Parks in Kenya and the Mkomazi National Park in Tanzania. A few samples

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*Dedicated to the memory of Professor Keith Alan Hobson – Pioneer of isotope ecology.

may have come from other regions, most likely from Tanzania. This study illustrates the value of combining genetics, isotope geochemistry, and population surveys in wildlife forensics studies.

1. Introduction

Transnational ivory trafficking severely impacts elephant populations, from driving population decline to spurring the evolution of loss of tusks , to increasing hybridization rates among forest and savanna elephants [1–5]. Spatially interpolated genetics have been used to understand the likely originating region of poached ivory recovered by law enforcement [2–6]. However, the large search footprint and coarse resolution limit focused management actions targeting areas of highest poaching concern or local policy development to address vulnerabilities such as corruption and poverty [4,7]. We add to spatial resolution by combining genetic information with strontium isotope ratios ($^{87}Sr/^{86}Sr$) determined by local geological knowledge to refine the likely source regions of illegally harvested ivory in eastern Africa. If carefully applied, these methods could provide targeted insight into geographic regions that may be hotspots for illegal poaching, providing the basis for government- and community-oriented policy decisions.

Genetic methods applied to elephant ivory provenance are able to identify the geographical centroid of origin to a 1° x 1° latitude/longitude location with an uncertainty radius of about 400 km [3]. This resolution significantly assists in tracking trade routes of illegal ivory post-poaching, illuminating part of the structures and methods used by transnational trafficking organizations [2,4,5]. Increasing the accuracy of origin assignments could significantly strengthen such law enforcement efforts.

In this paper, we determine characteristic mammal $^{87}Sr/^{86}Sr$ ratios across East Africa (called an '$^{87}Sr/^{86}Sr$ isoscape' [8]), which link mammals to the geologic bedrock that is the basis for bioavailable strontium [9,10]. Van der Merwe et al. [11] and Vogel et al. [12] recognized the utility of Sr and other isotopes related to geological substrates for determining ivory provenance; spatial interpolation of isotopic variation along landscapes has been useful in increasing the resolution from those early studies [13–15]. Coutu et al. [14] notably establish a strong link between bedrock and elephant ivory $^{87}Sr/^{86}Sr$ ratios in eastern Africa. Our strategy builds on other foundational isotope forensic work using $^{87}Sr/^{86}Sr$ ratios to study migration and origin patterns [16–22]. Elephants differ from some previously studied species because they have particularly large home ranges which can be up to many hundreds to thousands of square kilometres [23,24] and thus an individual $^{87}Sr/^{86}Sr$ ratio is integrated over a large area that may include multiple geological substrates. Previous studies, e.g. [20,25–27] have demonstrated high spatial heterogeneity of soils, plants, and rodents; our approach uses known origin samples that integrate over large spatial regions characteristic of savannah elephants, known to have a relatively large home range. Home range is important because Yang et al. [27] have shown that Sr turnover in elephants takes on the order of 2 years for blood serum to come to isotope equilibrium with the environment, and thus $^{87}Sr/^{86}Sr$ ratios in ivory will include a contribution of previous localities visited in the prior two years.

We present 973 new strontium isotope analyses of mammal samples from Africa. We use 616 samples from Eastern African samples with known locations to link to local geologic bedrock types in eastern Africa (Figure 1, Table 1). To assign origins to recently

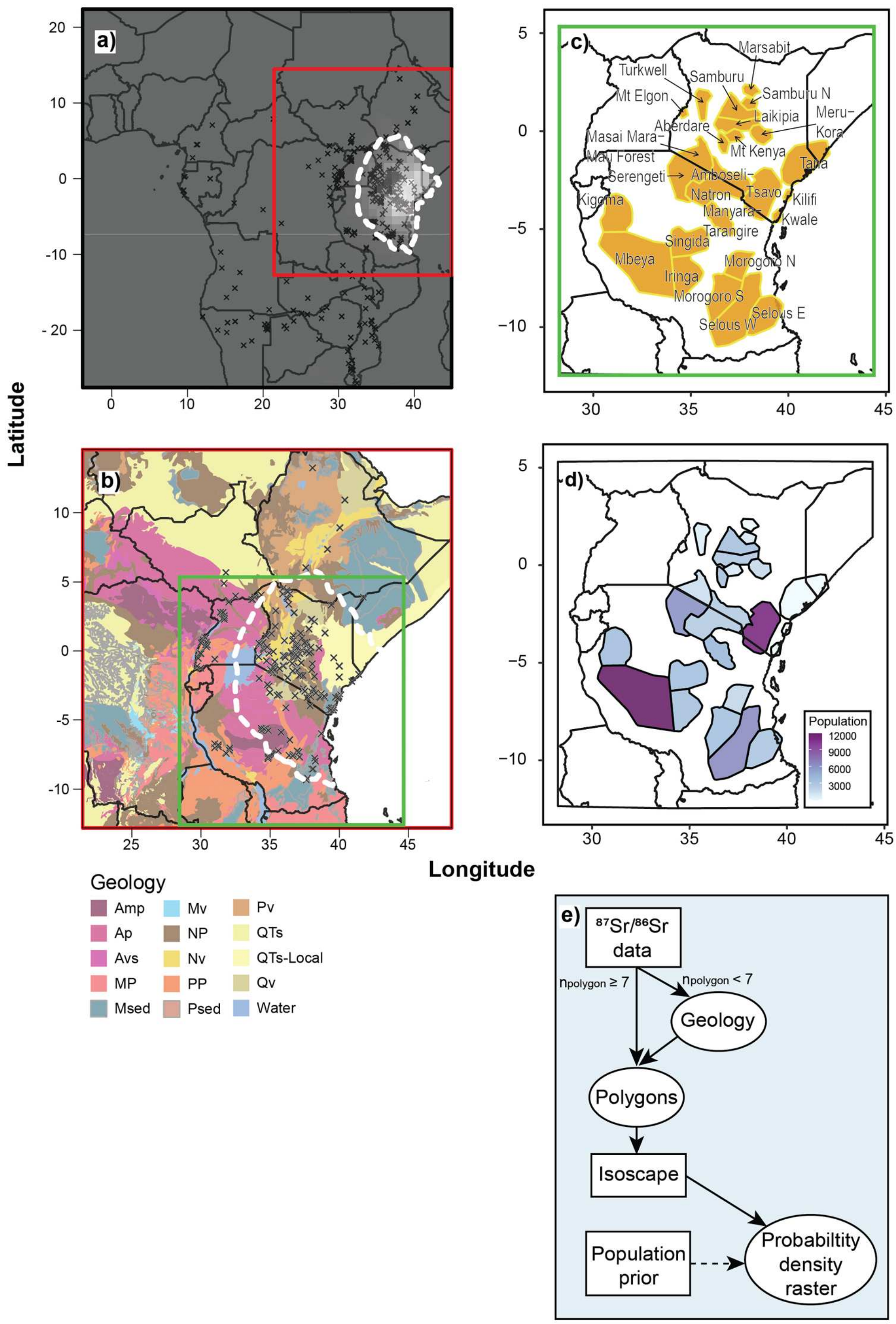

Figure 1. a) Aggregated genetic origin probability raster for 52 unknown-origin samples evaluated in this study, with locations of all samples collected for this study. b) Eastern Africa simplified geology with samples used in the isoscape development; with samples from eastern Africa used in this study. Green box shows area of Figure 1 c). c) 'Elephant Polygons' are considered in this study based on census data from Thouless et al. [28]. d) Relative population numbers of elephants within the Polygons. Country boundaries in Figure 1 b) are plotted using the rnaturalearth package [33].

Table 1. Characteristic $^{87}Sr/^{86}Sr$ ratios for geological substrates in region. Data from Appendix I. Geological age and lithologies for geological assignment types are in Table SI 2.1.1.

Geological assignment	n	$^{87}Sr/^{86}Sr$	1σ
Amp	11	0.7338	0.0075
Ap	79	0.7133	0.0046
Avs	12	0.7246	0.0105
MP	16	0.7165	0.0045
Msed	29	0.7128	0.0028
NP	156	0.7083	0.0019
Nv	108	0.7072	0.0016
PP	36	0.7218	0.0076
Pv	31	0.7057	0.0012
QTs-Local	19	0.7075	0.0009
Qv	119	0.7058	0.0011
Total	616		

seized ivory, we subset the areas of interest based on local elephant ranges as determined in the recent African continent-wide elephant census [28] and determine a characteristic $^{87}Sr/^{86}Sr$ ratio distribution for each of these areas, which we call 'Elephant Polygons'. We use both direct measurements from Elephant Polygons with a sufficient ($n > 6$) sample from within the polygon boundary, and we calculate characteristic $^{87}Sr/^{86}Sr$ ratios for less well sampled polygons used the weighted geological contribution to each of those polygons. We then examine 16 elephant samples of known origin, and a subset of 52 samples from three recent law enforcement seizures of ivory whose DNA-based geographical assignments were centered in the Kenyan–Tanzanian region of eastern Africa within the area of our sampling of geological substrates and Elephant Polygons. We ask whether the samples were all derived from a single region within Kenya–Tanzania, whether a single region dominated the seizures, or whether the samples were derived from many locations with no bias towards a single region. We discuss the utility of combined genetic and isotopic sourcing for determining the provenance of ivory and other illegally traded wildlife products.

2. Results and interpretation

2.1. Strontium isoscapes for ivory forensics

Southern Kenya and northern Tanzania can be characterized as being comprised of 14 geological substrates, ranging in age from Archean to Quaternary and including plutonic igneous rocks, volcanic igneous rocks, metamorphic rocks, sedimentary rocks, and Quaternary alluvial sediments derived from upstream outcrops. However, for wildlife forensic science studies, bio-available Sr must be considered rather than bedrock Sr variations across the landscape. Minerals weather at different rates [29], aerosols of dust and sea-spray contribute Sr to the landscape [25,30], and rivers bring upstream Sr into downstream landscapes [17]; all contribute to bioavailable Sr. Various approaches have been used to evaluate bio-available Sr in different landscape systems, e.g. [10,20,22,31], and it is evident that problem-specific approaches may use different datasets to evaluate bio-available Sr.

Elephant tusks have a hollow cone starting at the base. We sample the innermost part of the cone nearest the base, which integrates over a period of growth of approximately

3–6 months prior to death. Since elephants have a large home range measuring 100s to 1000s of km^2 [23,24,32] we use reference data from mammals that integrate over large areas. Samples include ivory, enamel, bone, hair, and dung. One region, the greater Tsavo ecosystem, included samples of all these materials; Table SI 3.1.1 shows that the different tissues have similar average $^{87}Sr/^{86}Sr$ isotope ratios and standard deviations although the different tissues integrate over different time periods (years for ivory, enamel, or bone; days for hair or dung), suggesting that the different materials equally characterized the local environment with respect to $^{87}Sr/^{86}Sr$ ratios.

Supplementary Information, Section 2 describes the baseline geological map and the combining of related geological units in this study. A more detailed geological map may be needed for local migration studies, especially where migration across geological distances of a few kilometres is the object of the study [19,20,22,34], or when evaluating dust versus weathering contributions from differing bedrocks [26].

Characteristic $^{87}Sr/^{86}Sr$ ratios for each geological substrate were determined by analysis of the 622 reference samples whose location could be confidently assigned to a geological substrate (with confidence levels of gps, g, or m ('Global Positioning System', 'good', 'medium', respectively; see SI 1.1 for detailed definitions of terms) and was from an animal with a relatively large home range. Table 1 shows the characteristic $^{87}Sr/^{86}Sr$ ratio for each of the 11 substrates from which we have measured data. Quaternary volcanic (Qv) regions, such as those associated with Mt Kenya or Mt Kilimanjaro, have the least radiogenic values and average 0.705, whereas the most radiogenic geological units are from the Archean, with $^{87}Sr/^{86}Sr$ average values as high as 0.734 for Amp (Archean metamorphic–plutonic). Figure 2a) shows $^{87}Sr/^{86}Sr$ by substrate. Although much of the data in this study will be applicable to other study areas, we have insufficient data to know if the geological substrates have consistent $^{87}Sr/^{86}Sr$ ratios continent-wide and therefore take a conservative approach to isoscape development for continental scale studies and apply this data only to eastern Africa at the present time.

For the purposes of this study, which is to determine the most likely origin of seized ivory samples, we take a different approach than most previous studies of $^{87}Sr/^{86}Sr$ isoscapes. For example, Janzen et al. [20] produce a high resolution $^{87}Sr/^{86}Sr$ isoscape of local parts of Kenya and Tanzania with the purpose of studying local migration patterns. Our basis for ivory provenance studies is to start with the current distribution of elephants in Africa using the survey of Thouless et al. [28], which identifies the areas in which elephants are found in Eastern Africa, with population estimates for each polygon. Based on the Voronoi coordinates with their inherent uncertainties for the location of the seized ivory samples we are studying, we consider the area of Eastern Africa from 5N to 10S latitude, and 30E to 42E longitude, and limit our search considerations to that area. Starting with the areas delineated in the continental survey, we characterize each polygon for its characteristic $^{87}Sr/^{86}Sr$ ratio as discussed below.

2.2. Elephant polygons

This study considers the provenance of ivory in three ivory seizures. Carbon-14 studies of seized ivory show that most ivory of recent seizures is from animals that died a few years before seizure by law enforcement [35], although at least one stockpile that was ca. 30 years old was compromised in the past decade [36]. No seized ivory from large

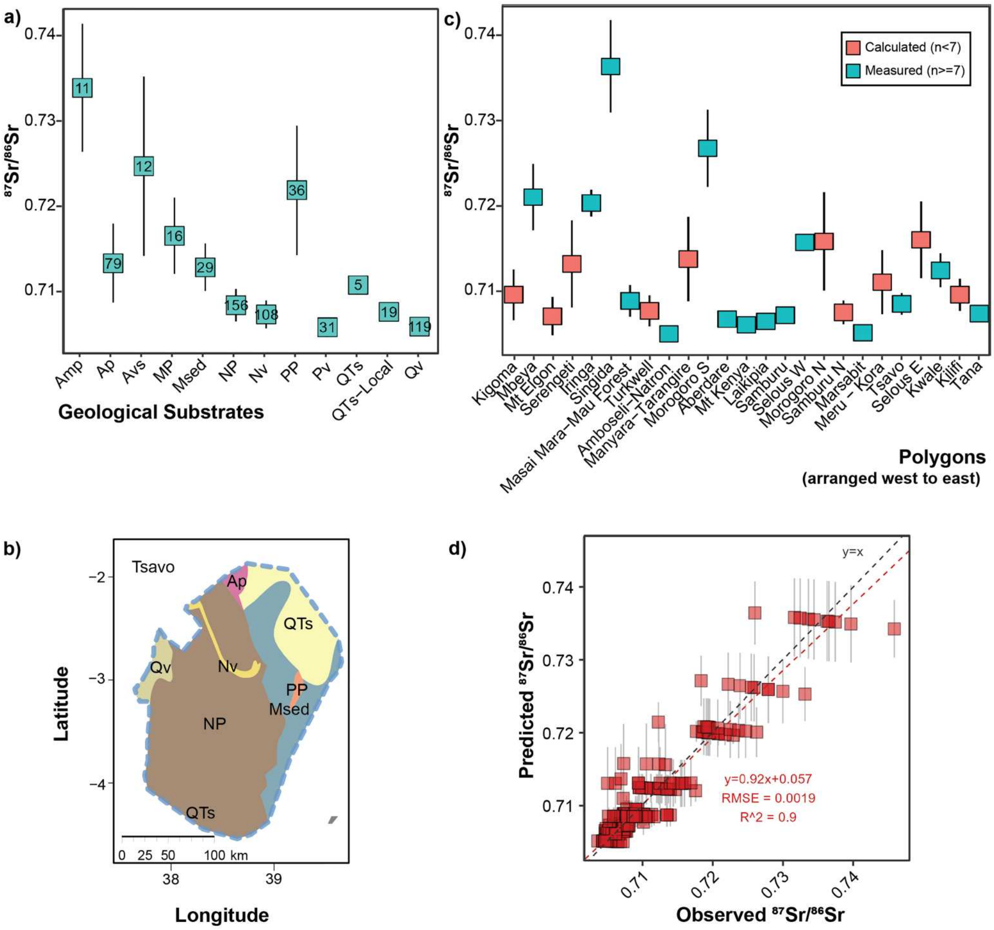

Figure 2. a) ^{87}Sr/^{86}Sr isotope measurements from geological substrates used in this study with average and one sigma uncertainty. Numbers represent sample size for the respective geological substrate. b) Example of an Elephant Polygon having multiple geological substrates within the boundaries of the polygon. c) Schematic showing the input of data used to make probabilistic geographic assignments. Genetic data was used to select samples of this study. d) Values determined in this study of Elephant Polygons are based on measured values (n ≥ 7 analyses for polygon) or determined by taking a weighted average based on fractions of geological substrates (n < 7 analyses for polygon). Also see Figure 3 a). e) Self-validation for Elephant Polygons with n ≥ 7 to compare the weighted-geology calculation methods with measured values. f) Cross-validation using leave-one-out approach between measured and predicted ^{87}Sr/^{86}Sr values for samples used in this study.

shipments (> 0.5 t) in the past 20 years has been demonstrated to be from animals that died before 1985. We therefore restrict our search to parts of Africa where elephants currently occur, excluding large parts of Africa where elephants were eradicated over the past 100+ years. The African Elephant Status Report [28] summarizes continent-wide survey data on elephant populations and provides maps of known and possible distributions of elephants in the twenty-first century; we use the shapefiles of the African Elephant Database (AED) of the IUCN/SSC African Elephant Specialist Group to limit search areas to 25 'Elephant Polygons' in our study area where elephants of modern poaching events could have originated. Our Elephant Polygons use the 'known' and 'possible' ranges of Thouless et al. [28]; they do not include areas categorized as 'doubtful'. Elephant Polygons of this study are shown in Figure 1c), and we have 384 samples within them. We use the continent-wide population estimates of Thouless et al. [28] (Figure 1 d)) as a population prior to derive the final probability determination ofthe place of origin of the unknown samples in this study. With a goal of determining the origin of illegal ivory in specific regions for law enforcement purposes, the Elephant Polygon approach is favoured over a continuous surface, raster-based isoscape where disparate geographic regions would be included together based solely on their similar $^{87}Sr/^{86}Sr$ ratios.

Elephant Polygon boundaries were designated in consideration of animal migration and integration of $^{87}Sr/^{86}Sr$ ratios across differing bedrock. Other studies covering different time periods, or using different taxa, would need to define other polygons specific to those studies.

Each Elephant Polygon contained multiple geological substrates. The 'Tsavo Polygon' illustrates this issue: it contains multiple geological substrates (Figure 2b)) and elephants can move freely throughout the defined polygon boundaries. Polygon areas ranged from about 2000–100,000 km^2; the largest fraction attributed to a single substrate in any polygon ranged between 39 and 99 %. Many of our known samples were from Elephant Polygons, and the $^{87}Sr/^{86}Sr$ value for most Elephant Polygons could be characterized using known samples found within the individual Elephant Polygons; for those polygons with $n > 7$ we used all samples within each respective polygon to determine a characteristic mean $^{87}Sr/^{86}Sr$ ratio and its standard deviation for that polygon. However, for polygons where the sample number was small (< 7), we calculated a characteristic $^{87}Sr/^{86}Sr$ ratio by weighting each geological substrate in each Elephant Polygon according to its fractional area within the polygon using samples only from Eastern Africa (Kenya, Tanzania, Uganda). We use this mixed-methods polygon and weighted-geology methods to assign $^{87}Sr/^{86}Sr$ ratios for all 25 Elephant Polygons (shown schematically in Figure 2c), with results in Figure 2d), Table 2). Figure 3 a,b) shows the $^{87}Sr/^{86}Sr$ characteristic of each polygon.

A comparison of measured values with calculated values for Elephant Polygons with $n \geq 7$ measurements shows agreement with a slope of 0.65 and an $r^2 = 0.902$ (Figure 2e)). The weighted-geology method gave lower values for two polygons (Morogoro S and Singida). A leave-one-out approach was used to cross-validate the model for assigning $^{87}Sr/^{86}Sr$ ratios to individual samples using the mixed methods measured-and-calculated polygons. The slope of the assignments was 0.92 with an r^2 value of 0.905 (Figure 2f); following Shao [37].

2.3. Probability-of-origin assignments

We examined 52 ivory tusks from 3 different ivory seizures made in 2012 and 2013: ARE, 05-13, 1.5 t; HKG, 10-12, 1.9 tB; KEN, 07-13, 3.3 t (seizures are named with a three letter ISO of the seizing country, month and year seized, and ivory weight in metric tonnes). Hereafter these seizures will be referred to as ARE, HKG, and KEN. ARE was a 1.5 t seizure in Dubai of the United Arab Emirates seized in May 2013. HKG was a 1.9 t seizure of ivory in Hong Kong in October 2012. KEN was a 3.3 t seizure of ivory made in the port of Mombasa, Kenya, in August 2013. Thus, all seizures were from ivory seized between October 2012 and August

Table 2. Areas and calculated $^{87}Sr/^{86}Sr$ values for Elephant Polygons as measured ($n \geq 7$) or based on area-weighted $^{87}Sr/^{86}Sr$ ratios ($n < 7$).

Polygon name	n[a]	$^{87}Sr/^{86}Sr$	±1s	Area (km²)	Population[b]
Aberdare	30	0.7067	0.0005	5252	3553
Amboseli-Natron	50	0.7051	0.0007	51215	2547
Iringa	11	0.7199	0.0015	29455	3529
Kigoma	calc	0.7096	0.0029	31123	3728
Kilifi	calc	0.7095	0.0018	2575	184
Kwale	20	0.7123	0.0019	3508	274
Laikipia	32	0.7065	0.0008	15564	2834
Manyara	calc	0.7138	0.0048	18270	4202
Marsabit	8	0.7052	0.0006	4831	100
Masai Mara-Mau Forest	36	0.7088	0.0018	18793	2531
Mbeya	11	0.7206	0.0037	101904	12083
Meru-Kora	calc	0.7111	0.0036	9775	1780
Morogoro N	calc	0.7158	0.0058	17885	1952
Morogoro S	9	0.7262	0.0044	33306	3635
Mt Elgon	calc	0.7071	0.0022	2175	200
Mt Kenya	20	0.7061	0.0006	5626	1024
Samburu	21	0.7072	0.0005	19501	3551
Samburu N	calc	0.7075	0.0014	4638	844
Selous E	calc	0.7163	0.0045	30185	3126
Selous W	7	0.7155	0.001	59586	6504
Serengeti	calc	0.7132	0.0049	33910	4559
Singida	10	0.7355	0.0053	30347	3635
Tana	8	0.7074	0.0005	43687	60
Tsavo	88	0.7085	0.0012	49659	11175
Turkwel	calc	0.7077	0.0018	10378	662

[a]Number of $^{87}Sr/^{86}Sr$ analyses within polygon. $^{87}Sr/^{86}Sr$ ratio calculated for polygons having $n < 7$, using proportional areas and $^{87}Sr/^{86}Sr$ of contributing geological substrates.
[b]Elephant populations from Thouless et al. (2016) assuming elephant populations are evenly distributed within regions contributing to individual Elephant Polygons

2013. Further details of these and other seizures are found in Wasser et al. [5]. We analyzed $^{87}Sr/^{86}Sr$ ratios for 16, 17, and 19 samples from ARE, HKG, and KEN, respectively.

DNA-based origin assignments placed all 52 unknown samples in the Kenya–Tanzania region [3] using Voronoi statistics for geographic assignment [2]; each had an uncertainty regarding the exact location of a region with an uncertainty of 370 ± 220 km based on comparing Voronoi coordinates with known locations for 16 samples, an uncertainty similar to that reported in [3]. Figure 1a,c) shows the general region of 'search' for all unknown samples. We consider all regions of Kenya and Tanzania as possible sources for any individual specimen.

For both our test and unknown samples we determined probability density functions using the assignR package [38]. This method assigns a probability based on the isotope distribution within a geographic region and the measured isotope value.

In our analysis, we first consider only probabilities based on $^{87}Sr/^{86}Sr$ ratios associated with each Elephant Polygon; this is the 'Sr-only method'. We then add the prior information of elephant population size within each Elephant Polygon; this uses both the $^{87}Sr/^{86}Sr$ ratio and a Population Prior and is termed the 'Sr + Pop method'. Because we have already used the genetic information to confine our search in the continent of Africa to the more restricted region of Kenya–Tanzania, both methods have genetic information as part of the overall assignment; we do not use the genetic information to further refine the geographic search area, but assume that each sample originated from one of the Polygons defined.

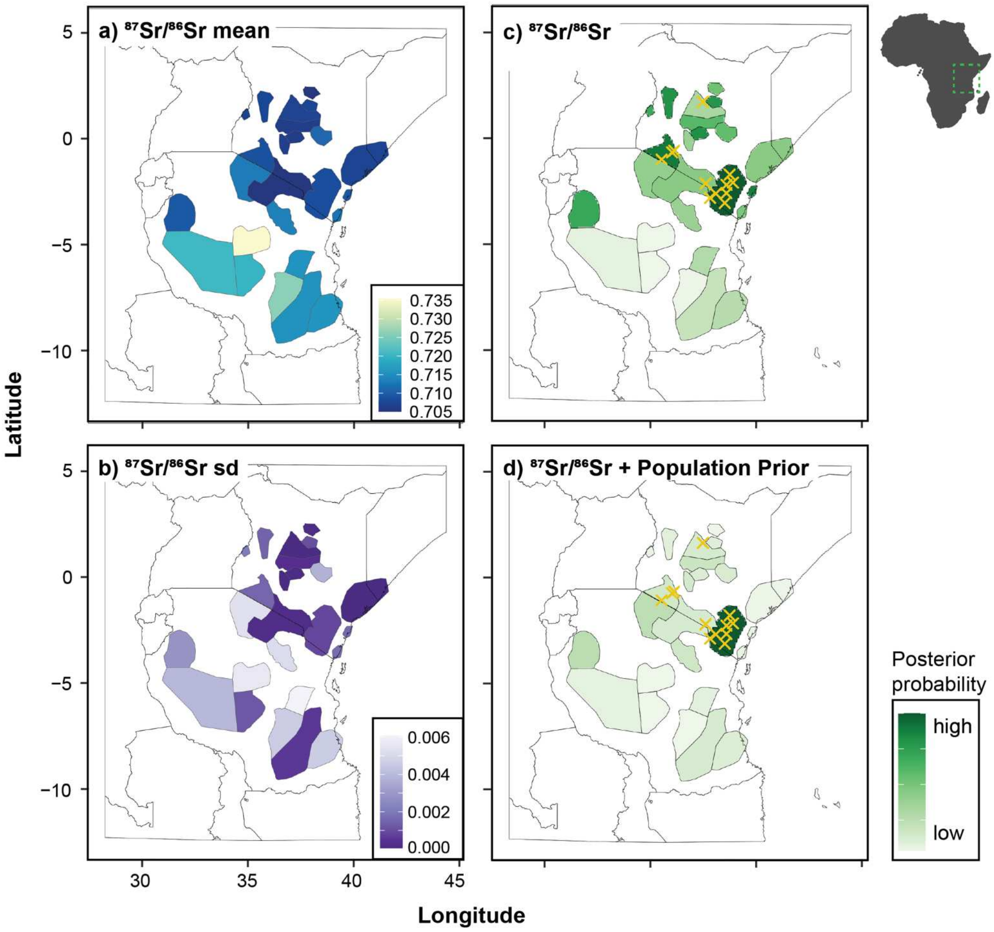

Figure 3. a) $^{87}Sr/^{86}Sr$ isoscape within our defined Elephant Polygon area; isoscape based on $^{87}Sr/^{86}Sr$ mean for each Elephant Polygon; isoscape based on $^{87}Sr/^{86}Sr$ mean for each Elephant Polygon. b) One sigma uncertainty associated with $^{87}Sr/^{86}Sr$ isoscape (from Table 2. c) Validation: Unioned assignment posterior probability distribution of known-origin validation samples; d) with added population prior. Locations of the 16 known origin samples shown as yellow crosses.

2.4. Application to samples

2.4.1. Application to the collection of known samples

Each of the 3 ivory seizures had a sample size between 16 and 19. We therefore selected 16 samples known to be from 4 Elephant Polygons in Kenya as validation samples. None were used for either the weighted geology or for determining characteristic $^{87}Sr/^{86}Sr$ values for Elephant Polygons. This suite included samples from the Amboseli-Natron (n = 3), Masai-Mara-Mau Forest (n = 4), Samburu (n = 2), and Tsavo (n = 7) Polygons. Thirteen of the 16 samples were located by GPS as indicated in Dataset II. Three were based on collectors' field notes and are estimated to be within less than 5 km of the collection site as denoted by the symbol 'g' in the Dataset II.

The 16 samples were elephant hair collected by the Kenya Wildlife Service. Both hair and ivory are formed from blood serum and so have the same isotope ratio at the time of formation. Hu et al. [38] showed irreversible uptake of Sr by hair during submersion in water so that it differs in its origin of Sr as compared to ivory; however, both origins (endogenous and exogenous) will record the local bioavailable Sr sources. Samples of different tissues from Tsavo National Park show that ivory and hair have indistinguishable $^{87}Sr/^{86}Sr$ ratios (SI Table 1.3.1) suggesting that any Sr uptake from the local environment maintained the local $^{87}Sr/^{86}Sr$ ratio.

The sixteen validation samples were assigned to Elephant Polygons using the Bayesian-based probability density functions in the assignR package [39]. Dataset V shows the probabilities for each of the test samples normalized so that the sum of probabilities for all Elephant Polygons is 1.

The $^{87}Sr/^{86}Sr$-only method applied to the test samples gives 4 samples each assigned to Tsavo and Tana, 3 samples to Mt Elgon, 2 to Kilifi, and a single sample each to Kwale, Marsabit, and Selous W. Each individual sample is discussed in the Supplementary Information Section 5.1. Such a widespread distribution is not a surprise because many of the Elephant Polygons have rather similar $^{87}Sr/^{86}Sr$ ratio distributions: for example, five Elephant Polygons have average $^{87}Sr/^{86}Sr$ ratios between 0.70771 and 0.70778 and it is difficult to determine the correct Elephant Polygons using $^{87}Sr/^{86}Sr$ ratios only.

The $^{87}Sr/^{86}Sr$ + Pop method results in 10 samples being attributed to Tsavo, two to Laikipia, and one each for Aberdares, Amboseli-Natron, Serengeti, and Selous W (see Appendix V). Therefore, the test results strongly favour the Tsavo Polygon as the dominant source of the test samples. Closer examination is warranted; however, it provides some instruction on interpretation. One known-origin Tsavo sample was erroneously assigned to the Amboseli-Natron Polygon; KWS-LFN-846 ($^{87}Sr/^{86}Sr$ = 0.70544) was collected at Lake Jipe and was from about 2 km from the upstream Amboseli-Natron Polygon (0.7051 ± 0.0007). This sample illustrates the problem of discrete boundaries when making assignments. Further examination of the individual samples in this data set shows that the Elephant Population prior is important information, for example diminishing the apparent importance of Tana compared to Tsavo; the two regions, although close to each other geographically and in their respective $^{87}Sr/^{86}Sr$ ratios, currently have vastly different elephant populations, 60 individuals for Tana compared to 11,175 in Tsavo based on the recent continent-wide survey of elephant populations [28]. The Tana region experienced heavy poaching several decades ago, significantly reducing its population, although it had a large population of elephants after European settlement in the late 1800s and early 1900s and was a favoured hunting area [40].

Figure 3 c,d) shows the Sr and Sr + Pop favoured distributions of the test samples; it shows that in aggregate the test samples are approximately aligned with their known origins. Employing both individual and seizure-level assignment approaches allows one to address complementary research aims. Individual assignments are effective for pinpointing the likely origin of single samples, providing detailed provenance information for each specimen. In contrast, aggregating assignments at the seizure level enables the identification of broader geographic patterns or recurring source regions, thus offering insights into the collective origins of groups of samples and highlighting areas that may be repeatedly implicated in wildlife trafficking. The latter could be useful for wildlife conservation efforts.

The limitations of Sr-only and also Sr + Pop become evident from examination of the test samples. Significant improvement is found by applying the Population prior to the Sr-only method, but still multiple geographic areas have substantial probabilities after applying the Population prior. If the genetic search areas could be improved to, for example, a radius of only 200 km, then distant polygons with similar $^{87}Sr/^{86}Sr$ ratios could be eliminated from consideration. In this study, we are considering all polygons within an area of approximately 10° longitude x 15° latitude, and so very distant polygons are being included for consideration for every sample. Such a reduction in the search area would be a rectangle of approximately 4° longitude and 4°latitude, and many fewer possible source areas would be in the search area.

2.4.2. Application to three ivory seizures: ARE, HKG, and KEN

The three ivory seizures, ARE, HKG, and KEN, have similar $^{87}Sr/^{86}Sr$ average ratios and their standard deviations, maximum and minimum values are similar (Table 3) suggesting that they may be related. We identified the most likely polygon-of-origin for each of the 52 unknown-origin samples (Dataset VI). We used the pre-defined genetic information that restricted our analysis to all 25 Elephant Polygons in Kenya and Tanzania using both the Sr-only and Sr + Pop methods as described above. Full assignment results for each of the unknown-origin samples for both the Sr-only and Sr + Pop methods are in Appendix VI. The aggregated results of the SR + Pop approach are shown in Table 4.

Three pairs of tusks were identified genetically as probably coming from the same elephants. Applying the approach detailed here, paired samples 116 and 117 from ARE were both assigned to the Tsavo Polygon, and 073 and 074 from KEN were both assigned to the Serengeti Polygon. However, the 145/146 pair from KEN was split with one assigned to Tsavo and the other to Samburu.

The Tsavo polygon was the most likely origin for the majority of the samples (Table 4 and Figure 4). Thirty-one of the 52 ivory samples from 49 individuals were assigned to the Tsavo polygon using the Sr + Pop method (Table 4). Four were assigned to Samburu, which has a similar but lower distribution of Sr isotope values to Tsavo; for these four samples, Tsavo had the next highest probability, just slightly lower than Samburu (Appendix VI). Four samples each were assigned to the Aberdares Polygon (0.7067 ± 0.0005) and to the Amboseli-Natron Polygon (0.7051 ± 0.0007), both of which had a significantly lower $^{87}Sr/^{86}Sr$ isotope ratio than Tsavo (0.7085 ± 0.0012). Nine samples were assigned to Selous W (n = 3) and the Serengeti (n = 6) Polygons, both of which had substantially higher $^{87}Sr/^{86}Sr$ distributions than Tsavo (see Table 2).

Thus, combining geological assignments with genetics suggests that about half to three quarters of the 52 samples from these three seizures most likely came from the Tsavo region; samples assigned to Samburu (not the Laikipia portion of the ecosystem) are well within the Tsavo distribution for $^{87}Sr/^{86}Sr$ isotope ratios. Although Samburu

Table 3. $^{87}Sr/^{86}Sr$ characteristics of each of the seizures ARE, HKG, and KEN.

Seizures	n	$^{87}Sr/^{86}Sr$	1σ	Min	Max
ARE, 05-13, 1.5 t,	16	0.70916	0.00254	0.70539	0.71387
HKG, 10-12, 1.9 tB	17	0.70907	0.00256	0.70448	0.71466
KEN, 07-13, 3.3 t	19	0.70834	0.00182	0.70482	0.71189

Table 4. Summed $^{87}Sr/^{86}Sr$ + Population assignments for ivory seizures ARE, HKG, and KEN.

Polygon name	ARE	HKG	KEN	ALL
Aberdare	0	0	0	0
Amboseli-Natron	1	1	2	4
Iringa	0	0	0	0
Kigoma	0	0	0	0
Kilifi	0	0	0	0
Kwale	0	0	0	0
Laikipia	0	0	1	1
Manyara-Tarangire	0	0	0	0
Marsabit	0	0	0	0
Masai Mara-Mau Forest	0	0	0	0
Mbeya	0	0	0	0
Meru-Kora	0	0	0	0
Morogoro N	0	0	0	0
Morogoro S	0	0	0	0
Mt Elgon	0	0	0	0
Mt Kenya	0	0	0	0
Samburu	2	3	2	7
Samburu N	0	0	0	0
Selous E	0	0	0	0
Selous W	2	1	0	3
Serengeti	2	2	2	6
Singida	0	0	0	0
Tana	0	0	0	0
Tsavo	9	10	12	31
Turkwel	0	0	0	0
ALL	16	17	19	52

also has a significant history of poaching in the twenty-first century [41], its elephant population is much smaller than that of the Tsavo region. Eight samples with low $^{87}Sr/^{86}Sr$ ratios came from regions that is characterized by volcanic terrains and these were assigned to the Aberdares or the Amboseli-Natron polygon; these samples have derived their $^{87}Sr/^{86}Sr$ ratios from a less radiogenic geological substrate than is predominantly found within the Tsavo Polygon. The Amboseli-Natron Polygon is bounded on the east by the Tsavo Polygon, and it is possible that those individuals could have strayed into the adjacent polygon or, like the 'test' sample (KWS-LFN-846) from Lake Jipe in Tsavo West National Park, could have obtained a 'non-radiogenic' $^{87}Sr/^{86}Sr$ ratio by the downstream contributions of rivers from Mt. Kilimanjaro. Likewise, the Aberdares region is not heavily poached and the samples assigned to the Aberdares are on the mixing line between Tsavo and Amboseli for Sr isotopes. After eliminating duplicated tusks, more than 38 of the 49 different individuals sampled are compatible with coming from the Tsavo Polygon. Five samples came from regions that are more highly radiogenic with respect to $^{87}Sr/^{86}Sr$ and samples with ratios > 0.712 (i.e. > 3σ outside the Tsavo window) are unlikely to come from Tsavo but rather they are most likely from Tanzania where polygons with more radiogenic (higher) $^{87}Sr/^{86}Sr$ ratios are found compared to Kenya. Further analysis will be needed to pinpoint their origins, but this analysis suggests compatibility with an origin from Serengeti or Selous W. Thus, we conclude that the Tsavo Polygon is the most likely origin for most (50–75 %) of the samples and with several samples possibly associated with the adjacent Amboseli-Natron Polygon (ca. 16 %), and with only a few samples from other regions in eastern Africa and likely from Tanzania.

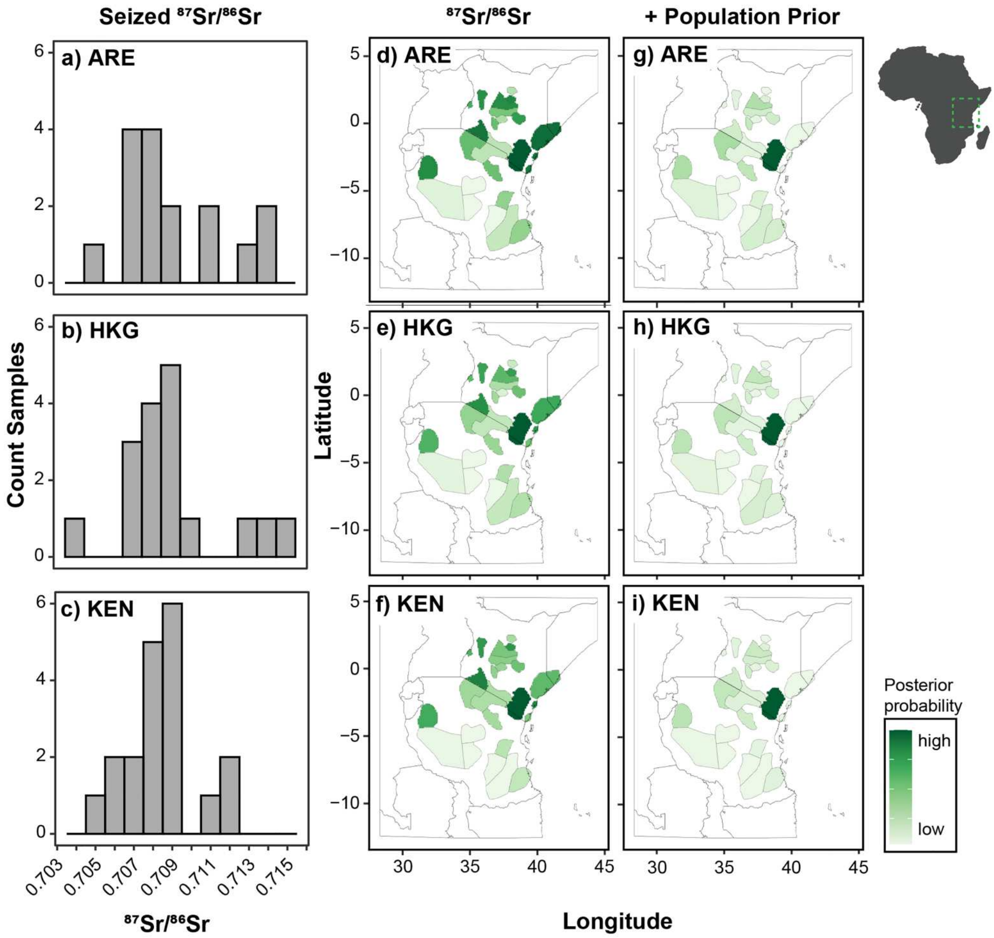

Figure 4. Aggregated assignments by seizure. a–c) Histograms of $^{87}Sr/^{86}Sr$ isotopes in each seizure (ARE, HKG, KEN). d–f) Aggregated probability distribution by seizure using $^{87}Sr/^{86}Sr$ method. g–i) Aggregated probability distribution by seizure using $^{87}Sr/^{86}Sr$ method with the population prior.

3. Discussion

The provenance of wildlife products, such as ivory, can be studied using a combination of genetics, bioavailable $^{87}Sr/^{86}Sr$ information, and population information. We applied these methods to ivory forensics from three ivory seizures using samples whose genetic locations, using Voronoi coordinates, gave a ‘search area’ centered on southeastern Kenya and northeastern Tanzania. Animal tissue and other samples from different geological substrates were analyzed for $^{87}Sr/^{86}Sr$ ratios to characterize the different substrates, which for this study were sub-divided into eleven mappable units. $^{87}Sr/^{86}Sr$ ratios ranged from 0.7054 for young Quaternary volcanics (Qv) to 0.7338 for Archean metamorphic and plutonic rocks (Amp). The larger Kenya–Tanzania region was sub-divided into 25 Elephant Polygons where elephants were known to occur in the twenty-first century, and each of these had an estimated $^{87}Sr/^{86}Sr$ isotope ratio based on the samples from within each polygon or based area-weighted geological distribution where the sample size was small ($n < 7$).

Using the combined genetics, bedrock assignments, and current population census information, we conclude that half to three-quarters of the samples from these three ivory seizures originate in the Tsavo region of southern Kenya; the remainder appears to be from several different regions. Some of those from outside the Tsavo polygon are from very non-radiogenic regions (possibly the Amboseli or Mt Kenya polygons), and some are from the radiogenic regions where Archean basement makes up an important fraction of the bedrock (e.g. Serengeti, Selous W).

The combined use of genetic information to provide 'search' areas for the application of $^{87}Sr/^{86}Sr$ isoscapes for wildlife forensics is a fruitful approach to region of origin assignment of illegal wildlife. Advances in genetics to reduce the 'search area' size will improve the identification of the region of origin; likewise, the addition of additional independent isotope systems, such as $^{143}Nd/^{144}Nd$, will add another dimension for region of origin identification.

4. Data and methods

4.1. Sample types

Animal tissues in this study from the African continent include museum specimens and other samples collected for research, and they include 211 previously published analyses [11,12,14,42] and 905 new analyses. The animals primarily included elephants and larger ungulates, which have significant home ranges. Tissues include dung, enamel, hair, bone, and ivory. Location, species, and tissues analyzed are tabulated in Appendices I, II, and III. Appendix I lists samples used for isoscape and elephant polygon development and includes 905 previously unreported $^{87}Sr/^{86}Sr$ measurements; Appendix II consists of 16 known origin samples not included in the isoscape and elephant polygon analysis; Appendix III consists of 52 ivory samples whose DNA analysis indicates a probable origin in Kenya or Tanzania.

4.2. $^{87}Sr/^{86}Sr$ method for bioapatite, hair and dung

Detailed methods for $^{87}Sr/^{86}Sr$ isotope analysis are given the Supplementary information (Section 1.2).

4.3 Geologic map

The geologic map used for this study is the GIS version of 'An updated geological map of Africa at 1/10 000 000 scale' [43]. This map organizes surficial geologic units into alluvium and sedimentary, metamorphic, and igneous rocks and associated age. We combined these units into 11 groups based on similarity in lithology and age to determine characteristic $^{87}Sr/^{86}Sr$ values for these geological groups (Table SI 3.1). More detail is found in the Supplementary Information, Section 2.

4.4. Polygon development

We used the Elephant Status Report [28] of Africa to define 'Elephant Polygons'; these areas are based on known and possible elephant ranges, using geological bedrock as boundaries between Elephant Polygons when possible. For each Elephant Polygon, we determined a characteristic $^{87}Sr/^{86}Sr$ ratio, with an uncertainty as defined below.

A few Elephant Polygons were dominated (> 75 %) by a single geological substrate, but most Elephant Polygons had significant fractions of multiple geological substrates contributing to the bioavailable strontium pool. For polygons with large numbers of samples (n > 6) from within a polygon, we used the average $^{87}Sr/^{86}Sr$ ratio as its characteristic value. For polygons with smaller 'n', we used the areal fractional contribution of the differing geological substrates to obtain a characteristic $^{87}Sr/^{86}Sr$ ratio for those polygons (Table SI 5.1).

4.5. Assignments

Individual assignments were created using the spatially explicit methods developed in the assignR package described in Ma et al. [39] to create probability density rasters. This semi-parametric Bayesian inversion method requires a rasterized version of the mean and sd of the $^{87}Sr/^{86}Sr$ isoscape and the $^{87}Sr/^{86}Sr$ ratio of the unknown origin sample. The pdRaster function geolocates potential origins of the unknown origin sample by producing a raster with cell values between 0 (no probability) and 1 (full probability), and where the sum of all raster cells equals 1. In Table 4, we aggregated each assignment by ranking Elephant Polygon-of-origin based on average likelihood of pixel values within each Elephant Polygons so as not to skew by polygon area. This approach is appropriate when the goal is to identify the most probable origin for each individual unknown sample, as it provides a focused assessment of likely provenance for single specimens. Alternatively, we also aggregated the data by seizure by unioning the assignment raster data (adding the posterior probability rasters). In Figure 3 c,d), this approach revealed that Tsavo has the highest aggregate posterior probability, followed by Masai-Mara, which are the two polygons with the most samples. This seizure-level approach is more appropriate when considering the prior knowledge that multiple samples from the same seizure may originate from the same location, and when the objective is to detect broader geographic trends or hotspots of origin across groups of samples. By combining the probabilistic assignments, this method allows for the identification of regions that are consistently implicated across multiple samples, which is valuable for understanding patterns at the population or trafficking level. Employing both individual and seizure-level assignment approaches allows us to address complementary research aims. Individual assignments are effective for pinpointing the likely origin of single samples, providing detailed provenance information for each specimen. In contrast, aggregating assignments at the seizure level enables us to identify broader geographic patterns and recurring source regions, offering insights into the collective origins of groups of samples and highlighting areas that may be repeatedly implicated in wildlife trafficking. The latter could be useful for wildlife conservation efforts.

4.6. Genetic methods

For the genetic analysis to assign search area, ivory was prepared as previously described [44–46] and genotyped for 16 microsatellite loci. Only samples successfully genotyped for 10 + loci were used in further analysis. Tusks were deemed to come from the same individual if they were mismatched at no more than 3 loci and all mismatches were consistent with allelic dropout. For the three seizures the amplification success rate was about 75 %: ARE (105 amplified out of 151 genotyped, 14 from same individual (i.e. 7 matches))*;* HKG (75 amplified out of 100, 6 matches)*;* KEN (128 amplified out of 185 genotyped (9 matches)).

Reference data for all analyses were version 5.32 of the elephant reference database [5], containing 1571 known-location savanna elephant *(Loxodonta africana)* samples and 678 known-location forest elephant *(L. cyclotis)* samples. Species assignment was done using EBhybrids version 0.991 [47]; all samples genotyped were identified as savanna elephants with high confidence. Individual elephant origin was estimated with SCAT version 3.0.2 [45] and seizure locations were refined using VORONOI version 2.0.1 [2] for each seizure separately, on the assumption that individual seizures come from constrained geographic areas relative to the entire species range. Location assignment accuracy is discussed in Wasser et al. [3].

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Data availability statement

Data for this paper are included as Appendices in the Supplementary Information. Data analyses were performed using R v3.4 in RStudio. Code and input data are provided in the Supplementary Material. All data sets and code deposited in Zenodo with DOI: 10.5281/zenodo.15528823.

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