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Strontium isotopes track female dispersal in Taï chimpanzees

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Abstract

Objectives: Chimpanzees (*Pan troglodytes*) are patrilocal, with males remaining in their natal community and females dispersing when they reach sexual maturity. However, the details of female chimpanzee dispersal, such as their possible origin, are difficult to assess, even in habituated communities. This study investigates the utility of $^{87}Sr/^{86}Sr$ analysis for (1) assessing Sr baseline differences between chimpanzee territories and (2) identifying the status (immigrant or natal) of females of unknown origin within the territories of five neighboring communities in Taï National Park (Côte d'Ivoire).

Materials and Methods: To create a local Sr isoscape for the Taï Chimpanzee Project (TCP) study area, we sampled environmental samples from TCP-established territories ($n = 35$). To assess dispersal patterns, 34 tooth enamel samples (one per individual) were selected from the Taï chimpanzee skeletal collection. $^{87}Sr/^{86}Sr$ analysis was performed on all 69 samples at the W.M. Keck Lab. The theoretical density and overlap of chimpanzee communities as well as generalized linear mixed models (GLMMs) were used to test each question.

Results: $^{87}Sr/^{86}Sr$ ratios for natal male chimpanzees ranged from 0.71662 to 0.72187, which is well within the corresponding environmental baseline range of 0.70774–0.73460. The local Sr isoscapes fit was estimated with the root-mean-square error value, which was 0.0048 (22% of the whole $^{87}Sr/^{86}Sr$ data range). GLMMs identified significant differences in $^{87}Sr/^{86}Sr$ ratios between natal and unknown North community origin groups, suggesting that after 1980, females of unknown origin could be immigrants to North community ($n = 7$, z-ratio $= -4.08$, $p = 0.0001$, power $= 0.94$).

Discussion: This study indicates that $^{87}Sr/^{86}$This study indicates that $^{87}Sr/^{86}Sr$ analysis can successfully identify immigrant females in skeletal collections obtained from wild chimpanzee communities, enabling the tracking of female dispersal patterns historically. There are, however, significant limitations within the scope of this study, such as (1) the absence of reliable maps for the TCP study area, (2) limited capacity for environmental sampling, (3) small sample sizes, and (4) tooth formation in wild chimpanzees.

KEYWORDS
chimpanzees, dispersal, enamel, isoscape, Sr isotopes

1 | INTRODUCTION

1.1 | Dispersal in chimpanzees

Natal dispersal upon reproductive maturity is common in many social animals, with one or both sexes leaving their natal community to seek novel mating opportunities, leading to a sex-biased dispersal pattern (Clutton-Brock & Lukas, 2012; Johnson & Gaines, 1990; Lawson Handley & Perrin, 2007; Li & Kokko, 2019). In chimpanzees (*Pan troglodytes*), typically only nulliparous females disperse (Goodall, 1986; Lee & Strier, 2015; Nishida, 2011; Parr & de Waal, 1999). Male chimpanzees are patrilocal, so they generally remain in their natal community for their lifetime (Inoue et al., 2008; Lehmann & Boesch, 2008, 2009; Moore et al., 2015). While there are some reports of females remaining in natal communities, female dispersal is much more likely and is often sustained by regular immigration of nulliparous females into studied communities (Gagneux et al., 1999; Hammond et al., 2006; Langergraber et al., 2007; Langergraber et al., 2014; Pusey & Packer, 1986; Walker & Pusey, 2020).

Chimpanzees are a territorial species and generally restrict their activity to a specific area (Boesch et al., 2006). The territory of a given social community can shift over time due to fluctuations in the number of adult males or in response to dynamics within the community's dominance hierarchy (Lehmann & Boesch, 2003; Lemoine et al., 2020). Female chimpanzee dispersal between communities can be high risk, due to travel through unknown territory and exposure to predators in unfamiliar feeding grounds (Boesch, 1991; Stumpf et al., 2009; Thompson, 2013). In Taï National Park (TNP) (Côte d'Ivoire), ongoing observational studies as part of the Taï Chimpanzee Project (TCP) have documented the dispersal of female chimpanzees for over 40 years (Boesch & Wittig, 2019; Lemoine et al., 2019). From these studies, it is estimated that most females disperse from their natal community upon sexual maturation, which occurs around 10 years of age, as signaled by pronounced sexual swellings (Boesch, 1997; Lemoine et al., 2019). However, some unknown circumstances result in a few staying to reproduce and raising their offspring with members of their natal community (Lemoine et al., 2019). In most dispersal events, predicting how far females travel to a new community or where they eventually immigrate is difficult. Although there are some rare instances of intercommunity migration of females and the arrival of females with infants, more often, female immigrants arrive unpredictably, and it is usually unknown where they emigrated from (Lemoine et al., 2019; Luncz & Boesch, 2014; Vigilant et al., 2001).Thus, much of what we know of chimpanzee natal dispersal is restricted to rare instances at long-term study sites where female origin and dispersal between different habituated populations may be tracked. Therefore, for most immigrants, researchers do not know how far females are traveling and what additional risks (natural or anthropogenic) they might encounter.

1.2 | The implications for a refined chimpanzee dispersal model

Understanding female dispersal also has implications for chimpanzee conservation. Western chimpanzees (*Pan troglodytes verus*) have undergone a dramatic population decline over the past two decades and are now considered critically endangered (Kühl et al., 2017). Even TNP, one of the last primary evergreen rainforests in West Africa and a protected refuge for western chimpanzees, was found to have one tenth of the expected population density of chimpanzees (Campbell et al., 2008). The rapid decline in western chimpanzees is related to a rising human population that has increased deforestation and poaching, and led to habitat fragmentation (Campbell et al., 2008; Kühl et al., 2017; Marchesi et al., 1995). Habitat fragmentation has been shown to increase the potential for inbreeding depression and subsequent population extinction (Knight et al., 2016). In environments that are impacted by habitat fragmentation, comparative data on female chimpanzee dispersal may be useful in contextualizing dispersal. Knowing how far females travel to find a new community allows us to better understand the risks associated with female dispersal and opens the doorway for expanding protected areas and assessing conservation need. Understanding female reproductive biology, including female dispersal patterns, is imperative for improving conservation efforts of western chimpanzees.

A clearer model of female chimpanzee dispersal can also help us understand how dispersal strategies evolved in our own species' ancestral lineage. Much of what we know about the social evolution of early hominins is limited by what is preserved in the fossil record, and contrasting interpretations of community dynamics and mating systems for hominins make the behavioral and socio-environmental context for early hominins unclear (Hill et al., 2011; Murdock, 1981; Wilkins & Marlowe, 2006). The reconstruction of hominin dispersal patterns using strontium (Sr) isotope analysis has been proposed as a useful proxy for behavioral trends that are not observable from the fossil record, such as philopatry, dispersal, landscape use, and community dynamics (Balter et al., 2012; Copeland et al., 2011; Hamilton et al., 2021). For instance, strontium isotope (^{87}Sr/^{86}Sr) ratios and Sr concentrations have been used to show differences in landscape use by early hominins, as well as to contend that early australopiths had a similar home range size, but different dietary breadths than anatomically modern humans (Balter et al., 2012; Copeland et al., 2011). The use of extant nonhuman primates has informed many behavioral models and assumptions about fossil hominins, often emphasizing sexual dimorphism of body size (Gordon et al., 2008; Lovejoy, 2009). Nonhuman primates, specifically within the genus *Pan*, are often used as analogues for early human dispersal models (Copeland et al., 2011; Lockwood et al., 2007). Yet given the remaining unknowns about dispersal in chimpanzees, additional sources of information about their origins and distance traveled would enrich the comparative model for apes (Koenig & Borries, 2012) and be useful in contextualizing emerging evidence for early African hominin mobility (Chazan, 2022; Heydari-Guran & Ghasidian, 2020).

1.3 | Strontium isotope geochemistry

Strontium isotope (^{87}Sr/^{86}Sr) analysis is a well-established method for provenance studies, and the ^{87}Sr/^{86}Sr ratios in animals are representative of the local environment (weathered bedrock and other sources) that are integrated into skeletal tissues when animals consume plant or animal food (Beard & Johnson, 2000; Bentley, 2006; Price et al., 2002). ^{87}Sr/^{86}Sr analysis uses the natural abundance of the radiogenic isotope ^{87}Sr, relative to the stable isotope ^{86}Sr, to assess the spatial variation among geological terrains (Bataille et al., 2020; Beard & Johnson, 2000; Bentley, 2006; Britton et al., 2020; Capo et al., 1998; Faure & Powell, 2012; Gosz et al., 1983; Hoppe et al., 2003; Hurst & Davis, 1981). Variations in ^{87}Sr/^{86}Sr measurements reflect the chemical composition and age of bedrock (Åberg, 1995). The ^{87}Sr/^{86}Sr ratio of a given bedrock terrain is determined by the radioactive decay of rubidium (^{87}Rb) to ^{87}Sr, with variations related to its age of formation and the initial abundance of Rb (Bentley, 2006).

Different types of bedrock underlying the soils and bodies of water on a landscape result in different ^{87}Sr/^{86}Sr ratios. The weathering of bedrock can release Sr into soils and water that is taken up by plants and animals (Bentley, 2006). Although different minerals in the rock, with different ^{87}Sr/^{86}Sr ratios, may weather at different rates, soil age or the depth at which plants root (thereby accessing weathered bedrock) can influence the regional environmental baseline or even isotopic ratios within a region (Crowley et al., 2017). Windborne dust, especially downwind of deserts or previously glaciated terranes (Aarons et al., 2017; Frumkin & Stein, 2004), and sea spray (Whipkey et al., 2000) can contribute Sr with isotopic ratios unrelated to the bedrock at a site. The balance of Sr supplied by local weathering versus these airborne sources can also affect the local environmental ^{87}Sr/^{86}Sr baseline.

Consequently, analyzing environmental samples and establishing a Sr isotope baseline for any given study area is critical. Bioavailable ^{87}Sr/^{86}Sr baselines are typically established by measuring soils, plants, and animal remains across a given study region (Bataille et al., 2020; Bataille & Bowen, 2012). These bioavailable ^{87}Sr/^{86}Sr baseline samples can then be used to create a heat map of the predicted ^{87}Sr/^{86}Sr spatial distribution, commonly referred to as a Sr isoscape. The use of Sr isoscapes has become standard practice, as they enable the prediction of an organism's origin based on the observed ^{87}Sr/^{86}Sr ratios in each study area. Measuring plants of varying kind and root depth has been shown to portray bioavailable Sr in an ecosystem accurately (Britton et al., 2020; Oelze et al., 2012).

The use of Sr isoscapes enables ^{87}Sr/^{86}Sr analysis to address broad questions related to the mobility and migration of various organisms, including primates (Balter et al., 2012; Bentley, 2006; Brennan et al., 2015; Copeland et al., 2011;Crowley & Godfrey, 2019; Dominy et al., 2020; Fannin et al., 2021; Koch et al., 1995; Sugiyama et al., 2022). However, ^{87}Sr/^{86}Sr analysis in primatology has thus far only been used to assess habitat use (Hamilton et al., 2019) and to identify the sex of philopatric and dispersing individuals (Hamilton et al., 2021). In this study, we use ^{87}Sr/^{86}Sr analysis of chimpanzee skeletal remains and environmental reference samples from five chimpanzee communities occupying neighboring territories in TNP to assess female chimpanzee immigrant status and mobility within the well-sampled North community. Specifically, we address the following questions:

1. Are there environmental baseline ^{87}Sr/^{86}Sr differences across Taï chimpanzee territories?
2. Do ^{87}Sr/^{86}Sr ratios differ among chimpanzee members of different Taï chimpanzee communities with distinct territories?
3. Are ^{87}Sr/^{86}Sr ratios able to discern the status (natal or immigrant) of Taï chimpanzee females and, if so, what do they reveal about the potential areas of origin for immigrant females from unknown chimpanzee communities?

2 | MATERIALS AND METHODS

2.1 | Study site

In 1978, the evergreen tropical rainforest of TNP(Figure 1; 5°45′ N, 7°7′ W), Côte d'Ivoire was registered as a Biosphere Reserve and in 1982 was added to the UNESCO World Heritage List due to its unique fauna, which includes the western chimpanzee (*P. troglodytes verus*) and 11 other primate species (Boesch & Boesch-Achermann, 2000; Guillaumet & Adjanohoun, 1971; Kolongo et al., 2006; Mangenot, 1950a, 1950b, 1955). At 5082 km², the park is one of the largest remaining areas of tropical rainforest in West Africa.[1] TNP consists of an ancient sloping peneplain broken by several rocky outcrops of Paleoproterozoic and Archean rock, which stand out from encircling plains as more or less isolated hills, including Mount Niénokoué (396 m) (Kolongo et al., 2006). A large zone of bedrock runs SW to NE across the park, dissected by tributaries that run parallel to it (Collinet et al., 1984; Rouw et al., 1990; Tagini, 1966, 1972). The TCP study area is largely composed of Paleoproterozoic volcanic-sedimentary bedrock, with small outcrops of Archean rock. The Cavally River separates Côte d'Ivoire from Liberia, with Archean bedrock on the Liberian side of the border (Petters, 1991). During December–January, the Harmattan season dry northeasternly winds deposit Saharan dust across TNP (Stoorvogel et al., 1997).

2.2 | Taï chimpanzees

Since 1979, the TCP has operated in a small section on the western side of TNP (400 km²), successfully habituating five neighboring chimpanzee communities to human observations and research (Boesch & Wittig, 2019; Wittig & Boesch, 2019). The habituated communities have been named per their original location within the study area: North community, South community, East community, and Middle community (Boesch & Boesch-Achermann, 2000). In 2014, the Pan African Programme (PanAf) began a census of a fifth community, called Northeast community (originally called Tai-R). In 2015, the TCP
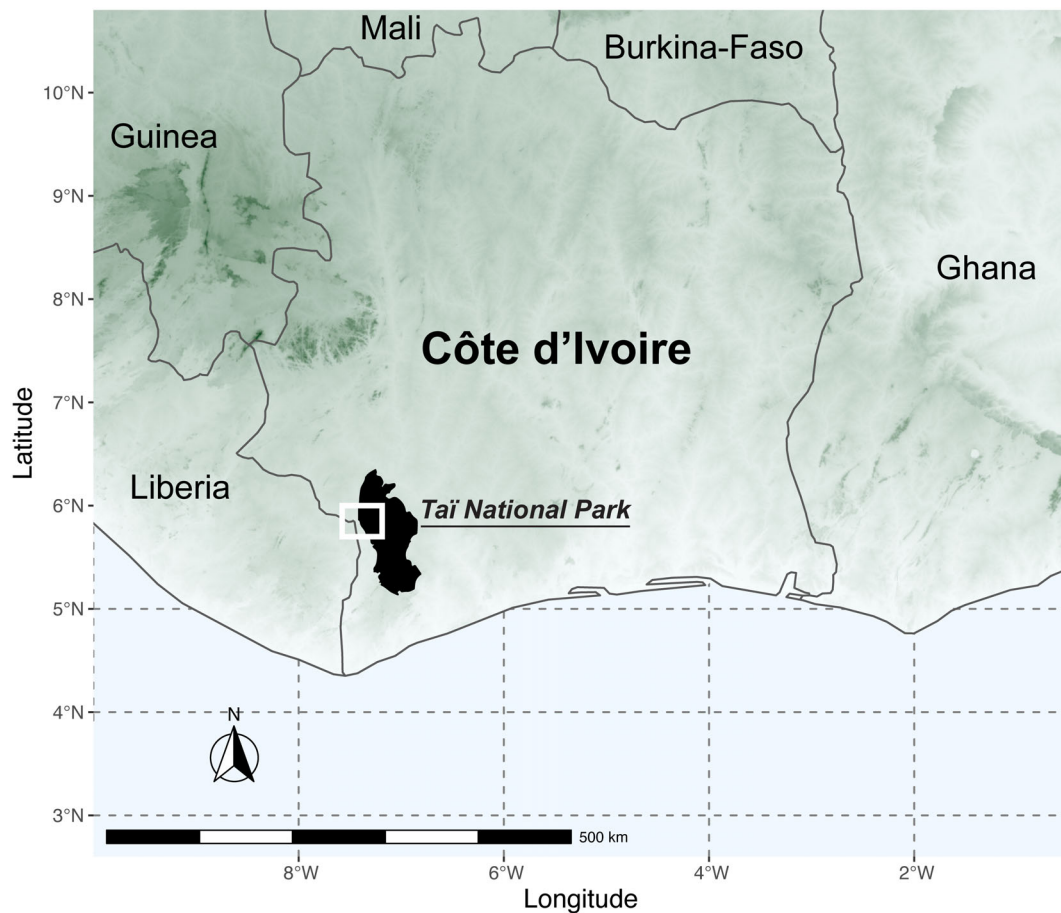
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FIGURE 1 Topographic map of Côte d'Ivoire, with the study site demarcated by a white rectangle, within Taï National Park. Dark green corresponds to a higher elevation, whereas light green corresponds to a lower elevation.

began the habituation of Northeast community, and this community has been followed since 2022 (Arandjelovic et al., 2020). Outside of the study area, to the northwest of North community, there is a chimpanzee community designated for ecotourism (Tai-E), which we will refer to as Northwest community (Boesch et al., 2021). Within the TCP study area as of 2019, 467 individuals have been identified, including 257 females, 192 males, and 18 individuals of indeterminate sex (Boesch & Wittig, 2019). Both subadult males and females range with adults of both sexes, using a similar proportion of the home range as their core area, and the individual life histories and genealogies have been well documented (Lehmann & Boesch, 2005).

The Taï chimpanzee skeletal collection is part of the long-term collection of the TCP, housed at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany (Boesch et al., 2006; Vigilant et al., 2001). Sampled chimpanzees (Table 1, n = 34) were born 1954–1997, with TCP demographic data collection beginning in 1980. Before habituation in 1979, North community's territory and size were estimated from focal follows and researcher observation. North camp was established in the central area where North community chimpanzees were first habituated, and subsequent trails to other chimpanzee communities were built out from there (Lemoine et al., 2019).

Based on researcher observations detailed in the TCP database, sampled individuals were classified as "natal," "unknown," or "reference." The "natal" category comprises resident males as well as females born in North community that had not migrated prior to death (n = 16). North community natal samples include adult (n = 3) and subadult males (n = 7), and subadults females (n = 6) that were born and died in North community's territory. The natal community is subdivided into pre-1980 (n = 2) and post-1980 (n = 14) to account for a lack of direct observation of North community (and its location) prior to 1980.

The "unknown" sampling category comprises possible immigrants to North community, and therefore includes adult females that were part of North community, but were not observed immigrating, making their origin unclear (n = 11). This community is further subdivided into "pre-1980" (n = 4) and "post-1980" (n = 7), depending on the timing of enamel formation. "Post-1980" includes females that formed tooth enamel when the location of North community (in which they died) is known, but their area of origin is unknown. For unknown females forming tooth enamel "pre-1980", we do not have direct observations of the location of North community, but we do have samples from males who formed tooth enamel between 1972 and 1980 who can supply a baseline for the community extending back in time. With one

exception (NF03, which formed enamel ~1960), all individuals sampled from North community formed enamel when the community occupied its historic range (1980–1999) or in an earlier interval when we can monitor territory with natal community $^{87}Sr/^{86}Sr$ ratios (Table 1). The historic range from 1980 to 1987 is estimated from researcher observation, where the territory of North community is generally known to surround North camp. All North community

individuals sampled in this study formed enamel within this historic pre-2000 territory of North community (here called North 1).

Lastly, the "reference" sampling category comprises resident males from the other chimpanzee communities in the TCP study area: South ($n = 4$), East ($n = 2$), and Middle ($n = 1$). Since both Northeast community and Northwest community have limited skeletal samples, we did not sample chimpanzees from these territories.

TABLE 1 Summary of Taï chimpanzees sampled ($n = 34$).

ID	Tooth	Sex	Origin	Time of birth	Age at death	ytf	Community	$^{87}Sr/^{86}Sr$	2 SE
NF03	M2	f	Unknown female (pre-1980)	1954[b]	39	1956–1961	North	0.71681	0.00001
NF01	M2	f	Unknown female (pre-1980)	1969[b]	23	1971–1977	North	0.71818	0.00001
NF02	M3	f	Unknown female (pre-1980)	1969[b]	25	1972–1980	North	0.71703	0.00001
NF09	M3	f	Unknown female (pre-1980)	1972[b]	27	1975–1980	North	0.71883	0.00001
NF11	M3	f	Unknown female (post-1980)	1973[b]	28	1976–1984	North	0.72218	0.00001
NF07	M2	f	Unknown female (post-1980)	1975[b]	19	1977–1983	North	0.72393	0.00001
NF08	M2	f	Unknown female (post-1980)	1976[b]	22	1978–1984	North	0.72051	0.00001
NF06	M2	f	Unknown female (post-1980)	1977[b]	16	1979–1985	North	0.72308	0.00001
NF10	M3	f	Unknown female (post-1980)	1978[b]	27	1981–1989	North	0.73049	0.00001
NF05	M2	f	Unknown female (post-1980)	1982[b]	12	1983–1988	North	0.72200	0.00001
NF04	M2	f	Unknown female (post-1980)	1982[b]	11	1984–1990	North	0.72081	0.00001
NF15	M3	f	Natal group (post-1980)	1979[b]	9	1982–1990	North	0.71639	0.00002
NF14	M2	f	Natal group (post-1980)	8/1/1984	6	1986–1992	North	0.71765	0.00001
NF13	dm[a]	f	Natal group (post-1980)	9/10/1987	5	1987–1987	North	0.72369	0.00001
NF17	M2	f	Natal group (post-1980)	6/5/1987	11	1989–1997	North	0.71924	0.00001
NF12	M1	f	Natal group (post-1980)	2/12/1991	3	1990–1993	North	0.71776	0.00001
NF16	M2	f	Natal group (post-1980)	11/24/1991	10	1993–1999	North	0.71761	0.00001
NM10	M3	m	Natal group (pre-1980)	1969[b]	25	1972–1980	North	0.72049	0.00001
NM07	M2	m	Natal group (pre-1980)	1971[b]	13	1973–1979	North	0.72030	0.00001
NM09	M3	m	Natal group (post-1980)	1975[b]	20	1978–1986	North	0.72179	0.00001
NM08	M3	m	Natal group (post-1980)	1980[b]	14	1983–1991	North	0.72089	0.00001
NM02	dm[a]	m	Natal group (post-1980)	2/6/1989	2	1989–1989	North	0.71901	0.00002
NM04	dm[a]	m	Natal group (post-1980)	12/10/1990	5	1990–1990	North	0.72016	0.00001
NM01	dm[a]	m	Natal group (post-1980)	11/3/1992	0.06	1992–1992	North	0.71826	0.00001
NM06	M2	m	Natal group (post-1980)	9/21/1991	10	1992–1997	North	0.71810	0.00001
NM05	M2	m	Natal group (post-1980)	10/7/1991	8	1993–1999	North	0.71960	0.00002
NM03	dm[a]	m	Natal group (post-1980)	8/31/1997	2	1997–1997	North	0.72076	0.00001
SM03	M3	m	Non-North group reference	1959[b]	40	1962–1970	South	0.72137	0.00001
SM01	M1	m	Non-North group reference	1979	19	1979–1983	South	0.72086	0.00001
SM02	M3	m	Non-North group reference	1989	25	1992–2000	South	0.72028	0.00001
SM04	M3	m	Non-North group reference	1991	adult	1994–2002	South	0.72029	0.00001
EM02	M2	m	Non-North group reference	unknown	adult	unknown	East	0.71662	0.00001
EM01	M3	m	Non-North group reference	1993[b]	14	1996–2004	East	0.71686	0.00001
MM01	M2	m	Non-North group reference	1983[b]	19	1985–1989	Middle	0.72187	0.00001

Note: Raw $^{87}Sr/^{86}Sr_{enamel}$ isotope ratios are included to 2 standard errors (SE). "ytf" is defined as the age of tooth formation when Sr accumulation begins. Age (years) represents the age in which the sampled individual died.
[a]For deciduous molars, lowercase letters correspond to deciduous dentition, and uppercase letters correspond to permanent dentition.
[b]Time of birth is estimated, as it was not witnessed by researcher.

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TABLE 2 Summary of environmental samples establishing the $^{87}Sr/^{86}Sr$ baseline for the different Taï chimpanzee territories ($n = 35$).

No.	Territory	Time slice	Species	Sample type	Latitude	Longitude	$^{87}Sr/^{86}Sr$	2SE	Source
257	North	North 1	*Afzelia bella*	Plant	5.8702	−7.3384	0.71952	0.00001	This study
1104	North	North 1	*Lissachatina fulica*	Snail shell	5.8863	−7.3162	0.71534	0.00001	This study
507	North	North 1	*Sterculia oblonga*	Plant	5.8771	−7.3336	0.71765	0.00002	This study
514	North	North 1	*Sterculia oblonga*	Plant	5.8708	−7.3299	0.71661	0.00002	This study
319	North	North 2	*Dialium aubrevillei*	Plant	5.8710	−7.3478	0.73460	0.00001	This study
445	North	North 2	*Parkia bicolor*	Plant	5.8760	−7.3467	0.72757	0.00001	This study
1096	North	North 2	*Lissachatina fulica*	Snail shell	5.8871	−7.3407	0.72632	0.00001	Wang et al., in review
1097	Northwest	Northwest	*Lissachatina fulica*	Snail shell	5.9267	−7.3571	0.72205	0.00001	Wang et al., in review
1098	Northwest	Northwest	*Lissachatina fulica*	Snail shell	5.9055	−7.3596	0.72219	0.00001	Wang et al., in review
1099	Northwest	Northwest	*Lissachatina fulica*	Snail shell	5.9053	−7.3399	0.72811	0.00001	Wang et al., in review
1100	Northwest	Northwest	*Lissachatina fulica*	Snail shell	5.9326	−7.3790	0.72233	0.00001	Wang et al., in review
1101	Northwest	Northwest	*Lissachatina fulica*	Snail shell	5.8960	−7.3570	0.72602	0.00002	Wang et al., in review
1102	Northwest	Northwest	*Lissachatina fulica*	Snail shell	5.9132	−7.3617	0.72207	0.00001	Wang et al., in review
1129	Northwest	Northwest	*Lissachatina fulica*	Snail shell	5.9181	−7.3703	0.7248	0.00001	Wang et al., in review
1289	Northwest	Northwest	*Coula edulis*	Nut shell	5.9309	−7.3640	0.72166	0.00001	Wang et al., in review
1306	Northwest	Northwest	*Coula edulis*	Nut shell	5.9312	−7.3466	0.72986	0.00001	Wang et al., in review
1103	Northeast	Northeast	*Lissachatina fulica*	Snail shell	5.8613	−7.3021	0.72102	0.00001	Wang et al., in review
1105	Northeast	Northeast	*Lissachatina fulica*	Snail shell	5.8713	−7.2939	0.72265	0.00001	Wang et al., in review
1106	Northeast	Northeast	*Lissachatina fulica*	Snail shell	5.8535	−7.3119	0.72297	0.00001	Wang et al., in review
1107	Northeast	Northeast	*Lissachatina fulica*	Snail shell	5.8534	−7.3073	0.72035	0.00001	Wang et al., in review
1127	Northeast	Northeast	*Lissachatina fulica*	Snail shell	5.8572	−7.3008	0.72215	0.00001	Wang et al., in review
1645	South	South	*Musanga cecropioides*	Plant	5.8012	−7.3192	0.72185	0.00001	This study
1646	South	South	*Coula edulis*	Plant	5.8180	−7.2992	0.71848	0.00001	This study
1682	South	South	*Parkia bicolor*	Plant	5.8301	−7.3328	0.71106	0.00001	This study
1684	South	South	*Musanga cecropioides*	Plant	5.8156	−7.3249	0.71987	0.00001	This study
1663	South	South	*Sarcophrynium brachystachyum*	Plant	5.8359	−7.3036	0.71753	0.00001	This study
1666	East	East	*Coula edulis*	Plant	5.8430	−7.2766	0.72078	0.00001	This study
1668	East	East	*Parkia bicolor*	Plant	5.8335	−7.2590	0.71394	0.00003	This study
1675	East	East	*Sterculia oblonga*	Plant	5.8240	−7.2842	0.70774	0.00001	This study
1676	East	East	*Dialium aubrevillei*	Plant	5.8139	−7.2792	0.72229	0.00001	This study
1649	Middle	Middle	*Coula edulis*	Plant	5.8516	−7.3337	0.71655	0.00001	This study
1655	Middle	Middle	*Sarcophrynium brachystachyum*	Plant	5.8444	−7.3336	0.71344	0.00001	This study
1657	Middle	Middle	*Coula edulis*	Plant	5.8392	−7.3356	0.71693	0.00001	This study

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TABLE 2 (Continued)

No.	Territory	Time slice	Species	Sample type	Latitude	Longitude	$^{87}Sr/^{86}Sr$	2SE	Source
1654	Middle	Middle	*Dialium aubrevillei*	Plant	5.8449	−7.3287	0.71842	0.00001	This study
1660	Middle	Middle	*Dialium aubrevillei*	Plant	5.8399	−7.3260	0.72190	0.00002	This study

2.3 | Dental sampling

For the 34 Taï chimpanzee samples, skulls were CT-scanned to record morphometric information prior to destructive sampling, and we used this 3D data to determine the best sampling locality on each tooth, avoiding microcracks and dental wear. We mechanically cleaned the sampling area with a diamond-tipped dental drill and then recovered about 50 mg of enamel reaching from the occlusal surface to the cementum-enamel junction, of which ~10 mg was used for subsequent $^{87}Sr/^{86}Sr$ analysis. Abraded enamel was placed in cleaned glass beakers and sonicated in ultrapure acetone to remove dust and exogenous contamination. Cleaned samples were then removed from the solution, transferred into clean Eppendorf tubes, and air dried in a sterile fume hood.

As tooth enamel forms during a specific developmental time window and does not subsequently remodel (Driessens & Verbeeck, 1990; White et al., 2011), the dental enamel samples in this study correspond to the following age ranges in years: ±1 year in utero (m1 and m2), in utero to 2.8 (M1), 1.8–5.6 (M2), and 3.6–8 (M3) (Schwartz et al., 2000; Smith et al., 2007; Smith et al., 2010). Lowercase and uppercase letters refer to deciduous and permanent molars, respectively. The $^{87}Sr/^{86}Sr$ ratios measured in deciduous molars, which formed in utero, are representative of the maternal body chemistry, given that virtually no placental discrimination of Sr isotopes has been shown (Shagina et al., 2007; Smith et al., 2022). Individual's year of tooth formation (ytf) is extrapolated from the date of birth and tooth type. For example, if an individual was born in 1980, and a third molar is sampled, we can estimate that the enamel formed between 8 and 9 years of age (from 1988 to 1989). We also include age at death (in years) for the individual (Table 1). We recognize that all birth dates are estimates based on observation for most individuals sampled, however, the relative range for dental tissue formation +/− 1 year should encompass errors in these estimates.

Female chimpanzees reach sexual maturity at around 10 years, often leaving their birth communities in the subsequent years. Therefore, all female permanent teeth used in this study are assumed to represent a predispersal isotope signal from their birth community's territory (Thompson, 2013). Deciduous premolars represent the $^{87}Sr/^{86}Sr$ range of the territory inhabited by the mother during gestation. Our samples include five deciduous molars, all from individuals with mothers that were North community residents while pregnant, and therefore should reflect the Sr isotope signature for North community's territory.

2.4 | Environmental sampling for Sr isoscape

To create a bioavailable Sr isoscape for the TCP study area, we sampled leaves of various chimpanzee plant foods from the TCP-established chimpanzee territories ($n = 14$) and used additional leaf samples ($n = 5$) from plants as part of a previous study in the surrounding TCP area (Lowry et al., 2021) (Table 2, Figure 2). In addition, we used data from nut (*Parinari excelsa*) and snail (*Lissachatina fulica*) shell fragments, which had been analyzed within the framework of a large-scale Sr isoscape project ($n = 16$, Wang et al., in review). Territory location and population density data collection began in 1984, detailing the temporal territory shifts of the TCP-habituated chimpanzee communities, and informed the environmental sampling of the historic range. An additional collection of ranging data began in the early 1990s, with records of exact GPS coordinates starting in 2013, informing the modern range of the North community (Wittig & Boesch, 2019).The environmental samples were binned by TCP-established community territories and their orientation within the study area (Figure 2): North, Northwest (Tai-E), Northeast (Tai-R, Pan African Programme), South, East, and Middle. Environmental samples collected as part of this study were georeferenced with a handheld GPS device, dried on site, stored in falcon tubes with silica, and transferred to the Primate Ecology and Molecular Anthropology lab at the University of California, Santa Cruz for analysis under import permits #PCIP-20-00092, -20-00377, and -21-00166.

Around the year 2000, the territory of North community shifted westward, due in part to a reduction in the number of adult males, and in part to pressure from Northeast community, which is known to have expanded westward around this time (see Figures S3–S6). To account for this shift in territory location and population density, the sampling area for North community is subdivided into two temporal groupings (see Figure 2), one "historic" North 1 (1980–1999) and one "modern" North 2 (2000–present). For both, highest presence density based on long-term focal follow data from the TCP database is the assumed territory for each grouping. North 1 represents the historical territory range from 1980 to 1999, when the territory was primarily restricted to the trails around North camp, with the main road constituting a border with a neighboring community with which North community had regular intercommunity encounters. North 2 represents 2000 to present when the territory shifted further west of the main road, away from North camp and the original trails, which aligns with the current ranging of North community. No chimpanzees were sampled from the modern population; therefore, the North 2 territory represents a potential location that individuals could have emigrated from. Northwest is an eco-tourism area that is northwest of North community and is not a TCP-defined study area, therefore, there is no data on territory location shifts or population density.

The territory shifts of the South, East, and Middle communities were not under study during the period that North community's territory shifted, as these communities were habituated later. However, based on direct researcher observations, we can report some more
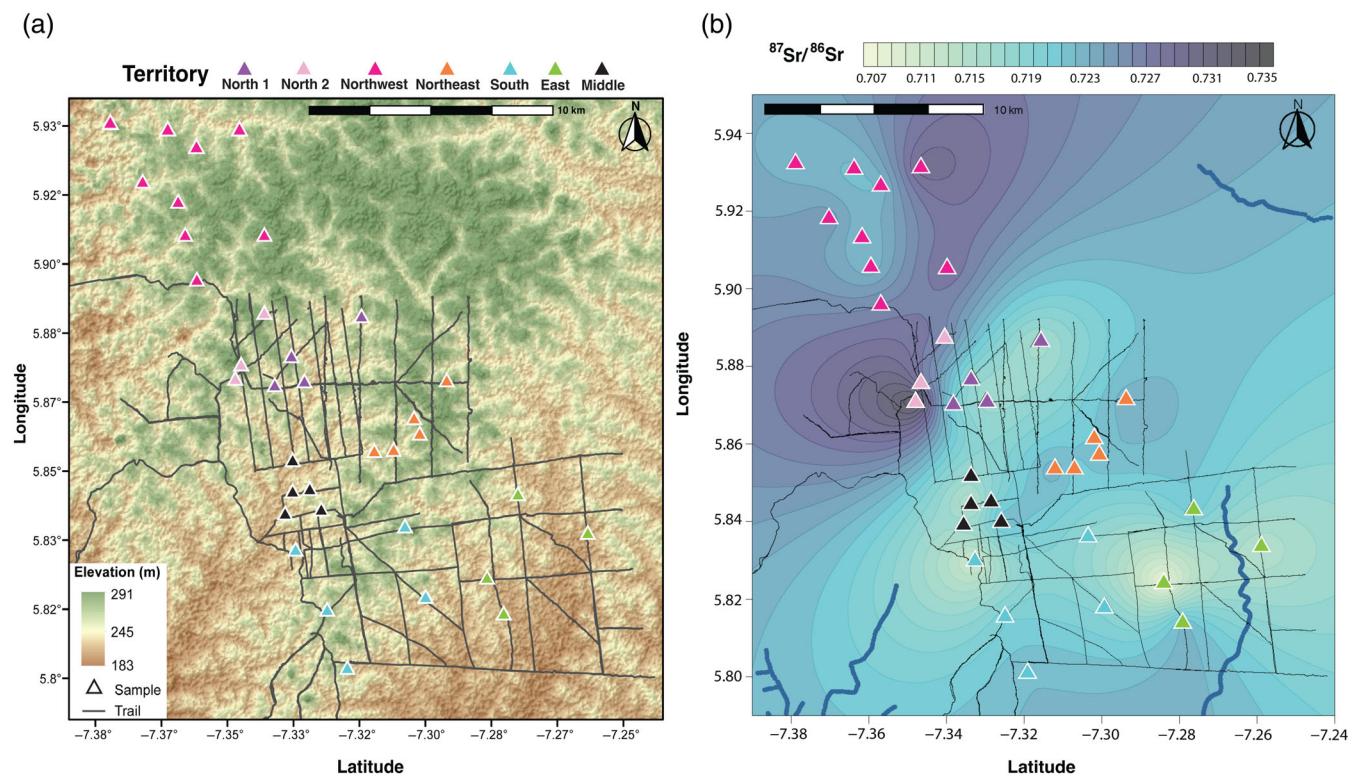
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FIGURE 2 Map of the environmental sample locations obtained from the Taï Chimpanzee Project (TCP) study area. (a) Digital elevation model of the TCP study area. Elevation is represented by the color scale, where light green represents higher elevation and brown represents lower elevation in meters (m). (b) Sr isoscape for the TCP area. Dark blue lines are rivers and streams, as visible on maps, and the overlying contour map is the kriging algorithm interpolation of $^{87}Sr/^{86}Sr$, forming a Sr isoscape of the region. The lighter contoured regions represent lower Sr isotope ratios, and the darker contoured regions represent higher Sr isotope ratios. Black lines indicate the trails and the relative extent of the TCP study area. North 1 represents the historic North community's territory from 1980 to 1999 ($n = 4$), and North 2 represents the modern North community's territory from 2000 to present ($n = 3$).

subsequent shifts in territorial locale. From 2014, South community, situated south of North community, has expanded their territory further southward, resulting in the expansion of the trail system (Boesch & Wittig, 2019; Lemoine et al., 2019). Since habituation, East community, located east of South community, is reported to have one of the largest territories, and is not known to have shifted its territory location (Kouakou et al., 2011). During the study period, Middle community, situated between North and South communities, did not shift its territory, however, as Middle community is no longer observed after experiencing a significant decline in numbers, it is unclear what the present territory is.

2.5 | $^{87}Sr/^{86}Sr$ analysis

Dried tooth samples were transferred to a clean lab setting where 10 mg was weighed into acid-washed Teflon beakers and digested in 1 mL triple-distilled, concentrated HNO_3 (15.9 M) at 120°C and subsequently evaporated to dryness on a hotplate. Dry leaf samples (~1–1.5 g), snail shell (10–15 mg), and nutshell (10–15 mg) were weighed into sonicated porcelain crucibles to be ashed in a muffle furnace at 800°C for 8 h. The resulting ash (~10 mg) was then weighed into

clean Teflon beakers and digested in 1 mL triple distilled, concentrated HNO_3 at 120°C, which was subsequently evaporated to dryness.

For chromatographic separation of Sr from other elements, we dissolved samples in 1 mL 3M HNO_3 for 2 h at 120°C along with one procedural blank. We followed the gravity flow column chromatography protocol outlined by Deniel and Pin (2001) modified after Copeland et al. (2008). Briefly, as samples were dissolving, 1 mL 50–100 μm Sr-spec™ resin (Eichrom Technologies) was loaded in Bio-Rad™ gravity-flow chromatography columns, rinsed twice with 10 mL ultrapure water (18.2 M Ω cm) obtained from a Milli-Q Element water purification system, then conditioned with 3 mL of 3M HNO_3. Dissolved samples were carefully loaded onto the columns, drop by drop, then captured and reloaded twice to maximize the amount of Sr binding to the resin. After three washes with 500 μL 3M HNO_3, the Sr was eluted with 1.5 mL MQ H_2O into a clean Teflon beaker and evaporated to dryness under the presence of two drops of phosphoric acid (H_3PO_4), which helps to concentrate the sample while drying.

For measurement of the samples on a thermal ionization mass spectrometer (Phoenix62, Isotopx) in the UC Santa Cruz W.M. Keck Isotope Laboratory, we resolved the visible Sr pellet in 1 μL of tantalum chloride ($TaCl_5$) activator, which was then loaded onto degassed

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rhenium filaments, alongside the international standard, SRM NIST987. Procedural blanks were measured on an Element XR high-resolution ICP-MS in the UC Santa Cruz Plasma Analytical lab to quantify possible cross-contamination or impurity of reagents. Internal precision (in percentages) and analytical blank concentrations (in parts per million) are reported in the results section.

2.6 | Data analysis

All analyses and visualizations were created using R, with a significance level of $\alpha = 0.05$ (R Core Development Team, 2024). The full dataset is provided in Table 1 for all individuals and Table 2 for all environmental samples.

To assess how $^{87}Sr/^{86}Sr$ differences in chimpanzee enamel and the environment vary in the TCP study area, we conducted the following: (1) established a local isoscape from environmental samples from the territories of four habituated communities (North, South, East, and Middle communities) and from two neighboring territories (Northeast and Northwest communities), then assessed if there are significant $^{87}Sr/^{86}Sr$ differences among environmental samples consistent with the territories of chimpanzee communities, (2) assessed if there are $^{87}Sr/^{86}Sr$ differences in chimpanzee enamel samples between communities, and (3) compared the $^{87}Sr/^{86}Sr$ ratios between individuals binned as "unknown" females with females that have a known natal community, to validate the "unknown" females' origin status (immigrant or native).

2.6.1 | Establish a local isoscape from environmental samples

We explored the differences in $^{87}Sr/^{86}Sr$ between the following territories: North 1 ($n = 4$), North 2 ($n = 3$), Northeast ($n = 4$), Northwest ($n = 9$), South ($n = 5$), East ($n = 4$), and Middle ($n = 5$) (Table 2). To verify that sample type (plant, nutshell, and snail shell) did not cause heteroscedasticity, we assessed the homogeneity of variance between territories (North [North 1–2], Northeast, Northwest, South, East, and Middle) using the "stats" package in R (Bartlett, 1937; R Core Development Team, 2024). To test if there were differences in Sr environmental baselines between TCP-established territories, we fitted two generalized linear mixed models (GLMMs) with a beta distribution (Bolker et al., 2009) using the "glmmTMB" package in R 4.2.1 (Brooks et al., 2022; Magnusson et al., 2017; R Core Development Team, 2024). Mixed model fit was validated using the "DHARMa" package in R (Hartig & Hartig, 2017). In the hypothesis (full) model, $^{87}Sr/^{86}Sr$ data from environmental samples are predicted by territory, as a fixed effect and sample type (plant, nutshell, and snail shell) was included as a random effect. In the null model, $^{87}Sr/^{86}Sr$ data from environmental samples are only predicted by sample type, as the random effect (Table S1). Since there are small sample sizes for North 1 ($n = 4$), North 2 ($n = 3$), and East ($n = 4$), the Akaike information criterion was corrected for small sample sizes (AICc). Then, the "MuMIn" package was used to compare the full and null models and select the model

with the best fit, that is, the model with the lowest AICc scores (Anderson & Burnham, 2004; Barton & Barton, 2015). An estimated marginal means post hoc analysis was performed to assess the significance of pairwise differences in $^{87}Sr/^{86}Sr$ ranges between territories. Estimated marginal means in log-odds ratio scale were computed, and *p*-values adjusted for multiple comparison by Bonferroni using the 'emmeans' package in R (Lenth et al., 2021). Since we have a small sample size per territory ($n < 10$), we also performed a power analysis for each pairwise difference generated by the 'emmeans' package (Kumle et al., 2021).

To create a Sr isoscape of the study area, we constructed $^{87}Sr/^{86}Sr$ contour maps with the environmental $^{87}Sr/^{86}Sr$ dataset ($n = 35$) and a Kriging algorithm in the Surfer software package (Figure 2). Kriging is a geostatistical gridding method that produces maps by interpolating irregularly spaced data points to express the trends within a dataset (Cressie, 1990, 2015; Journel & Journel, 1989; PL & Srivastava, 1989). Although direct researcher observations remark on inselberg outcrops emerging from volcanic tuffs in the TCP study area, a detailed geological map of TNP or the TCP study area is not available. Therefore, we were not able to use random forest modeling to build a local isoscape (Bataille et al., 2018). We can only show predicted $^{87}Sr/^{86}Sr$ trends across the TCP study area in relation to topographic and hydrologic features in the surrounding landscape (Figure 2).

2.6.2 | Are there significant $^{87}Sr/^{86}Sr$ differences in chimpanzee enamel samples between chimpanzee communities?

To validate the environmental baseline and Sr isoscape for the TCP study area, we analyzed $^{87}Sr/^{86}Sr$ ratios in enamel bioapatite from resident chimpanzees ($n = 17$). The resident chimpanzees are only associated with TCP-established communities included in the sample population: North community ($n = 10$), South community ($n = 4$), East community ($n = 2$), and Middle community ($n = 1$). Subadult females were omitted, as only males were sampled from the reference communities, to ensure a balanced sample size and prevent overrepresenting North community individuals. The R 'stats' package was used to compare the theoretical density and distribution of the $^{87}Sr/^{86}Sr$ ratios in enamel bioapatite from resident chimpanzees in TCP-established communities (R Core Development Team, 2024). Since the overall sample size is small for the reference male group ($n = 7$), we assessed the overlap between $^{87}Sr/^{86}Sr$ ratios relative to the North community natal males. First, we used R "fitdistrplus" to fit the $^{87}Sr/^{86}Sr$ ratios for post-1980 North community natal males with a beta distribution and calculated the 2.5% (0.718) and 97.5% (0.722) quantiles (Delignette-Muller & Dutang, 2015). Next, we assessed if the $^{87}Sr/^{86}Sr$ ratios of the pre-1980 natal males ($n = 2$) were different from post-1980 natal males ($n = 8$) by plotting the $^{87}Sr/^{86}Sr$ ratios of North community pre-1980 natal males onto the theoretical density of post-1980 natal males. Since pre-1980 natal males fell within the quantiles of post-1980 natal males, we included them in this group ($n = 10$, Figure S1) and calculated the new 2.5% (0.717) and 97.5%

(0.722) quantiles. Next, we assessed if the ^{87}Sr/^{86}Sr ratios of the other TCP-established communities (South, East, and Middle) fell within the quantiles of the theoretical density of all North community natal males ($n = 10$).

2.6.3 | Do ^{87}Sr/^{86}Sr ratios of unknown females correspond to those of natal individuals?

To test if ^{87}Sr/^{86}Sr ratios can discern unknown Taï chimpanzee female origin status (natal or immigrant) within North community ($n = 27$), we compared unknown females from pre-1980 ($n = 4$) and post-1980 ($n = 7$) to all native North community residents ($n = 16$). North community residents includes males ($n = 10$) and subadult females ($n = 6$), representing the pre-dispersal population, which we use as a local baseline for North community. To test if there were differences between origin groups (pre-1980 unknown female, post-1980 unknown female, and post-1980 natal community), we fitted and validated two GLMMs. For the full model, ^{87}Sr/^{86}Sr from enamel samples is predicted by the origin community (natal post-1980, unknown female pre-1980, and unknown female post-1980) as a fixed effect. Sample type (dm, M1, M2, and M3) is included as a random effect to account for differences in age and tooth formation range. In the null model, ^{87}Sr/^{86}Sr data from North community chimpanzee enamel samples are only predicted by sample type, as a random effect. AICc, which is corrected for small sample size was used to compare the full and null models and select the model with the best fit. A post hoc analysis was run to see the pairwise comparisons between origin groups and determine which origin groups are significantly different in ^{87}Sr/^{86}Sr ratios. Since we have a small sample size per origin group ($n < 20$), we also performed a power analysis for each pairwise difference generated by the "emmeans" package (Kumle et al., 2021). Following a power analysis, we also explore the individual origin of unknown females. To do this, we use the interquartile range (IQR) of North community residents ($n = 16$) multiplied by 1.5 (IQR $\times$ 1.5) to determine potential outliers, and likely individual immigrants.

3 | RESULTS

We successfully obtained ^{87}Sr/^{86}Sr ratios from all teeth and plant samples. The NIST-987 standard after 7 cycles of data collection had an average ratio of 0.710422 ± 0.00004 (2σ) (McArthur et al., 2001). Internal precision for strontium runs is typically 0.00069% SE. Total procedural blanks for strontium are <0.0003 ppm.

3.1 | Establish a local isoscape from environmental samples

^{87}Sr/^{86}Sr ratios for the environmental baseline range from 0.70774 to 0.73460, with precision reported to 2 SE (see Table 2). To assess the

fit of the Sr isoscape (Figure 2), we used the root-mean-square error (RMSE), where the ordinary kriging resulted in an RMSE value of 0.0048 (22% of the whole ^{87}Sr/^{86}Sr data range). There were no significant differences in variance of ^{87}Sr/^{86}Sr ratios within TCP-established territories (bartlett, $K^2 = 11.1$, $df = 6$, $p > 0.05$). The full model had a lower AICc and GLMMs identified significant differences in ^{87}Sr/^{86}Sr between territories, where territory was a fixed effect and sample type was a random effect (summarized in Supporting Information, Tables S1 and S2, Figure 3). There was a statistically significant difference in ^{87}Sr/^{86}Sr for the territories North 2 (Wald-Z Statistic = 5.38, $p < 0.00001$), Northwest (Wald Z-Statistic = 4.29, $p < 0.00001$), and East (Wald Z-Statistic = 115.74, $p < 0.00001$), as well as Northeast (Wald Z-Statistic = 2.58, $p < 0.01$). A post hoc analysis showed significant pairwise differences between East-North 2 (z-ratio = −5.38, $p < 0.0001$), East-Northwest (z-ratio = −4.19, $p = 0.0006$, 0.80), Middle-North 2 (z-ratio = −5.11, $p < 0.0001$), Middle-Northwest (z-ratio = −3.83, $p = 0.003$), North 1-North 2 (z-ratio = −4.96, $p < 0.0001$), North 1-Northwest (z-ratio = −3.64, $p = 0.006$), North 2-Northeast (z-ratio = 3.27, $p = 0.02$), North 2-South (z-ratio = 4.98, $p < 0.0001$), and Northwest-South (z-ratio = 3.65, $p = 0.005$) (estimated marginal means, with a p-value adjustment in Bonferroni method; Table S2, Figure 3). However, there was only intermediate to high power for East-Northwest (power = 0.80), Middle-Northwest (power = 0.63), North 1-Northwest (power = 0.66), and North 2-Northeast (power = 0.98). Any intermediate-high power values where there was no significant effect noted in the GLMMs were ignored.

3.2 | Are there significant ^{87}Sr/^{86}Sr differences in chimpanzee enamel samples between chimpanzee communities?

^{87}Sr/^{86}Sr ratios for resident male chimpanzees ranged from 0.71662 to 0.72187 (Table 1, Figure 3). Since there was a small sample size for reference males, no statistical tests were performed, and we exclusively assess the ^{87}Sr/^{86}Sr ratios for the "reference" resident males ($n = 7$) relative to the North community natal males ($n = 10$). The mean and median ^{87}Sr/^{86}Sr ratios for North community natal males are 0.71993 and 0.72023, respectively. The ^{87}Sr/^{86}Sr ratios for resident males from South ($n = 4$) and Middle ($n = 1$) communities males fell within the 2.5% (0.717) and 97.5% (0.722) quantile range of North community natal males (summarized in Supporting Information, Figure S2). The ^{87}Sr/^{86}Sr ratios for resident males from East community ($n = 2$) fell outside of the 2.5% (0.717) and 97.5% (0.722) quantile range of North community natal males. This suggests that the ^{87}Sr/^{86}Sr ratios for East community males does not overlap with North community natal males, however, due to the small sample size, we are not able to test the statistical significance of this pattern. Within the entire TCP study area, there was an average mismatch of 0.003 between natal males and their respective territories (Figure 3).
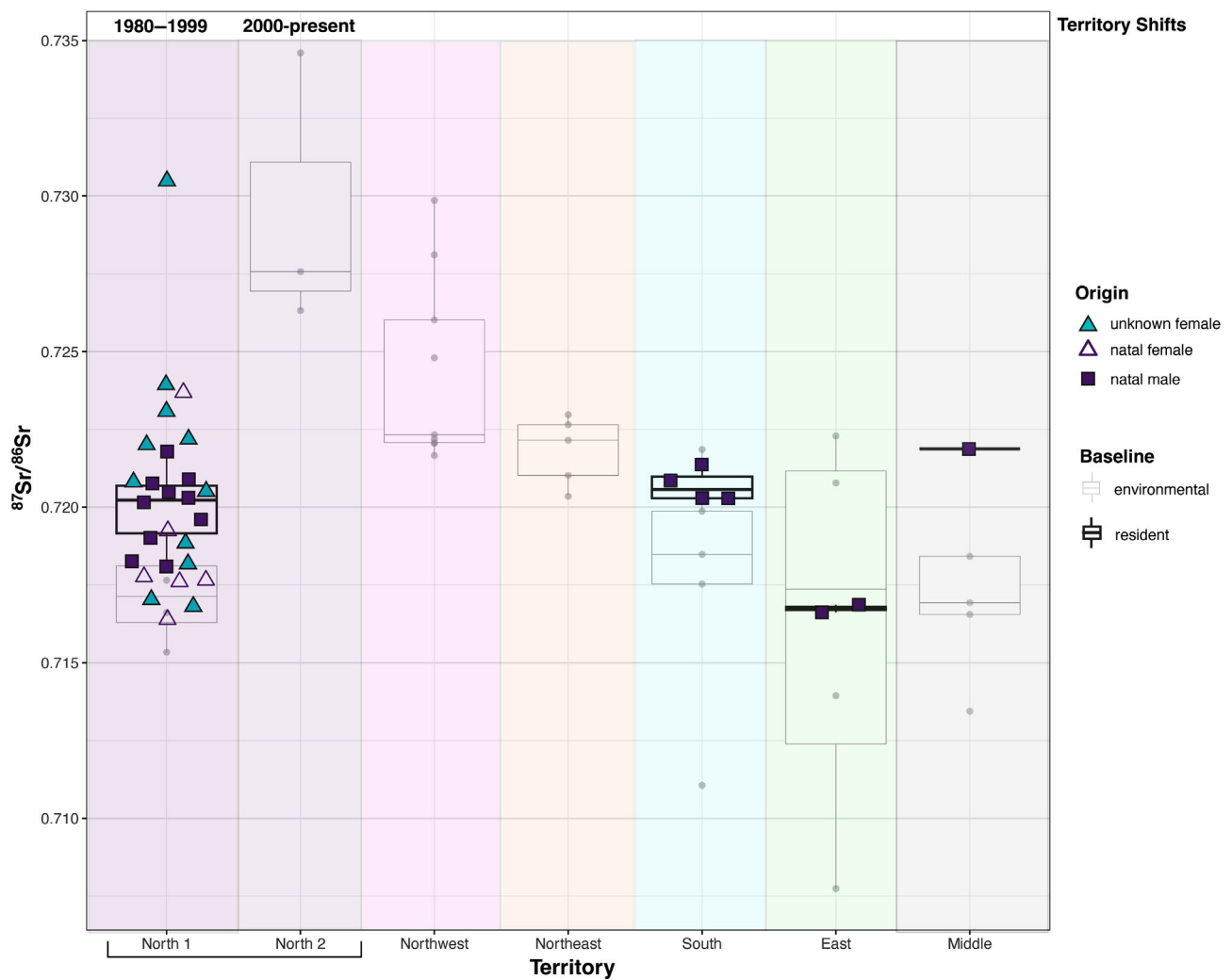
FIGURE 3 Boxplot illustrating the environmental variation in ^{87}Sr/^{86}Sr by territory, including territories of neighboring chimpanzee communities. For each chimpanzee territory, the black boxplots represent the median, upper, and lower quartiles for the ^{87}Sr/^{86}Sr data obtained from resident males. In contrast, gray boxplots represent the ^{87}Sr/^{86}Sr baseline obtained from environmental data. Open triangles are natal subadult females not included in the resident chimpanzee baseline. Cyan triangles designate females of unknown natal status. North comprises individuals that formed tooth enamel before 1980 ($n = 6$) and after 1980 ($n = 21$), as well as environmental baseline samples that represent the historical (1980–1999) and modern (2000–present) territory location shifts. The areas Northwest and Northeast are represented only by environmental samples.

3.3 | Do ^{87}Sr/^{86}Sr ratios of unknown females correspond to those of natal individuals?

The ^{87}Sr/^{86}Sr ratios for adult females of unknown origin from pre-1980 (n = 4) and post-1980 (n = 7) ranged from 0.71681 to 0.73049 (Table 1, Figure 4). The full model had a lower AICc and GLMMs identified significant differences in ^{87}Sr/^{86}Sr ratios between adult female origin groups, where origin group was a fixed effect, and tooth type was a random effect (Table S3). Complete model outputs are available in Supporting Information, Tables S3 and S4, Figure 4. In the origin community, ^{87}Sr/^{86}Sr ratios in unknown females from post-1980 significantly differed from the North natal community (z-ratio = 4.08, p < 0.000001; Figure 4). A post hoc analysis (estimate marginal means, with a p-value adjustment in Bonferroni method, Table S4) showed a

significant pairwise difference between unknown females and North community residents post-1980 (z-ratio = −4.08, p = 0.0001, power = 0.94), as well as between unknown females post-1980 and pre-1980 (z-ratio = 4.41, p < 0.0001, power = 1.00). However, there were no significant differences between unknown females pre-1980 and North community residents post-1980 (z-ratio = 1.47, p = 0.42, power = 0.31).

The IQR × 1.5 was 0.71944 ± 0.004 for North community residents (n = 16). When comparing unknown females (n = 11) to North community residents (0.715–0.723), we found that 2 out of the 11 unknown females (NF07 and NF10) had ^{87}Sr/^{86}Sr ratios that were outside of this range (18%, 0.724–0.730). While 9 out of 11 unknown females (NF01, NF02, NF03, NF04, NF05, NF06, NF08, NF09, and NF11) were within the ^{87}Sr/^{86}Sr ratios

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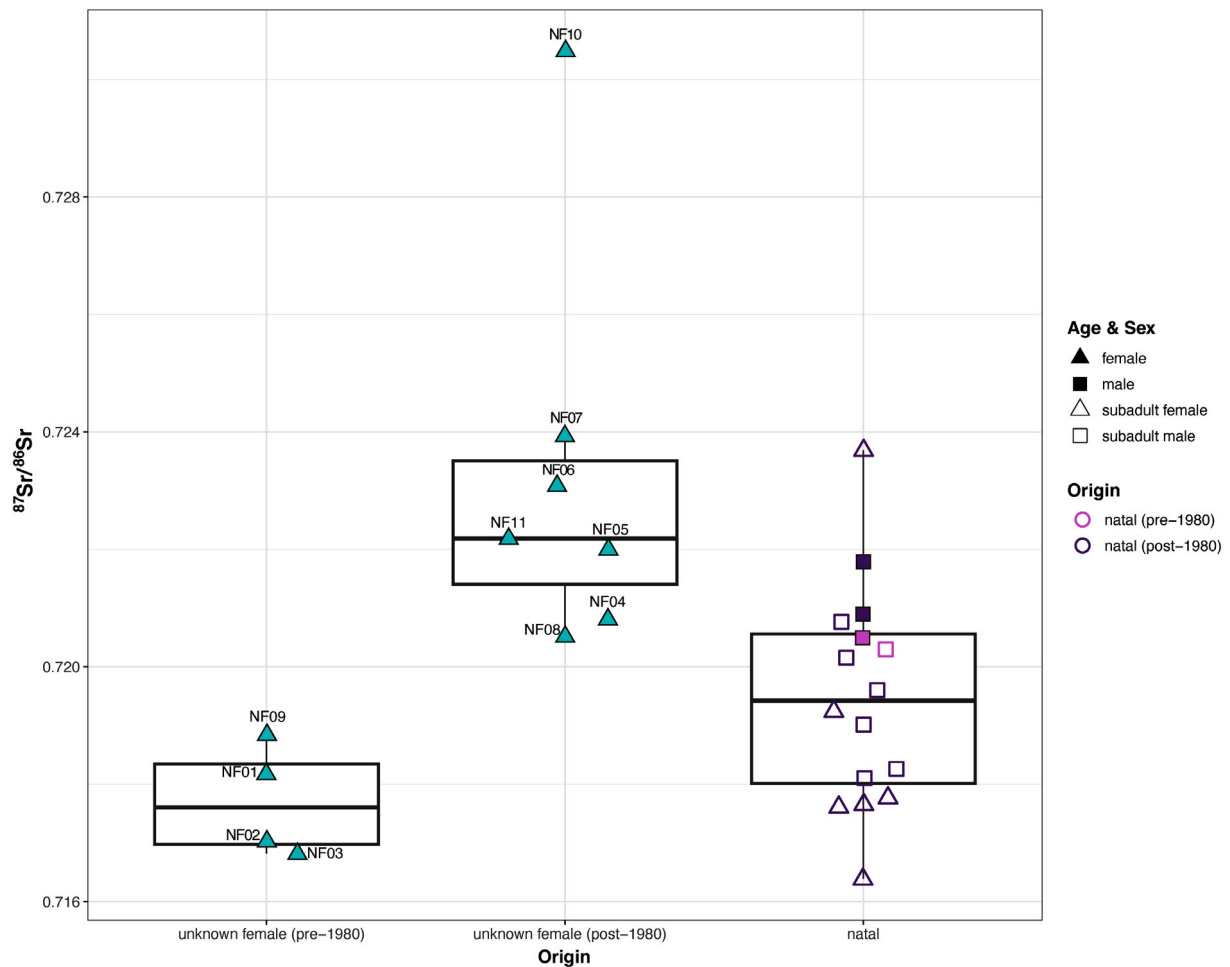The Official Journal of the American Association of Biological Anthropologists

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FIGURE 4 Boxplots illustrating the $^{87}Sr/^{86}Sr$ variation by origin group. Boxplots consist of the median, upper, and lower quartiles, representing the interquartile range (IQR). Values beyond the vertical bars ("whiskers") fall beyond 1.5 × IQR and are significant outliers. Unknown females comprises individuals that formed tooth enamel "before 1980" ($n = 4$) and "after 1980" ($n = 7$). North "natal" comprises individuals that formed tooth enamel before 1980 ($n = 2$) and after 1980 ($n = 14$).

IQR × 1.5 range (82%, 0.715–0.723) of North community residents (Figure 4).

4 | DISCUSSION

In this study, we measured the $^{87}Sr/^{86}Sr$ ratios of chimpanzee enamel from four communities and developed, with locally sourced environmental samples, a local isoscape of their territories (North, South, and East, Middle), as well as two neighboring territories (Northwest and Northeast). We show that the $^{87}Sr/^{86}Sr$ baselines differ between TCP chimpanzee territories and among some Taï chimpanzee communities. We demonstrate that natal males and subadult (predispersal) females can be used to establish a chimpanzee community's $^{87}Sr/^{86}Sr$ baseline. This combined approach allowed us to use $^{87}Sr/^{86}Sr$ ratios to assess which females of unknown origin may have migrated to the TCP-established North community. However, the exact region that these females could have originated remains unclear and would require more extensive environmental sampling of TNP. There is a

general mismatch between the local environmental and resident individual enamel $^{87}Sr/^{86}Sr$ data within each territory, which demands further exploration in the future (Figure 3).

The TCP study area is highly heterogeneous in $^{87}Sr/^{86}Sr$ ratios (Figure 2b), which is in line with our observations of general geological heterogeneity in the field but was not supported by the low resolution of geological maps available for this part of Côte d'Ivoire. Within the TCP study area, the environmental $^{87}Sr/^{86}Sr$ ratios range from 0.708 to 0.735, a remarkable range for a relatively small study area of less than 400 km². However, we do recognize that some variation in $^{87}Sr/^{86}Sr$ ratios could be missed by our relatively small sample size ($n < 10$) for each chimpanzee territory. Even more radiogenic $^{87}Sr/^{86}Sr$ ratios, ranging from 0.724 to 0.767, have been measured approximately 50–60 km southeast at the ecotourism site of Djouroutou (Wang et al., in review). This demonstrates that there is immense geological variability within TNP that early geological surveys from the greater park region could not account for (Rouw et al., 1990). It is also noteworthy that the observed $^{87}Sr/^{86}Sr$ range within the TCP study area aligns with what is reported for Saharan dunes (0.713–

0.737), suggesting that there could be a strong influence of the Harmattan season (Stojanowski & Knudson, 2011). Dusts from the Sahara Desert, specifically from the sand dunes in Libya and Chad can have Sr concentrations ranging from 76 to 202 ppm, and Rb concentrations ranging from 53 to 67 ppm (Gross et al., 2016). Therefore, it is possible that within Taï, the $^{87}Sr/^{86}Sr$ variability in plants and the slightly higher $^{87}Sr/^{86}Sr$ ratios for chimpanzee enamel are driven by the seasonal influx of Sahara dust (Frumkin & Stein, 2004). The Harmattan dust typically reaches the TNP in early January and is estimated to deposit around 60–100 kg/ha in the Taï forest (Stoorvogel et al., 1997; Wittig, 2018). There was a strong influence of the Harmattan between 1992 and 2009, which overlaps with tooth formation periods of some of the sampled individuals (Table 1; Schulz-Kornas et al., 2019). During the Harmattan, Taï chimpanzees have even been found to respond with less chewing, leading to larger fecal particle size during Harmattan season (Schulz-Kornas et al., 2019). We propose that the seasonal influx of dust during the Harmattan also influences the $^{87}Sr/^{86}Sr$ characteristics of Taï forest, and as a result, could contribute to the isotopic mismatch between resident chimpanzees and their territories.

We found isotopic differences between neighboring chimpanzee territories. For the historic North community territory, we found that Middle and South communities overlapped in the isotopic baselines from environmental $^{87}Sr/^{86}Sr$ and chimpanzee enamel $^{87}Sr/^{86}Sr$ ratios, suggesting geological homogeneity across these territories. When considering the environmental $^{87}Sr/^{86}Sr$ ratios for modern North community territory (referred to as North 2 in Tables 1, S1, and S2), there are significant differences in $^{87}Sr/^{86}Sr$ ratios when compared with the territories of historic North community (referred to as North 1 in Tables 1, S1, and S2), South community, East community, Middle community, and Northeast community (Table S2). However, the statistical power was low for the comparisons between the modern North community and East (0.02), Middle (0.01), historic North (0.01), and South (0.29) community's territories (Table S2). This could suggest the following: (1) there was a high Type II error, since we used the more conservative Bonferroni method, (2) there was high variance among the samples, and (3) the sample size was too small to detect an effect. In spite of this, high statistical power when comparing the Northwest and Northeast territories suggest that these territories are indeed statistically different from the other territories (Table S2 and Figure 3). The modern North community appears to be characterized by higher geological heterogeneity than the historic North territory, which could be related to the proximity to the prominent granite outcrops (inselbergs) in the Northwest territory (Figures 2, 3, and S6). Similarly, in the northwestern, northeastern, and western parts of the TCP area, we found more radiogenic $^{87}Sr/^{86}Sr$ baseline ratios (Tables S1 and S2, Figure 2), likely driven by inselbergs in these regions (see elevation in Figure 2a). In contrast, the Middle, East, and South regions are marked by lower $^{87}Sr/^{86}Sr$ ratios (Tables S1 and S2, Figures 2 and 3), which could be related to the influx of extrinsic sediment from the Cavally and Sassandra rivers (Goldstein & Jacobsen, 1987). Indeed, water-related weathering and erosion, which affect the Sr concentration in river runoff, can result in lower

$^{87}Sr/^{86}Sr$ ratios in riparian environments (Capo et al., 1998; Sillen et al., 1998).While there are some inselbergs in South, and East territories, we suggest that the environmental $^{87}Sr/^{86}Sr$ ratios are possibly driven by increased weathering related to several small river systems (Figures 2b and 3; Luncz et al., 2016). Particularly in East territory, we know of well-documented offshoots of the Cavally River, which could influence the distinct pattern in $^{87}Sr/^{86}Sr$ ratios observed in this area (Hamilton et al., 2019; Poszwa et al., 2002; Poszwa et al., 2004).

The overall heterogeneity in geology, landscape, and the reported $^{87}Sr/^{86}Sr$ ratios allowed us to detect differences between neighboring chimpanzee territories and resident individuals of these neighboring communities. We found that $^{87}Sr/^{86}Sr$ ratios from resident males in the East community (0.716) did not overlap with those from resident males in the North community (0.717–0.722, Figure S2). However, all other chimpanzee reference communities (South and Middle) were within the $^{87}Sr/^{86}Sr$ range of North community resident males (Figure S2). The unique $^{87}Sr/^{86}Sr$ ratios for East community could be related to the riparian environment in this territory, or the isotopic variation in this community may not have been captured by our small sample size ($n = 2$). We also found that in North community, $^{87}Sr/^{86}Sr$ ratios differed between resident males and resident subadult females, where females have lower $^{87}Sr/^{86}Sr$ ratios (Figure 4). In fact, predispersal subadult females appear to align better with the environmental baseline for North community (see Figure 3). This unexpected sex difference could possibly be related to diet, with subadult females engaging more in nut-cracking (Boesch & Boesch, 1984). Subadult males do engage in hunting and meat eating, but meat is less than 1% of the overall diet (Bertin & Wittig, 2019; Boesch & Boesch, 1989). Other studies have suggested that meat must make up 90% of a diet before influencing $^{87}Sr/^{86}Sr$ ratios, due to low concentrations of Sr and Ca (Burton & Price, 2002; Burton & Wright, 1995; Runia, 1987). Therefore, we propose that the sex difference could be related to the $^{87}Sr/^{86}Sr$ variation in plants and more females participating in nut-cracking relative to males.

The combination of the environmental isotope data from the TCP study area and our comparison with resident individuals allowed us to assess the migratory history of several adult females of unknown origin who resided in North community as adults. First, we show that there is a significant difference in $^{87}Sr/^{86}Sr$ ratios between unknown females pre-1980 (0.717–0.719, $n = 4$) and post-1980 (0.719–0.730, $n = 7$). Since unknown females pre-1980 (0.71771) do not overlap with pre-1980 natal males (0.72039), which are shown to align with post-1980 natal males (Figure S1), it is unclear if this relates to an unknown territory shift in pre-1980 North community residents pre-1980, a sex-difference in diet, or a potential origin locality with similar $^{87}Sr/^{86}Sr$ ratios to the historic North community's territory. The lower variance in $^{87}Sr/^{86}Sr$ ratios for unknown females pre-1980 could also indicate a much smaller population density relative to post-1980. Additionally, since pre-1980 unknown females overlap with East community (Figure 4), it is possible that the territory of North community was oriented slightly more east, where there is an area with lower $^{87}Sr/^{86}Sr$ ratios (Figure 2b). However, additional environmental samples will be needed to confirm this.

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From direct observations in the Taï chimpanzees, it is estimated that around 88% of females disperse from their natal territory (Boesch, 1997; Lemoine et al., 2019). For the historically well-studied North community, we show that females of unknown origin post-1980 ($n = 7$) are significantly different from resident individuals post-1980. However, due to our small sample size, this could be influenced by two females that have much higher $^{87}Sr/^{86}Sr$ ratios (0.723 and 0.730) than the mean for pre-1980 unknown females (0.71734, $n = 3$) and post-1980 unknown females (0.72124, $n = 6$). In spite of this, all unknown females are within the $^{87}Sr/^{86}Sr$ range of the larger TCP study area (Figures 3 and 4), suggesting that these females might come from neighboring communities or the other parts of the Taï forest with similar $^{87}Sr/^{86}Sr$ ratios. Our isotope data suggests that only two females (NF07 and NF10) categorized as of unknown origin in North community indeed did not overlap with the $^{87}Sr/^{86}Sr$ ratios of North territory at the time their teeth formed, nor do they match resident males and subadult females. This suggests they likely migrated to North Community from elsewhere. It is possible that these females could be from areas in the modern North (0.726–0.735), Northwest (0.722–0.729), Northeast (0.720–0.723), or territories that have more radiogenic $^{87}Sr/^{86}Sr$ ratios like those observed for Djouroutou (0.724–0.767, Wang et al., in review). Nine of these females (NF01, NF02, NF03, NF04, NF05, NF06, NF08, NF09, and NF11) were within the $^{87}Sr/^{86}Sr$ IQR × 1.5 (0.715–0.723) of North community residents, suggesting that they are in line with the median $^{87}Sr/^{86}Sr$ ratio for North community natives, but it is also possible that they could be from a territory with similar $^{87}Sr/^{86}Sr$ ratios further away. Since there is a significant overlap between the historic North community territory (0.716–0.719) with the South community (0.711–0.722) and Middle community territory (0.713–0.722), we also suggest that these nine females may be from other TCP-established territories (see Figure 4). However, without more extensive environmental sampling of the TNP, it is possible other areas within TNP have similar $^{87}Sr/^{86}Sr$ ratios, therefore exact locations of origins are difficult to determine.

4.1 | Limitations and further considerations

There are several constraints within the scope of this study, such as the absence of reliable geological maps for our study area, the limited environmental sampling, and the isotopic mismatch between resident chimpanzees and their territories. We recommend the consideration of these limitations in future work that employs $^{87}Sr/^{86}Sr$ analysis in tracking female dispersal in skeletal remains of great apes, as well as the limitations of using $^{87}Sr/^{86}Sr$ ratios to inform early hominin dispersal models.

A main limitation of this study is that there are very little geological data available for TNP and almost none for the TCP study area (Collinet et al., 1984; Kolongo et al., 2006; Rouw et al., 1990). This limited our ability to build a more robust local and regional isoscape using machine learning approaches (e.g. see Bataille et al., 2020) that could have taken geological and other environmental factors into

consideration and allowed us to make predictions on female origins inside and outside of the TCP study area. Further, as a result of the limited scope of this study, we primarily sampled the local TCP study area to determine the isotopic variation within and across neighboring chimpanzee territories. More extensive environmental sampling of the larger TNP forest would expand this study's Sr isoscape and allow for a more nuanced interpretation of the possible origins of immigrant females.

We also found lower $^{87}Sr/^{86}Sr$ ratios in environmental samples compared with the respective resident $^{87}Sr/^{86}Sr$ ratios for several chimpanzee communities and their territories (see Figure 3). These isotopic mismatches could be related to variation in nutrient sources and/or variation in sampled plants' rooting depths (Grimstead et al., 2017). Chimpanzees tend to consume foods from a variety of sources (fruit, leaves, bark, pith, termites, ants, and primates) (Bertin & Wittig, 2019), resulting in a mixed dietary $^{87}Sr/^{86}Sr$ signal relative to any single measured plant, which will primarily obtain its $^{87}Sr/^{86}Sr$ ratios from the immediate soil substrate (Wright, 2005). Another possible explanation is that there is variation in rooting depths for the tree species sampled in this study (*Sarcophrynium brachystachyum*, *Musanga cecropioides*, *Parkia bicolor*, *Afzelia bella*, *Sterculia oblonga*, *Coula edulis*, and *Dialium aubrevillei*). Overall, trees are described as diverse in $^{87}Sr/^{86}Sr$ ratios due to their variable rooting depths (Poszwa et al., 2004). In primary tropical rainforests, however, the humus layer is commonly shallow, and rooting depth is overall low. In fact, none of the species sampled are known to exhibit unusually deep root systems (Koffi et al., 2022). However, foliar Sr levels still might differ in terms of nutrient sourcing, and their ability to sequester Sr from wind-blown dust, such as those that are associated with the Harmattan season discussed above (Grimstead et al., 2017). It is also possible that historical territory shifts occurred and resulted in the mismatch between the resident chimpanzee $^{87}Sr/^{86}Sr$ ratios and the environmental $^{87}Sr/^{86}Sr$ ratios measured from environmental samples in their present-day territories. It is also worth noting that the other chimpanzee communities (South: 1997, Middle: 2000, East: 2005, Northeast: 2015) were habituated much later than North community (ca. 1985, after Boesch & Wittig, 2019; Lemoine et al., 2019), and therefore territory shifts before tooth enamel formation of resident community members remain unknown and unaccounted for. Since habituation, South community shifted their territory further south, which could explain the difference in $^{87}Sr/^{86}Sr$ ratios between their historic and modern territory (Boesch & Wittig, 2019). The single male sampled for Middle community formed its enamel prior to habituation, and it is possible that his community occupied a slightly different territory before they were habituated in 2000.

Hence, when sampling skeletal tissues from chimpanzees to study natal dispersal, the limitations in the recently observed past of the study subjects need to be considered, particularly in long-term research projects with historic skeletal collections, such as the TCP. Ideally, we would be able to measure a pre- and post-dispersal isotope ratio from the same skeleton to identify natal dispersal over larger distances. This could be achieved by sampling early and late forming teeth from the same individual, as is increasingly done in archeological

human populations, for example (Knipper et al., 2017). However, given that in chimpanzees all teeth form and mineralize well before natal dispersal (<9 years old), this is not an option. It is possible that bone could capture a postdispersal isotope signal incorporated over a lifetime, although, bone is prone to Sr contamination (Hoppe et al., 2003), especially in the case of museum-curated specimens, which may have been chemically treated for preservation purposes. While sampling teeth and bone could be an option, this would limit research to historic populations.

There are possible alternatives to skeletal tissues for studying the elusive migration of female chimpanzees, such as hair. In humans, the ^{87}Sr/^{86}Sr ratios of hair can indicate an individual's geographical origin (Vautour et al., 2015), and hair can easily be collected from great ape sleeping nests (Oelze, 2016; Oelze et al., 2011; Oelze et al., 2020). However, isotope ratios in chimpanzee hair can be expected to only record several months of an individual's life (Oelze, 2016). Therefore, hair samples would need to be collected from very recently immigrated females, who are commonly unhabituated, and thereby inaccessible for sampling from researchers. This presents an unfortunate dilemma when considering the future applications of ^{87}Sr/^{86}Sr analysis to assess natal dispersal in African great apes, and with that, their use as points of reference when studying early hominin natal dispersal. One solution to this dilemma is the habituation of numerous neighboring chimpanzee communities, which is time and cost intensive, yet increasingly common at long-term field sites. In theory, this would enable direct observations and occasional monitoring of the transition of a habituated female from one community into another, and the potential to witness the social challenges immigrant females may face in their new social community, as well as the unique cultural transitions she might engage in (Luncz & Boesch, 2014). Another solution is to use multiproxy isotope profiles (C, N, O, H, S, and Pb) coupled with DNA analysis, which has been useful in identifying individuals and tracking origin in forensic cases (Bartelink & Chesson, 2019). Complementing multiproxy methods with ^{87}Sr/^{86}Sr analysis has the potential to improve our assessment of the migration patterns between multiple chimpanzee communities. When considering historic and modern migration patterns, the integration of ^{87}Sr/^{86}Sr analysis offers crucial geographical information, which can significantly reduce the potential origin locales when attempting to identify possible migrants.

AUTHOR CONTRIBUTIONS

Renee D. Boucher: Conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (supporting); investigation (lead); methodology (lead); project administration (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Roman M. Wittig:** Project administration (lead); resources (lead); supervision (equal); writing – review and editing (equal). **Sylvain R. T. Lemoine:** Investigation (equal); methodology (equal); resources (equal); software (equal); validation (equal); writing – review and editing (equal). **Aleksey Maro:** Investigation (supporting); resources (equal); writing – review and editing (equal). **Xueye Wang:** Data curation (equal); methodology (supporting); software (equal); visualization (equal); writing – review and editing (equal). **Paul L. Koch:** Formal analysis (supporting); investigation (supporting); methodology (supporting); project administration (equal); supervision (lead); writing – original draft (equal); writing – review and editing (equal). **Vicky M. Oelze:** Conceptualization (lead); data curation (equal); formal analysis (equal); funding acquisition (lead); investigation (equal); methodology (equal); project administration (lead); resources (lead); supervision (lead); writing – original draft (equal); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

OPEN RESEARCH BADGES

This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at https://github.com/rdbouche/Strontium-isotopes-track-female-dispersal-in-Ta-chimpanzees/tree/main.

DATA AVAILABILITY STATEMENT

The full dataset is provided in Table 1 for all individuals and Table 2 for all environmental samples.

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ENDNOTE

[1] According to the *Office Ivorien des Parcs et Réserves* TNP was enlarged in 2018 (http://www.oipr.ci/index.php/parcs-reserves/parcs-nationaux/parcnational-de-tai).

REFERENCES

Aarons, S. M., Aciego, S. M., Arendt, C. A., Blakowski, M. A., Steigmeyer, A., Gabrielli, P., Sierra-Hernández, M. R., Beaudon, E., Delmonte, B., Baccolo, G., May, N. W., & Pratt, K. A. (2017). Dust composition changes from Taylor Glacier (East Antarctica) during the last glacial-interglacial transition: A multi-proxy approach. *Quaternary Science Reviews*, 162, 60–71.

Åberg, G. (1995). The use of natural strontium isotopes as tracers in environmental studies. *Water, Air, and Soil Pollution*, 79, 309–322.

Anderson, D., & Burnham, K. (2004). *Model selection and multi-model inference*. Springer.

Arandjelovic, M., Boesch, C., Campbell, G., Hohmann, G., Junker, J., Kouakou, Y., Kühl Hjalmar, Leendertz Fabian, Leinert Vera, Murai Mizuki, Oelze Victoria, Rabanal Louisa, Robbins Martha, Vergnes Virginie, Wagner Oliver, Head Jojo Möbius, Y. (2020). *Pan African Programme: The cultured chimpanzee. Guidelines for research and data collection*. Wild Chimpanzee Foundation.

Balter, V., Braga, J., Télouk, P., & Thackeray, J. F. (2012). Evidence for dietary change but not landscape use in South African early hominins. *Nature*, 489(7417), 558–560.

Bartelink, E. J., & Chesson, L. A. (2019). Recent applications of isotope analysis to forensic anthropology. *Forensic Sciences Research*, 4(1), 29–44.

Bartlett, M. S. (1937). Properties of sufficiency and statistical tests. *Proceedings of the Royal Society of London*, 160(901), 268–282.

Barton, K., & Barton, M. K. (2015). Package 'mumin'. Version 1. 439.

Bataille, C. P., & Bowen, G. J. (2012). Mapping 87Sr/86Sr variations in bedrock and water for large scale provenance studies. *Chemical Geology*, 304, 39–52.

Bataille, C. P., Crowley, B. E., Wooller, M. J., & Bowen, G. J. (2020). Advances in global bioavailable strontium isoscapes. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 555, 109849.

Bataille, C. P., von Holstein, I. C., Laffoon, J. E., Willmes, M., Liu, X.-M., & Davies, G. R. (2018). A bioavailable strontium isoscape for Western Europe: A machine learning approach. *PLoS One*, 13(5), e0197386.

Beard, B. L., & Johnson, C. M. (2000). Strontium isotope composition of skeletal material can determine the birth place and geographic mobility of humans and animals. *Journal of Forensic Science*, 45(5), 1049–1061.

Bentley, R. A. (2006). Strontium isotopes from the earth to the archaeological skeleton: A review. *Journal of Archaeological Method and Theory*, 13(3), 135–187.

Bertin, B. Z. B. G., & Wittig, R. (2019). Long-term diet of the chimpanzees (*Pan troglodytes verus*) in Taï National Park: Interannual variation in consumption. In C. Boesch, R. Wittig, C. Crockford, L. Vigilant, T. Deschner, & F. Leendertz (Eds.), *The chimpanzees of Taï Forest: 40 years of research*. Cambridge University Press.

Boesch, C. (1991). The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour*, 117(3–4), 220–241. https://doi.org/10.1163/156853991X00544

Boesch, C. (1997). Evidence for dominant wild female chimpanzees investing more in sons. *Animal Behaviour*, 54(4), 811–815.

Boesch, C., & Boesch, H. (1984). Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *Journal of Human Evolution*, 13(5), 415–440.

Boesch, C., & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology*, 78(4), 547–573.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: Behavioural ecology and evolution*. Oxford University Press.

Boesch, C., & Wittig, R. (2019). Demography and life history of five chimpanzee communities in Taï National Park. In C. Boesch, R. Wittig, C. Crockford, L. Vigilant, T. Deschner, & F. Leendertz (Eds.), *The chimpanzees of the Taï Forest: 40 years of research* (pp. 159–177). Cambridge University Press.

Boesch, C., Gotanegre, A., Hillers, A., Kouassi, J., Boesch, H., Kizila, P., & Normand, E. (2021). Lessons learned while protecting wild chimpanzees in West Africa. *American Journal of Primatology*, 83(4), e23209.

Boesch, C., Kohou, G., Néné, H., & Vigilant, L. (2006). Male competition and paternity in wild chimpanzees of the Taï forest. *American Journal of Physical Anthropology*, 130(1), 103–115.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Brennan, S. R., Zimmerman, C. E., Fernandez, D. P., Cerling, T. E., McPhee, M. V., & Wooller, M. J. (2015). Strontium isotopes delineate fine-scale natal origins and migration histories of Pacific salmon. *Science Advances*, 1(4), e1400124.

Britton, K., Le Corre, M., Willmes, M., Moffat, I., Grün, R., Mannino, M. A., Woodward, S., & Jaouen, K. (2020). Sampling plants and malacofauna in 87Sr/86Sr bioavailability studies: Implications for Isoscape mapping and reconstructing of past mobility patterns. *Frontiers in Ecology and Evolution*, 8(446), 579473. https://doi.org/10.3389/fevo.2020.579473

Brooks, M., Bolker, B., Kristensen, K., & Maechler, M. (2022). Package 'glmmTMB'.

Burton, J. H., & Price, T. D. (2002). The use and abuse of trace elements for paleodietary research. In *Biogeochemical approaches to paleodietary analysis* (pp. 159–171). Springer.

Burton, J. H., & Wright, L. E. (1995). Nonlinearity in the relationship between bone Sr/Ca and diet: Paleodietary implications. *American Journal of Physical Anthropology*, 96(3), 273–282.

Campbell, G., Kuehl, H., Kouamé, P. N. G., & Boesch, C. (2008). Alarming decline of West African chimpanzees in Côte d'Ivoire. *Current Biology*, 18(19), R903–R904.

Capo, R. C., Stewart, B. W., & Chadwick, O. A. (1998). Strontium isotopes as tracers of ecosystem processes: Theory and methods. *Geoderma*, 82(1–3), 197–225.

Chazan, M. (2022). Early hominin group size: A perspective from Bestwood 1, Northern Cape Province, South Africa. *Quaternary International*, 614, 7–15. https://doi.org/10.1016/j.quaint.2021.05.017

Clutton-Brock, T. H., & Lukas, D. (2012). The evolution of social philopatry and dispersal in female mammals. *Molecular Ecology*, 21(3), 472–492. https://doi.org/10.1111/j.1365-294X.2011.05232.x

Collinet, J., Monteny, B., & Pouyaud, B. (1984). In J. L. Guillaumet, G. Couturier, & H. Dosso (Eds.), *Le milieu physique. Pp in: Recherche et aménagement en milieu forestier tropical humide: le Projet Taï de Côte d'Ivoire* (Vol. 15). UNESCO. Notes du MAB.

Copeland, S. R., Sponheimer, M., de Ruiter, D. J., Lee-Thorp, J. A., Codron, D., le Roux, P. J., Grimes, V., & Richards, M. P. (2011). Strontium isotope evidence for landscape use by early hominins. *Nature*, 474(7349), 76–78.

Copeland, S. R., Sponheimer, M., le Roux, P. J., Grimes, V., Lee-Thorp, J. A., de Ruiter, D. J., & Richards, M. P. (2008). Strontium isotope ratios (87Sr/86Sr) of tooth enamel: A comparison of solution and laser ablation multicollector inductively coupled plasma mass spectrometry methods. *Rapid Communications in Mass Spectrometry*, 22(20), 3187–3194.

Cressie, N. (1990). The origins of kriging. *Mathematical Geology*, 22(3), 239–252.

Cressie, N. (2015). *Statistics for spatial data*. John Wiley & Sons.

Crowley, B. E., & Godfrey, L. R. (2019). Strontium isotopes support small home ranges for extinct lemurs. *Frontiers in Ecology and Evolution*, 7, 490. https://doi.org/10.3389/fevo.2019.00490

Crowley, B. E., Miller, J. H., & Bataille, C. P. (2017). Strontium isotopes (87Sr/86Sr) in terrestrial environmental and palaeoenvironmental research: Empirical efforts and recent advances in continental-scale models. *Biological Reviews*, *92*(1), 43–59.

Delignette-Muller, M. L., & Dutang, C. (2015). fitdistrplus: An R package for fitting distributions. *Journal of Statistical Software*, *64*, 1–34.

Deniel, C., & Pin, C. (2001). Single-stage method for the simultaneous isolation of lead and strontium from silicate samples for isotopic measurements. *Analytica Chimica Acta*, *426*(1), 95–103.

Dominy, N. J., Ikram, S., Moritz, G. L., Wheatley, P. V., Christensen, J. N., Chipman, J. W., & Koch, P. L. (2020). Mummified baboons reveal the far reach of early Egyptian mariners. *eLife*, *9*, 60860. https://doi.org/10.7554/eLife.60860

Driessens, F. C., & Verbeeck, R. (1990). *Biominerals*. CRC press.

Fannin, L. D., Yeakel, J. D., Venkataraman, V. V., Seyoum, C., Geraads, D., Fashing, P. J., Nguyen, N., Fox-Dobbs, K., & Dominy, N. J. (2021). Carbon and strontium isotope ratios shed new light on the paleobiology and collapse of *Theropithecus*, a primate experiment in graminivory. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *572*, 110393.

Faure, G., & Powell, J. L. (2012). *Strontium isotope geology* (Vol. 5). Springer Science & Business Media.

Frumkin, A., & Stein, M. (2004). The Sahara–East Mediterranean dust and climate connection revealed by strontium and uranium isotopes in a Jerusalem speleothem. *Earth and Planetary Science Letters*, *217*(3–4), 451–464.

Gagneux, P., Boesch, C., & Woodruff, D. S. (1999). Female reproductive strategies, paternity and community structure in wild West African chimpanzees. *Animal Behaviour*, *57*(1), 19–32.

Goldstein, S. J., & Jacobsen, S. B. (1987). The Nd and Sr isotopic systematics of river-water dissolved material: Implications for the sources of Nd and Sr in seawater. *Chemical Geology: Isotope Geoscience Section*, *66*(3), 245–272. https://doi.org/10.1016/0168-9622(87)90045-5

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Belknap Press of Harvard University Press.

Gordon, A. D., Green, D. J., & Richmond, B. G. (2008). Strong postcranial size dimorphism in *Australopithecus afarensis*: Results from two new resampling methods for multivariate data sets with missing data. *American Journal of Physical Anthropology*, *135*(3), 311–328.

Gosz, J. R., Brookins, D. G., & Moore, D. I. (1983). Using strontium isotope ratios to estimate inputs to ecosystems. *Bioscience*, *33*(1), 23–30.

Grimstead, D. N., Nugent, S., & Whipple, J. (2017). Why a standardization of strontium isotope baseline environmental data is needed and recommendations for methodology. *Advances in Archaeological Practice*, *5*(2), 184–195. https://doi.org/10.1017/aap.2017.6

Gross, A., Palchan, D., Krom, M. D., & Angert, A. (2016). Elemental and isotopic composition of surface soils from key Saharan dust sources. *Chemical Geology*, *442*, 54–61. https://doi.org/10.1016/j.chemgeo.2016.09.001

Guillaumet, J.-L., & Adjanohoun, E. (1971). La végétation de la Côte d'Ivoire. *Le milieu naturel de la Côte d'Ivoire*, (50), 166–262. https://www.documentation.ird.fr/hor/fdi:16372

Hamilton, M. I., Fernandez, D. P., & Nelson, S. V. (2021). Using strontium isotopes to determine philopatry and dispersal in primates: A case study from Kibale National Park. *Royal Society Open Science*, *8*(2), 200760.

Hamilton, M. I., Nelson, S. V., Fernandez, D. P., & Hunt, K. D. (2019). Detecting riparian habitat preferences in "savanna" chimpanzees and associated fauna with strontium isotope ratios: Implications for reconstructing habitat use by the chimpanzee-human last common ancestor. *American Journal of Physical Anthropology*, *170*(4), 551–564.

Hammond, R. L., Lawson Handley, L. J., Winney, B. J., Bruford, M. W., & Perrin, N. (2006). Genetic evidence for female-biased dispersal and gene flow in a polygynous primate. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1585), 479–484.

Hartig, F., & Hartig, M. F. (2017). *Package 'DHARMa'*. R Development Core Team.

Heydari-Guran, S., & Ghasidian, E. (2020). Late Pleistocene hominin settlement patterns and population dynamics in the Zagros Mountains: Kermanshah region. *Archaeological Research in Asia*, *21*, 100161. https://doi.org/10.1016/j.ara.2019.100161

Hill, K. R., Walker, R. S., Božičević, M., Eder, J., Headland, T., Hewlett, B., Hurtado, A. M., Marlowe, F., Wiessner, P., & Wood, B. (2011). Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science*, *331*(6022), 1286–1289.

Hoppe, K. A., Koch, P. L., & Furutani, T. (2003). Assessing the preservation of biogenic strontium in fossil bones and tooth enamel. *International Journal of Osteoarchaeology*, *13*(1–2), 20–28.

Hurst, R. W., & Davis, T. E. (1981). Strontium isotopes as tracers of airborne fly ash from coal-fired power plants. *Environmental Geology*, *3*(6), 363–367. https://doi.org/10.1007/bf02473525

Inoue, E., Inoue-Murayama, M., Vigilant, L., Takenaka, O., & Nishida, T. (2008). Relatedness in wild chimpanzees: Influence of paternity, male philopatry, and demographic factors. *American Journal of Physical Anthropology*, *137*(3), 256–262.

Johnson, M. L., & Gaines, M. S. (1990). Evolution of dispersal: Theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics*, *21*(1), 449–480.

Journel, A. G., & Journel, A. G. (1989). *Fundamentals of geostatistics in five lessons* (Vol. 8). American Geophysical Union Washington.

Knight, A., Chapman, H. M., & Hale, M. (2016). Habitat fragmentation and its implications for endangered chimpanzee *Pan troglodytes* conservation. *Oryx*, *50*(3), 533–536. https://doi.org/10.1017/S0030605315000332

Knipper, C., Mittnik, A., Massy, K., Kociumaka, C., Kucukkalipci, I., Maus, M., Wittenborn, F., Metz, S. E., Staskiewicz, A., Krause, J., & Stockhammer, P. W. (2017). Female exogamy and gene pool diversification at the transition from the Final Neolithic to the Early Bronze Age in central Europe. *Proceedings of the National Academy of Sciences*, *114*(38), 10083–10088. https://doi.org/10.1073/pnas.1706355114

Koch, P. L., Heisinger, J., Moss, C., Carlson, R. W., Fogel, M. L., & Behrensmeyer, A. K. (1995). Isotopic tracking of change in diet and habitat use in African elephants. *Science*, *267*(5202), 1340–1343. https://doi.org/10.1126/science.267.5202.1340

Koenig, A., & Borries, C. (2012). Hominoid dispersal patterns and human evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *21*(3), 108–112.

Koffi, K. K. S., Dosso, K., Barot, S., Wittig, R. M., Aristophanous, M., Moretto, P., Koné, I., & Seydou, T. (2022). *Chimpanzees, dung beetles and seed dispersal: Implications for habitat conservation of the West African chimpanzee Pan troglodytes verus in Taï National Park, Côte d'Ivoire*. Research Square.

Kolongo, T. S. D., Decocq, G., Yao, C. Y. A., Blom, E. C., & Van Rompaey, R. S. (2006). Plant species diversity in the southern part of the Tai National Park (Côte d'Ivoire). *Biodiversity and Conservation*, *15*(7), 2123–2142.

Kouakou, C. Y., Boesch, C., & Kuehl, H. S. (2011). Identifying hotspots of chimpanzee group activity from transect surveys in Taï National Park, Côte d'Ivoire. *Journal of Tropical Ecology*, *27*(6), 621–630. https://doi.org/10.1017/S0266467411000423

Kumle, L., Võ, M. L.-H., & Draschkow, D. (2021). Estimating power in (generalized) linear mixed models: An open introduction and tutorial in R. *Behavior Research Methods*, *53*(6), 2528–2543.

Kühl, H. S., Sop, T., Williamson, E. A., Mundry, R., Brugière, D., Campbell, G., Cohen, H., Danquah, E., Ginn, L., Herbinger, I., Jones, S., Junker, J., Kormos, R., Kouakou, C. Y., NGoran, P. K., Normand, E., Shutt-Phillips, K., Tickle, A., Vendras, E., ... Boesch, C. (2017). The critically endangered western chimpanzee declines by 80. *American journal of primatology Supplement*, *79*(9), e22681. https://doi.org/10.1002/ajp.22681

Langergraber, K. E., Rowney, C., Crockford, C., Wittig, R., Zuberbühler, K., & Vigilant, L. (2014). Genetic analyses suggest no immigration of adult females and their offspring into the Sonso

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community of chimpanzees in the Budongo Forest Reserve, Uganda. *American Journal of Primatology*, 76(7), 640–648.

Langergraber, K. E., Siedel, H., Mitani, J. C., Wrangham, R. W., Reynolds, V., Hunt, K., & Vigilant, L. (2007). The genetic signature of sex-biased migration in patrilocal chimpanzees and humans. *PLoS One*, 2(10), e973.

Lawson Handley, L., & Perrin, N. (2007). Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology*, 16(8), 1559–1578.

Lee, P. C., & Strier, K. B. (2015). Complexities of Understanding Female Dispersal in Primates. In T. Furuichi, J. Yamagiwa, & F. Aureli (Eds.), *Dispersing Primate Females*. Primatology Monographs. Springer.

Lehmann, J., & Boesch, C. (2003). Social influences on ranging patterns among chimpanzees (*Pan troglodytes verus*) in the Tai National Park, Cote d'Ivoire. *Behavioral Ecology*, 14(5), 642–649.

Lehmann, J., & Boesch, C. (2005). Bisexually bonded ranging in chimpanzees (*Pan troglodytes verus*). *Behavioral Ecology and Sociobiology*, 57(6), 525–535. https://doi.org/10.1007/s00265-004-0891-5

Lehmann, J., & Boesch, C. (2008). Sexual differences in chimpanzee sociality. *International Journal of Primatology*, 29(1), 65–81. https://doi.org/10.1007/s10764-007-9230-9

Lehmann, J., & Boesch, C. (2009). Sociality of the dispersing sex: The nature of social bonds in West African female chimpanzees, *Pan troglodytes*. *Animal Behaviour*, 77(2), 377–387.

Lemoine, S., Boesch, C., Preis, A., Samuni, L., Crockford, C., & Wittig, R. M. (2020). Group dominance increases territory size and reduces neighbour pressure in wild chimpanzees. *Royal Society Open Science*, 7(5), 200577. https://doi.org/10.1098/rsos.200577

Lemoine, S., Crockford, C., & Wittig, R. (2019). Spatial integration of unusually high numbers of immigrant females into the South Group: Further support for the bisexually bonded model in Taï chimpanzees. In C. Boesch, R. Wittig, C. Crockford, L. Vigilant, T. Deschner, & F. Leendertz (Eds.), *The chimpanzees of the Taï Forest: 40 years of research*. Cambridge University Press.

Lenth, R., Singmann, H., Love, J., Buerkner, P., & Herve, M. (2021). emmeans: Estimated marginal means, aka least-squares means. R Package Version 1 (2018).

Li, X. Y., & Kokko, H. (2019). Sex-biased dispersal: A review of the theory. *Biological Reviews*, 94(2), 721–736.

Lockwood, C. A., Menter, C. G., Moggi-Cecchi, J., & Keyser, A. W. (2007). Extended male growth in a fossil hominin species. *Science*, 318(5855), 1443–1446.

Lovejoy, C. O. (2009). Reexamining human origins in light of *Ardipithecus ramidus*. *Science*, 326(5949), 74–74e78.

Lowry, B., Wittig, R. M., Pittermann, J., & Oelze, V. (2021). Stratigraphy of stable isotope ratios and leaf structure within an African rainforest canopy with implications for primate isotope ecology. *Scientific Reports*, 11(1), 1–11.

Luncz, L. V., & Boesch, C. (2014). Tradition over trend: Neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females. *American Journal of Primatology*, 76(7), 649–657. https://doi.org/10.1002/ajp.22259

Luncz, L. V., Proffitt, T., Kulik, L., Haslam, M., & Wittig, R. M. (2016). Distance-decay effect in stone tool transport by wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*, 283(1845), 20161607. https://doi.org/10.1098/rspb.2016.1607

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Bentham, K., Bolker, B., & Brooks, M. M. (2017). Package 'glmmtmb'. R Package Version 0.2.0.

Mangenot, G. (1950a). Essai sur les forêts denses de la Côte d'Ivoire. *Bulletin de la Société Botanique de France*, 97(7–9), 159–162.

Mangenot, G. (1950b). Les forêts de la Côte d'Ivoire. *Bulletin de la Société Botanique de France*, 97(7–9), 156–157.

Mangenot, G. (1955). Etude sur les forêts des plaines et plateaux de la Côte-d'Ivoire. *Etudes éburnéennes*, 16(4), 6–61.

Marchesi, P., Marchesi, N., Fruth, B., & Boesch, C. (1995). Census and distribution of chimpanzees in Cote dIvoire. *Primates*, 36, 591–607.

McArthur, J. M., Howarth, R., & Bailey, T. (2001). Strontium isotope stratigraphy: LOWESS version 3: Best fit to the marine Sr-isotope curve for 0–509 Ma and accompanying look-up table for deriving numerical age. *The Journal of Geology*, 109(2), 155–170.

Moore, D. L., Langergraber, K. E., & Vigilant, L. (2015). Genetic analyses suggest male philopatry and territoriality in savanna-woodland chimpanzees (*Pan troglodytes schweinfurthii*) of Ugalla, Tanzania. *International Journal of Primatology*, 36, 377–397.

Murdock, G. P. (1981). *Atlas of world cultures*. University of Pittsburgh Press.

Nishida, T. (2011). *Chimpanzees of the lakeshore: Natural history and culture at*. Cambridge University Press.

Oelze, V. M. (2016). Reconstructing temporal variation in great ape and other primate diets: A methodological framework for isotope analyses in hair. *American Journal of Primatology*, 78(10), 1004–1016.

Oelze, V. M., Fuller, B. T., Richards, M. P., Fruth, B., Surbeck, M., Hublin, J.-J., & Hohmann, G. (2011). Exploring the contribution and significance of animal protein in the diet of bonobos by stable isotope ratio analysis of hair. *Proceedings of the National Academy of Sciences*, 108(24), 9792–9797. https://doi.org/10.1073/pnas.1018502108

Oelze, V. M., Koch, J. K., Kupke, K., Nehlich, O., Zäuner, S., Wahl, J., Weise, S. M., Rieckhoff, S., & Richards, M. P. (2012). Multi-isotopic analysis reveals individual mobility and diet at the early Iron Age monumental tumulus of Magdalenenberg, Germany. *American Journal of Physical Anthropology*, 148(3), 406–421.

Oelze, V. M., Percher, A. M., Nsi Akoué, G., El Ksabi, N., Willaume, E., & Charpentier, M. J. E. (2020). Seasonality and interindividual variation in mandrill feeding ecology revealed by stable isotope analyses of hair and blood. *American Journal of Primatology*, 82(12), e23206. https://doi.org/10.1002/ajp.23206

Parr, L. A., & de Waal, F. B. (1999). Visual kin recognition in chimpanzees. *Nature*, 399(6737), 647–648.

Petters, S. W. (1991). *Regional geology of Africa*. Springer.

PL, I. E., & Srivastava, R. (1989). *An introduction to applied geostatistics*. Oxford University Press.

Poszwa, A., Dambrine, E., Ferry, B., Pollier, B., & Loubet, M. (2002). Do deep tree roots provide nutrients to the tropical rainforest? *Biogeochemistry*, 60(1), 97–118.

Poszwa, A., Ferry, B., Dambrine, E., Pollier, B., Wickman, T., Loubet, M., & Bishop, K. (2004). Variations of bioavailable Sr concentration and 87Sr/86Sr ratio in boreal forest ecosystems. *Biogeochemistry*, 67(1), 1–20.

Price, T. D., Burton, J. H., & Bentley, R. A. (2002). The characterization of biologically available strontium isotope ratios for the study of prehistoric migration. *Archaeometry*, 44(1), 117–135.

Pusey, A., & Packer, C. (1986). Dispersal and philopatry. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 150–166). University of Chicago Press.

R Core Development Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rouw, A. d., Vellema, H., & Blokhuis, W. A. (1990). *Land unit survey of the Tai region south-west Cote d'Ivoire*. (p. 222). The Tropenbos foundation, Ede.

Runia, L. T. (1987). Strontium and calcium distribution in plants: Effect on palaeodietary studies. *Journal of Archaeological Science*, 14(6), 599–608.

Schulz-Kornas, E., Stuhlträger, J., Clauss, M., Wittig, R. M., & Kupczik, K. (2019). Dust affects chewing efficiency and tooth wear in forest dwelling Western chimpanzees (*Pan troglodytes verus*). *American Journal of Physical Anthropology*, 169(1), 66–77.

Schwartz, G. T., Reid, D. J., Dean, M., & Chandrasekera, M. S. (2000). Aspects of tooth crown development in common chimpanzees (*Pan troglodytes*) with a note on the possible role of sexual dimorphism in canine growth. *Proceedings of 11th International Symposium on Dental Morphology*, Oulu.

Shagina, N. B., Tolstykh, E. I., Fell, T. P., Harrison, J. D., Phipps, A. W., & Degteva, M. O. (2007). In utero and postnatal haemopoietic tissue doses resulting from maternal ingestion of strontium isotopes from the Techa River. *Radiation Protection Dosimetry*, *127*(1–4), 497–501. https://doi.org/10.1093/rpd/ncm357

Sillen, A., Hall, G., Richardson, S., & Armstrong, R. (1998). 87Sr/86Sr ratios in modern and fossil food-webs of the Sterkfontein Valley: Implications for early hominid habitat preference. *Geochimica et Cosmochimica Acta*, *62*(14), 2463–2473.

Smith, T. M., Austin, C., Ávila, J. N., Dirks, W., Green, D. R., Williams, I. S., & Arora, M. (2022). Permanent signatures of birth and nursing initiation are chemically recorded in teeth. *Journal of Archaeological Science*, *140*, 105564.

Smith, T. M., Reid, D. J., Dean, M. C., Olejniczak, A. J., & Martin, L. B. (2007). Molar development in common chimpanzees (*Pan troglodytes*). *Journal of Human Evolution*, *52*(2), 201–216.

Smith, T. M., Smith, B. H., Reid, D. J., Siedel, H., Vigilant, L., Hublin, J.-J., & Boesch, C. (2010). Dental development of the Taï Forest chimpanzees revisited. *Journal of Human Evolution*, *58*(5), 363–373.

Stojanowski, C. M., & Knudson, K. J. (2011). Biogeochemical inferences of mobility of early Holocene fisher-foragers from the southern Sahara Desert. *American Journal of Physical Anthropology*, *146*(1), 49–61. https://doi.org/10.1002/ajpa.21542

Stoorvogel, J. J., Van Breemen, N., & Jassen, B. H. (1997). The nutrient input by Harmattan dust to a forest ecosystem in Côte d'Ivoire, Africa. *Biogeochemistry*, *37*(2), 145–157. https://doi.org/10.1023/A:1005734225727

Stumpf, R. M., Thompson, E. M., Muller, M. N., & Wrangham, R. W. (2009). The context of female dispersal in Kanyawara chimpanzees. *Behaviour*, *146*(4–5), 629–656.

Sugiyama, N., Sugiyama, S., Cagnato, C., France, C. A. M., Iriki, A., Hughes, K. S., Singleton, R. R., Thornton, E., & Hofman, C. A. (2022). Earliest evidence of primate captivity and translocation supports gift diplomacy between Teotihuacan and the Maya. *Proceedings of the National Academy of Sciences*, *119*(47), e2212431119. https://doi.org/10.1073/pnas.2212431119

Tagini, B. (1966). Esquisse géotechnique de la Côte d'Ivoire. Rapport SO. DE.MI. 107, 94.

Tagini, B. (1972). *Notice explicative à la carte géologique de la Côte d'Ivoire au 1/2 000 000*. SODEMI.

Thompson, M. E. (2013). Reproductive ecology of female chimpanzees. *American Journal of Primatology*, *75*(3), 222–237.

Vautour, G., Poirier, A., & Widory, D. (2015). Tracking mobility using human hair: What can we learn from lead and strontium isotopes? *Science & Justice*, *55*(1), 63–71.

Vigilant, L., Hofreiter, M., Siedel, H., & Boesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Sciences*, *98*(23), 12890–12895. https://doi.org/10.1073/pnas.231320498

Walker, K. K., & Pusey, A. E. (2020). Inbreeding risk and maternal support have opposite effects on female chimpanzee dispersal. *Current Biology*, *30*(2), R62–R63.

Wang, X., Bocksberger, G., Agbor, A., Angedakin, S., Aubert, F., Ayuk Ayimisin, E, Bailey, E., Barubiyo, D., Bessone, M., Bobe, R., Bonnet, M., Boucher, R., Brazzola, G., Brewer, S., Lee, K., Carvalho, S., Chancellor, R., Cipoletta, C., Cohen, H., … Oelze, V. M. (in review). Strontium isoscape of sub-Saharan Africa allows tracing origins of victims of the transatlantic slave trade.

Whipkey, C., Capo, R. C., Chadwick, O., & Stewart, B. (2000). The importance of sea spray to the cation budget of a coastal Hawaiian soil: A strontium isotope approach. *Chemical Geology*, *168*(1–2), 37–48.

White, T. D., Black, M. T., & Folkens, P. A. (2011). *Human osteology*. Academic Press.

Wilkins, J. F., & Marlowe, F. W. (2006). Sex-biased migration in humans: What should we expect from genetic data? *BioEssays*, *28*(3), 290–300.

Wittig, R. (2018). Tai chimpanzees. In J. Vonk & T. K. Shackelford (Eds.), *Encyclopedia of animal cognition and behavior*. Springer International Publishing.

Wittig, R., & Boesch, C. (2019). Observation protocol and long-term data collection in Taï. In C. Boesch, R. Wittig, C. Crockford, T. Deschner, L. Vigilant, & F. Leendertz (Eds.), *The chimpanzees of Taï Forest: 40 years of research*. Cambridge University Press.

Wright, L. E. (2005). Identifying immigrants to Tikal, Guatemala: Defining local variability in strontium isotope ratios of human tooth enamel. *Journal of Archaeological Science*, *32*(4), 555–566.

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