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Matrilineal population structure and distribution of the Angolan giraffe in the Namib desert and beyond



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ABSTRACT

The distribution maps of giraffe (Giraffa) subspecies in southern Africa are based on historical assumptions, yet some populations have likely been misidentified, hindering effective conservation efforts. Particularly, the populations in Zimbabwe are poorly studied, and translocations, such as the 1991 movement of giraffe from Namibia's Etosha National Park to mitigate the human-induced decline of Namibia's desert-dwelling giraffe in the lower Hoanib and Hoarusib Rivers, was concluded without consideration of genotype. Mitochondrial DNA sequence analyses from cytochrome b and control region revealed that instead of the South African giraffe subspecies (G. giraffa giraffa), the Angolan giraffe (G. g. angolensis) occurs in southern Zimbabwe's Bubye Valley Conservancy. Furthermore, Namibia's desert-dwelling giraffe and those from Etosha National Park form distinct matrilineal lineages within the Angolan giraffe subspecies clade. Thus, despite the translocation and proximity of the Etosha National Park, the Etosha giraffe genotype has not spread amongst the desert-dwelling giraffe. Use of mutation rate estimates indicates that there has been no matrilineal exchange between Etosha and the desertdwelling giraffe for ca. 40,000 years. While philopatry could produce distinct mitochondrial lineages, the short geographical distance and long time involved, makes it more likely that the Etosha giraffe cannot successfully compete with a putatively better adapted desert-dwelling giraffe. The analyses also show that the distribution of the Angolan giraffe extends further eastwards than expected. These findings provide important implications for giraffe conservation, and translocation in particular, which may not always be an effective means of improving genetic diversity.

1. Introduction

Giraffe (*Giraffa*) as a single species have recently been classified as "Vulnerable" on the IUCN RedList, due to a decline of approximately 40% over the past three decades [1]. However, the classification did not consider that genetic taxonomy suggests four distinct species of giraffe, which in turn has important implications for giraffe conservation [2]. To date, the distribution of the currently recognized nine subspecies [2] is not well understood, because most distribution maps are based on historical assumptions and anecdotal evidence.

In southern Africa, the southern giraffe (*G. giraffa*) is divided into two subspecies: the South African giraffe (*G. g. giraffa*) mainly occurring in Botswana, South Africa, Zambia and Zimbabwe, and the Angolan giraffe (*G. g. angolensis*) prevalent primarily throughout Botswana and Namibia (Fig. 1). In southern Africa, the distinction between the southern giraffe subspecies is historically based on pelage pattern, morphometrics and geography [3]. However, the pelage pattern of the

two subspecies is very similar and, therefore, the geographic distribution of the subspecies in southern Africa is uncertain [1]. Genetic analyses of most populations are missing, and only few giraffe studies have been undertaken in Zimbabwe [4–6]. These studies led to varying classifications over the years as either Angolan or South African giraffe subspecies [5,7,8].

In Namibia, the Angolan giraffe occurs naturally across the central and northern parts of the country with major populations in Etosha National Park (ENP), communal northwestern Namib Desert and private land throughout the country. The pelage of the desert-dwelling giraffe is often paler in comparison to Angolan giraffe from ENP [9] and a status as separate subspecies has been suggested [10]. However, genetic studies so far did not find differences to justify a separate subspecies or population [9,11,12]. In 1991, 22 giraffe individuals were translocated from western ENP to the lower Hoarusib River to augment the desert-dwelling giraffe population, which at the time comprised approximately 100 individuals [9]. However, failure to conduct pre-

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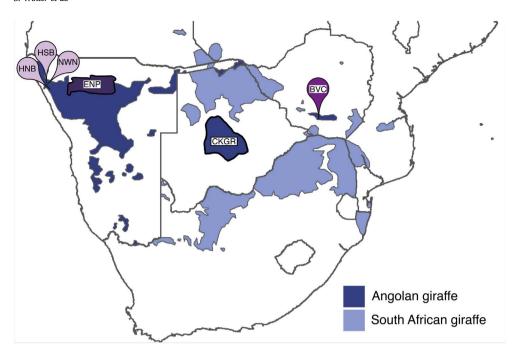


Fig. 1. The distribution of the southern giraffe subspecies. Map of southern Africa highlighting the assumed distribution of southern giraffe subspecies, as estimated by the Giraffe Conservation Foundation, 2017. Labeled pins represent the main sampling locations for this study: Hoanib River Catchment (HNB), Hoarusib River Catchment (HSB), northwestern Namibia (NWN), and Bubve Valley Conservancy (BVC). Areas with a black frame indicate the location of two additional major Angolan giraffe populations, the Etosha Nationalpark (ENP) in Namibia, and the Central Kalahari Game Reserve (CKGR) in Botswana. According to the new findings, the giraffe population of the BVC in Zimbabwe is shown as the Angolan giraffe and not as expected South African giraffe subspecies. It illustrates the dispersed distribution of the Angolan giraffe to the east in southern Africa.

and post-translocation surveys impeded assessment of translocation success [9].

Genetic analysis of mitochondrial DNA is a powerful tool to aid in distinguishing giraffe subspecies [2,12,13]. Here, cytochrome b and the control region from 33 southern giraffe, including Namibia's desert-dwelling and Bubye Valley Conservancy (BVC) giraffe from Zimbabwe (Fig. 1), were analyzed, to determine the biogeography of southern giraffe and to investigate whether the translocation of giraffe from a nearby population increased the genetic diversity of the desert-dwelling giraffe in Namibia.

2. Material and methods

Tissue samples from southern giraffe individuals were obtained by remote biopsy darting in southern Zimbabwe's BVC (n=10), as well as the desert-dwelling giraffe of the lower Hoanib (HNB) (n=13) and Hoarusib (HSB) (n=3) River catchments, and other regions of northwestern Namibia (NWN) (n=7) (Fig. 1). Similarly, reticulated giraffe (G. reticulata) samples were collected at Ishaqbini Conservancy (n=4) in Kenya, to add wild reticulated giraffe to the dataset of all giraffe species and subspecies. All samples were collected by the Giraffe Conservation Foundation (GCF) and partners with permits from the respective governments. Biopsy samples were preserved in 99% ethanol. DNA was isolated using the NucleoSpin* Tissue kit (Macherey-Nagel). Cytochrome b and control region were PCR amplified using the VWR Taq DNA Polymerase 2X Master Mix with 2.0 mM MgCl₂. PCR amplification and sequencing followed previously published protocols [13].

Cycle sequencing was performed using the BigDye terminator sequencing kit 3.1 (Applied Biosystems) and analyzed on an ABI 3730 DNA Analyzer, manually edited in Geneious version 6.1.8 [14] and aligned using MAFFT version 7 [15]. All data generated during this study are available from GenBank under the accession numbers KY865101 - KY865174. Accession numbers for additional data analyzed in the current study can be found in the references (see Supplementary material, Table S1).

Published sequences from other giraffe (sub)species were aligned to Okapi (*Okapia johnstoni*) orthologs, which served as an outgroup in the full sample analysis (see Supplementary material, Table S1). A reduced dataset limited to southern giraffe where six northern giraffe (*G. camelopardalis*) individuals served as an outgroup, allowed for higher resolution depiction of topology.

BEAST version 1.8.3 [16] using an uncorrelated lognormal relaxed clock [17] and 20 million MCMC chains produced Bayesian phylogenies. The HKY+4G+ I substitution model [18] was suggested by jModelTest2 [19]. Convergence of the BEAST run was evaluated in Tracer version 1.6.0 [20]. A maximum clade credibility tree was generated using TreeAnnotator version 1.8.3 [21] with 10% burnin. Additionally, we used MEGA version 7.0.16 [22] to calculate a Maximum-Likelihood tree under HKY+4G+ I and Geneious version 6.1.8 [14] for Neighbor-Joining tree analysis under HKY. Both analyses were performed with 100 bootstrap replicates.

Statistical parsimony networks of both mtDNA loci were calculated using TCS version 1.21 [23] with a connection limit of 95%. Haplotypes for Angolan giraffe individuals were coded with DnaSP version 5.10.01 [24] for both loci separately. Principal Component Analysis (PCA) was performed using adegenet [25] for R version 3.3.2.

3. Results

Aligning 1140 nt of the cytochrome b gene and 418 nt of control region sequences yielded a 1558 bp long dataset for each of the 116 giraffe individuals. Fig. 2a shows a Bayesian tree for the South African and Angolan giraffe only. Tree analyses using Maximum Likelihood or Neighbor-Joining, and a Bayesian tree that includes all (sub)species, are shown in Supplementary material (Figs. S1-3) and generally agree with the tree shown in Fig. 2a. Surprisingly, nine giraffe from the BVC, southern Zimbabwe, which were expected to be South African giraffe, form a distinct clade and group within the Angolan giraffe lineage close to a cluster of giraffe from the Central Kalahari Game Reserve (CKGR) in Botswana (Fig. 2a). Individual BVC007 groups outside the BVC cluster, being closely related to the desert-dwelling giraffe. Except for two giraffe individuals (NWN03 and HNB101), the desert-dwelling giraffe (HNB, HSB, and NWN) form a distinct cluster with significant support (posterior probability ≥0.95), within the Angolan giraffe clade. In the tree analysis and haplotype networks giraffe from ENP form two distant clades. One splits at the basis of Angolan giraffe, and one is reconstructed as sistergroup to the desert-dwelling giraffe (Fig. 2a). While these branches are not significantly supported, the two distinct clades within the ENP population could be explained by an "out of Etosha" radiation with the ENP as origin of an Angolan giraffe dispersal to the east, followed by a back-migration into ENP.

Assuming a human mitochondrial mutation rate 0.118/sites/Myr

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