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Validating local knowledge on camels: Colour phenotypes and genetic variation of dromedaries in the Nigeria-Niger corridor

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ABSTRACT

The traditional camel breeding concept of pastoralists in the Nigeria-Niger corridor favours certain dromedary colour phenotypes, which are associated with distinct economic and behavioural traits. With the increasing requirement of sustainable food sources in desert environments the economic interest in Nigerian dromedaries has also been growing. In this study we used mitochondrial and microsatellite data to understand if the observed colour phenotypes correspond to genetically distinct groups and whether these groups reflect the breeding concept of camel pastoralists in the Nigeria-Niger corridor. Our results showed that Nigerian dromedaries are composed of a homogenous gene pool with no specific clustering according to coat colour. Significant but low nuclear and mitochondrial differentiation was detected only between dark-brown and black-brown camels. In addition to little evidence for population structure, Nigerian dromedaries exhibited a high genetic diversity, which could be explained by continuous gene flow with other populations during the annual transhumant voyage embarked upon by pastoralists on both sides of the Nigeria-Niger corridor. In comparison to local pastoralists' knowledge, the molecular genetic data do not support a clear distinction into breeds (*Ja, Kurri,* and *Kala*) based on coat colour differences.

1. Introduction

The relationship between traditional, indigenous knowledge systems (Nwokoma, 2012) and technical, systematic animal production is highly interesting but ambivalent. In general two perspectives prevail: first, explaining indigenous knowledge through scientific methods of enquiry and experimentation and second, using indigenously generated facts to strengthen scientific concepts. In domestic species, the classical definition of a breed is defined as animals that, through selection and reproduction, have come to resemble one another and pass those traits uniformly to their offspring (Desilva and Fitch, 1995). Lush (1994) in his definition of a breed stated "a breed is a group of domestic animals, termed such by common consent of the breeders, [….]." Harmonizing the two aforementioned definitions, Köhler-Rollefson (1997) mentioned that a domestic animal population may be regarded as a breed, if the animals fulfil the criteria of (*i*) being subjected to a common utilization pattern, (*ii*) sharing a common habitat/ distribution, (*iii*) representing largely a closed gene pool, and (*iv*) being regarded as distinct by their breeders.

Pastoralists possess a wealth of untapped indigenous knowledge which, when properly harnessed, can reveal new insights into the complex interaction between animals and their herders. One example of such knowledge is the breeding goal of camel pastoralists in northern Nigeria. Based on coat colour Mohammed (2000) defined four major camel types in livestock markets of north-western Nigeria: sand-brown, grey-white, dark-brown, and pied ecotypes. In addition, Abdussamad et al. (2011) reported white, brown-black and black phenotypes in the Nigeria-Niger corridor. The definition of ecotype encloses the notion of a population (or a breed) that is genetically adapted to a specific habitat and transmits these traits to the next generation (FAO, 2007). A phenotype, on the other hand, is an organism's expressed physical traits, which are determined by an individual's genotype and expressed genes, and environmental influences (Bailey, 2012). With regard to the coat colour diversity present in the Nigeria-Niger corridor, we aimed to understand whether these dromedaries are representative of different genetic lineages. *I.e.*, do these individuals represent several independent breeds (possible

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ecotypes), or a single population (one breed) with extensive phenotypic variation?

Camel pastoralists in the Nigeria-Niger corridor manage camel livestock towards an "ideal" herd rather than an "ideal" animal, as is the case with the conventional concept of animal breeding (Abdussamad et al., 2011). One group of breeders insists that a camel of different coat colour is distinct from another camel in terms of specific economic traits. This is irrespective of the fact that these animals co-exist in the same habitat with a high probability of unsupervised mating. Their breed concept can be referred to as a 'utility school of thought'. Another group of herders, following a 'pedigree school of thought', is convinced that the expression of certain economic traits has nothing to do with coat colour, but is purely based on the pedigree (Abdussamad et al., 2011). Regardless of the school of thought, the dark-brown *Ja* phenotype is the favourite "ideal" animal for camel pastoralists in the Nigeria-Niger corridor. Indeed, dark-brown camels, as well as the pied-coloured (*Bule*) and grey-white dromedaries, are associated with high milk production during the rainy season. The brown-black *Kurri* breed is described as resistant to the dry season, while grey-white camels are considered as strong and beautiful but poor performing during the dry season. Overall, most breeders prefer to keep an assortment of phenotypes in their herds as a possible survival strategy that supports pastoral life in a fragile ecosystem (Abdussamad et al., 2011). The breeding approach of the Nigeria-Niger corridor pastoralists is therefore not in line with the concept of conventional animal breeding, which aims at maintaining a closed gene pool.

In northern Nigeria, the molecular characterization of camel phenotypes/breeds is an ambitious task due to the general lack of interest in research on dromedaries. According to Mohammed (2000), the dromedary camel is seen as a "foreign animal" to the agricultural research personnel in Nigeria. He further mentioned that this attitude might be responsible for the scanty information and misconceptions about dromedaries, which are generally considered to be of bad temperament and difficult to handle. The social prejudices against camel owners are another bottleneck to the development of dromedary husbandry in Nigeria, since they are judged as foreigners from Niger Republic, where most of the traditional herders originate (Mohammed, 2000). Currently, an emerging economical and zootechnical interest for camels is probably due to the threat of desertification that is now afflicting sub-Saharan Africa and the necessity of developing coping strategies. The camel, known for its resilience to dry land conditions, is certainly the best candidate for mitigation of drought effects on pastoral communities and populations facing threats of desertification.

Indigenous knowledge has received considerable attention in the context of research for agricultural development, being espoused as an important but underutilized resource (Kugonza et al., 2012; Warren, 1991). For example, current recommendations by the Food and Agriculture Organization (FAO, 2007) suggest, "In the absence of breed association records or molecular studies, the views of the livestock keepers themselves perhaps provide the best indication of breed identity." However, little work has aimed at testing the compatibility and complementarity of indigenous *versus* experiment-based, scientific knowledge (Walker et al., 1997). This study uses a molecular genetic approach to examine camel breeding goals and evaluates the results in the context of pastoralists' indigenous knowledge (Abdussamad et al., 2011). In Nigeria a genetic characterization and economic evaluation of camel phenotypes has not been performed so far. Using mitochondrial and microsatellite data, the current study intends to determine (*i*) if the identified colour phenotypes are genetically distinct groups and (*ii*) if these groups are reflecting the breeding concept of camel pastoralists in the studied area.

2. Materials and methods

2.1. Sample collection and DNA extraction

In total we sampled 75 dromedaries brought to the Garin Alkali livestock market in Bursali Local Government Area of Yobe State in northeastern Nigeria. They comprised the following colour phenotypes: 21 brown-black (BB; *Kurri* breed), 18 dark-brown (DB; *Ja*), 26 sandbrown (SB; *Kala*), 5 grey-white (GW) and 5 others (OT) consisting of 2 white, 2 pied-cross (*Kubule*) and 1 pied coloured (*Bule*) individuals. The phenotypes/breeds were selected based on the information of the Nigerian pastoralists. Respectively, Nigerian pastoralists relate DB dromedaries with high milk yield, the BB camels with strength during the dry season, and the GW phenotype as poor performers during the dry season but beautiful and with high milk yield during the rainy season (Abdussamad et al., 2011). Details about the study area have been previously described (Abdussamad et al., 2011). Detailed information on the dromedaries included in this study is listed in Table S1. Genetic material was obtained from hair samples collected from the tail of each camel. Hair samples were digested using non-commercial lysis buffer (Pfeiffer et al., 2004) and DNA was extracted with the NucleoSpin®-Tissue Kit (Macherey-Nagel). Blank controls were included in every set of extractions and during further amplification steps.

2.2. DNA amplification, genotyping and sequencing

We amplified alleles at different size ranges using 18 microsatellite markers pooled in five multiplexes according to fragment length and fluorescence labelling (Table S2). Genotyping runs were performed with the MegaBACE 1000 and electropherograms were evaluated with Genetic Profiler v2.2 (GE Healthcare). Mitochondrial DNA primers (Table S3) were used to amplify a fragment containing portions of the cytochrome b gene (MT-CYTB), the tRNAs Threonine and Proline, and the control region (MT-CR); spanning positions nt15120–nt151981 in the *Camelus dromedarius* mitochondrial genome (gb|EU159113.1). PCR amplification was performed following Silbermayr et al. (2010) and sequencing was done in both directions on the MegaBACE 1000. The resulting electropherograms were evaluated and aligned using CodonCode Aligner v3.0.2 (CC Corporation).

2.3. Statistical analyses

Due to the absence of accurate and standardized pedigrees, we used Coancestry (Wang, 2011) to estimate pairwise relatedness coefficients (r) for all nuclear genotypes. Closely related individuals ($r \geq 0.5$; Wang, 2011) were excluded from further analysis. Mitochondrial diversity indices such as number of haplotypes, number of polymorphic sites, mean number of pairwise differences (k) and haplotype diversity (H_d) were computed using DNAsp 5.1.0.1 (Librado and Rozas, 2009). The latter measurement is equivalent to the expected heterozygosity for diploid data and is defined as the probability that two randomly chosen haplotypes are different in the sample. Nucleotide diversity (π) based on the average number of pairwise differences (Nei, 1987), Watterson's θ_s, population pairwise differentiation Φ_{ST}, and an analysis of molecular variance (AMOVA) were calculated using Arlequin v3.11 (Excoffier and Lischer, 2010) with the Tamura and Nei substitution model (Tamura and Nei, 1993). Deviations from Hardy–Weinberg equilibrium for each locus in the population ($H1$ = heterozygote deficiency; default parameters) and the presence of null alleles were tested with Genepop (Rousset, 2008). Estimates of microsatellite diversity within populations including total number of alleles (TNA), mean number of alleles (MNA), allelic richness (Ar) standardized for a minimum of

eight individuals per population, observed (H_O) and expected (H_E) heterozygosities, and nuclear pairwise F_{ST} values corrected for multiple testing were calculated using MSAnalyzer 4.05 (Dieringer and Schlötterer, 2003). Genetix (Belkhir et al., 1999) was used to infer the population-based inbreeding coefficient F_{IS}, which describes the average deficiency or excess of heterozygotes in each group (Weir and Cockerham, 1984).

Population structure at the mitochondrial level was inferred using Bayesian clustering for linked loci in Baps 6 (Corander and Tang, 2007). We used Network 4.6.1.1. (Bandelt et al., 1999) to construct the median joining network (MJN) by selecting default parameters. Using Structure v2.3 (Pritchard et al., 2000), population structure at the nuclear level was inferred at 200,000 Markov Chain Monte Carlo steps after a burn-in of 20,000 steps under an admixture model allowing correlated allele frequencies. Five independent simulations for each K (2–8) were performed to determine the most probable clustering solution through the modal distribution of DeltaK (Evanno et al., 2005). We obtained graphical representations of these statistics using Structure Harvester v0.6.94 (Earl and vonHoldt, 2012) and concatenated the results from multiple runs for each K with Clumpp (Jacobsson and Rosenberg, 2007). Final graphs were drawn with R (R Core Team, 2014). Population demographic changes under the assumption of no selection acting on the mitochondrial control region were assessed with DNAsp using the pairwise mismatch distribution and two neutrality tests, Tajima's D and Fu's FS with 10,000 permutations, respectively.

3. Results

In this study we investigated the genetic diversity and population structure of 75 Nigerian dromedaries representing five different phenotypes (BB, DB, SB, GW and OT) with the aim to detect potential accordance between population genetic structure and traditional breeding strategies. After removing closely related individuals ($r \geq 0.5$) as well as samples with unreliable or low genotyping success as they were collected non-invasively (Goossens et al., 1998), we considered $n=51$ mitochondrial sequences (Table S4) and $n=39$ microsatellite genotypes for downstream analysis (Table S5).

3.1. Mitochondrial and nuclear genetic diversity

In the 862 bp-long mtDNA fragment amplified in 51 individuals we detected 14 polymorphisms (13 transitions, one transversion) segregating into twelve haplotypes and with a haplotype (gene) diversity $H_d=0.751 \pm 0.056$ (Table 1). The pairwise nucleotide diversity π was calculated at 0.00236 ± 0.001, while the mean number of differences between all pairs of haplotypes equalled $k=2.036 \pm 1.163$. Among the five investigated populations (BB, DB, SB, GW and OT), H_d and π ranged between 0.476 and 0.897, and from 0.001 to 0.004, respectively (Table 1).

The total number of alleles in the 39 individuals genotyped at 18 microsatellite loci was 101 with a MNA of 5.61 per locus over all studied camels. The MNA for the four populations (BB, DB, SB and GW) ranged between 3.17 and 4.28 per locus per population. The allelic richness (Ar) per locus calculated for a population based on a minimum sample size of eight diploid individuals ranged from 3.65 to 4.01. The level of genetic diversity in the total Nigerian dromedary population measured as H_O and H_E was 0.52 and 0.63, respectively. The inbreeding coefficient F_{IS} ranged between 0.05 in the BB and 0.20 in the SB dromedaries (Table 1). Four of the 18 loci (YWLL44, CVRL03, CVRL07 and CMS50) were out of HWE after correcting for multiple testing (Bonferroni correction for 18 independent tests) due to heterozygote deficiency (Table S2).

3.2. Population structure and demographic inferences

In the MJN (Fig. 1) the twelve detected haplotypes grouped parsimoniously in two haplogroups with four polymorphisms fixed between them. One of the haplogroups showed a star-shaped figure with a dominant haplotype, which represented 47% of the studied camels. Among the 51 mitochondrial sequences, BAPS analysis revealed four haplogroups as the best clustering solution (posterior probability, PP=0.74; Fig. S1). At the nuclear level, Bayesian clustering implemented in Structure uncovered no population differentiation for a theoretical number of ancestral

Table 1
Genetic diversity of dromedary camel populations (mitochondrial DNA and microsatellite data).

Pop	mtDNA (862 bp)						
	n	Haplotypes	Var. sites	H_d	π	k	θ_s
BB	13	8	12	0.897 (0.067)	0.004 (0.002)	3.188 (1.761)	3.867 (1.778)
DB	15	5	5	0.476 (0.155)	0.001 (0.001)	0.785 (0.603)	1.538 (0.848)
SB	14	7	9	0.857 (0.065)	0.003 (0.002)	2.419 (1.395)	2.830 (1.359)
GW	5	3	7	0.700 (0.218)	0.003 (0.002)	2.828 (1.784)	3.360 (2.085)
OT	4	2	1	0.667 (0.204)	0.001 (0.001)	0.669 (0.628)	0.545 (0.545)
Total	51	12	14	0.751 (0.056)	0.002 (0.001)	2.036 (1.163)	3.112 (1.166)

Pop	Microsatellite (18 loci)						
	n	TNA	MNA	Ar	H_O	H_E	F_{IS}
BB	11	69	3.83 (1.9)	3.65	0.54	0.58	0.05*
DB	13	76	4.22 (1.9)	3.83	0.53	0.63	0.14*
SB	10	77	4.28 (2.6)	4.01	0.51	0.64	0.20*
GW	5	57	3.17 (1.5)	na	0.47	0.57	0.18*
OT	na	na	na	na	na	na	na
Total	39	101	5.61 (3.4)	3.90	0.52	0.63	0.16*

BB=brown-black; DB=dark-brown; SB=sand-brown; GW=grey-white; OT=others (pied coloured, pied coloured cross and white); n=number of individuals; Var. sites=variable sites; H_d=haplotype diversity; π=nucleotide diversity based on number of pairwise nucleotide differences; k=mean number of pairwise differences; θ_s=Watterson's theta based on the number of segregating sites; TNA=total number of alleles; MNA=mean number of alleles per locus; Ar=allelic richness per locus calculated for a population based on minimum sample size of 8 diploid individuals; H_O/H_E=observed/expected heterozygosity; F_{IS}=inbreeding coefficient; na=not applicable.

* $p < 0.001$; standard deviations are given in parentheses.

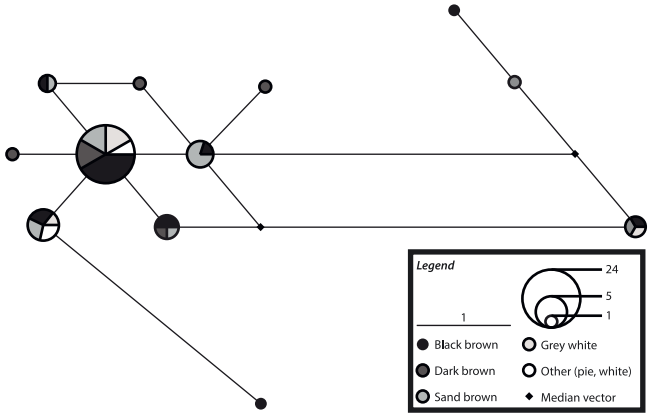

Fig. 1. Median joining network displaying the maximum parsimony relationship between the mitochondrial haplotypes obtained from 51 Nigerian dromedary camels.

Table 2
Population pairwise distances based on the 862-bp mtDNA sequences (Φ_{ST}; below diagonal) and 18 microsatellite loci (F_{ST}; above diagonal).

	BB	DB	SB	GW	OT
BB	–	0.031***	0.020	0.032	na
DB	0.056*	–	−0.003	0.014	na
SB	−0.047	0.061	–	0.006	na
GW	−0.144	0.055	−0.115	–	na
OT	−0.040	0.179*	0.043	−0.052	–

BB=brown-black; DB=dark-brown; SB=sand-brown; GW=grey-white; OT=others (pied coloured, pied coloured cross and white); na=not applicable.
*$p < 0.05$ **$p < 0.01$. ***$p < 0.001$.
Sample sizes are given in Table 1.

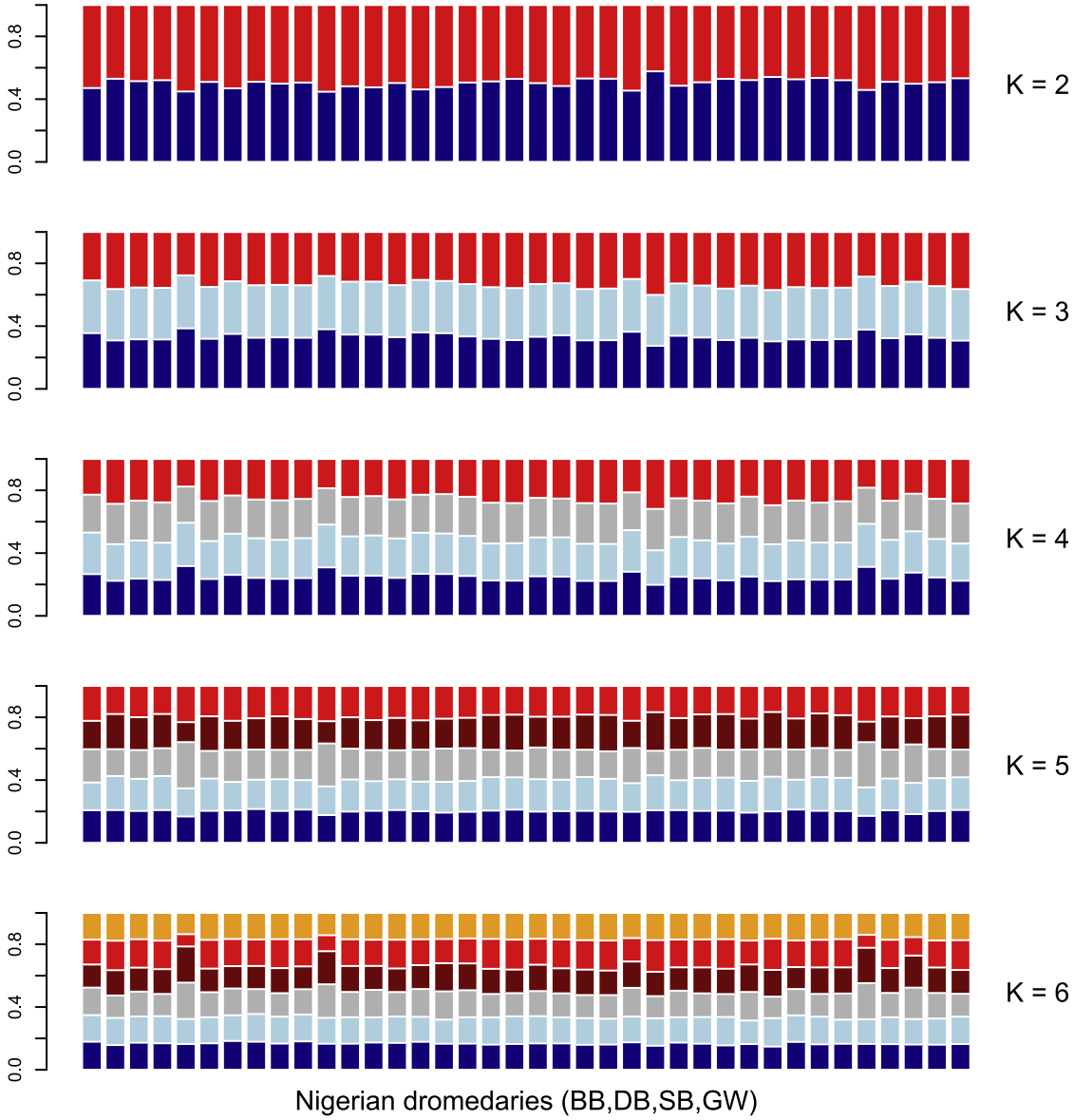

Fig. 2. Structure bar plot representing the individual assignment probabilities of the 39 Nigerian dromedaries to 2–6 theoretical genetic ancestry groups (clusters).

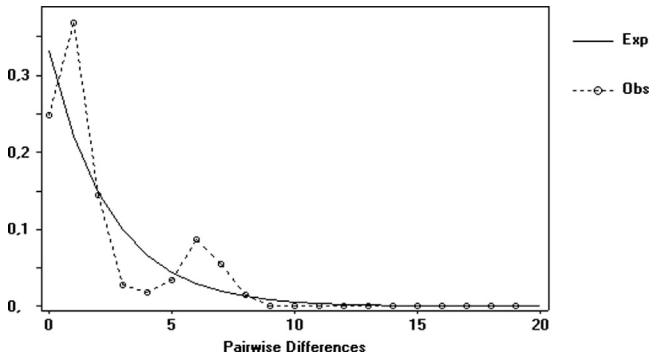

Fig. 3. Mismatch distribution of 51 mitochondrial sequences of Nigerian dromedary camels.

populations set to $K=2$–8 (Fig. 2). The optimal cluster solution of $K=6$ (DeltaK; Fig. S2) resulted in no biologically meaningful clustering and confirmed that all the investigated Nigerian dromedary populations share a similar ancestry. Consequently, the AMOVA analysis detected that all of the mitochondrial (100%) and most of the nuclear (99.74%) variation were present among individuals in the respective populations and not between populations. Mitochondrial Φ_{ST} revealed significant differences between DB and BB ($\Phi_{ST}=0.056$), and between DB and OT ($\Phi_{ST}=0.179$) dromedaries. Significant nuclear differentiation only existed between DB and BB ($F_{ST}=0.031$) populations (Table 2). The pairwise mismatch distribution showed a multimodal curve (Fig. 3), which is typical for a stable population. Although the neutrality tests Tajimas's D (-1.064; $p>0.10$) and Fu's FS (-3.609; $p>0.05$) provided negative values indicating possible population expansion, they were not significantly different from zero.

4. Discussion

We used molecular methods (mitochondrial and microsatellite genotyping) to assess the genetic diversity in northern Nigerian dromedaries and to validate breed discrimination and breeding concepts of camel pastoralists in the Nigeria-Niger corridor. Based on local knowledge, the colour phenotypes of Nigerian dromedaries are associated with distinct economic traits, *e.g.* higher milk yield or drought resistance. Accordingly, herders favour specific phenotypes like the dark-brown camels. We screened 75 individuals belonging to five different colours/breeds (DB, BB, SB, GW and OT) to identify possible associations between phenotypes and genetic structuring.

4.1. Colour phenotypes and population differentiation

We detected 12 different haplotypes in the 51 Nigerian dromedaries. The observed haplotype structure, however, was not related to the coat colour phenotypes, as DB, SB, GW and BB dromedaries shared haplotypes, including the one in highest frequency (47%; Fig. 1). The lack of association between mitochondrial haplogroups and coat colour/breed was also reflected in the Bayesian analysis of population structure, where the *Ja* (DB), *Kurri* (BB) and *Kala* (SB) camels were situated within the same cluster (Fig. S1). Likewise, based on nuclear microsatellite alleles we could not assign individual camels to distinct clusters as all dromedaries from the studied populations shared a common ancestry, irrespective of their coat colour and breed affiliation (Fig. 2). A similarly low population structure has been reported in Australian feral dromedaries, where only little genetic differentiation between populations has been observed (Spencer and Woolnough, 2010). A small historical founder size has been suggested as a possible explanation for the lack of distinct groups (Spencer and Woolnough, 2010). Poor genetic differentiation and low nuclear F_{ST} values (0.009) were also found in Kenyan dromedaries (Mburu et al., 2003). Likewise, a study of southern African dromedaries indicated a close relationship between camels from South Africa, Botswana and Namibia (Nolte et al., 2005). Similarly to these studies, we observed unrestricted gene flow between the different Nigerian camel phenotypes as the pairwise genetic comparisons between the Nigerian breeds resulted in low differentiation levels and were only significant between DB and BB camels ($F_{ST}=0.03$; Table 2). In a meta-analysis comparing dromedaries from the Canary Islands with populations from the Arabian Peninsula, Pakistan and Africa population structure was observed between Canary Islands/Algerian, Saudi Arabian/Pakistan and Kenyan camels, respectively. However, no breed differentiation within the countries was reported (Schulz et al., 2010).

4.2. Genetic diversity and demographic development

Irrespective of their low population structure, dromedaries in the Nigeria-Niger corridor exhibit a high genetic diversity ($H_E=0.625$) comparable to some extent to that of Saudi Arabian ($H_E=0.652$; Mahmoud et al., 2013), southern African ($H_E=0.604$; Nolte et al., 2005) and Pakistani ($H_E=0.640$; Schulz et al., 2010) camels. Dromedary populations from Australia (Spencer and Woolnough, 2010), the Canary Islands (Schulz et al., 2010) and Kenya (Mburu et al., 2003) had lower genetic diversity with H_E values ranging between 0.538 and 0.586, possibly a result of inbreeding and/or founder effects from a limited number of source individuals (Spencer and Woolnough, 2010). Interestingly, we found similar levels of mitochondrial genetic diversity ($H_d=0.725$) in Nigerian dromedaries compared to Mongolian domestic Bactrian camels (Chuluunbat et al., 2014). The high amount of genetic diversity observed in Nigerian dromedaries could be explained by constant gene flow and exchange between other dromedary populations from neighbouring countries; for instance, during the annual transhumant voyage embarked upon by pastoralists on both sides of the Nigeria-Niger corridor. This assumption should be confirmed by genetic comparisons with other dromedary populations (*e.g.* Algeria, Libya, Egypt, Sudan).

Non-panmictic population structure or the presence of related camels in the sample set, despite our cut-off ($r\geq 0.5$), might explain the excess of homozygotes and deviations from HWE, resulting in the high F_{IS} values observed in the Nigerian dromedary population. We cannot exclude that the increase in F_{IS} might result from the presence of null alleles in genotyped markers, even with multiple genotyping repetitions (Table S2). However, BB camels presented a low F_{IS} (0.05) measure for the loci screened in this study (Table 1).

The star-like shape of the main haplogroup (one big haplotype with many small satellites one mutational step apart) in the MJN (Fig. 1) hinted to an expanding population, therefore we performed additional analysis to investigate demographic parameters in the Nigerian dromedaries. Although the mismatch distribution showed a multi-modal curve typical for a stable population we observed the highest peak at the pairwise differences of one, which indicates recent population expansion. The modelled curve displayed a smooth distribution, which could account for an expanding population (Fig. 3). Likewise, the neutrality tests resulted in negative values (although not significant), which might hint to demographic expansion while assuming absence of selection (Rogers and Harpending, 1992).

5. Conclusion

We conclude that the Nigerian dromedaries are composed of a homogenous gene pool as no distinct population differentiation

was observed. These results do not support the clear distinction into breeds (*e.g. Ja*, *Kurri* and *Kala*) and the breeding concept of the pastoralists based on coat colour differences. Future studies might use candidate genes approaches to investigate loci under putative selection such as the KIT (tyrosine-protein kinase) gene for spotted coat colour (Fontanesi et al., 2010; Reinsch et al., 1999) or the MC1R (melanocortin 1 receptor) gene for the red-brown/black phenotype (Fontanesi et al., 2009; Andersson, 2001). In literature, we did not find any correlation between coat colour genes and milk or meat traits. Therefore, if the breeding goals for dromedaries *de facto* are an increase in milk and meat production, it is recommended to start classical breeding programmes with exact recording and selection of the desired phenotypes, *e.g.* milk yield, milk fat and protein content or weight gain. It is noteworthy, however, that pastoralists in the Nigeria-Niger corridor select for an "ideal" multi-purpose herd (Abdussamad et al., 2011) with widely distributed phenotypes and high diversity, rather than for single, high-performance camels. With increasing changes in climate conditions and desertification we should keep the traditional breeding concepts in mind and consider carefully the next steps for genetic selection and improvement in dromedaries.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.livsci.2015.07.008.

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