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Research Article

Dark grey gazelles *Gazella* (Cetartiodactyla: Bovidae) in Arabia: Threatened species or domestic pet?

Torsten Wronski[1,*], Hannes Lerp[2], Eva V. Bärmann[3], Thomas M. Butynski[4], Martin Plath[5]

[1] *Faculty of Science, School of Natural Sciences and Psychology, Liverpool John Moores University, James Parsons Building, Byrom Street, Liverpool, L3 3AF, UK*
[2] *Natural History Collections, Museum Wiesbaden, Friedrich-Ebert-Allee 2, 65185 Wiesbaden, Germany*
[3] *Zoological Research Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany*
[4] *Lolldaiga Hills Research Programme, Sustainability Centre Eastern Africa, P.O. Box 149, Nanyuki 10400, Kenya*
[5] *College of Animal Science and Technology, Northwest A&F University, Yangling 712100, P.R. China*

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Abstract

True gazelles (genus *Gazella*) are a prime example of a mammalian group with considerable taxonomic confusion. This includes the descriptions of several dark grey taxa of questionable validity. Here, we examined captive dark grey putative Neumann's gazelle *Gazella erlangeri*. Our concerted efforts to retrieve mitochondrial sequence information from old museum specimens of two dark grey gazelles, putative *G. erlangeri* and putative Muscat gazelle *G. muscatensis*, were unsuccessful. We did, however, find the mtDNA haplotypes of extant putative *G. erlangeri* to be nested within the haplotype variation of the Arabian gazelle *G. arabica*. The observed population genetic divergence between *G. arabica* and putative *G. erlangeri* (based on 11 nuclear microsatellites) was driven by genetic impoverishment of putative *G. erlangeri*. These results, along with morphological signatures of domestication (e.g., reduced brain case size), suggest genetic bottle necks and domestication effects as a consequence of prolonged captive breeding. Three hypotheses are discussed: (a) *G. erlangeri* and/or *G. muscatensis* are valid species but are now extinct; (b) one or both taxa represent phenotypic variation within *G. arabica* and, therefore, are synonyms of *G. arabica*; and (c) captive stocks, exhibiting the effects of domestication and inbreeding, are the sources for the descriptions of *G. erlangeri* and *G. muscatensis*. As concerns the conservation of gazelles, based on current knowledge, we strongly advise against using putative *G. erlangeri* for any introduction initiative but recommend the continued captive management of putative *G. erlangeri*.

Introduction

Captive breeding programs are often initiated when natural populations are at the brink of going extinct. In some cases, the captive stock was established from a few wild individuals (e.g., Arabian oryx *Oryx leucoryx* (Pallas, 1777) and Asian crested ibis *Nipponia nippon* (Temminck, 1835); Yu et al., 2006; Li et al., 2014). In Arabian oryx, four of the last 11 free-living individuals were transferred from a remnant Omani natural population to the Phoenix Zoo (Henderson, 1974; Grimwood, 1988). In the course of 20 years, this captive population — augmented by animals held in zoological gardens and private collections — grew to 123 individuals. This enabled several reintroduction programs (Abu Jafar and Hays-Shahin, 1988; Abu-Zinada et al., 1988; Stanley Price, 1989; El Alqamy et al., 2011). Today, reintroduced populations of Arabian oryx occur in Arabia (El Alqamy et al., 2011; Islam et al., 2011a), leading to a reclassification of the "Degree of Threat" status for this species from "Endangered" to "Vulnerable" (Marton-Lefèvre, 2011; IUCN, 2013).

In other cases, the species was extinct in the wild but captive stocks were available. One example is the scimitar-horned oryx *Oryx dammah* (Cretzschmar, 1826) (Newby, 1988). In 1985, the first successful reintroduction program for this species was implemented in the Bou-Hedma National Park, southern Tunisia (Bertram, 1988).

Not all captive breeding programs have, however, been established for conservation purposes. One famous example is Père David's deer *Elaphurus davidianus* Milne-Edwards, 1866. Following its extinction in the wild in 220 AD, this species survived only in the former Imperial Hunting Park near Beijing. At present, several zoological gardens are working to increase captive breeding stock (ISIS, 1996), and the species has been successfully reintroduced in southern China (Cao, 1993).

One major question associated with long-term captive populations is, "Does allelic variation of the current captive population represent that of the extinct wild population?" (Briscoe et al., 1992; Allendorf et al., 2012; Li et al., 2014). Genetic drift obviously plays an important role when effective population sizes are small. Moreover, artificial selection and captive conditions can lead to the fixation of alleles that are no longer counter selected by natural selection. Ample evidence indicates that, due to domestication processes, species undergo morphological changes after many generations in captivity. These include changes in skull shape, brain volume, postcranial skeleton, and digestive tract (Hemmer, 1990; Clutton-Brock, 1999; O'Regan and Kitchener, 2005). Behavioral alterations include reduced anti-predator and flight responses (e.g., Price, 1999, 2002).

This paper reports a case of an enigmatic captive breeding population of true gazelles (genus *Gazella*). Due to habitat destruction, competition with domestic livestock, and hunting with fire arms, dogs, and vehicles, gazelle numbers declined dramatically in Arabia during the 20^{th} Century (Thouless et al., 1991; Cunningham and Wacher, 2009). Saudi gazelle *Gazella saudiya* Carruthers and Schwarz, 1935, the Ar-

*Corresponding author
Email address: t_wronski@gmx.de (Torsten Wronski)

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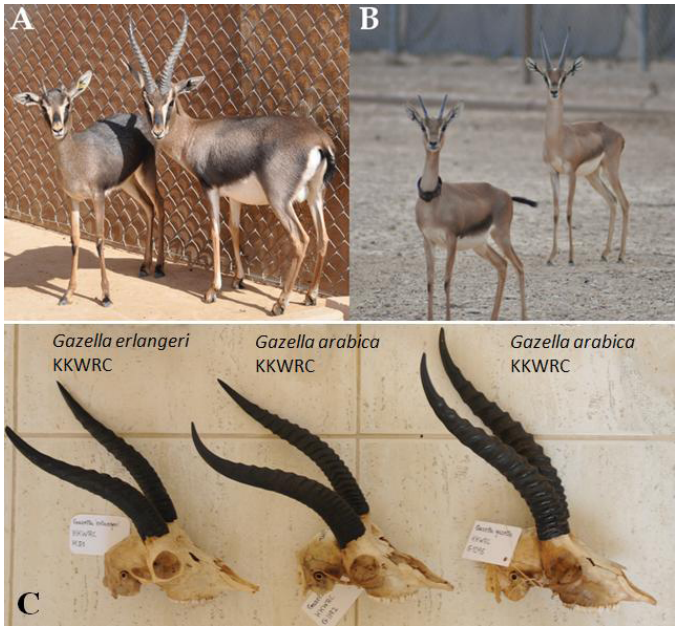

Figure 1 – Adult female (left) and adult male (A) putative Neumann's gazelle *Gazella erlangeri* and (B) adult female (left) and adult male Arabian gazelle *Gazella arabica* at King Khalid Wildlife Research Centre. (C) Skulls of adult male putative *G. erlangeri* and adult male *G. arabica* at KKWRC. Skulls of putative *G. erlangeri* are noticeably smaller than those of *G. arabica,* while skulls of *G. arabica* exhibit much more variation than those of putative *G. erlangeri.* Photographs by Hannes Lerp and Torsten Wronski.

abian form of dorcas gazelle *Gazella dorcas* (Linnaeus, 1758) (Hammond et al., 2001; Lerp et al., 2011), is extinct (Habibi and Williamson, 1997; Thouless et al., 1997). Natural populations of Arabian sand gazelle *Gazella marica* Thomas, 1897 probably no longer exist, but this species has been successfully reintroduced (Cunningham and Wacher, 2009). The third gazelle species in Arabia, Arabian gazelle *Gazella arabica* Lichtenstein, 1827, persists in reintroduced and remnant natural populations (Islam et al., 2011b; Wronski et al., 2011; Boug et al., 2012; Wronski and Butynski, 2014). The taxonomic position of *G. arabica* has puzzled generations of scientists (Groves and Harrison, 1967; Lange, 1972; Harrison and Bates, 1991; Vassart et al., 1995; Groves, 1996, 1997; Groves and Grubb, 2011; Hadas et al., 2015). Only recently have molecular and morphometric analyses demonstrated the distinctness of *G. arabica* from mountain gazelle *G. gazella* (Pallas, 1766) of the Levant (Wronski et al., 2010a; Bärmann et al., 2013a; Lerp et al., 2013; Hadas et al., 2015).

Beyond the above-mentioned species, several questionable gazelle taxa have been described and named on the basis of sightings, drawings, obscure historical reports, and museum specimens, some of which are of unknown provenance: *Gazella cora* Smith, 1827; *G. vera* Gray, 1850; *G. muscatensis* Brooke, 1874; *G. erlangeri* Neumann, 1906; *G. arabica hanishi* Dollman, 1927; *G. bilkis* Groves and Lay, 1985; *G. gazella farasani* Thouless and Al Bassri, 1991; *G. dareshurii* Karami and Groves, 1993; and *G. acaciae* Mendelssohn, Groves and Shalmon, 1997 (see also Bärmann et al., 2013b, 2014). It seems likely that most of these are variants of *G. arabica*, as recent molecular and morphological analyses found no evidence for additional species in Arabia (Rebholz and Harley, 1997; Wronski et al., 2010a; Bärmann et al., 2013a; Lerp et al., 2014). A thorough genetic analysis of the type material will be necessary, however, to clarify the synonymy or distinctness of these taxa.

In 1987, a group of phenotypically similar, yet distinct, gazelles (Fig. 1a) was presented to the officials of the National Wildlife Research Centre (NWRC) in Saudi Arabia by the Emir of Najran. In 1994, seven gazelles, phenotypically similar to those gifted by the Emir of Najran in 1987, were confiscated from a pet shop in Jeddah (Greth and Williamson, 1992, 1996). Captive populations of this gazelle are currently held at Al Wabra Wildlife Preservation (AWWP) in Qatar and at King Khalid Wildlife Research Centre (KKWRC) in Saudi Arabia (Greth and Williamson, 1992; Blacket, 2001; Hammer, 2010). These animals are of particular interest in that they exhibit striking phenotypic similarity to what, after more than 100 years of confusing taxonomic revisions and reassignments, is today referred to as Neumann's gazelle *Gazella erlangeri* (Neumann, 1906; Greth and Williamson, 1992; Groves, 1996, 1997; Groves and Grubb, 2011). Likewise, there is also phenotypic similarity to Muscat gazelle *Gazella muscatensis* Brooke, 1874 (Groves and Grubb, 2011).

Several features of these gazelles can be interpreted as the result of domestication and/or inbreeding. Relative to *G. arabica*, they are small, robustly built, have a short cranial length, lack sexual dimorphism in body size, and the hair of the dorsum and sides is much greyer (Fig. 1; see "phenotype b" in Wronski et al., 2010b). Even though no quantitative behavioral data are available, they are obviously much tamer/docile than typical captive *G. arabica*.

We used a combined phylogenetic, population genetic, and morphological approach to assess the taxonomic status and evolutionary history (including potential domestication effects) of putative *G. erlangeri*. Quantitative data on the morphometry of adult skulls were obtained using 24 linear measurements. Phylogeographic analysis of mitochondrial DNA sequences (1007 bp cytochrome b) was employed to unravel the phylogenetic relationships to the presumed sister species, *G. arabica*. An attempt was made to retrieve DNA from historic skins of gazelles referred to as *G. erlangeri* and *G. muscatensis* following state-of-the-art protocols for low DNA yields from tanned skins. Finally, allelic variation at 11 nuclear microsatellite loci was used to investigate genetic variability in captive putative *G. erlangeri* and wild and captive *G. arabica*, and to detect hybrids.

Materials and methods

Sampling of captive putative *G. erlangeri* and *G. arabica*

Samples were obtained from 16 captive specimens that exhibited the phenotype of *G. erlangeri*. Samples were obtained from animals at KKWRC, but originating from NWRC (N=11), a pet shop in Jeddah (N=1), the private collection of the Emir of Najran (N=1), the private collection of the Prince of Taif (N=2), and Al Areen Wildlife Sanctuary in Bahrain (N=1; Tab. 1). The latter specimen was identified as *G. muscatensis* by Al Areen Wildlife Sanctuary, but it is phenotypically *G. erlangeri*. To infer the origin of maternally inherited mitochondrial DNA of putative *G. erlangeri*, we compared previously published cytochrome b sequences with those of *G. arabica* (Tab. 1, grouping similar to Lerp et al., 2014). To compare these samples with *G. arabica*, we reanalysed a data set comprised of 55 wild and captive *G. arabica* specimens from three areas in Arabia (Lerp et al., 2014).

DNA extraction and genotyping

DNA extraction of captive putative *G. erlangeri* samples and amplification of 11 nuclear microsatellite markers (BM302, BM415, CSSM043, Texan19, BM4505, SR-CRSP6, MCM38, Inra40, OarFCB304, RM088, Texan6) was conducted as described in Lerp et al. (2014).

Museum skin samples

Samples of tanned skin were obtained from gazelles referred to as *G. erlangeri* (N=3) and *G. muscatensis* (N=2) housed in the Natural History Museum, London, and the Museum für Naturkunde, Berlin (Supplemental Tab. S1). These samples were processed under clean conditions with sterile scalpels, UV radiated pipettes, and sterilized tubes to avoid contamination. DNA was extracted using the QIAamp DNA Micro Kit (Qiagen, Hilden). For each sample, twice as much Proteinase K and extraction buffer was used than recommended by the manufacturer. Each sample was incubated overnight at 56 °C to ensure complete tissue lysis. No carrier-RNA was used during DNA extraction. A third washing step, using 250 µl pure ethanol, was added to the protocol to maximize DNA yield. Two elution steps with 50 µl and 250 µl elution buffer were conducted. For each sample, a second DNA extraction was conducted while adding 20 µl dithiothreitol before incubating

Table 1 – Summary of captive adult specimens of putative *Gazella erlangeri* (*N*=16), and wild and captive adult specimens of *Gazella arabica* (*N*=55) included in the phylogenetic and population genetic analyses.

Taxon	Origin	Wild/captive	Number of samples in phylogeographic analysis (Genbank access numbers)	Number of samples in population genetic analyses
G. erlangeri	NWRC	Captive	2[1](JN410350, JN410351)	9
G. erlangeri	Pet shop, Jeddah	Captive	1 (JN410348)	1
G. erlangeri	Emir of Najran	Captive	1 (JN410349)	1
G. erlangeri	Prince of Taif	Captive	0	2
G. erlangeri	Al Areen	Captive	0	1
G. arabica	North Arabia[2]	Wild	8 (JN410224, KC188740, KC188741, KC188744, KC188745, KC188747, KC188748, KC188759)	12
G. arabica	Southwest Arabia[2]	Wild and captive	5 (JN410261, JN410355, KC188761, KC188762, KC188765)	22
G. arabica	East Arabia[2]	Wild and captive	2 (JN410353, KU560648)	14

[1] Samples not included in population genetic analyses.
[2] See Lerp et al. (2014) for detailed information on samples.

overnight to degenerate keratinous structures. For each batch of 7 to 15 samples extracted in parallel, a negative control was performed to ensure that the reaction chemicals did not contain DNA. Two positive controls were conducted using fresh material (*G. arabica* and putative *G. erlangeri*). DNA content was measured using a NanoDrop 1000 spectrophotometer. DNA content of museum samples ranged from to 20.7 to 195.5 ng/µl in the 50 µl elution.

A fragment of 287 base pairs (bp) length of the cytochrome b gene was amplified using gazelle-specific primers (forward primer g8F 5'-ACA CCC GAA AGA CCC ACC CAC T-3' and reverse primer 295R 3'-CCA TAG TAG AGG CCT GTC C-5') derived from a data set of putative *G. erlangeri* and *G. arabica* cytochrome b sequences (see below). Primers were tested and amplified well for putative *G. erlangeri* and *G. arabica*. All PCR amplifications were performed in a 20 µl reaction volume using 14 µl ABgene Thermo-Start master mix including 0.25 U DNA polymerase, 0.2 mM dNTP, 1.5 mM $MgCl_2$, and 1.1× reaction buffer, as well as 2 µl of each primer and 2 µl DNA template. Amplifications were performed under "relaxed" PCR conditions; initial denaturation (15 min at 95 °C), followed by 40 cycle steps of 1 min at 94 °C (denaturation), 1 min at 50 °C (primer annealing), 1 min at 72 °C (elongation) and, finally, one extension step (10 min at 72 °C). Amplification success was determined using gel electrophoresis.

Because amplicons were not obtained from museum specimens, PCR conditions were altered in two ways: (1) $MgCl_2$ concentration was increased to 2.5 mM; (2) DNA concentrations were reduced by dilution (1:10 and 1:100), or increased by concentrating DNA from different extractions using Amicon Ultra Centrifugal Filters 30K. In cases where these two alterations did not result in amplification, a second PCR was run using the prior PCR reaction mix as a template.

To test for PCR inhibitors in the eluted DNA sample, a "spike"-PCR was performed by mixing 1 µl of fresh *G. arabica* DNA with 1 µl DNA from a museum specimen. This mixture was used as a template. No PCR inhibitors were detected.

Phylogeographic analysis

A mitochondrial cytochrome b sequence alignment of 19 previously published and new sequences (Tab. 1) was constructed. The software TCS 1.21 (Clement et al., 2000) was used to construct a statistical parsimony (SP) network. The connection limit was set to 95%. Arlequin 3.5.1.3 (Excoffier and Lischer, 2010) was used to calculate pairwise F_{ST}-values between groups.

Population genetic analyses

Arlequin 3.5.1.3 (Excoffier and Lischer, 2010) was used to calculate expected heterozygosity (H_E) and observed heterozygosity (H_O), and to test for deviations from Hardy-Weinberg-Equilibrium (HWE). HP-Rare (Kalinowski, 2005) with rarefaction was used to calculate per-locus allelic richness for each group. A repeated measures ANOVA in SPSS 21 was applied to test for group differences. Levene's test for homoscedasticity revealed no violation of the assumption of equal variances (p=0.85). Null alleles were detected in the microsatellite data set of *G. arabica* (Lerp et al., 2014). Therefore, FreeNA (Chapuis and Estoup, 2007) was used to estimate pairwise F_{ST}-values by excluding null alleles and 95% confidence intervals based on 50000 bootstrap replicates. STRUCTURE 2.3.4 (Pritchard et al., 2000) was employed to identify the number of genetically distinct clusters (K) in the combined data set of putative *G. erlangeri* and *G. arabica*. For each value of K=1 through K=7, 10 iterations were run with 10^5 generations being discarded as burn-in, followed by a sampling phase of 10^5 iterations. Each simulation was performed using an ancestry model incorporating admixture, a model of correlated allele frequencies, but without prior information corresponding to the origin of the samples. The "recessive alleles" setting implemented in STRUCTURE was used to estimate null allele frequencies for each locus in the clusters and to correct for null alleles in the respective analyses (for methodological details see Senn and Pemberton, 2009). To detect the uppermost level of population differentiation, the method presented by Evanno et al. (2005) was applied using STRUCTURE HARVESTER 0.6.94 (Earl and VonHoldt, 2011). This allows for a batch application of STRUCTURE results.

Skull morphometry

Twenty-four linear measurements (Supplemental Tab. S2, Fig. S4) were taken (by the same person) from 31 skulls from adult animals at KKWRC (seven putative *G. erlangeri*: five males, two females; 24 *G. arabica*: 18 males, six females). For four specimens, one or two measurements were missing due to incomplete skulls. These were replaced with the average values of the other specimens belonging to the same taxon and sex. Another six gazelles, labelled "*G. muscatensis*", originating from the Batinah coastal area in northern Oman, were measured for comparison with captive putative *G. erlangeri*. These six specimens, three males (HZM 6.4049, HZM 11.4114, HZM 26.4534) and three females (HZM 4.4047, HZM 7.405, HZM 12.4115), are housed in the Museum of the Harrison Institute in Sevenoaks, Kent, UK. Measurements were taken by the Curator, Malcolm Pearch, and analysed together with the other measurements to reveal possible similarities or differences between putative *G. erlangeri* and putative *G. muscatensis*.

The data were explored using a Principle Component Analysis (PCA) with $\log_{10}$-transformed measurements as recommended by Keene (1995) (Fig. 4, Tab. 2). Four principal components with Eigenvalues >1 were obtained. These were used as input variables in a discriminant function analysis (DFA) with cross-validation to test for the distinctness of putative *G. erlangeri* and *G. arabica*. In order to identify the effects of possible domestication on braincase variables and snout length, all measurements were tested for significant differences between putative *G. erlangeri* and *G. arabica* using two-way ANOVA, while including sex as another factor (Tab. 3). All morphometric analyses were conducted with SPSS 21.

Table 2 – Principal component analysis for 24 skull measurements from adult putative *Gazella erlangeri* (*N*=7) and adult *Gazella arabica* (*N*=24). Bold font indicates variables with high (>|0.6|) factor loadings for the first two components. Full name of each skull measurement abbreviation (i.e., "variable") are given in Tab. 3 and Supplemental Tab. S2.

	Factor loading				Extraction
Variable	**PC1**	**PC2**	**PC3**	**PC4**	**communality**
BPL	0.610	0.065	-0.478	0.386	0.754
CBL	0.209	0.028	0.698	0.338	0.646
DFH	0.504	**0.639**	-0.241	0.261	0.789
DFO	0.587	0.37	-0.512	-0.038	0.746
DH	-0.56	**0.718**	0.040	0.088	0.838
DOC	**0.883**	0.055	-0.07	-0.139	0.807
HBD	-0.238	**0.653**	0.412	-0.413	0.823
HD1	**0.864**	-0.349	0.082	-0.236	0.93
HD2	**0.902**	-0.339	0.014	-0.168	0.957
HL	**0.847**	-0.313	0.002	-0.22	0.863
HTD	0.388	-0.514	-0.199	0.144	0.475
IB	**0.892**	0.022	0.231	0.142	0.868
LF+P	**0.820**	0.052	0.221	0.162	0.75
LL	0.717	0.298	0.132	0.113	0.633
LP	0.387	-0.086	0.61	0.517	0.796
MWH	0.548	**-0.749**	0.137	-0.029	0.882
OD	0.557	0.557	-0.001	-0.228	0.673
OHB	**0.879**	0.099	-0.158	-0.235	0.863
OHO	**0.879**	0.001	-0.16	-0.189	0.834
WAO	**0.918**	0.278	0.079	-0.003	0.927
WB	0.691	0.313	0.367	-0.077	0.717
WBA	0.662	0.031	0.347	-0.264	0.629
WPP	0.744	0.073	-0.393	0.35	0.837
ZW	**0.828**	0.264	-0.039	0.109	0.768
Eigenvalues	11.88	3.33	2.24	1.36	
% of variance	49.49	13.86	9.33	5.68	

Results

Phylogeographic analysis

Extensive efforts to retrieve mtDNA sequences from museum specimens referred to as *G. erlangeri* and *G. muscatensis* were unsuccessful, probably because the tanning procedures had damaged all DNA. Statistical parsimony network analysis of putative *G. erlangeri* from KKWRC and *G. arabica* cytochrome b sequence variation found two haplotypes in putative *G. erlangeri* (differing by a single substitution) and nine haplotypes in *G. arabica* (differing by one to 16 mutational steps; Fig. 2). Most haplotypes were separated by one or two mutational steps. The maximum distance between adjoining haplotypes was eight mutational steps.

Haplotypes of putative *G. erlangeri* did not form a monophyletic group (i.e., they clustered within the haplotype variation of *G. arabica*). There was some genetic structure within *G. arabica* with two clades separated by eight mutational steps (Fig. 2). The first clade predominantly comprised specimens from northern Arabia while the second clade (including putative *G. erlangeri* haplotypes) mostly contained specimens from south-western and eastern Arabia. Clades showed geographic range overlap, however, with one individual from south-western Arabia assigned to clade 1 and one individual from northern Arabia assigned to clade 2. These two major clades are congruent with the findings, using only mitochondrial markers, of Lerp et al. (2014) (i.e., low gene flow among eastern, western, and northern populations). Pairwise F_{ST}-values between geographic groups of putative *G. erlangeri* and *G. arabica* revealed only two significant values; between putative *G. erlangeri* and northern *G. arabica* (F_{ST}=0.65, p=0.02), and between northern *G. arabica* and south-western *G. arabica* (F_{ST}=0.41, p=0.02).

Population genetic analyses

Five (BM302, BM415, Texan19, RM088, Texan6) of 11 microsatellite loci were monomorphic in putative *G. erlangeri* but polymorphic in *G. arabica* (Supplemental Tab. S3). Of the remaining six loci, four showed no deviations from HWE in putative *G. erlangeri* (BM4505: H_O=0.818, H_E=0.628; CSSM043: H_O=0.545, H_E=0.619; SR-CRSP6: H_O=0.692, H_E=0.508; INRA40: H_O=0.400, H_E=0.533), while two loci did (MCM38: H_O=0.462, H_E=0.760, p=0.02; OarFCB304: H_O=0.357, H_E=0.601, p=0.03). Only one locus (MCM38) showed no length range overlap between putative *G. erlangeri* and *G. arabica* (Supplemental Tab. S3). Allelic richness differed significantly among groups ($F_{3,30}$=42.73, p<0.001). A post hoc test (Student-Newman-Keuls Method) revealed significant differences for almost all pair-wise comparisons ($p\leqslant$0.006). Only the comparison between eastern *G. arabica* and northern *G. arabica* was not significant (p=0.86).

Allelic richness (mean±SD) was 2.17±1.34 in putative *G. erlangeri*, 4.79±1.43 in northern *G. arabica*, 5.87±1.77 in south-western *G. arabica*, and 4.72±1.70 in eastern *G. arabica*. Estimated pairwise F_{ST}-values between putative *G. erlangeri* and all three *G. arabica* groups exceeded 0.2, while being much lower among them (F_{ST}<0.06). STRUCTURE HARVESTER indicated K=2 genetic clusters to be the uppermost level of population differentiation (ΔK=93.4; Fig. 3a). Here, all putative *G. erlangeri* were assigned to a genetic cluster (with $Q\geqslant$0.94) that was almost absent in *G. arabica* (a single individual of *G. arabica* showed an assignment of Q=0.42 while all others had $Q\leqslant$0.17; Fig. 3b).

At K=4, genetic assignment of putative *G. erlangeri* was also exclusive to a single genetic cluster ($Q\geqslant$0.97) with *G. arabica* not assigned to this cluster ($Q\leqslant$0.30; Fig. 3b). Furthermore, population genetic structure within *G. arabica* was uncovered, but the assignment did not represent geographic groups (Fig. 3b; see Lerp et al., 2014 for details).

Skull morphometry

Principal component analysis of the 24 linear skull measurements retrieved four principal components with Eigenvalue >1.0. Variables with highest factor loadings for PC1 were those reflecting differences in horn length (HL), horn diameter (HD1, HD2), occipital height (OHB, OHO), braincase length (DOC, LF+P), skull width (WAO, ZW), and inter-bullae distance (IB), while variables with highest factor loadings for PC2 were horn base distance (HBD), distance between horn pedicles (DH), horn width (MWH), and distance from front of the skull to horn base (DFH) (Tab. 2). For visualization of differences between the sexes and among groups, PC1 and PC2 (together accounting for 63.3% of the total variance) were plotted (Fig. 4).

PC1 and PC2 showed significant differences for equality of means (t_{30}=3.31, p=0.002 for PC1; t_{30}=2.29, p=0.029 for PC2) and were used

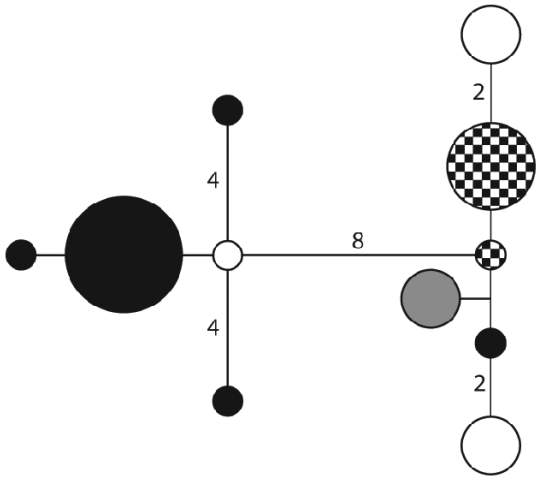

Figure 2 – Statistical parsimony network based on a 1007 bp fragment of cytochrome b (19 sequences) for putative Neumann's gazelle *Gazella erlangeri* and Arabian gazelle *Gazella arabica*. Circle sizes are proportional to the number of individuals with the corresponding haplotype (smallest circles represent one individual). Length of the connecting line is proportional to one mutation step. The number of mutation steps is, otherwise, stated. Putative *G. erlangeri* haplotypes (checkered) and *G. arabica* haplotypes from northern (black), south-western (white), and eastern (grey) Arabia are shown.

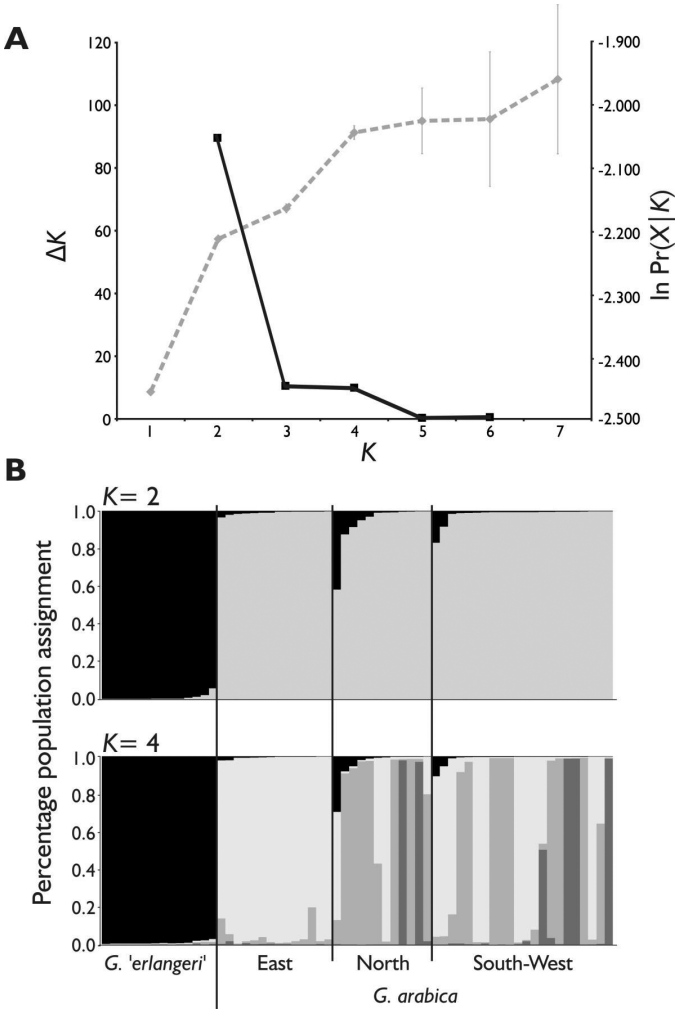

Figure 3 – Individual assignment to different numbers of genetic clusters for putative Neumann's gazelle *Gazella erlangeri* and Arabian gazelle *Gazella arabica* inferred from STRUCTURE analysis. (A) Estimated ln Pr (X|*K*) (grey diamonds) and Δ*K* (black squares) as a function of *K*. (B) Percentage assigned to inferred genetic clusters for *K*=2 and *K*=4 per specimen. Animals were sorted by *Q*-values for the *G. erlangeri* cluster for each group.

as dependent variables in a DFA to test for the distinctness of the two taxonomic groups. In both classifications — the one using original data as well as the cross-validation analysis — 30 of 31 skulls (96.8%) were correctly classified, with only one *G. arabica* male assigned to *G. erlangeri*. In a subsequent analysis, in which only male specimens were considered, this male was again classified as *G. erlangeri*. In this DFA, the weighting for PC2 (standardized canonical discriminant function coefficient=0.90) was much higher than for PC1 (0.23). This reflects the high impact of horn distance and horn width on the classification of males. All six female *G. arabica* were correctly classified by this DFA, while one of the two putative *G. erlangeri* females was assigned to G. arabica.

The additional analyses that included the six putative *G. muscatensis* specimens from the Harrison Institute showed a similar picture: principal components 1 and 2 received axis loadings from the same measurements as in the original analysis (e.g., braincase length and height, horn diameter and width, and skull width, had high positive loadings in PC1, while horn distance received negative loadings). There were a few measurements that behaved differently in the two analyses, especially condylo-basal length (CBL), zygomatic width (ZW), and horn base distance (HBD). These had high loadings in PC1 or PC2 in the original analysis but much lower loadings (mainly in PC3 and PC4) in the additional analysis. All specimens belonging to the dark morph (putative *G. erlangeri* and putative *G. muscatensis*) deviated in the same direction from those of the rufous morph (*G. arabica*) in PC1 and PC2 (Supplemental Fig. S5); both groups were distinguished unambiguously in the DFA (using PC1 and PC2 as dependent variables), where 97.3% of cases were correctly classified (only one *G. arabica* female was placed into the *G. erlangeri* cluster). Obvious differences between captive putative *G. erlangeri* and putative *G. muscatensis* became apparent along PC2 and PC3.

In line with our prediction that *G. erlangeri* is a domesticated form of *G. arabica*, we found indications for reduced brain dimensions and other signatures indicative of domestication. For example, brain case length (LF+P), occipital height (OHB, OHO), brain case width (WB), and snout length (DFH, DFO) were significantly reduced (Tab. 3). Furthermore, there were significant differences in orbital diameter (OD), lacrimal length (LL), skull width (WAO), zygomatic width (ZW), maximum width of horns sheaths (MWH), horn length (HL), horn pedicle diameter 1 and 2 (HD1,2), distance orbit to condyle (DOC), and horn base distance (HBD; Tab. 3). All other measurements showed no significant differences between putative *G. erlangeri* and *G. arabica* (Tab. 3).

Discussion

Despite efforts to obtain sequence information from museum specimens of putative *G. erlangeri* and putative *G. muscatensis*, no PCR products were retrieved. In the past, museum skins were often tanned using a cocktail of chemicals to prevent biological infestation. This process often leads to a complete denaturalization of DNA. This precludes a rigorous discussion of the taxonomic status of *G. erlangeri* and *G. muscatensis*. As such, one could argue that one or both are valid taxa that are extinct in the wild. Studies comprising mitochondrial sequence information from *G. gazella*, *G. arabica*, *G. marica*, and *G. saudiya* samples collected during the past few decades throughout Arabia present no support for the current existence of other species of gazelle in Arabia (Hammond et al., 2001; Wronski et al., 2010a; Wacher et al., 2011; Lerp et al., 2014).

The case of *G. erlangeri* is difficult to resolve. Neumann (1906) compared the lectotype of *G. arabica* in the Museum für Naturkunde with a drawing of *G. arabica* in Sclater and Thomas (1898) (pl. 49). Neumann thought that this drawing represented a greyer variant of *G. arabica* originating from Lahadsch (= Lahej = Lahij), north of Aden, south-western Yemen. He introduced the subspecific name "*erlangeri*" to account for this difference and based this new taxon on the drawing labelled "*G. arabica*" in Sclater and Thomas (1898). The animal after

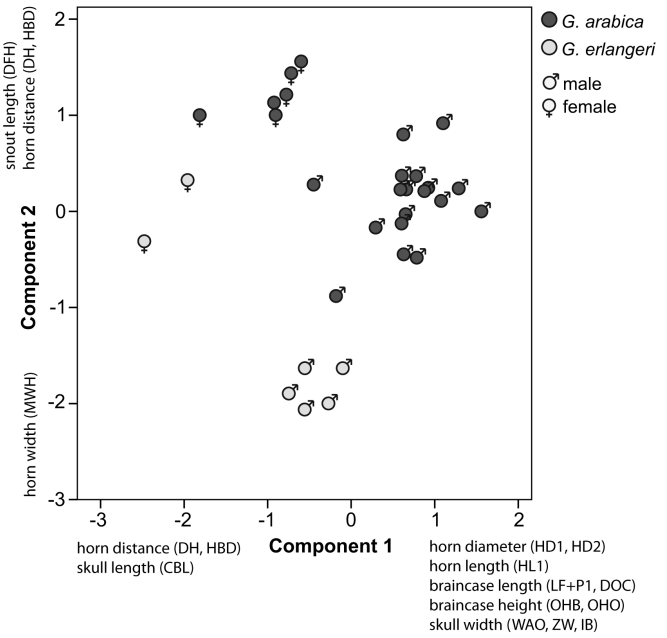

Figure 4 – Principal component analysis of adult putative Neumann's gazelle *Gazella erlangeri* (*N*=7) and adult Arabian gazelle *Gazella arabica* (*N*=24) skulls using 24 linear measurements. Component 1 mainly reflects differences in horn length and diameter, occipital height, braincase length, and skull width. Component 2 is mostly influenced by horn distance and width, as well as distance from snout tip to horn base.

Table 3 – Results of two-way ANOVAs on 24 skull measurements of adult putative *Gazella erlangeri* (*N*=7) and adult *Gazella arabica* (*N*=24). Significant differences are highlighted in bold font.

Skull measurement	Abbreviation	Factor	$F_{1,27}$	*p*
Basi-palatal length	BPL	species	1.72	0.2
		sex	3.86	0.06
		species × sex	0.23	0.63
Condylo-basal length	CBL	species	0.17	0.69
		sex	0.0071	0.93
		species × sex	3.65	0.07
Distance front to horns	DFH	species	17.34	**<0.001**
		sex	0.1	0.75
		species × sex	0.082	0.78
Distance front to orbit	DFO	species	5.32	**0.03**
		sex	1.73	0.2
		species × sex	0.18	0.68
Distance between horns pedicles	DH	species	0.78	0.39
		sex	130.91	**<0.001**
		species × sex	8.11	**0.008**
Distance orbit to condyle	DOC	species	9.67	**0.004**
		sex	17.63	**<0.001**
		species × sex	0.016	0.9
Horn base distance	HBD	species	8.06	**0.008**
		sex	6.68	**0.015**
		species × sex	0.42	0.52
Horn pedicle diameter 1	HD1	species	11.19	**0.002**
		sex	163.2	**<0.001**
		species × sex	2.3	0.14
Horn pedicle diameter 2	HD2	species	9.59	**0.005**
		sex	153.45	**<0.001**
		species × sex	0.013	0.91
Horn length	HL	species	15.57	**<0.001**
		sex	173.24	**<0.001**
		species × sex	7.91	**0.009**
Horn tip distance	HTD	species	2.45	0.13
		sex	16.66	**<0.001**
		species × sex	0.4	0.54
Inter-bullae distance	IB	species	10.01	**0.004**
		sex	16.13	**<0.001**
		species × sex	0.85	0.37
Length of frontal+parietal	LF+P	species	8.96	**0.006**
		sex	10.93	**0.003**
		species × sex	0.016	0.9
Length of lacrimal	LL	species	19.97	**<0.001**
		sex	4.25	**0.049**
		species × sex	0.22	0.65
Length of parietal	LP	species	1.15	0.29
		sex	1.42	0.24
		species × sex	0.22	0.64
Maximum width of horns sheats	MWH	species	5.23	**0.031**
		sex	37.63	**<0.001**
		species × sex	0.32	0.58
Orbit diameter	OD	species	15.9	**<0.001**
		sex	0.16	0.7
		species × sex	1.62	0.21
Occipital height	OHB	species	10.79	**0.003**
		sex	15.26	**<0.001**
		species × sex	0.63	0.43
Occipital height	OHO	species	8.4	**0.007**
		sex	19.78	**<0.001**
		species × sex	0.055	0.82
Width across orbits	WAO	species	57.27	**<0.001**
		sex	29.64	**<0.001**
		species × sex	0.52	0.48
Width of braincase	WB	species	15.63	**<0.001**
		sex	3.44	0.075
		species × sex	0.91	0.35
Width of basioccipital anterior	WBA	species	3.6	0.068
		sex	6.86	**0.014**
		species × sex	0.13	0.73
Width across paroccipital processes	WPP	species	2.21	0.15
		sex	4.27	**0.049**
		species × sex	0.43	0.52
Zygomatic width	ZW	species	24.22	**<0.001**
		sex	11.14	**0.002**
		species × sex	0.09	0.76

which the drawing was made, an adult male brought to the Gardens of the Zoological Society of London from Aden in the early 1890s, was, to our knowledge, not preserved. There are, however, museum specimens from the type locality. In Berlin, there is a skin labelled "type of *G. erlangeri* (=*G. lahadchensis*)", collected in Lahadsch (date and collector unknown). This specimen (ZMB_MAM_89578) is, however, not the *G. erlangeri* holotype and is not mentioned in Neumann (1906).

In the case of *G. muscatensis*, the description is based on a single dark grey specimen obtained by Major C. B. Evan Smith in August 1873 from Muscat, Oman (Brooke, 1874). It is conceivable that the holotype of *G. muscatensis* either represents natural variation within *G. arabica* or is a domesticated *G. arabica*.

This study focussed on captive putative *G. erlangeri*. These animals show striking similarities with the descriptions of *G. erlangeri* and *G. muscatensis*, especially their dark grey dorsum and sides. They are also shorter and more robustly built than the typical, gracile, *G. arabica* (Fig. 1). Our morphological analyses found evidence of domestication processes congruent with *a priori* predictions derived from studies on domestic animals (Kruska, 1987; Hemmer, 1990; Clutton-Brock, 1999; O'Regan and Kitchener, 2005). These include smaller brain case and shorter snout length. Our population genetic analysis detected considerably lower genetic variation within putative *G. erlangeri* than in *G. arabica* (Lacy, 1987; Briscoe et al., 1992). We suspect that these findings indicate prolonged captive breeding in combination with small effective population size. The low sexual dimorphism in body size in putative *G. erlangeri* compared to other gazelles in the Middle East (Wronski et al., 2010b) also supports this suspicion (O'Regan and Kitchener, 2005).

The dark grey hair of putative *G. erlangeri* might be a by-product of domestication (i.e., selection for tame individuals). In a study on silver fox, a melanistic form of red fox *Vulpes vulpes* (Linnaeus, 1758), Belyaev (1969) demonstrated that artificial selection for increased tameness had pleiotropic effects on the morphological and physiological phenotype. Foxes were rigorously selected for tame, dog-like, behaviour and subsequently showed a range of morphological and physiological traits characteristic of domestic animals (Trut et al., 2009). While putative *G. erlangeri* were not actively selected for tameness in breeding centres, they are today much calmer and tamer than *G. arabica* in the same centres. This suggests artificial selection for increased tameness before conservation breeding began. The high number of fixed alleles and the two mitochondrial haplotypes that clustered within *G. arabica* further support the view that putative *G. erlangeri* represent a domestic form of *G. arabica*.

Many authors cite the ancient Egyptian drawings of gazelles (and other antelopes) being hand-fed as evidence for their domestication (e.g., Clutton-Brock, 1999). Archaeological evidence suggests that gazelles in the Middle East were, if not domesticated, at least managed (Legge, 1972, 1977). Moreover, the sacrifice of gazelles is frequently mentioned in ancient Egyptian tomb inscriptions (Diamond, 1999; Thesaurus Linguae Aegyptiae, 2014). As late as the first half of the 20^{th} Century, people in Iraq kept gazelles for meat and the manufacture of Torah scrolls, even in urban homes and gardens (Amar and Nissan, 2009). Gazelles are still traded in pet markets in the Middle East (Bailey, 2003; Soorae et al., 2008; Bachmann, 2010; Lerp et al., 2014; see Introduction).

Another possibility for dark grey putative *G. erlangeri* (phenotype b in Wronski et al., 2010b) is that they represent a mountain variant of *G. arabica*. Ungulates that occur on mountains tend to be darker than their lowland conspecifics (Groves and Grubb, 1974; Moodley and Bruford, 2007). *Gazella erlangeri* were thought to occur in the mountains of south-western Yemen, and in the mountains of western Saudi Arabia as far north as Thuwal, north of Jeddah (Groves, 1996, 1997). Investigations in this region, however, found only *G. arabica* haplotypes (Wronski et al., 2010a) and *G. arabica* with reddish hair (Boug et al., 2012).

In this study, phylogeographic analysis could not resolve the origin of *G. erlangeri*. Thus, it remains possible that *G. erlangeri* originated from south-eastern Arabia — from where *G. muscatensis* was de-

scribed (Brooke, 1874). The putative *G. muscatensis* specimens from the Harrison Institute showed high similarity to captive putative *G. erlangeri*, although the PCA found differences that separated both groups. However, these differences could either be based on real disparities in skull dimensions, or stem from measurement inconsistencies, as the two groups were measured by different persons. It is, thus, possible that a distinct form of gazelle called *G. muscatensis* existed in Oman, and that captive presumed *G. erlangeri* stem from this now extinct form. Genetic analyses using novel hybrid-capture techniques and measurements of cranial capacity might solve this question (Knapp and Hofreiter, 2010).

Although unlikely, we cannot reject the hypothesis that putative *G. erlangeri* and/or putative *G. muscatensis* are descendants of an extinct taxon. In-other-words, at least one taxon — *G. erlangeri* or *G. muscatensis* — could be a valid species. It is conceivable that some microsatellite alleles became fixed through genetic drift in a small population, and mitochondrial introgression from *G. arabica* occurred. This has been observed in American bison *Bison bison* Linnaeus, 1758, which show higher mitochondrial than autosomal cattle ancestry (Hedrick, 2010). The apparent effects of prolonged captive breeding and domestication in putative *G. erlangeri* bring into question the value to conservation of the current captive populations.

Conclusions

The most parsimonious conclusion concerning the taxonomic status of *G. erlangeri* is that this species never existed. Perhaps, *G. erlangeri* represents an extinct colour morph of *G. arabica* from which domestic pet gazelles (phenotype b, Wronski et al., 2010b) were derived. If so, this may also be the source for the description of *G. muscatensis* (Brooke, 1874). In terms of conservation, based on current knowledge, we strongly advise against using putative *G. erlangeri* for any introduction initiative. We do, however, recommend that this attractive, docile, and scientifically interesting gazelle be maintained and effectively managed in captivity for its potential educational, cultural, research, and conservation values.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Museum skin samples of putative *Gazella erlangeri* and putative *Gazella muscatensis* used in this study.

Table S2 Skull measurements taken in this study.

Table S3 Descriptive statistics of genetic variation at 11 microsatellite loci used in this study of *Gazella arabica* and putative *Gazella erlangeri*.

Figure S4 Skull measurements used in this study of adult *Gazella arabica* and adult putative *Gazella erlangeri*.

Figure S5 Principal component analysis of skulls of adult *Gazella arabica*, putative *Gazella erlangeri*, and putative *Gazella muscatensis*.