



Taxonomy and Translocations of African Mammals: A Plea for a Cautionary Approach

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Abstract: Ecotourism can fuel an important source of financial income for African countries and can therefore help biodiversity policies in the continent. Translocations can be a powerful tool to spread economic benefits among countries and communities; yet, to be positive for biodiversity conservation, they require a basic knowledge of conservation units through appropriate taxonomic research. This is not always the case, as taxonomy was considered an outdated discipline for almost a century, and some plurality in taxonomic approaches is incorrectly considered as a disadvantage for conservation work. As an example, diversity of the genus Giraffa and its recent taxonomic history illustrate the importance of such knowledge for a sound conservation policy that includes translocations. We argue that a fine-grained conservation perspective that prioritizes all remaining populations along the Nile Basin is needed. Translocations are important tools for giraffe diversity conservation, but more discussion is needed, especially for moving new giraffes to regions where the autochthonous taxa/populations are no longer existent. As the current discussion about the giraffe taxonomy is too focused on the number of giraffe species, we argue that the plurality of taxonomic and conservation approaches might be beneficial, i.e., for defining the number of units requiring separate management using a (majority) consensus across different concepts (e.g., MU-management unit, ESU—evolutionary significant unit, and ECU—elemental conservation unit). The taxonomically sensitive translocation policy/strategy would be important for the preservation of current diversity, while also supporting the ecological restoration of some regions within rewilding. A summary table of the main translocation operations of African mammals that have underlying problems is included. Therefore, we call for increased attention toward the taxonomy of African mammals not only as the basis for sound conservation but also as a further opportunity to enlarge the geographic scope of ecotourism in Africa.

Keywords: Africa; mammal subspecies; biotic homogenization; *Giraffa*; game tourism; taxonomy; *Panthera leo*; ECU

1. Introduction

When dealing with Africa's biodiversity, we should not be tempted to fall into the belief of studying and conserving a piece of Eden that escaped the ruinous consequences of human impact. This is not certainly true, but see [1,2], yet wildlife diversity and abundance had—and still has—an obvious role in shaping Western perceptions of Africa as a unique place on Earth [3,4].

African biomes are also a unique laboratory for scientific research that explores the forces that governed evolutionary history. Dealing with such diverse issue as humans' evolutionary history or the relationship between tectonic activity and cichlids' speciation [5], Africa appears as a unique setting to reach a better knowledge of how biodiversity



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Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). developed. Moreover, African mammals have been a classic subject for scientific inquiries dealing with evolution for more than a century now, e.g., [6–17].

Mammal diversity, particularly the richness of relatively large-sized species, fueled at first a growing interest in Africa by hunters from all over the world. Later, a conservation movement developed (aside from a few pioneers such as Carl Akeley), mainly influenced by those researchers—such as George B. Schaller and Ian Douglas-Hamilton—studying charismatic species such as African elephants, lions, gorillas and chimpanzees. The same species and African wildlife biomass and diversity are now the target of a multi-millionaire tourism industry that makes wildlife a highly profitable business for private operators and African countries [18]. This has led to an increased role in active management of some mammal species, including a growing occurrence of translocations as a means to repopulate or restock protected areas that have lost their native stock of some of the most charismatic species [19–22], to realize the optimal management for threatened taxa (e.g., [23,24] in the case of the Cape mountain zebra) or for the ecological restoration of particular regions (e.g., [25,26]). Active management operations are often valuable from the conservation point of view, but some of them have been inappropriate or even damaging to the genetic integrity of autochthonous populations of particular species (cf. [27] for mitigation translocation cases), such as in the case of the wildebeest (see [28-30]), or whole communities (for evaluation of ungulate translocations, especially in Southern Africa, see [21,31,32]).

In the present contribution, we aimed to critically review translocations of some mammals in Africa as a conservation tool, partly using giraffes as a case-study because of the current progress in understanding their diversification across Africa and emphasizing some causes of concern relating the possible negative outcomes for the conservation of evolutionary history in a unique continent. Following an increasing emphasis on financial viability, many extralimital species—i.e., species that historically did not occur in an area—or stocks of atypical phenotypes (under "intentional genetic manipulation" [21]) were introduced into private and public reserves to increase public experiences with the intention of increasing ecotourism attractions [33]. Although translocations are not a totally new tool in African conservation, it seems that many current projects are being realized primarily for financial reasons rather than conservation considerations. Another factor that often determines and influences the translocations is the need to create private game reserves dedicated to trophy hunting. This phenomenon is especially widespread in South Africa [34], and, often, the purpose of increasing income is to the detriment of conservation because moving species and subspecies well outside their original ranges increases the risk of hybridization between closely related species or subspecies [35,36]. A similarly questionable type of operation is to create fenced private reserves with the aim of attracting tourists to observe animal species, especially large mammals, including those that had never been locally present there in historic times.

According to [37], there are at least seven types of translocation for which conservation is not the primary aim (note that species conservation may be an associated aim and protection of individual animals of threatened species may be a primary aim): non-lethal management of problem animals, commercial and recreational, biological control, aesthetic, religious, wildlife rehabilitation, and animal rights activism.

2. What Do We Know about Large Mammal Diversity?

Wildlife managers, like most tourists, are convinced that our knowledge of large African mammals is more than satisfactory, as demonstrated from the large number of books existing on the subject e.g., [38,39]. Field guides, in particular, are suspected to vehicle an assuring view concerning our taxonomic knowledge of mammals [40]. Most users are unaware that such tools as field guides are intended to help identify what people see in a given place (i.e., to distinguish a bushbuck, *Tragelaphus scriptus* (Pallas, 1766) from a sitatunga *T. spekii* Speke, 1863; taxonomy follows predominantly [41]) but say nothing about the number of taxa, their phyletic relationships, and the rank accorded inside the

sitatunga and the bushbuck concepts [42]. Diatribes regarding taxonomic subdivisions of even the most well-known African mammals are widespread (e.g., African elephants [43], ungulates [44], felids [45], and canids [46]), including many species that are commonly relocated through the African continent (see Table 1). Wildlife managers are often convinced that wildlife was ubiquitous before humans exerted a strong pressure on it, which also leads to local extirpations.

Table 1. Some selected cases of mammalian translocations in Africa, with uncertain outcomes, including goals and consequent problems. Taxonomy follows predominantly [41].

Species	Original Range	Translocated to	Purpose	Aftermath	References
Damaliscus pygargus phillipsi Harper, 1939	Northeast South Africa	Southwest South Africa, Botswana, Mozambique, Namibia, Swaziland, Zimbabwe, Angola	Hunting restocking, conservation, eco-tourism	Genetic integrity of D. p. pygargus (Pallas, 1767); invasive in Angola	[19,47,48]
Connochaetes taurinus (Burchell, 1824)	Northern South Africa	Southern South Africa	Hunting, restocking	Genetic integrity of <i>Connochaetes gnou</i> (Zimmermann, 1780)	[30]
Equus zebra hartmannae Matschie, 1898	Namibia	Western Cape, Eastern Cape (South Africa)	Introduction	Genetic integrity of <i>E. z. zebra</i> Linnaeus, 1758	[49]
<i>Equus grevyi</i> Oustalet, 1882	Kenya	Kenya (outside natural range)	Conservation (favor range expansion)	Genetic integrity due to hybridization with <i>E. quagga boehmi</i> Matschie, 1892	[50,51]
Aepyceros melampus petersi Bocage, 1879	Namibia, Angola	Angola, Namibia	Conservation	Possible hybridization with <i>A.m. melampus</i> (Lichtenstein, 1812)	[52]
Hippotragus equinus koba (Gray, 1872)	West Africa	South Africa	Hunting, restocking	genetic integrity of <i>H.</i> <i>e. equinus</i> (É. Geoffroy Saint-Hilaire, 1803)	[19,53]
Redunca fulvorufula fulvorufula (Afzelius, 1815)	South Africa	Namibia	Conservation	Introduction in a new area outside the historic range; possible competition with other species, sanitary problems, etc.	[54]
Tragelaphus angasii Angas, 1849	South Africa	Botswana, Namibia, Angola	Hunting	Competition and hybridization with <i>T. strepsiceros</i> (Pallas, 1766); competition with <i>T. scriptus</i> (Angola)	[47,55]
<i>Hippotragus niger</i> (Harris, 1838) ssp.	Tanzania, Zambia, Mozambique, Malawi	South Africa	Conservation	Genetic integrity of different subspecies; possible hybridization with <i>H. equinus</i>	[56,57]
Hippotragus equinus ssp.	Namibia, Botswana, South Africa	South Africa	Hunting, conservation	Genetic integrity of different subspecies	[58,59]
Antidorcas marsupialis marsupialis (Zimmermann, 1780)	South Africa	South Africa	Hunting, introduction	Possible hybridization with <i>A. m. hofmeyri</i> Thomas, 1926	[60]

Species	Original Range	Translocated to	Purpose	Aftermath	References
Tragelaphus spekii gratus P. L. Sclater, 1880 (?)	Unknown locality	The Gambia	Tourism, aesthetic reasons	Introduction? reintroduction? population probably extinct	[61]
Diceros bicornis michaeli Zukowski, 1965	Kenya	South Africa	Conservation restocking	Genetic integrity of D. b. bicornis (Linnaeus, 1758)	[62,63]
Diceros bicornis michaeli	South Africa (ranches), EAZA zoos	Tanzania	Conservation restocking, and reintroduction	Genetic integrity of D. b. michaeli	[64–66] (see reference [66] in case of ex situ stock)
Diceros bicornis ssp.	All areas	East Africa	Conservation	Possible genetic erosion of Masai Mara population with recognized traces of gene pool of <i>D. b.</i> <i>longipes</i> Zukowski, 1949	[66]
Ceratotherium simum simum (Burchell, 1817)	Kenya (ranch)	Uganda	Conservation?	Introduction of one allochthonous subspecies into previous range of extinct <i>C. s. cottoni</i> (Lydekker, 1908)	[67]
Ceratotherium simum simum	South Africa	Kenya, Zambia	Conservation	creation of new nuclei outside the historic range	[68]
Beatragus hunteri (Sclater, 1889)	Southeast Kenya	Kenya (Tsavo East NP)	Conservation	Creation of a new population outside the natural range	[69,70]
Taurotragus oryx oryx (Pallas, 1766)	South Africa	Senegal	Tourism, aesthetic reasons	Possible competition, and genetic integrity of <i>T. derbianus</i> <i>derbianus</i> (Gray, 1847)	[71–73]
Kobus ellipsiprymnus ellipsiprymnus (Ogilby, 1833)	South Africa	Senegal	Tourism, aesthetic reasons	Genetic integrity of K. e. unctuosus (Laurillard, 1842)	[71,72]
Oryx gazella gazella (Linnaeus, 1758)	South Africa	Senegal	Tourism, aesthetic reasons	Introduction in an area where it has never been present	[71,72]
Panthera leo cf. melanochaita (H. Smith, 1842) (ex P. l. krugeri (Roberts, 1929))	South Africa	Rwanda	"Reintroduction"	Introduction outside the natural range. In Rwanda, was formerly present as <i>P. l. azandica</i> (Allen, 1924)	[74]

Table 1. Cont.

Taxonomic research, on the contrary, evidences the existence of discrete morphological (and sometimes genetic) discontinuity inside globally perceived "species," with geographic patterns that often follow well-known biogeographical subdivisions of Africa, and sometimes an abrupt taxa's limits congruent with biomes and vegetation types changes are observed [75]. Although we may detect areas of apparent intergradations between clearly different "forms" (for the African buffalo, see [76,77]), there are few doubts about the existence of a long and complicated history of adaptation, separation, retraction, and advancement of geographic ranges of different taxa following climate changes, which must be summarized by a not so simple taxonomy, as is often requested by some stakeholders and researchers [78,79]. Finally, complex taxonomies are also difficult to translate into national and international legislations; yet, this is vital for effective conservation policy to maintain current levels of biodiversity [80].

3. Translocations and Conservation

Table 1 shows some selected cases of translocation of African mammals that caused or may cause serious genetic-conservation, as well as sanitary problems or other undesirable conservation consequences.

Regrettably, in some cases, as with the black rhinoceros *Diceros bicornis*, the issue remains a highly academic one as extirpation of most rhinoceros populations preceded modern evidence-based conservation management [66,81]. In the latter decades, the increasing attention to tourism by several African countries led to growing attention to protected areas and, if needed, to the reintroductions of species that became historically extinct in these regions [25,82,83]. Hybridization between distinct taxa is a common result of translocations in South Africa, where several genera such as Connochaetes and Aepyceros are involved [21,84]. The same threat is now spreading elsewhere, a case in point being the managed populations of two Taurotragus species in the same area in Senegal; one being the critically endangered *Taurotragus derbianus derbianus* whose genetic integrity is potentially threatened by the imported T. oryx oryx—fortunately in this case, no hybrids have yet been detected based on microsatellite markers [73]. In the same private "reserves" in Senegal, several species, including Ceratotherium simum simum, Kobus ellipsiprymnus ellipsiprymnus, Tragelaphus strepsiceros strepsiceros, Aepyceros melampus melampus, Oryx gazella gazella, and Giraffa camelopardalis giraffa have been introduced from South Africa [71,72] (see also Table 1), which is a fact that raise some concern, especially in cases of animal escapes. Ironically, translocations may also be responsible for the extinction of pure genetic lineages via hybridization, thereby negatively impacting endangered, indigenous, and rare species. Owing to a general neglect of taxonomy-following the so-called "taxonomic inertia" period described by [40]—it is highly probable that the hybridization problem is greatly undervalued in conservation circles. However, a more subtle danger is the general distortions of the genetic landscape, especially of wild ungulates, as is often reported in North America and Europe [85] but also from Africa [86], which may preclude further research, and which may create management problems that cannot be properly anticipated.

Poor taxonomic knowledge coupled with translocations may also lead to conservation initiatives that have only an aesthetic value and, more seriously, may divert attention from real priorities. On the other hand, we know that funds and conservation interest is not homogeneous in Africa [87], and, therefore, we may accept that the extant of biodiversity we risk to lose is greater than we think, especially outside East and South Africa.

4. Giraffes as a Case Study

The last decade saw an unparalleled interest in giraffe taxonomy, starting with studies by [82,88,89]. We associate this unprecedented progress with the use of various data types, increased sampling of studies and availability of the data, various expert knowledge, and the tuning of arguments via numerous discussions [44,90–94]. Currently, we have increasing knowledge about giraffe morphological differentiation [44,77,88], phylogenetic structure and timing of differentiations of current or extinct populations [89,95–100], gene flow [44,100,101], unique genomic signatures [102], and potential ecological factors responsible for the restricted gene flow [75]. Giraffes are thus becoming the model case study for the testing of species delimitation in mammals, similarly as cetaceans became the extraordinary model for understanding the various aspect of their and general vertebrate evolution in unprecedented detail [103,104].

Departing from the classical monotypic taxonomic account dominating the 20th century, Colin Groves and Peter Grubb considered that an eight species arrangement better

interpreted available morphological data [44]; for the basic overview of giraffe taxonomy across the 20th and 21st centuries, see Table 2. This latter work, adopting a phylogenetic species concept, was not always accepted by several researchers, yet, in the *Giraffa* case, subsequent genetic works were unanimous in always accepting more than one species. Four species were accepted by [99] and more recently by [100]—Giraffa camelopardalis (Linnaeus, 1758); G. reticulata De Winton, 1899; G. giraffa (Boddaert, 1785); and G. tippelskirchi Matschie, 1898—while [97] recognized three species: Giraffa camelopardalis, G. giraffa, and G. tippelskirchi. Although a step forward, several gaps in available data and interpretation were evident, as too often these reviews were based on previous arrangements without a critical examination of geographic and taxonomic gaps. [94] rightly stressed the taxonomic history of the taxon G. g. rothschildi Lydekker, 1903 to evidence the lack of consensus and possible negative setbacks for conservation. A preponderance of scientists have followed the conservative IUCN protocol and continue to refer to the different kinds of giraffes using the one species/nine subspecies account [94], although this view can be quite dangerous, or at least controversial, for conservation. For example, the materials related to [99] specifically posters a "Giraffe conservation guide" and provided a clear and alarming conservation message to the public about the patchy distribution with declining trends in many northern populations. Recently, an important contribution came from [98], which also included genetic data from key museum specimens belonging to now extinct populations. Among the most important findings include the description of a new—historically extinct—taxon from Senegal, G. camelopardalis senegalensis Petzold, Magnant, and Hassanin, 2020, which went extinct around 1970; the revalidation of G.g. wardi Lydekker, 1904; and a stricter geographical delimitation of the nominal G. c. camelopardalis, which make this taxon, the Nubian giraffe, another example of a taxon "allowed to slip into extinction unnoticed" [40]. The better definition of conservation units or ECUs is a greater priority today than fixing the number of species, considering that taxonomy is particularly relevant when translocations are considered a key conservation component [105]. Petzold and collaborators [98] have contributed to better delineate conservation units, especially in the northern continental sector that has traditionally received scarcer conservation attention and where biogeographical barriers, such as the Nile Basin, have been scarcely considered in mammal taxonomic studies [106,107]. The western giraffe, G. c. peralta Thomas, 1898 emerges unanimously as a distinct taxonomic unit and hence as a conservation priority. Translocations to create more populations should be promoted, whereas the creation of breeding populations of extralimital taxa, such as the G. c. giraffa imported from South Africa to Senegal in the Bandia Private Reserve [108], pose more than a question regarding their conservation relevance and possible interference with long-term G. c. peralta conservation. Regrettably, it can be hypothesized that tourism development in West Africa may lead to further attempts to reconstruct a "true African wildlife experience" for naïve tourists through the importation of stocks from South African wildlife reserves, de facto enlarging a problem of genetic pollution that is already widespread in South Africa [19]. In another critical region, the Nile Basin, translocations have a critical role to play in re-establishing species to their former range [109]. It is vital however that each remaining nominal taxon/population is managed separately, avoiding premature lumping based on scattered evidence and a lack of awareness of biogeographical and ecological barriers. For example, [110] had already proposed a close phyletic relationship between the subspecies rothschildi, cottoni Lydekker, 1904 and *antiquorum* (Swainson, 1835), and although genetic data seems to confirm this, the adaptive significance of some morphological features of rothschildi (dark coloration and two additional posterior horns in the males) are still unknown. Considering the fact that some authors specify in detail some morphological differences between camelopardalis and rothschildi, and other taxa [110–112], it would be worthwhile to inspect their validity using modern statistical methods (e.g., multivariate methods, discriminant analysis). Still more controversial seems the inclusion of the taxon *congoensis* Lydekker, 1903 as a synonym of antiquorum, considering that his original descriptor considered it an intermediate between northern and southern giraffes because of completely spotted limbs (a southern characteristic) and a well-developed frontal horn (a northern characteristic) [110,113]. The putative taxon *congoensis* is actually restricted to the Garamba National Park on the left side of the White Nile, whereas putative *cottoni* is found on the other side of the White Nile, which is apparently a non-trivial zoogeographical barrier.

In their recent genetic work [98], Petzold and collaborators evidenced how the nominal *G. c. camelopardalis* must now be considered extinct. This is further evidence of the relevance of sampling museum specimens from type locality [114] even if we have to correct these authors by circumscribing the type locality of *camelopardalis* to the Setit River (in present day Sudan and Eritrea), a well-known area for giraffe zoo collectors in the 19th and first half of the 20th centuries [115,116]. According to [98], the residual giraffe populations from the Gambella and Omo NPs in Southwest Ethiopia belong to *rothschildi*, but, as the only survivors in a complex biogeographical region east of the Nile that is still partially unexplored biologically [117], we recommend affording great priority to their conservation.

In summary, translocations of giraffes have a long tradition [105]. Some represent a helpful conservation management tool, as we mentioned above, but some others are questionable from a conservation perspective, at least until we have a clear understanding of separable conservation units in some key regions that have so far received little attention.

Table 2. Giraffe taxa recognized in the 20th and 21st centuries across several basic sources, which seemed to assess giraft	fes
independently and/or using different data.	

Source	[110,118]	[111]	[119]	[120]	[121]	[122]	[112]	[39]
Data Used	C+SSH	C+SSH	U(M)	U(M)	U(M)	U(M)	С	U(M)
aethiopica					camelopardalis			
africana								
angolensis	х	х	х	х	х	х	x	х
antiquorum	х	x	х		х	х	х	
australis biturigum	capensis				giraffa camelopardalis	giraffa camelopardalis		
camelopardalis		х	х	х	x	x	х	х
capensis	х	х			giraffa	giraffa		
congoensis	х	х			camelopardalis	camelopardalis		х
cottoni	х	х			rothschildi	rothschildi		
giraffa			х	х	х	х	х	х
hagenbecki		reticulata			reticulata	reticulata		
infumata		х			angolensis	angolensis		
maculata		capensis			giraffa	giraffa		
nigrescens	х	reticulata			reticulata	reticulata		
peralta	х	х	х	х	х	х	х	х
, renatae								
reticulata	x *	х	х	х	х	х	x	х
rothschildi	х	х	х	х	х	х	x	
senegalensis								
schillingsi	tippelskirchi	tippelskirchi			tippelskirchi	tippelskirchi		
senaariensis		camelopardalis			antiquorum	antiquorum		
thornicrofti	х	x		х	x	x	x	х
tippelskirchi	х	х	х	х	х	х	x	х
typica	х	camelopardalis			camelopardalis			
wardi	х	х			giraffa			
valid taxa	2.13	2.13	1.8	1.8	1.0	1.0	1.0	1.8
(sp.; ssp.)	2,15	2,15	1,0	1,0	1, 9	1, 9	1,9	1,0
Source	[123]	[88]	[41]	[82]	[124]	[125]		
Data used	U(M)	C+mtDNA+SSH+SSI	U(M)	mtDNA+STRs	U(M+G)	BSI+C+mtDI	NA+SSI	H+SSI
aethionica			camelopardalis					
africana			camelopardalis					
angolensis	oiraffa	x or giraffa?	oiraffa	x *	x	x		
antiauorum	x	x or camelopardalis?	camelopardalis	not sampled	x	x		
australis			giraffa			and the second se		
biturigum			camelovardalis					
camelopardalis	х	х	X	not sampled	x	x		
cavensis	giraffa		giraffa			giraffa		
convoensis	antiauorum		camelovardalis			0		
congoensis	antiquorum		camelopardalis			- "		

cottoni			rothschildi			camelopardalis
giraffa	х	х	х	x *	х	x
hagenbecki			reticulata			
infumata	giraffa		çiraffa			angolensis
maculata	8		giraffa			0
niorescens			reticulata			
neralta	antiquorum	v or camelonardalis?	camelonardalis	v *	v	x
ranataa	иниционит	x of cumetopurtuitis:	camelopardalis	А	~	x
reticulata	X	X	cumetopuruutis	× *	X	X
rothochildi	x camelonardalic	x	X	х х *	X	x camalonardalic
romocalonaia	ситеюритиинз	x	x	A	X	cumeiopuruuiis
seneguiensis			timedalerinali			
schuungsi						
senaariensis			cameioparaalis	. 11		
thornicrofti	х	x	x	not sampled	x	x
tippelskirchi	х	x	X	X *	х	x
туріса			camelopardalis			
wardi	gıraffa		giraffa			gıraffa
valid taxa	1:6	1: min. 6	1:6	6; min. 6, up	1:9	1:8
(sp.; ssp.)	-, -	_,	_, •	to 11	-, -	_, •
Source	[126]	[44,91]	[99–101]	[97,98]		
Data used	U	C+SSH+SSI+mtDNA	G+mtDNA+nDNA	C+mtDNA+nI	DNA+SSH+S	SI
aethionica				G. c.		
истории				camelopardalis		
africana						
anaolanaia		× *	x (as subspecies of G.	C a ainaffa		
angolensis	х	X *	giraffa)	G. g. giraffa		
				x (as subsp.		
antiquorum	х	x *	x (as subsp. of G.	of G.		
1			camelopardalis)	camelopardalis)		
australis				G. o. oiraffa		
440114110				G. g. girujju G. c		
biturigum				camelonardalis		
camelonardalis	x	x *	x *	x *		
canensis	~	~ airaffa	A	C a airaffa		
сиреныя		gtrujju		G. g. girujju G. c		
congoensis		antiquorum?		antiquorum		
				uniquorum C		
cottoni		camelopardalis		G. C.		
a in a ffa		. *	*	antiquorum		
giraffa	x	X	X	X ··		
hagenbecki				G. <i>C</i> .		
				reticulata		
infumata		giraffa		reticulata G. g. wardi		
infumata maculata		giraffa		reticulata G. g. wardi G. g. giraffa		
infumata maculata nigrescens		giraffa		reticulata G. g. wardi G. g. giraffa G. c.		
infumata maculata nigrescens		giraffa		reticulata G. g. wardi G. g. giraffa G. c. reticulata		
infumata maculata nigrescens		giraffa	x (as subsp. of G	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp.		
infumata maculata nigrescens peralta	x	giraffa x *	x (as subsp. of <i>G</i> .	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G.		
infumata maculata nigrescens peralta	x	giraffa x *	x (as subsp. of <i>G</i> . <i>camelopardalis</i>)	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis)		
infumata maculata nigrescens peralta renatae	x	giraffa x *	x (as subsp. of G. camelopardalis)	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis)		
mfumata maculata nigrescens peralta renatae	x	giraffa x *	x (as subsp. of G. camelopardalis)	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp.		
infumata maculata nigrescens peralta renatae reticulata	x	giraffa x * x *	x (as subsp. of <i>G.</i> <i>camelopardalis</i>) x *	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G.		
infumata maculata nigrescens peralta renatae reticulata	x x	giraffa x * x *	x (as subsp. of <i>G.</i> <i>camelopardalis</i>) x *	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis)		
infumata maculata nigrescens peralta renatae reticulata	x x	giraffa x * x *	x (as subsp. of <i>G.</i> <i>camelopardalis</i>) x *	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp.		
infumata maculata nigrescens peralta renatae reticulata rothschildi	x x x	giraffa x * x * camelopardalis	x (as subsp. of <i>G.</i> <i>camelopardalis</i>) x * <i>G. c. camelopardalis</i>	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G.		
infumata maculata nigrescens peralta renatae reticulata rothschildi	x x x	giraffa x * x * camelopardalis	x (as subsp. of G. camelopardalis) x * G. c. camelopardalis	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis)		
infumata maculata nigrescens peralta renatae reticulata rothschildi	x x x	giraffa x * x * camelopardalis	x (as subsp. of G. camelopardalis) x * G. c. camelopardalis	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp.		
njumata maculata nigrescens peralta renatae reticulata rothschildi senegalensis	x x x	giraffa x * x * camelopardalis	x (as subsp. of <i>G.</i> camelopardalis) x * G. c. camelopardalis	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G.		
njumata maculata nigrescens peralta renatae reticulata rothschildi senegalensis	x x x	giraffa x * x * camelopardalis	x (as subsp. of G. camelopardalis) x * G. c. camelopardalis	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G.		
infumata maculata nigrescens peralta renatae reticulata rothschildi senegalensis	x x x	giraffa x * x * camelopardalis	x (as subsp. of G. camelopardalis) x * G. c. camelopardalis	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) g. t.		
injumata maculata nigrescens peralta renatae reticulata rothschildi senegalensis schillingsi	x x x	giraffa x * x * camelopardalis	x (as subsp. of G. camelopardalis) x * G. c. camelopardalis	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) camelopardalis) G. t. tippelskirchi		
njumata maculata nigrescens peralta renatae reticulata rothschildi senegalensis schillingsi	x x x	giraffa x * x * camelopardalis	x (as subsp. of G. camelopardalis) x * G. c. camelopardalis	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) g. t. tippelskirchi G. c.		
infumata maculata nigrescens peralta renatae reticulata rothschildi senegalensis schillingsi senaariensis	x x x	giraffa x * x * camelopardalis	x (as subsp. of G. camelopardalis) x * G. c. camelopardalis	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) f. t. tippelskirchi G. c. antiauorum		
infumata maculata nigrescens peralta renatae reticulata rothschildi senegalensis schillingsi senaariensis	x x x	giraffa x * x * camelopardalis	x (as subsp. of G. camelopardalis) x * G. c. camelopardalis	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis)		
infumata maculata nigrescens peralta renatae reticulata rothschildi senegalensis schillingsi senaariensis thornicrofti	x x x	giraffa x * x * camelopardalis	x (as subsp. of <i>G.</i> <i>camelopardalis</i>) x * <i>G. c. camelopardalis</i> x (as subsp. of <i>G.</i>	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) g. t. tippelskirchi G. c. antiquorum x (as subsp. of G.		
injumata maculata nigrescens peralta renatae reticulata rothschildi senegalensis schillingsi senaariensis thornicrofti	x x x	giraffa x * x * camelopardalis x *	x (as subsp. of <i>G.</i> <i>camelopardalis</i>) x * <i>G. c. camelopardalis</i> x (as subsp. of <i>G.</i> <i>tippelskirchi</i>)	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) G. t. tippelskirchi G. c. antiquorum x (as subsp. of G.		
njumata maculata nigrescens peralta renatae reticulata rothschildi senegalensis schillingsi senaariensis thornicrofti timelskirchi	x x x	giraffa x * x * camelopardalis x *	x (as subsp. of <i>G.</i> <i>camelopardalis</i>) x * <i>G. c. camelopardalis</i> x (as subsp. of <i>G.</i> <i>tippelskirchi</i>)	reticulata G. g. wardi G. g. giraffa G. c. reticulata x (as subsp. of G. camelopardalis) x (as subsp. of G. camelopardalis) G. t. tippelskirchi G. c. antiquorum x (as subsp. of G.		

Table 2. Cont.

Table 2. Cont.

typica				G. c. camelopardalis
wardi		giraffa		x (as subsp. of <i>G. giraffa</i>)
valid taxa (sp.; ssp.)	1;9	8; not recognized	4; 7	3; 10

Taxa recognized as valid are labelled by "x." Taxa recognized as species are labelled by "*." Synonyms of specific taxa are specified when they were noted by particular authors. Abbreviations: BSI—body size, C—coloration, G—genomic data, mtDNA—mitochondrial DNA, nDNA—nuclear DNA, sp.—species, ssp.—subspecies, SSH—skull shapes, SSI—skull size, STRs—microsatellites, U—unspecified, U(M)—unspecified (presumably morphology), and U(M+G)—unspecified (presumably morphological and genetic data).

5. Discussion

As the current discussion about giraffe taxonomy is too focused on the number of species, we argue that the plurality of taxonomic and conservation approaches might be beneficial in order to unify conservation priorities, contra e.g., [127]; see also the comments on taxonomic instability in [128]. Taxonomists often use some particular species concept (for review see [129]), and population/evolutionary geneticists describe interesting results but often without presenting formal taxonomic actions [130,131] and/or alternatively using some standard conservation units—usually management unit (MU), evolutionary significant unit (ESU), cf. [132], or elemental conservation unit (ECU), cf. [133]. The reasons for diverse approaches are various, from the objective (e.g., lost or inaccessible type material, unsuccessful isolation of DNA from type series, difficulty to have samples from same regions) to the subjective (personal adherence to a particular approach based on various reasons or scarce knowledge of taxonomic practice); moreover, a consensus about the "species" label is often hardly obtainable, albeit units deserving conservation attention could be identical or very similar. This is also the case with giraffes (Table 2), because these populations—angolensis, antiquorum, camelopardalis, giraffa, peralta, reticulata, rothschildi, thornicrofti, and tippelskirchi—have been recognized as valid taxa in at least 13 of 18 reviewed sources since 1904 (Table 2). The concordance about the uniqueness of these populations and the latest assessments of giraffes, e.g., [97–101] are quite considerable. Therefore, we recommend using several criteria to define basic taxonomic and conservation units contemporarily (cf. [66] in the case of Diceros bicornis using MU, ESU, and higher level ESUs) in conservation management plans and programs in order to find the majority consensus on which "lineages" deserve conservation attention. This approach would meet integrative taxonomy standards [134]. Robuchon and collaborators [135] offered an excellent framework for evaluation of the impact of species splitting on species prioritysetting that is more than recommended for accommodating new taxonomic knowledge in conservation strategies. Genomic data holds enormous potential to resolve species delimitation and recognize demographic history and adaptive potential in detail [136]; its usage should be recommended for future studies. The common practice (e.g., making sequences and other data available on GenBank and/or dryad data platforms as much as possible) should be continued, because it enables independent data testing and uses different approaches. Additionally, we highly recommend associating photographs and/or basic descriptions of the phenotype/size of the DNA voucher specimens, as proposed by [137].

As some current genomic assessments have recognized significant differentiation of populations, specifically in plains zebra *Equus quagga* Boddaert, 1785 [138] or tiger *Panthera tigris* (Linnaeus, 1758) [139], which have been recognized as undifferentiated based on small number of loci (zebras [130]) and some phenotype and ecological features (tigers [140]), we argue for a precautionary principle in conservation management [128,135,141].

Africa is a diverse continent with a growing ecotourism industry. Charismatic megavertebrates are particularly searched by tourists and "big game" hunters, but small-scale tourism may furnish valuable income to communities protecting valuable or appealing populations such as the Niger giraffe *G.* (*camelopardis*) *peralta*, the Bor maneless zebra *E. quagga borensis* Lönnberg, 1921, or the mountain nyala *Tragelaphus buxtoni* (Lydekker,

1910); income may also be generated by active promotion of a more sensitive mammal watching activity [142].

A further threat is represented by conservative taxonomies that are proposed by conservation groups without a real review of new and old data, as has been recently the case with the IUCN/SSC Cat Specialist Group [45]. Acceptance of a two-subspecies arrangement largely based on some genetic data seems to overly neglect the great phenotypic diversity still found, for instance, in lion Panthera leo (Linnaeus, 1758) [143,144] and ignores some studies that highlight genetic divergence promoted by ecological discontinuity [145,146] that seems to support a new paradigm to explain microevolutionary divergence in widespread, large-sized carnivores [147]. Therefore, without forgetting or underestimating the composite problems of lion conservation, and of coexistence/interaction with humans involving this highly charismatic species [148,149], taxonomic issues deserve to be included in the future conservation strategies of this charismatic species. Paradoxically, tourists (but also trophy hunters) may be greatly interested in phenotypic lion diversity, and works such as [143] may provide the input for further travels in different regions of Africa and the promotion of new conservation/tourism projects for little-known, overlooked populations such as those of Southwestern Ethiopia. Regrettably, genetic considerations alone have suggested merging quite distinct captive populations of two gazelle subspecies Nanger dama dama (Pallas, 1766) and N. d. mhorr (Bennett, 1833) [150]. Apart from pure scientific considerations [151], this line of action should preclude the possibility for Western Sahara communities to have a part in managing for their own welfare a unique ungulate taxon, which is an important incentive for local ecotourism; this is a view opposed to that recently presented in [152].

6. Conclusions

It should be emphasized that the taxonomically sensitive translocation policies [153] would be important for the preservation of current diversity but also for the ecological restoration of some regions within rewilding, which could be essential for the preservation of some unique (often refugee) species [154,155]. Considering the restricted distribution of some giraffe taxa [98,156] and its important role in communities as flower predators [157], giraffe translocations [105] have a great potential that should be utilized for future generations.

Furthermore, the creation in Africa of fenced private or state wildlife reserves filled with exotic stocks not only have a disputable educative effect on tourists and also on local wildlife managers, actually creating or perpetuating a homogenized idea of "African wildlife," but even create the possibility of concrete dangers. In fact, some species can escape by crossing the fences, which has already happened, and the potential exists to create free allochthonous extra-range nuclei and also to undermine the genetic integrity of native subspecies possibly present in the areas surrounding the reserves.

It is time that conservation biologists recognize the immense threat that taxonomical oversight coupled with the great economic significance of tourism poses to the diversity and integrity of the "genetic landscape" (that is, the evolutionary landscape) of large mammals in Africa. If we wish to preserve such heritage, keeping it as unmodified as possible to future generations of African people and investigators, we need to act now with an urgent change of attitude toward these issues.

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