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The lions of Somalia: a review of available morphological and socio-ecological data

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Abstract

There is an increased recognition of the threat status of the African lion (*Panthera leo*), once a widespread top predator of open African habitats. However, our knowledge about the biology of the species is often based on a few study sites in South and East Africa, and the present subspecific taxonomy developed by the IUCN reinforces an idea of homogeneity of the species in Africa. A synthesis of available knowledge regarding the lions of Southern Somalia, formerly proposed as a distinct subspecies, *Panthera leo somaliensis* is presented. Particular attention is paid to the issue of manelessness in males, a phenomenon that has been studied in Tsavo (N.E. Kenya) but it is highlighted for the first time for the Southern Somalia region. Although our data cannot lead to a definitive answer about the taxonomic status of Somali lions, there is enough evidence to call for further studies and conservation efforts, also in the light of the increased evidence of genetic discontinuity in lions associated with strong ecological barriers.

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Introduction

Whereas *Panthera leo* (Linnaeus, 1758) remains one of the most charismatic African predators, the majority of biological data on this species originated from a few African sites, such as the Serengeti high plains ecosystem of Tanzania and Kenya (Patterson, 2007). Ecological knowledge derived from such patchy distributions contributes to the difficulty in conserving the species as a whole given it is currently declining across its range (Bauer et al., 2015; Trinkel and Angelici, 2016). Very little is known about the lions of North-East Africa, although regions such as 'Nubia' and 'Sennar' (i.e. present-day North-East Sudan and adjoining Eritrea and Western Ethiopia) were among the first to be exploited for wildlife by western zoos and circuses in modern times (Rothfels, 2002).

The lions of the Horn of Africa remained largely unsampled in the first biomolecular researches investigating *P. leo* phylogeography (Barnett et al., 2006; 2009; Dubach et al., 2013), although, recent studies on *P. leo* phylogeography such as Barnett et al. (2014) and Bertola et al. (2016) used genetic samples of lions from both Ethiopia and Somalia. Furthermore, craniometric investigations (i.e. Christiansen, 2008; Mazak, 2010) that supported the validity of some of the traditionally recognized subspecies did not feature specimens from the Horn of Africa (including Somalia).

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Recently, studies on the variability of secondary sexual characters in male lions and its possible taxonomic and socio-ecological meaning have increased, with a particular focus on the maneless lions in Tsavo National Park, Kenya (Kay and Patterson, 2002; Nagel et al., 2003; Yamaguchi et al., 2004; Patterson, 2004; 2007; Gnoske et al., 2006; Patterson et al., 2006). However, the general absence, or very scarce development of a mane in lions from Somalia, as reported in the 20th century literature (Tedesco Zammarano, 1930; Funaioli, 1959; Fagotto, 1985) has been overlooked in these recent studies.

Somali lions, often referred to as the subspecies *P. l. somaliensis* (Noack, 1891) have been grossly overlooked in the last decades, particularly after the long period of civil unrest afflicting Somalia, and probably also due to the lack of specimens in museums. This subspecies was considered as a valid taxon by Azzaroli and Simonetta (1966) in their review on Somali carnivores. These authors also offered a brief overview on the taxonomical history of the Somali lion subspecies *P. l. somaliensis*, which they opted to assign to Hollister (1918) while regarding the original *Felis leo* var. *somaliensis* (Noack, 1891) a '*nomen dubium*'. Their main reason was the fact that Noack based his description on two live specimens in the Berlin Zoological Garden, with an uncertain geographic origin (listed broadly as 'Somali Peninsula') (Noack, 1891). Furthermore, the specimens themselves subsequently went missing. Specimens of Somali lions of rigorously ascertained origin were published by Hollister (1918), though the two specimens from Somalia lived in the National Zoo of Washington DC, United States (Azzaroli and Simonetta, 1966). In 1964, Zukowsky described the subspecies *P. l. webbiensis* on the basis of an adult male specimen from Ogaden (Ethiopia) preserved in the Naturhistorisches Museum Wien and another male that had lived at a German Zoo (Osnabrück), originating from the Mogadishu area (Zukowsky, 1964). Subsequent revisions such as those of Mazák (1968) and Hemmer (1974) regarded *P. l. somaliensis* as a valid taxon, or a synonym of *P. l. nubicus* (Blainville, 1843) with *P. l. webbiensis.* It is also worth noting that in Mazák's revision, *P. l. somaliensis* was regarded as the lion subspecies of East Africa. Thus, other taxa whose descriptions were based on lions from African regions other than Somalia (i.e. the current Tanzania, Ethiopia, Kenya, Uganda, and Congo) were regarded as synonyms of *P. l. somaliensis*.

The recent proposed systematic arrangement of the lion, as well as that of many other felid species, was carried out exclusively on genetic data (Kitchener et al., 2017). This review divides *P. leo* into only two subspecies: *P. l. leo* (Linnaeus, 1758), which includes the Asiatic lions and the lions of Western, Central, and Eastern Africa up to more or less the Ethiopian Rift Valley; and *P. l. melanochaita* (Smith, 1842), which includes all remaining Eastern and Southern African lions. According to this work, all the other described lion subspecies are considered as synonyms with one of the two subspecies, and there is little consideration to any morphological or morphometric differences between the various populations. However, differences between geographically close lion populations have been highlighted through both morphological and genetic analyses (Tende et al., 2014a; b). The fact that two major lion phylogeographic lineages exist does not command a parsimonious approach according to which only two subspecies can be recognized. It is somewhat paradoxical that while even the species rank is accorded a degree of subjectivity owing to sampling bias and the lack of discreteness of evolutionary processes (Padial and De la Riva, 2021), a robust objective criteria is required for the subspecies rank, although the 75% rule is already available and may result in more biologically meaningful trinomials (i.e. Patten and Unitt, 2002).

Such a restrictive criteria for subspecies rank adopted by IUCN could be dangerous and damaging for the preservation of lion biodiversity as it underestimate the significance of geographical variation, and may also favor remixing between different populations following restocking or translocations (cf. Bertola et al., 2021; Gippoliti et al., 2021). Bertola et al. (2021), accepted the Kitchener et al. (2017) taxonomic arrangement, but proposed the consideration of a much greater number of genetic 'lineages' as possible conservation units, *de facto* recognizing the limits of the subspecific arrangement proposed Kitchener et al. (2017). Therefore, alternative taxonomic hypotheses such as those of Barnett et al. (2014), that recognized five subspecies, should be more seriously tested given the potential relevance for management actions, specifically in light of the lack of data from certain regions throughout the range of the species.

In this review, we evaluate the available data on the Somali lion found in Italian literature. As the old Italian literature on Somali mammals appears to be little-known, specimens stored in Italian museums may contribute to historical information on the species in the region (Gippoliti, 2006; Gippoliti and Amori, 2011; Gippoliti and Fagotto, 2012; Gippoliti et al., 2014). Regarding lions, de Beaux (1924) considered the species still in need of study due to a lack of specimens in Italian museums. Further specimens of Somali lion were discussed by Azzaroli and Simonetta (1966). Therefore, our aim is to review all biological data concerning Somali lions – especially of southern Somalia – in order to contribute to their taxonomic knowledge while underlining their own morphological, ecological and socio-behavioral characteristics in the framework of other better-known East African populations. We collected photos of wild and captive male lions from

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Somalia in order to assess the degree of variability found in their mane development. Furthermore, we carried out multivariate morphometric comparisons of skull measurements, including those of Somali lions reported by the Institute of Zoology by Florence University and the Centro di Ecologia Tropicale of the National Research Council (CNR) (Azzaroli and Simonetta, 1966). Although only sketchy observations are available, it seemed worthwhile to review what is known on the social organization about Somali lion putative *Panthera leo somaliensis* (Noack, 1891) and to put it in a general context. Lastly, we reviewed all the data concerning the past distribution of lions in Somalia and reported the latest data about their current distribution and conservation.

Material and Methods

Available literature on the zoology and big game hunting in the former '*Somalia Italiana*' was reviewed to extract data and photos concerning lion morphology, ecology, social organization and distribution.

When appropriate, a distinction was made between the 'Oltregiuba' Region (South of the Juba River close to the Kenyan border, or Jubaland for British researchers), the "Interfluvial Region" (the area located between the Juba and the Webi Shebeeli Rivers, possibly the most well-known of Somali areas), and Central-North Somalia. These data were integrated with those originating from the former 'British Somaliland' in order to generate a broader picture on Somali lions (Fig. 1)

In order to describe the stages of mane development in adult lions, we used the classification proposed by Gnoske et al. (2006) which consists of eight categories ranging from I (total absence of mane) to VIII (maximum mane extension around the head, and ventrally).

In this study we did not follow the systematic review proposal by Kitchener et al. (2017), but we preferred to tentatively stick to the position of Hollister (1918) which recognizes more than one lion putative subspecies in East Africa with the aim of evaluating comparisons between different populations (putative subspecies), and the Somali lions (cf. also Wozencraft, 2005).

Cranial measurements

The available cranial measurements of Somali lions taken by Azzaroli and Simonetta (1966) were compared with the ones of *P. l. nyanzae,* (Heller, 1913), and *P. l. massaica* (Neumann, 1900), two other East African subspecies, reported by Hollister (1918). Due to the sexual dimorphism of this species, males and females were analyzed separately. Only adult specimens were included in the analysis.

The male sample (Supplementary Table 1) consisted of 5 specimens belonging to *P. l. somaliensis*, 7 to *P. l. massaica* and 7 to *P. l. nyanzae*. The female sample (Supplementary Table 2) consisted of 5 *P. l. somaliensis*, 13 *P. l. massaica*, and 12 *P. l. nyanzae*. For each specimen 6 linear measurements were used: Greatest length (GLS), Condylo-basal length (CBL), Greatest length of nasals (GLN), Interorbital breadth (IOB), Bizygomatic breadth (BZB), and Mandible length (ML). These definitions follow Mazák (2010). The adult specimen "n.4 Tozzi" from Azzaroli and Simonetta (1966), listed as unknown sex, was included in the females as its measurements were consistent with those of the other females. For four values, Azzaroli and Simonetta (1966) reported the range of the measurements. In those cases, we used the arithmetic means of the ranges.

The analyses were carried out in the R statistical environment v 4.0.5 (R Core Team, 2021). Some missing data were present in our samples (CBL= 5.56% among males; GLS= 3.33% and CBL= 3.33% for females). In order to produce a complete set of measurements, missing data were imputed with the predictive mean matching method implemented by the R package mice v 3.12 (van Buuren and Groothuis-Oudshoorn, 2011).

Table 1: Means in mm for each subspecies of the different measurements of male specimens.

Putative subspecies	GLS	CBL	GLN	IOB	BZB	ML
Panthera leo massaica	359.14±14.84	321.86±8.51	107.00±7.07	73.14±4.56	244.14±14.09	250.00±9.16
Panthera leo nyanzae	354.57±12.75	318.14±10.88	104.00±5.38	69.00±2.83	231.00±14.29	244.57±8.18
Panthera leo somaliensis	329.00±21.51	298.00±15.2	96.00±4.64	66.00±5.34	227.20±11.14	224.60±13.43

Table 2: Pairwise non-parametric MANOVA. The F-values are reported above the diagonal while the p-values are reported below the diagonal. Significant values are reported in **bold**.

Putative subspecies	*Panthera leo massaica*	*Panthera leo nyanzae*	*Panthera leo somaliensis*
Panthera leo massaica		1.491	9.335
Panthera leo nyanzae	0.212		5.834
Panthera leo somaliensis	**0.006**	**0.024**	

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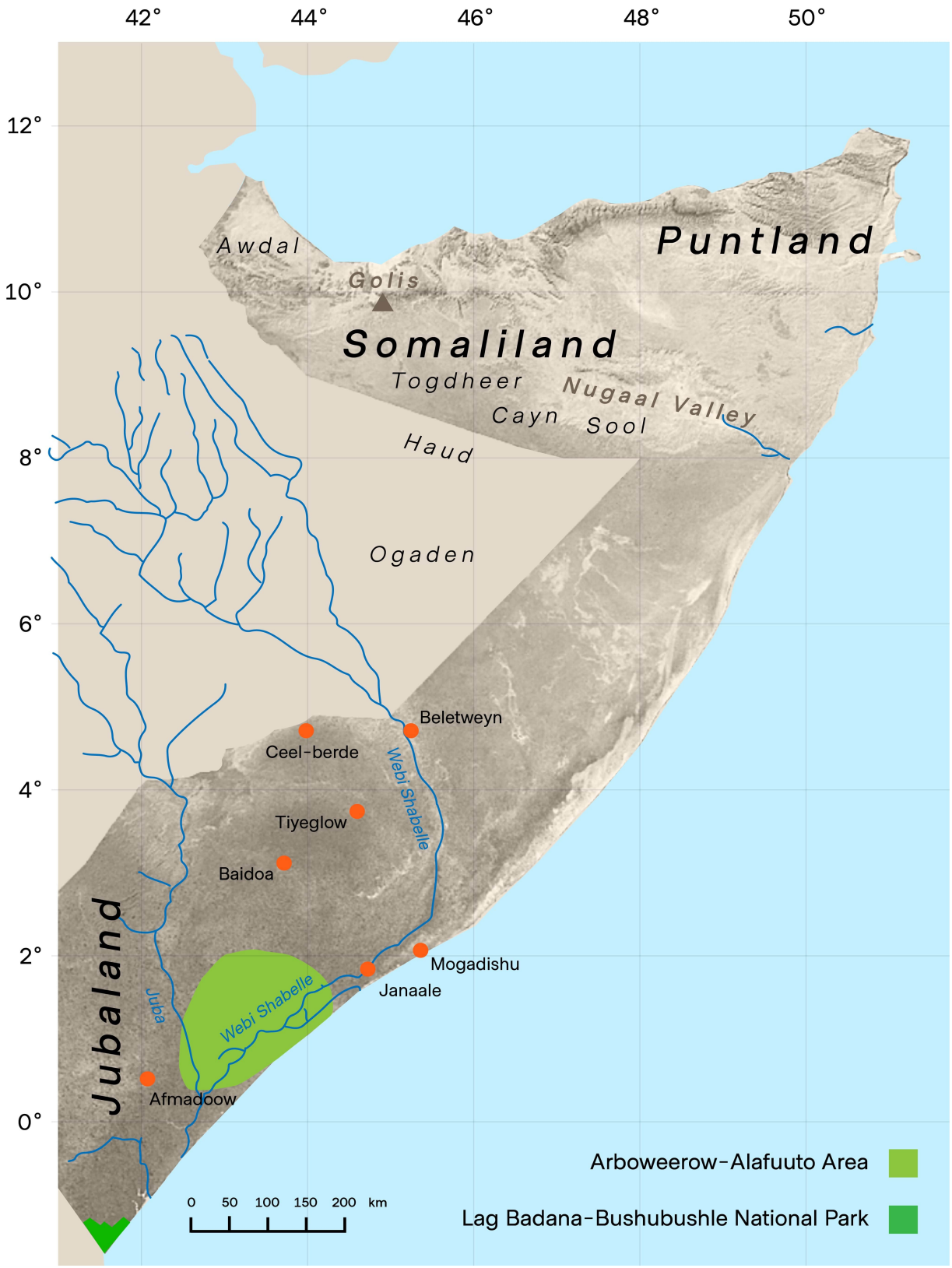

Figure 1: Map of Somalia which features all the location mentioned in the paper (drawn by I. Tkacenko). Orange dots indicate towns and villages.

In order to explore the patterns of morphological variability, a standardized Principal Component Analysis (PCA) was carried out on the two datasets with the R package stats (R Core Team, 2021). Subsequently, we calculated the arithmetic means of the measurements for each subspecies with the R package stats (R Core Team, 2021). A linear discriminant analysis (LDA) followed by *a posteriori*

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classification was carried out in order to assess whether cranial measurements are a good predictor for putative subspecies classification. For these analyses, the R package MASS v. 7.3-55 (Venables anf Ripley, 2002) was used. We then calculated the arithmetic means of the measurements for each subspecies with the R package stats (R Core Team, 2021).

Finally, in order to assess the presence of a statistical significance of the differences among the biometric measurements of the three subspecies non-parametric MANOVA (npMANOVA) (Anderson, 2001) was carried out on the two datasets. In case of a significant result, a pairwise npMANOVA implemented in the R package RVAideMemoire v 0.9-78 (Hervé, 2018) was carried out to assess which groups presented significant differences. Both tests were carried out with 999 randomizations and the significance levels for pairwise npMANOVA were corrected with the false discovery rate (FDR) method (Benjamini and Hochberg, 1995). P-value was set at 0.05.

Results

Morphology and mane development

Wild Somali lions show a very light coloration which is said to conceal them perfectly in the Somali environment, and was the main character leading Noack to describe the *somaliensis* subspecies (Noack, 1891:120). This seems a common trend among Somali mammals (de Beaux, 1924), a fact of interest considering the refugium history of this mainly dry region (cf. Agnelli et al., 1990; Kingdon, 1990). Scortecci (1937) described it as pale ochraceus ('ocracea pallida'). This is also confirmed by a skin observed in the V. Tedesco Zammarano collection and a mounted skin in the Verona Natural History Municipal Museum (MCSNV). According to Peel (1900), lions in Somaliland differ greatly in color from dark tawny-yellow brown to light yellow. There is no difference between dorsal and ventral coloration. It is interesting to note that the same pattern is not visible in captive Somali lions held in Italian zoos, although regrettably we lack specific reports on the issue. Furthermore, both de Beaux (1915) and Hollister (1917) had reported that wild-born lions gradually became darker after being held for some time in zoos.

Regarding mane development, a distinction must be made between wild and captive animals. Fagotto (1985b) reported that 'The most important characteristic is the absence of the mane: a fully grown male has no mane at all in the typical Somali subspecies. Only a few and very short hairs are present on the sides of the neck'. Wild males usually present poor manes and longer dark manes are an exception (Peel, 1900), while captive Somali lions develop richer manes (Tedesco Zammarano, 1930). As a matter of fact, captive lions tend to develop richer manes than their wild counterparts (Pocock, 1931; Mazák, 1968) and Somali lions are no exception to this (Tedesco Zammarano, 1930). The presence of poorly developed manes in Somali lions has been generally explained by the abundance of thick and thorny vegetation in their habitat. Furthermore, this explanation was also recently proposed for the presence of maneless lions in Tsavo (Kays and Patterson, 2002). Swayne (1903), on the basis of his experience in British Somaliland, stressed the importance of climatic factors, noting that lions at a higher altitude had more developed manes. Elliot (1897) was so disappointed regarding the lion skins he saw in Somaliland (at any altitude) to write 'I decided it would not properly represent the real lion in collection and so after procuring a specimen or so, we paid no attention to them except when they were accidently met with'. According to Funaioli (1957), hunters could distinguish Somali male lions only by their more robust body and size of footprints, a fact confirmed by Lombardi (1958). The shooting of females instead of males occurred more than once (N. Forin, pers. comm. to S. Gippoliti).

A trophy of a male Somali lion maintained in the V. Tedesco Zammarano private collection (Fig. 2) shows the typical scarce development of the mane in adult Somali lions, while a more developed one is evident in a photo of a wild-shot male ('Sul Moròr') with some dental problems, and with a twisted claw, which had become a man eater, along the Juba River (Tedesco Zammarano, 1929; 1930) (Fig. 3). Two photos of dead males (courtesy of Mr N. Forin) show poorly developed manes and an absence of abdominal fur (Figs. 4–5) which appear to have reached stage II in the classification proposed by Gnoske et al. (2006). The same general lack of manes was reported from Oltregiuba (the Jubaland of British) (Ward and Sorrell, 1950). Two other photos (Figs. 6–7) of adult males from Jubaland show type I or type IV mane respectively. Another image of a stuffed Somali lion in the MCSNV appears to show a type II mane (Fig. 8).

Although live Somali lions have frequently been imported to Italy, few photographic documents can be unambiguously attributed to them. Among these, we find one showing V. Tedesco Zammarano with 'Faf' (Fig. 9), a male Somali lion taken in Somalia and subsequently donated to the 'Giardino Zoologico' (Zoo) of Rome around 1922. This lion presents a fair mane (type V) which appears to be richer than the ones of wild lions; it does not extend into the abdomen. Another photo from the Giardino Zoologico (Fig. 10) depicts a male named 'Altair' who was acquired in North Somalia (Obbia) as a cub, and lived in Rome for several years. The mane (type VI or VII) is well developed and there is evidence that it is darker posteriorly without being black. Lastly a captive male of the Somali lion in the Al Ain Zoo, UAE (Fig. 11) shows a clear mane type V with an abdominal fold and no elbow tuft.

To some extent, the mane development of Somali males seems similar to mane development observed in

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the extant Asian population of the Gir Forest, *P. l. persica* (Meyer, 1826), rather than the other African populations. Furthermore, the last two captive specimens show an abdominal fold typically associated with the Asiatic subspecies. However, the scanty available evidence presented here suggests that the captive Somali lions do not show the extreme mane development and color change reported for captive Asian lions (Barnett et al., 2007; Lupták and Csurma, 2009). Interestingly, wild Asian lions appear to show elbow tuft and belly fringe that are well-developed in association with a poorly developed mane which appears nonetheless different from the one of Somali lions (Pocock, 1931). It should be stressed that mane extent and color is not determined only by environmental parameters, as often argued (Christiansen, 2008), otherwise we should have all black-maned lions in European zoos. Furthermore, age or seasonal changes in mane color in captive lions have never been observed (S. Gippoliti, pers. obs.). Therefore, it would be useful to analyze these morphological similarities and differences in the light of what is known concerning their social organization.

Figure 2: Somali lion (putative *P. l. somaliensis*) head formerly in the private collection by V. Tedesco Zammarano in Rome, Italy. In this case it is difficult to safely attribute a category of mane due to the poor state of conservation of the sample. However, it would appear to be a type II mane.

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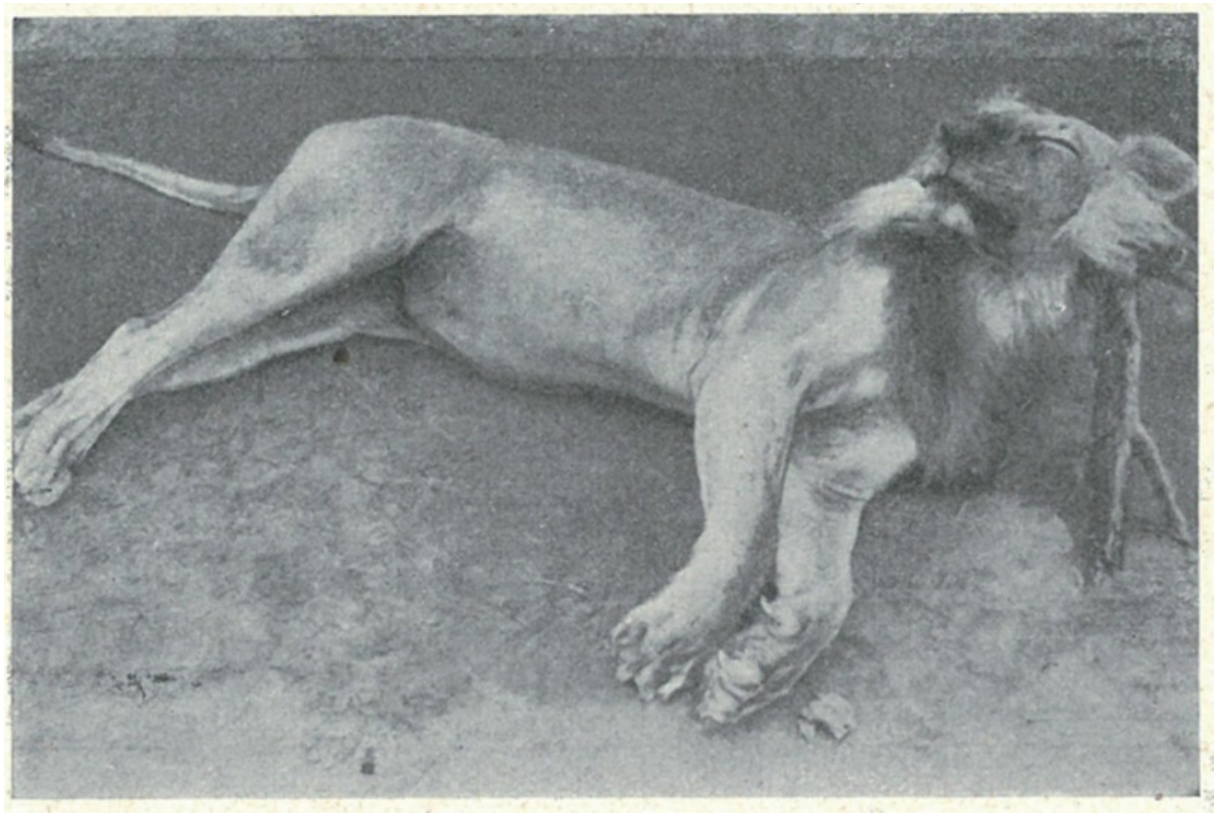

Figure 3: A maneater Somali lion (putative *P. l. somaliensis*), Interfluvial Somali region, (Tedesco Zammarano, 1929). Mane type V.

Figure 4: Somali lion (putative *P. l. somaliensis*), Afmadow (Jubaland) in 1971 (photo by N. Forin). Mane type II.

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Figure 5: Somali lion (putative *P. l. somaliensis*) at Afmadow (Jubaland) (photo N. Forin). Mane type II.

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Figure 6: A very large male (putative *P. l. somaliensis*), from Oltregiuba (Jubaland) (Ricci, 1965). Mane type I.

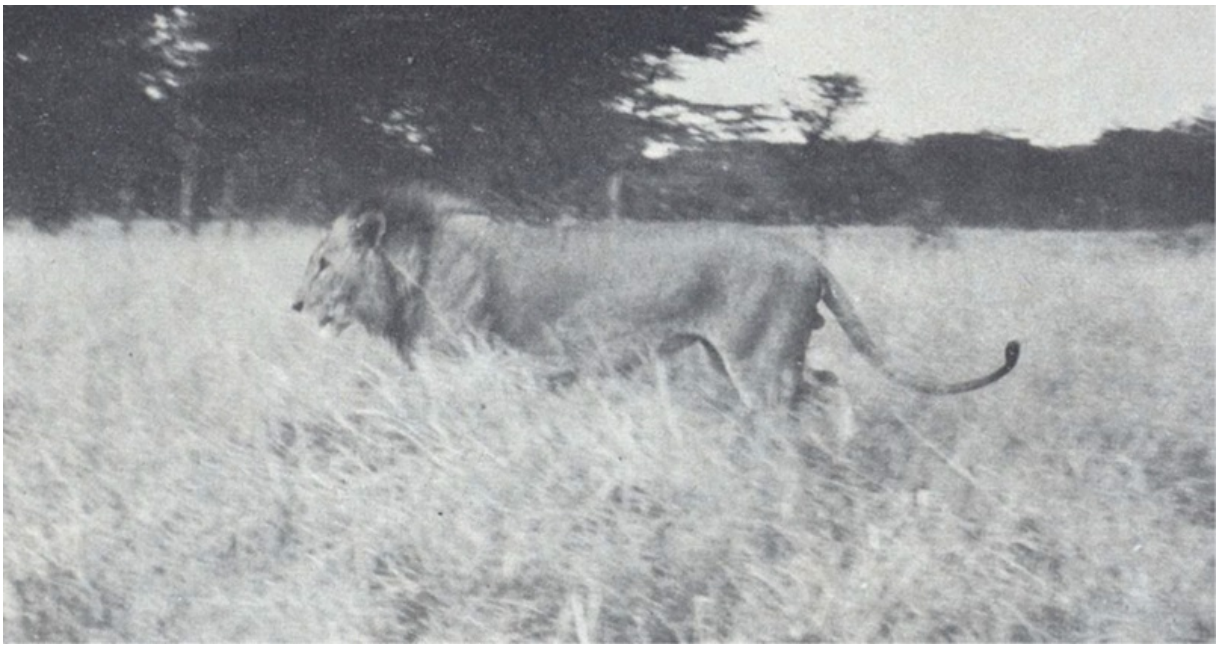

Figure 7: A rare photo of a live Somali lion (putative *P. l. somaliensis*) from Oltregiuba (Jubaland) (Tamagnini, 1962). Mane type IV.

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Figure 8: Somali lion (putative *P. l. somaliensis*) at Verona Natural History Municipal Museum (photo S. Gippoliti). Mane type II.

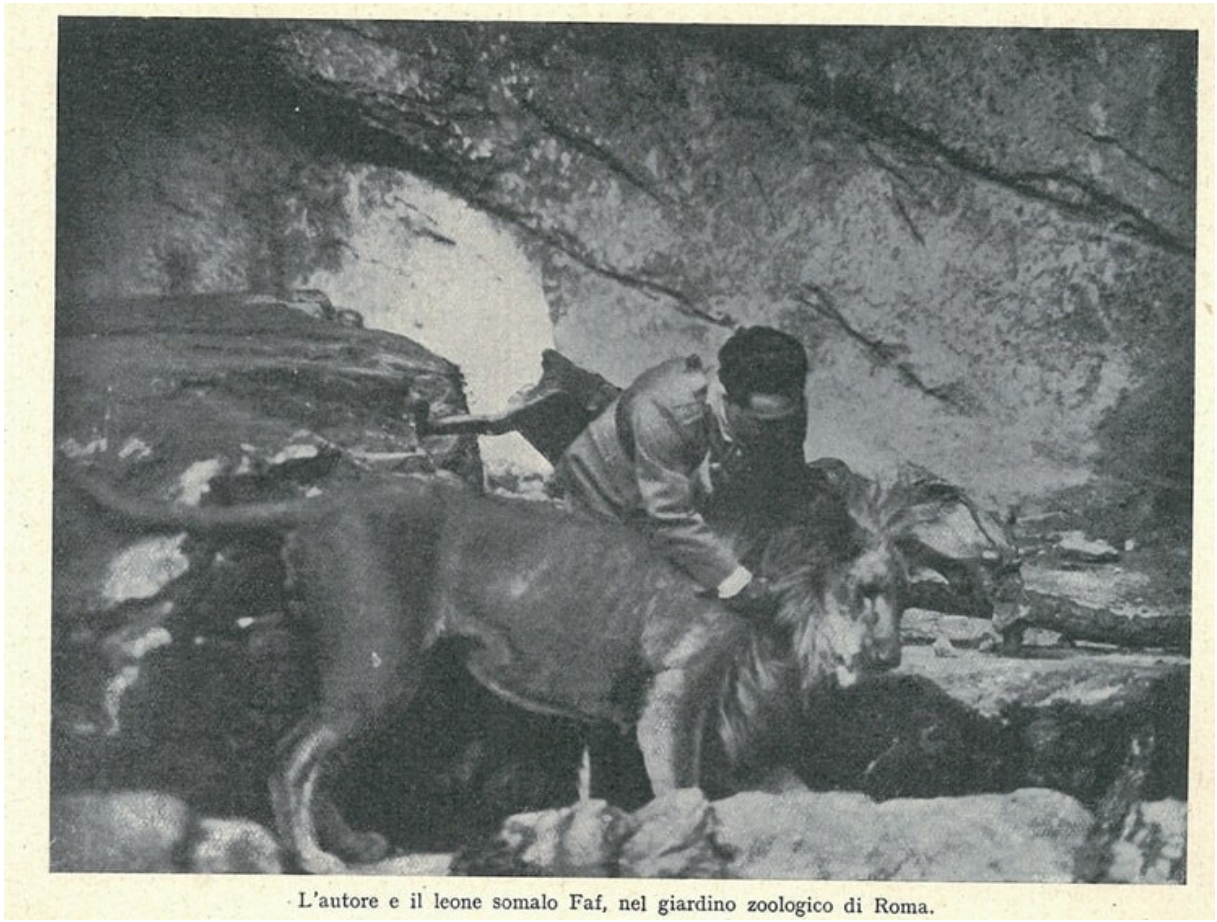

Figure 9: V. Tedesco Zammarano with 'Faf' a Somali lion (putative *P. l. somaliensis*) in the Giardino Zoologico, Rome. Mane type V.

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Figure 10: The Somali lion (putative *P. l. somaliensis*) Altair at the Giardino Zoologico, Rome, Italy. Mane seems type VI or VII.

Figure 11: A Lion family with Somali origin (Al Ain Zoo, UAE). There is an external similarity with specimens from Chad for example or other North-East African countries. Mane of this adult male in captivity is type V. Photo by Wolfgang Dreier (Luptak and Csurma, 2009).

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Craniometric measurements

Males

The PCA shows that the first component explains a considerable amount of morphological variation as it explains 74.04% of the total variance whereas the second and third axis explain respectively 17.42% and 3.66% of the total variance. Together they explain 95.12% of the whole variance. The graph of PCA axis 1 and 2 (Fig. 12) shows that the specimens belonging to *P. l. somaliensis* are well differentiated from the other two subspecies. However, the plotting of the other axis (PC2 with PC3 and PC3 with PC4) shows a major overlapping of the three subspecies. The variable contribution plots show that variables GLS, ML, and CBL influence the variation of the first axis while IOB, GLN, and BZB influence the variation of the second axis. Furthermore, GLN and BZB also contribute to the variation of the third axis.

Table 1 shows the means of each measurement for each subspecies. It can be noted that *P. l. somaliensis* presents the lowest means for each category. The LDA (Fig. 13) shows a clear distinction of *P. l. somaliensis* from the other two subspecies which overlap. The first axis explains 85.63% of the sample's variance while the second one 14.37%. The *a posteriori* test classified correctly 80% of *P. l. somaliensis* specimens and 71.43% of the other two subspecies. Furthermore, the non-parametric MANOVA indicates the presence of a statistically significant difference among the values of the three subspecies (F= 5.8941, P-value= 0.003). As shown in Table 2, the pairwise non-parametric MANOVA confirms the presence of a statistically significant difference between *P. l. somaliensis* and the other subspecies.

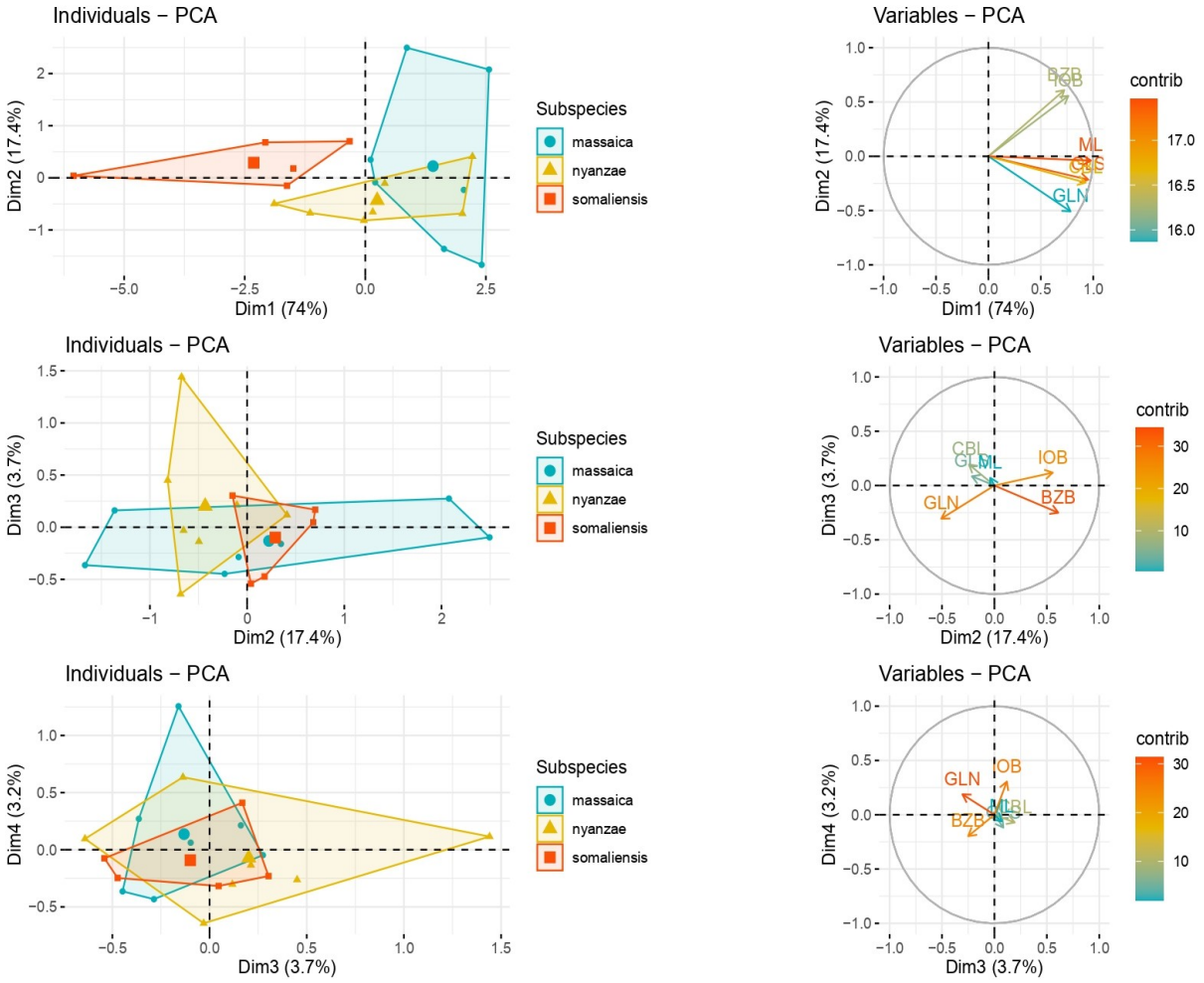

Figure 12: Principal Component Analysis for the males. Different subspecies are indicated by different colors. PC axis 1 to axis 4 and associated variables contributions are reported.

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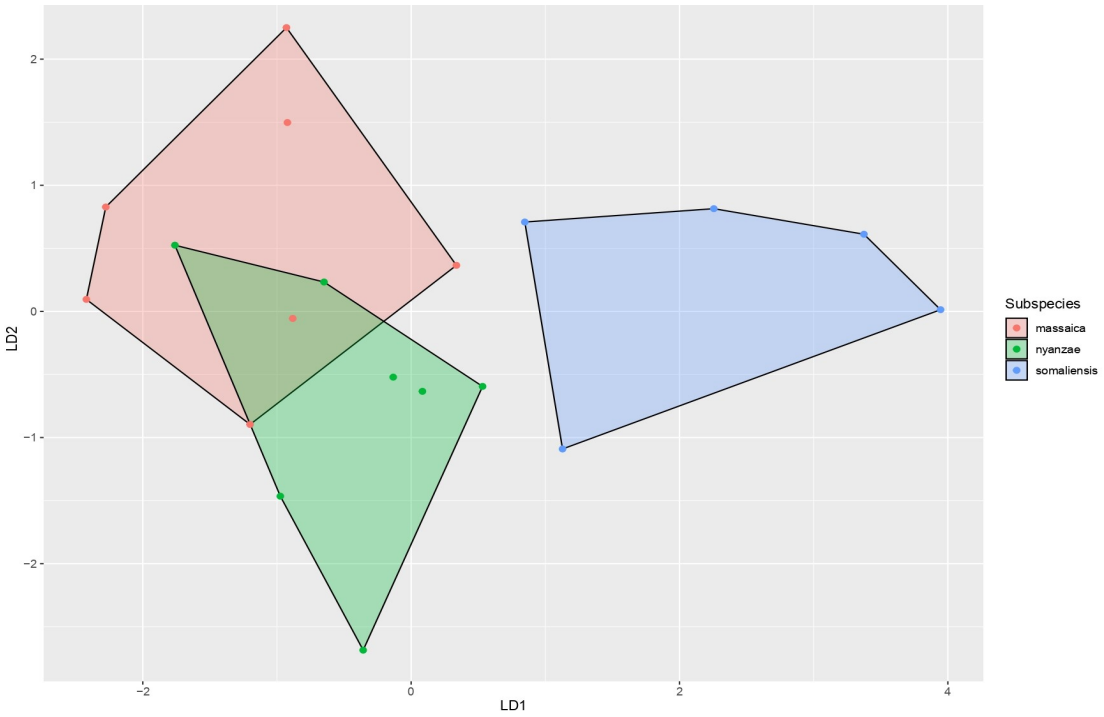

Figure 13: Linear Discriminant Analysis for the males. Different subspecies are indicated by different colors.

Females

The PCA shows that the first three components explain respectively 69.8%, 9.91%, and 9.17% of the total variance, amounting to 88.87% of the sample variance. Differently from the males, the graph of PCA axis 1 and PCA axis 2 (Fig. 14) shows a considerable overlap of the three subspecies, as do the graphs of PC2 and PC3 and of PC3 and PC4. As with the males, the variable contribution plots show that variables GLS, ML, and CBL influence the variation of the first axis ION, GLN, and BZB influence the variation of the second axis, with the latter two also contributing to the variation of the third axis.

Table 3 shows the means of each variable for each subspecies. Like the males, the LDA (Fig. 15) shows a clear distinction of *P. l. somaliensis* from the other two subspecies which overlap. The first axis explains 97.6% of the sample's variance while the second one 2.4%. The a posteriori test classified correctly 80% of *P. l. somaliensis* specimens and 61.54% of *P. l. massaica* and 55.33% of *P. l. nyanzae*the females of *P. l. somaliensis* present the lowest means for each category. However, the non-parametric MANOVA indicates the absence of a statistically significant difference among the three subspecies (F= 2.282, P-value= 0.088).

Social organization

It is generally reported that the pride represents the basic social unit in lions, the only known wild social felid (Yamaguchi et al., 2004). However, no multi-female pride has so far been observed in Somalia, nor can adult multi-male associations be confirmed. According to a professional hunter, generally only solitary lions were observed, heard at dusk, and eventually hunted (N. Forin, pers. comm.). Funaioli reported to us a direct observation of a trio consisting of an adult male, an adult female and one juvenile in the South region of the Juba River (U. Funaioli, pers. comm.). Of the eight direct observations reported by V. Tedesco Zammarano during two hunting expeditions (1915–16 and 1921–22) in the interfluvial area of Somalia, two involved single individuals, four two individuals, and two a trio (a female with two juveniles and two adult males and one female). On the other hand, Mosse (1913) reported in Somaliland a group of 6 lions consisting of 3–4 lioness and two young males. It is remarkable that maneless lions from the Tsavo ecosystems have been seen associated with prides of typical size (Patterson, 2004). It is also worth noting that, if Somali lion males are smaller than males from nearby South-Western regions, while females have a similar size, sexual dimorphism is lesser accentuated in putative *P. l. somaliensis*. This may be a further consequence of peculiar environmental conditions and scarce prey abundance.

Historical range

Peel (1900) undertook two expeditions into the interior of Somaliland and reported that lions were very rare in the Haud region, a vast savannah located in the South-West used by pastorals for grazing during the wet season, but mentions that few lions were remaining in the Awdal region (Gudibursi areas).

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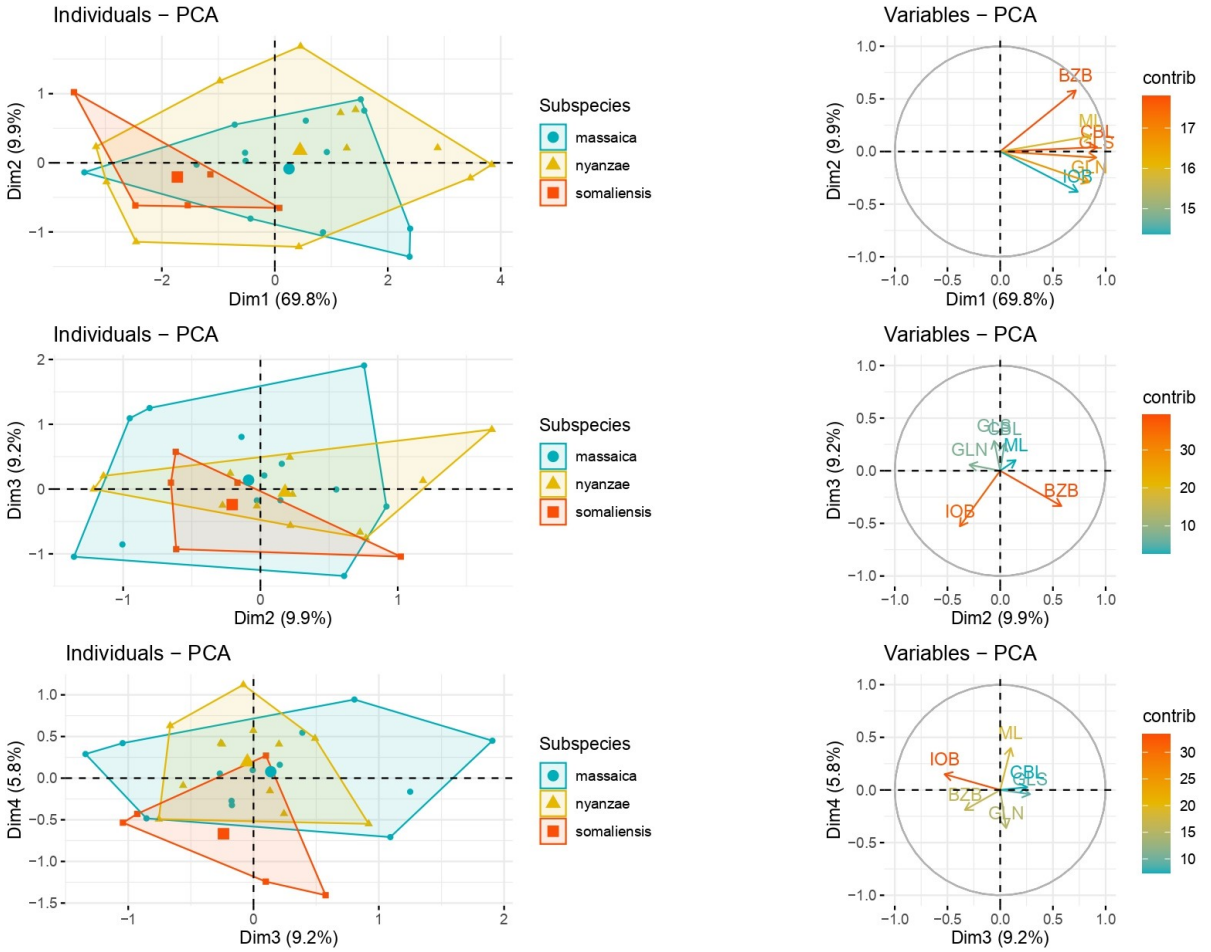

Figure 14: Principal Component Analysis for the females. Different subspecies are indicated by different colors. PC axis 1 to axis 4 and associated variables contributions are reported.

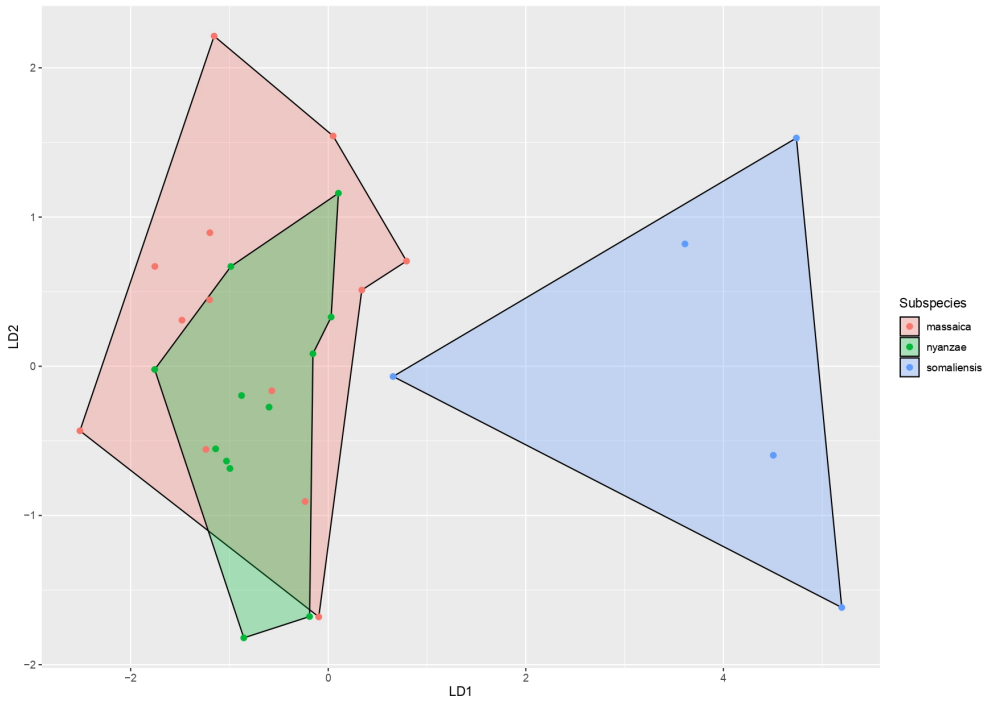

Figure 15: Linear Discriminant Analysis for the females. Different subspecies are indicated by different colors.

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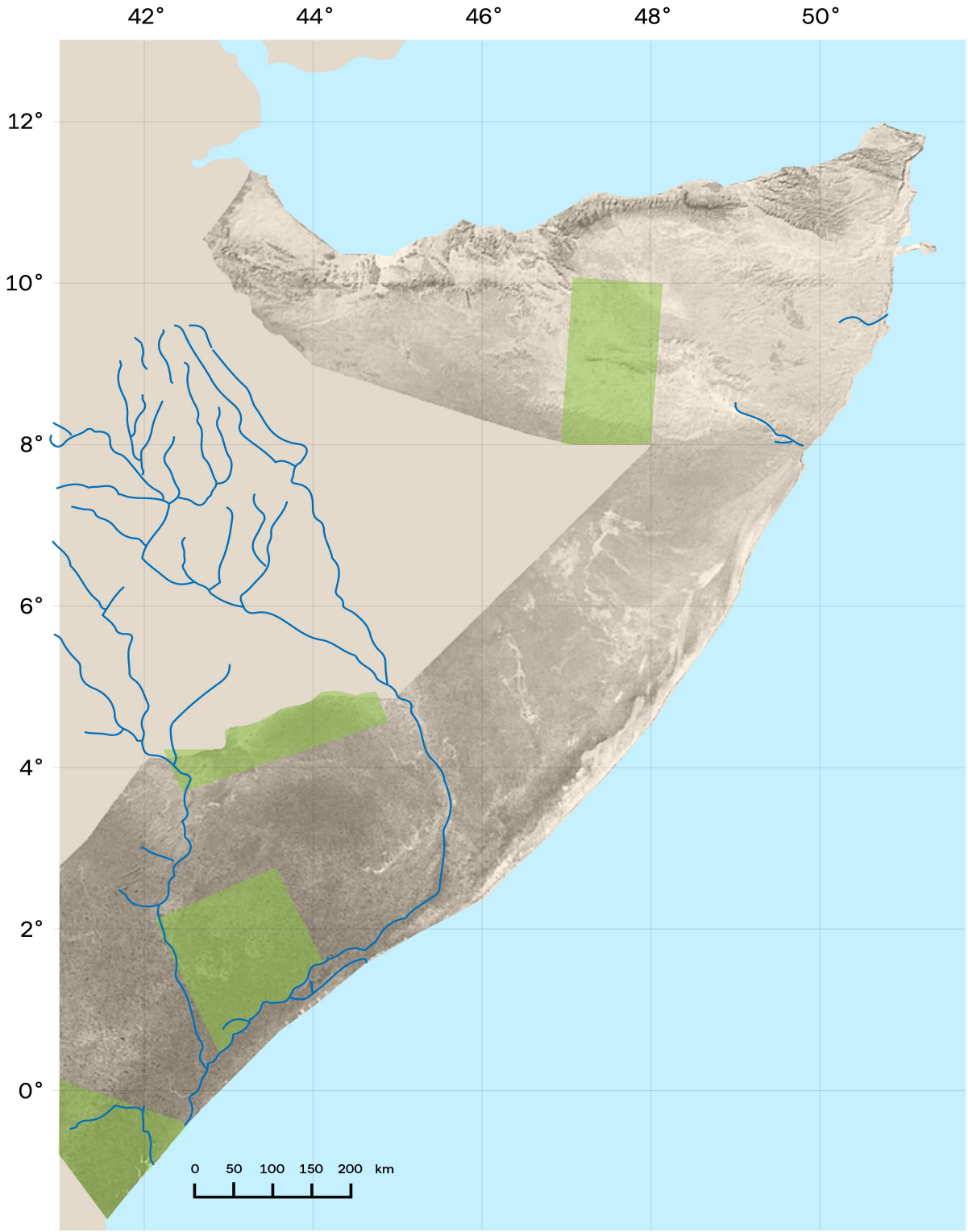

Figure 16: Map Current distribution of lions in Somalia (drawn by O.G. Amir, modified by I. Tkacenko). The green polygons indicate the areas where lion presence has been estimated

Table 3: Means in mm for each subspecies of the different measurements of female specimens.

Putative subspecies	GLS	CBL	GLN	IOB	BZB	ML
Panthera leo massaica	295.31±7.42	265.23±6.83	89.69±5.02	59.38±3.55	193.77±6.27	204.15±5.06
Panthera leo nyanzae	295.17±11.75	266.25±9.09	88.92±5.33	59.83±3.81	196.08±9.29	205.00±5.67
Panthera leo somaliensis	284.60±12.44	260.80±4.38	86.80±3.03	57.80±3.03	191.00±3.39	192.00±5.52

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Ten years later Drake-Brockman (1910) visited North Somalia and reported that lions were very rare, but the species was still present in the Haud, in the Nugaal Valley (located in the North East of Somalia) and in the Ogaden region (now part of Ethiopia). He reported that lions used to wander to Golis Mountain up to the Red Sea area, perhaps to follow their prey such as the Sacred Baboons *Papio hamadryas* (Linnaeus, 1758), which are common in these areas even today roaming in large numbers on the hills and in the valleys of Somaliland. In the 1930's, Scortecci (1937) reported that lions were also common in the Haud region.

Fourteen years later Hunter (1951) conducted a seven-year long survey in Somaliland and reported that lions were commonly distributed all over Somaliland, though the species favored mountain areas with juniper forest (*Juniperus procera*), higher plateaus with thick bush, and well-watered lowlands. A decade later, Funaioli and Simonetta (1967) reported that during their field observations, conducted from 1958 to 1966, lions were widely distributed in the North and Southern of Somalia. However, central regions were sparsely populated by lions due to the decline of woodland cover, an increase in livestock population, and the poisoning campaigns carried out by livestock herders.

During the 1980's, Fagotto (1985a) mentioned that the lion population had declined overall in the country and that a significant population could be found only in the Lower Shabelle and Lower Juba regions. In 1985 Fagotto shot an adult male lion in Janaale village, 100 km south of Mogadishu (Fagotto, 1985b). In 2006, lions were still present in their stronghold of the lower Sheebeli, even though such evidence came from lion cubs sold in Mogadishu (Amir, 2006).

Present distribution and conservation status

Currently, lions are mainly distributed in the Southern part of Somalia while some smaller populations are present in the Northern part of Somalia and in the riverine areas (Fig. 14). However, it must be noted that the current population of lions in Somalia is very difficult to estimate due to prolonged conflict and persisting insecurity. It is likely that the populations in these areas are threatened by the illegal trade of cubs and indiscriminate killing due to the proliferation of weapons in Somalia. However, it is still possible to hope that Somali lions will be studied and protected when political stability is reached again in Somalia.

The two areas in Southern Somalia which present consistent lion populations are the Arboweero-Alafuuto area, located in the lower part of the Shabelle River, and the Lag Badana-Bushubushle National Park. In 2017, the presence of lions was also confirmed in areas adjacent to the National Park to the South-West of the Juba River up to the border with Kenya (Amir et al, 2017).

In most of the Northern regions of Somalia, the lion population has been extirpated. However, some areas such as the Nugaal Valley, the Eastern part of the Golis Mountains, and the Sool and Cayn regions (located in Somaliland) may hold few individuals. In these areas, killings of female camels by lions were reported during 2021. A lioness was last sighted on 24th April 2021 in the Geed-dheer and Cankalaalaad areas of the Widhwidh district in the Togdheer region. Lions have also been recently reported in the contested areas between the Somaliland and Puntland, which people and livestock tend to avoid due to recurrent conflicts. There have been no recent lion sightings in central Somalia.

The presence of lions in the Interfluvial Region was confirmed between late 2020 and 2021 in an area located in the North, between the towns of Tiyeglow, Baidoa, Ceel-berde, and Beletweyn close to the border with Ethiopia; no conflict with livestock was reported in this area.

Discussion

This review leads us to understand how the lions of Somalia have never been considered enough: we still do not know much about their taxonomic identity, and less, if not anecdotal news, is known about their ecology and behavior. As already mentioned, Somalia's difficult political-administrative situation does not help scientists or research groups to undertake studies in this direction. However, we have collected as far as possible all available data.

Regarding the morphology, the cranial measurements indicate that, in both sexes, *P. l. somaliensis* tends to be smaller than other East African putative subspecies such as *P. l. nyanzae* and *P. l. massaica*. According to the LDA cranial measurements allow us to distinguish *P. l. somaliensis* from the other two putative subspecies. However, according to the non-parametric MANOVA only in the males the values are significantly different between subspecies (with the taxon *somaliensis* significantly smaller than the other two) while the differences between females are not significant. This is also partially indicated by the PCA as the plots between PC1 and PC2 (which together explain nearly 89% of variability in males and 80% in females) show a clear differentiation of *P. l. somaliensis* from the two other putative subspecies in males and an overlapping in females. Recent lion taxonomy revisions such as Lupták and Csurma (2009) synonymized these three putative subspecies with *P. l. nubica* and indicated nonetheless *P. l. somaliensis* as a slightly smaller subpopulation. Furthermore, Mazák (1968), who synonymized *P. l. nyanzae* and *P. l. massaica* with *P. l. somaliensis*, reported that the taxon presents considerable variability (i.e. 250-300 cm body length in males and 220-270 cm in females; GLS ranges between 336 and 382.8 mm in males and between 277 and 312 mm in females). This highlights the fact that lion putative subspecies from East Africa present considerable morphological

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variability. Interestingly, although measurements by Azzaroli and Simonetta (1966) of specimens from former Italian Somalia were not taken into account for his revision, Mazák (1968) reported that lions from both former Italian Somalia and Somaliland featured poorly developed manes. However, since our measurements belong only to a small sample of individuals, it would be interesting to carry out similar analysis on a larger dataset, even though it is not easy to obtain Somali lion samples.

We have also seen how wild males either present a poor mane or are often lacking one (Figs. 2–8). On the other hand, if kept in captivity (Figs. 9–11) they present normally developed manes. These types of mane in wild males seem similar (but not exactly the same) to those found in the Tsavo ecosystems, in Kenya (Kays and Patterson 2002; Patterson 2004), which is not far from the Somali border. Lönnberg (1912) assigned a scantly maned male shot north of Guaso Nyiro (Kenya) to *P. l. somaliensis*. It has been stated that those manes could depend on the particular type of habitat where they live, especially in the South-Western sector of the country, including the Trans-Juba, that is, a particular type of arid savannah full of thorny shrubs and bushes (Kays and Patterson, 2002). It is not known with absolute certainty whether all the lion populations of Somalia have this characteristic, even if lions from other parts of the country, i.e. from the North East or North West, or even from the Ethiopian region of Ogaden seem to be consistent with this phenotypic aspect (Peel, 1900; Elliot, 1907; Zukowsky, 1964). The fact that mane variability in lions depends on climatic differences (i.e. temperatures and rainfall) is well known (Patterson, 2007). It is worth noting that in Bertola et al. (2016) lions form the Aberdare National Park, in North Kenya, which present thicker manes (Kays and Patterson, 2002), belong to the same cluster as Somali lions in the median network based on the *cytb* haplotype while lions from Tsavo, which present manes similar to the ones of Somali lions, belong to a different cluster. However, Barnett et al. (2014) reported that Somali lions belonged to the same cluster as Tsavo lions in a median network based on the *cytb* haplotype. Thus, some studies regarding a possible admixture between lions from Somalia and Kenya may be useful. It has to be said that Barnett et al. (2014) and Bertola et al. (2016) based their study on the maternally inherited mtDNA, thus mtDNA population genetic studies would reflect maternally directed natal-site fidelity and gene flow while the biparentally inherited nDNA assists in quantifying the levels of gene flow between subpopulations for both sexes (Tende et al, 2014a). Furthermore, since lions show high rates of male-biased difference in dispersal patterns (Pusey and Packer, 1987), different distributions of genetic variation among populations for maternally (mtDNA) versus biparentally (nDNA) inherited molecular markers are expected (Tende et al., 2014a). For this reason, we argue that a population genetic study based on both mDNA and nDNA may be useful to determine whether an admixture between lion populations in North Kenya (i.e. those of Tsavo and Aberdare) and in the Somali arid region has taken place, given the nearness to the Somali border.

The social organization and behavior of the Somali lion are very little known. According to the available data, lions in Somalia hunt or live individually or at the most in pairs or accompanied by another younger individual, probably their offspring. This type of social organization is very similar to the observations made on the West African lions, sensu *P. l. senegalensis* (Meyer, 1826) which, curiously, are also devoid of mane or present a barely hinted mane (Mazák, 1968; Rosevear, 1974; Angelici et al., 2015; Angelici and Rossi, 2017). A possible preliminary interpretation of the first results obtained on craniometric differences, although as said they concern a limited sample of individuals, could refer to the fact that often in social mammal species with large groups (with a high degree of polygyny), including the lion, there is a more marked sexual dimorphism distorted towards males, than in solitary mammals or with primitive sociability (i.e. Clutton-Brock et al., 1980; Lindenfors et al., 2002, 2007; Cassini, 2020), even if there exist reverse cases (Law, 2019). This correlation, at an evolutionary level, has also been demonstrated with regard to the dimensions relative to the skeleton, including the skull (Morris and Carrier, 2016). So, both in Somali lions and in West African lions, which have a less developed sociality with pairs of specimens or at most few social individuals, there is a sexual dimorphism, in phenotype characters and in size, less pronounced than in lions with larger and more organized groups (i.e. Angelici et al., 2015). This would explain the reason why the males of *P. l. somaliensis* are smaller in size than other Eastern-African lions, while the females show overlapping data with those of other eastern populations. In both carnivores and primates, the most dimorphic species are those in which competition among males for access to females is relatively intense (Cassini, 2020). It seems that species with uni-male, multi-female breeding systems tend to be more dimorphic than monogamous species (Gittleman and Van Valkenburgh, 1997).

Furthermore, a correlation between brain volume and sociality in carnivores was proposed by Hemmer (1978) with more social species presenting higher brain volumes than less social species. Although this theory was rejected (Glitterman, 1986), it is worth noting that more solitary lion subspecies such as *P. l. persica* (Meena, 2009) and *P. l. leo* (Mazák, 1968) present significantly lower brain volumes than other subspecies (Hemmer, 1971; Yamaguchi et al., 2009). Yamaguchi et al. (2009) reported that Sub-Saharan lion putative subspecies present a non-significant difference in their brain volume. However, all the

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East Africa lions were encompassed under *P. l. nubica*. Thus, it would be interesting to study whether *P. l. somaliensis* presents a significantly smaller brain volume than other East African putative subspecies, *sensu* Hollister (1918).

Conclusions

In conclusion, this review does not allow us to draw a definitive conclusion about the taxonomic nature of the lions of Somalia, and a broader approach including lion populations from Ethiopia and nearby countries is needed. Nonetheless, the review of old literature and the morphometrical analysis (albeit based on a small sample) indicate that this population presents noteworthy morphological and socio-ecological characteristics (i.e. smaller males compared to other Eastern African subspecies and smaller social units) which prompt us to suggest further studies on this population for conservation reasons. Furthermore, wild males of putative *P. l. somaliensis* appear to have scanty or non-existent manes, such as the lions of the Tsavo National Park in Kenya. While this character has been associated with environmental factors, we argue that further genetic studies are needed to assess whether there exists a genetic continuum between these two populations.

It should be noted that the recent acceptance of only two subspecies in *P. leo*, following the results of phylogenetic researches seems at least premature and certainly dangerous for the conservation of some lion populations (cf. Gippoliti et al., 2021). Concordance between molecular research and subspecies rank is a self-inflicted burden that is not required by the somewhat elastic and subjective subspecies rank as generally acknowledged (Patten and Remsen, 2017). The reported geographical limit between *P. l. leo* and *P. l. melanochaita* (Curry et al., 2020) is a biogeographical non-sense, Western Ethiopia and Eritrea belong to the same ecoregion as Eastern Sudan – as evidenced by the recent discovery of an endemic primate species (Gippoliti, 2017). This is probably due to a mixture of scarce sampling and ignorance of Africa biogeography, and therefore we call for a caution in accepting such taxonomy by conservation bodies. The identification of several valid subspecies, or even of ESU's, can make us better understand and highlight populations differing for ecology, behavior and physiology in order to better preserve biodiversity (i.e. Winker, 2010). Indeed, many times, underestimating this aspect has led to overlooking the urgency of conservation action in some regions, causing unnecessary loss of biodiversity (i.e. Angelici and Rossi, 2018; Gippoliti and Groves, 2020). Aside from taxonomy, conservation biologists must reconsider the importance of protecting local populations to avoid future translocations of naive predators that may increase conflicts with human communities in countries where humans and wildlife must find a difficult coexistence.

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Conflict of interest

All the authors declare that there are no conflicting issues related to this review article.

References

Agnelli, P., Azzaroli, M. L. and Simonetta, A. M. (1990). Some remarks on the mammals of Somalia. *Biogeographia–The Journal of Integrative Biogeography*, 14 (1): 499–513. https://doi.org/10.21426/B614110361

Amir, O. G. (2006). Wildlife trade in Somalia. *Report to the IUCN/SSC Antelope Specialist Group*. 28 pp.

Amir, O. G., De Leeuw, J. and Koech, G. (2017). *Assessment of the Biological in terrestrial and marine landscape of the proposed Lag Badana National Park and surrounding in Jubaland, Somalia. Working paper N0.251*. World Agroforestry Centre. Nairobi, Kenya. 38 pp.

Anderson, M. J. (2001). A new method for nonparametric multivariate analysis of variance. *Austral Ecology*, 26 (1): 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Angelici, F. M. and Rossi, L. (2017). Further lion, *Panthera leo senegalensis* Meyer, 1826, sightings in Mole National Park,Ghana, and possible first serval *Leptailurus serval* Schreber, 1776 record after 39 years (Mammalia Felidae). *Biodiversity Journal*, 8 (2): 749–752.

Angelici, F. M. and Rossi, L. (2018). A new subspecies of grey wolf (Carnivora, Canidae), recently extinct, from Sicily, Italy. *Bollettino del Museo Civico di Storia Naturale di Verona, Botanica Zoologia*, 42: 3–15. https://doi.org/10.1101/320655

Angelici, F. M., Mahama, A. and Rossi, L. (2015). The lion in Ghana: its historical and current status. *Animal Biodiversity and Conservation*, 38 (2): 151–162. https://doi.org/10.32800/abc.2015.38.0151

[Downloaded from jad.lu.ac.ir on 2024-04-23]

[DOR: 20.1001.1.2676685.2022.4.2.5.7]
[DOI: 10.52547/JAD.2022.4.2.2]

Azzaroli, L. and Simonetta, A. M. (1966). Carnivori della Somalia ex italiana. *Monitore Zoologico Italiano. Supplemento*, 1 (1): 102–195. https://doi.org/10.1080/03749444.1966.10736741

Barnett, R., Yamaguchi, N., Barnes, I. and Cooper, A. (2006). The origin, current diversity and future conservation of the modern lion (*Panthera leo*). *Proceedings Royal Society B: Biological Sciences*, 273 (1598): 2119–2125. https://doi.org/10.1098/rspb.2006.3555

Barnett, R., Yamaguchi N., Shapiro, B. and Nijman, V. (2007). Using ancient DNA techniques to identify the origin of unprovenanced museum specimens, as illustrated by the identification of a 19th century lion from Amsterdam. *Contributions to Zoology*, 76 (2): 87–94. https://doi.org/10.1163/18759866-07602002

Barnett, R., Shapiro, B., Barnes, I., Ho, S. Y. W., Burger, J., Yamaguchi, N., Higham, T. F. G., Wheeler, H. T., Rosendahl, W., Sher, A. V., Sotnikova, M., Kuznetsova, T., Baryshnikov, G. F., Martion, L. D., Harington, C. R., Burns, J. A. and Cooper, A. (2009). Phylogeography of lions (*Panthera leo* ssp.) reveals three distinct taxa and a late Pleistocene reduction in genetic diversity. *Molecular Ecology*, 18 (8): 1668–1677. https://doi.org/10.1111/j.1365-294x.2009.04134.x

Barnett, R., Yamaguchi, N., Shapiro, B., Ho, S. Y. W., Barnes, I., Sabin, R., Werdelin, J., Cuisin, J. and Larson, G. (2014). Revealing the maternal demographic history of *Panthera leo* using ancient DNA and a spatially explicit genealogical analysis. *BMC Evolutionary Biology*, 14 (1): 1–11. https://doi.org/10.1186/1471-2148-14-70

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L. T. B., Macdonald, D. W. and Packer, C. (2015). Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings National Academy of Sciences*, 112 (48): 14894–14899. https://doi.org/10.1073/pnas.1500664112

Benjamini, Y. and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B: Biological Sciences*, 57: 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Bertola, L. D., Jongbloed, H., Van Der Gaag, K. J., De Knijff, P., Yamaguchi, N., Hooghiemstra, H., Bauer, H., Henschel, P., White, P. A., Driscoll, C. A., Tende, T., Ottosson, U., Said, Y., Vrieling, K. and De Iongh, H. H. (2016). Phylogeographic patterns in Africa and high resolution delineation of genetic clades in the Lion (*Panthera leo*). *Scientific Reports*, 6 (1): 1–11. https://doi.org/10.1038/srep30807

Bertola, L. D., Miller, S. M., Williams, V. L., Naude, V. N., Coals, P., Dures, S. G., Henschel, P., Chege, M., Sogbohossou, E. A., Ndiaye, A., Kiki, M., Gaylard, A., Ikanda, D. K., Becker, M. S. and Lindsey, P. (2021). Genetic guidelines for translocations: Maintaining intraspecific diversity in the lion (*Panthera leo*). *Evolutionary Applications*, 00, 1–18. https://doi.org/10.1111/eva.13318

Blainville de, H. M. D. (1843). *Ostéographie ou description iconographique comparée du squelette et du système dentaire des cinques classes d'animaux vertébrés récents et fossils pour servir de base a la zoologie et la géologie. Mammifères. Carnassiers. Vol. 2*. Arthus Bertrand, Paris, France. 1006 pp.

Cassini, M. H. (2020). A mixed model of the evolution of polygyny and sexual size dimorphism in mammals. *Mammal Review*, 50 (1): 112–120. https://doi.org/10.1111/mam.12171

Christiansen, P. (2008). On the distinctiveness of the Cape lion (*Panthera leo melanochaita* Smith, 1842), and a possible new specimen from the Zoological Museum, Copenhagen. *Mammalian Biology*, 73 (1): 58–65. https://doi.org/10.1016/j.mambio.2007.06.003

Clutton-Brock, T., Albon, S. and Harvey, P. (1980). Antlers, body size and breeding group size in the Cervidae. *Nature*, 285 (5766): 565–567. https://doi.org/10.1038/285565a0

Curry, C. J., Davis, B. W., Bertola, L. D., White, P. A., Murphy, W. J., and Derr, J. N. (2021). Spatiotemporal genetic diversity of lions reveals the influence of habitat fragmentation across Africa. *Molecular Biology and Evolution*, 38 (1): 48–57. https://doi.org/10.1093/molbev/msaa174

de Beaux, O. (1915). Sull'opportunità di indicare nelle descrizioni osteologiche le caratteristiche individuali ed anormali e lo stato di conservazione dei soggetti. *Monitore Zoologico Italiano*, 26: 261–267.

de Beaux, O. (1924). Mammiferi della Somalia italiana. Elenco delle specie e sottospecie finora riconosciute presentii, con annotazioni di Sistematica e Zoo-geografia. *Atti della Accademia Ligure di Scienze e Lettere*, 3: 149–168.

Drake-Brockman, R. E. (1910). *Mammals of Somaliland*. Hurst and Jackson, London, UK. 201 pp.

Dubach, J. M., Briggs, M. B., White, P. A., Ament, B. A. and Patterson, B. D. (2013). Genetic perspectives on 'Lion Conservation Units' in Eastern and Southern Africa. *Conservation Genetics*, 14 (4): 741–755. https://doi.org/10.1007/s10592-013-0453-3

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[DOI: 10.52547/JAD.2022.4.2.2]

Dures, S. G., Carbone, C., Savolainen, V., Maude, G. and Gottelli, D. (2020). Ecology rather than people restrict gene flow in Okavango-Kalahari lions. *Animal Conservation*, 23 (5): 502–515. https://doi.org/10.1111/acv.12562

Elliot, D. G. (1897). List of mammals obtained by the Field Columbian Museum (East African) Expedition to Somali-land in 1896. *Field Columbian Museum Publication*, 19: 109–155.

Fagotto, F. (1985a). Larger animals of Somalia in 1984. *Environmental Conservation*, 12 (3): 260–264. https://doi.org/10.1017/s0376892900016015

Fagotto, F. (1985b). The lion in Somalia. *Mammalia (Paris)*, 49 (4): 587–588

Funaioli, U. (1957). *Fauna e caccia in Somalia*. Governo della Somalia, Ministero per gli Affari Economici, Dipartimento Agricoltura e Zootecnia, Mogadishu, Somalia. 98 pp.

Funaioli, U. (1959). I mammiferi della Somalia. Cenni sul loro interesse nell'economia del paese. Primo elenco. *Rivista di Agricoltura Subtropicale e Tropicale*, 53: 176–196, 335–355.

Funaioli, U. and Simonetta, M. (1967). The Mammalian fauna of Somali Republic: status and conservation problem. *Italian Journal of Zoology*, 74 (Supplement): 285–347. https://doi.org/10.1080/03749444.1966.10736746

Gippoliti, S. (2006). Zammarano's monkey *Cercopithecus mitis zammaranoi* de Beaux, 1923: The forgotten monkey of Somalia. *African Primates*, 6 (1–2): 26–32.

Gippoliti, S. (2017). On the taxonomy of *Erythrocebus* with a re-evaluation of *Erythrocebus poliophaeus* (Reichenbach, 1862) from the Blue Nile Region of Sudan and Ethiopia. *Primate Conservation*, 31: 53–59.

Gippoliti, S. (2020). Everything mammal conservation biologists always wanted to know about taxonomy (but were afraid to ask). *Journal for Nature Conservation*, 54: 125793. https://doi.org/10.1016/j.jnc.2020.125793

Gippoliti, S. and Amori, G. (2011). A new species of mole-rat (Rodentia, Bathyergidae) from the Horn of Africa. *Zootaxa*, 2918 (1): 39–46. https://doi.org/10.11646/zootaxa.2918.1.4

Gippoliti, S. and Fagotto, F. (2012). On the greater kudu *Tragelaphus strepsiceros* in Central and Southern Somalia. *Mammalia*, 76 (3): 323–325. https://doi.org/10.1515/mammalia-2012-0005

Gippoliti, S. and Groves, C. P. (2020). Cryptic problematic species and troublesome taxonomists: A tale of the Apennine bear, and the Nile White Rhinoceros, *In*: Angelici, F. M. and Rossi, L. (Eds.), *Problematic wildlife II. New conservation and management challenges in the human-wildlife interactions*. pp. 509–527. https://doi.org/10.1007/978-3-030-42335-3_16

Gippoliti, S., Amori, G., Castiglia, R., Colangelo, P. and Capanna, E. (2014). The relevance of Italian museum collections for research and conservation: the case of mammals. *Rendiconti Lincei*, 25 (3): 351–357. https://doi.org/10.1007/s12210-014-0304-2

Gippoliti, S., Robovský, J. and Angelici, F. M. (2021). Taxonomy and translocations of African mammals: A plea for a cautionary approach. *Conservation*, 1 (2): 121–136. https://doi.org/10.3390/conservation1020011

Gittleman, J. L. (1986). Carnivore brain size, behavioral ecology, and phylogeny. *Journal of Mammalogy*, 67 (1): 23–36. https://doi.org/10.2307/1380998

Gittleman, J. L. and Van Valkenbug, B. (1997). Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny, and behavioural ecology. *Journal of Zoology*, 242 (1): 97–117. https://doi.org/10.1111/j.1469-7998.1997.tb02932.x

Gnoske, T. P., Celesia, G. G. and Kerbis Peterhans, J. C. (2006.) Dissociation between mane development and sexual maturity in lions (*Panthera leo*): solution to the Tsavo riddle?. *Journal of Zoology*, 270 (4): 551–560. https://doi.org/10.1111/j.1469-7998.2006.00200.x

Heller, E. (1931). New races of carnivores and baboons from Equatorial Africa and Abyssinia. *Smithsonian Miscellaneous Collections*, 61 (19): 1–12.

Hemmer, H. (1971). Intraspezifische Unterschiede der relativen Hirngrösse beim Löwen (*Panthera leo* L.). *Experientia*, 27 (12): 1500–1501.

Hemmer, H. (1974). Untersuchungen zur Stammesgeschichte der Pantherkatzen (Pantherinae), Teil III: Zur Artgeschichte des Löwen *Panthera (Panthera) leo* (Linnaeus 1758). *Veröffentlichungen der Zoologischen Staatssammlung München*, 17: 167–280.

Hemmer, H. (1978). Socialization by intelligence: social behavior in carnivores as a function of relative brain size and environment. *Carnivore*, 1: 102–105.

Hervé, M. (2018). RVAideMemoire: testing and plotting procedures for biostatistics. R package version 0.9-69, 3. Available at https://CRAN.R-project.org/package=RVAideMemoire

Hollister, N. (1917). Some effects of environment and habit on captive lions. *Proceedings of the United States National Museum*, 53 (2196): 177–193.

Hollister, N. (1918). East African mammals in the United States National Museum, pt. 1: Insectivora, Chiroptera, and Carnivora. *Bulletin of the United States National Museum*, 99: 1–194.

Hunter, J. A. (1951). *A general survey of the Somaliland protectorate 1944–1950. Final report on economic survey and reconnaissance of British Somaliland Protectarate. 1944–1950 Colonial Development and Welfare Scheme D.484*. General survey of the Somaliland Protectorate 1944–1950, Hargeisa, Somaliland Protectorate. 204 pp.

[Downloaded from jad.lu.ac.ir on 2024-04-23]

[DOR: 20.1001.1.2676685.2022.4.2.5.7]
[DOI: 10.52547/JAD.2022.4.2.2]

Kays, R. and Patterson, B. D. (2002). Mane variation in African lions and its social correlates. *Canadian Journal of Zoology*, 80 (3): 471–478. https://doi.org/10.1139/z02-024

Kingdon, J. (1990). *Island Africa: The Evolution of Africa's rare animals and plants*. Collins, London, UK. 287 pp.

Krásová, J., Mikula, O., Šumbera, R., Horáková, S., Robovský, J., Kostin, D. S., Martynov, A. A., Lavrenchenko, L. A. and Bryja, J. (2021). The Rufous Sengi is not *Elephantulus*-Multilocus reconstruction of evolutionary history of sengis from the subfamily Macroscelidinae. *Journal of Zoological Systematics and Evolutionary Research*, 59 (4): 918–932. https://doi.org/10.1111/jzs.12460

Kitchener, A. C., Breitenmoser-Würsten, C., Eizirik, E., Gentry, A., Werdelin, L., Wilting, A., Yamaguchi, N., Abramov, A. V., Christiansen, P., Driscoll, C., Duckworth, J. W., Johnson, W., Luo, S.-J., Meijaard, E., O'Donoghue, P., Sanderson, J., Seymour, K., Bruford, M., Groves, C., Hoffmann, M., Nowell, K., Tim-mons, Z. and Tobe, S. (2017). A revised taxonomy of the Felidae. The final report of the Cat Classification Task Force of the IUCN/SSC Cat Specialist Group. *Cat News Special Issue*, 11. 80 pp.

Law, C. J. (2019). Solitary meat-eaters: solitary, carnivorous carnivorans exhibit the highest degree of sexual size dimorphism. *Scientific Reports*, 9 (1): 15344. https://doi.org/10.1038/s41598-019-51943-x

Lindenfors, P., Tullberg, B. S. and Biuw, M. (2002). Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behavioral Ecology and Sociobiology*, 52 (3): 188–193 https://doi.org/10.1007/s00265-002-0507-x

Lindenfors, P., Gittleman, J. L. and Jones, K. E. (2007). Sexual size dimorphism in mammals, *In*: Fairbairn, D. J., Blanckenhorn, W. U. and Székely, T. (Eds.), *Sex, size and gender roles: Evolutionary studies of sexual size dimorphism*. Oxford University Press, Oxford, UK. pp 16–26. https://doi.org/10.1093/acprof:oso/9780199208784.003.0003

Linnaeus, C. (1758). *Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis*. *Tenth edition Vol. 1.* Laurentii Salvii, Stockholm, Sweden. 824 pp.

Lombardi, A. (1958). *L'amico degli animali racconta*. SEI, Turin, Italy. 217 pp.

Lönnberg, E. (1912). *Mammals collected by the Swedish zoological expedition to British East Africa, 1911*. Almqvist and Witkells, Uppsala and Stockholm, Sweden. 228 pp.

Lupták, P. and Csurma, L. (2009). The external variability and taxonomy of recent and extinct subspecies of lion (*Panthera leo*). *Gazella*, 36: 33–150.

Mazák, V. (1968). Der Löwe. *Das Pelzgewerbe*, 19 (3): 3–27.

Mazák, J. H. (2010). Geographical variation and phylogenetics of modern lions based on craniometric data. *Journal of Zoology*, 281 (3): 194–209. https://doi.org/10.1111/j.1469-7998.2010.00694.x

Meena, V. (2009). Variation in social organisation of lions with particular reference to the Asiatic Lions *Panthera leo persica* (Carnivora: Felidae) of the Gir forest, India. *Journal of Threatened Taxa*, 1 (3): 158–165. https://doi.org/10.11609/JoTT.o2095.158-65

Meyer, J. N. (1826) *Dissertatio inauguralis anatomico-medica de genere felium*. Ph.D. thesis. University of Vienna, Vienna, Austria.

Moore, A. E., Cotterill, F. P. D., Winterbach, C. W., Winterbach, H. E. K., Antunes, A. and O'Brien, S. J. (2016). Genetic evidence for contrasting wetland and savannah habitat specializations in different populations of lions (*Panthera leo*). *Journal of Heredity*, 107 (2): 101–103. https://doi.org/10.1093/jhered/esv097

Morris, J. S. and Carrier, D. R. (2016). Sexual selection on skeletal shape in Carnivora. *Evolution*, 70 (4): 767–780. https://doi.org/10.1111/evo.12904

Mosse, A. H. E. (1913). *My Somali book. A record of two shooting trips*. Sampson Low, Marston and Co., London, UK. 372 pp.

Nagel, D. S., Hilsberg, A., Benesch, A. and Scholtz, J. (2003). Functional morphology and fur pattern in recent and fossil *Panthera* species. *Scripta Geologica*, 126: 227–239.

Neumann, O. (1900). Die von mir in den Jahren 1892–95 in Ost und Central Africa, speciell in den Massai-Ländern und den Ländern am Victoria Nyansa gesammelten und beobachten Säugethiere. *Geographie und Biologie der Thiere*, 13: 529–562.

Noack, T. (1891). Beiträge zur Kenntnis der Säugetier-Fauna von Ostafrika. *Jahrbuch Hamburgischen Wissenschaftlichen Anstalten*, 9: 74–159.

Padial, J. M. and De la Riva, I. (2021). A paradigm shift in our view of species drives current trends in biological classification. *Biological Reviews*, 96 (2): 731–751. https://doi.org/10.1111/brv.12676

Patten, M. A. and Unitt, P. (2002). Diagnosability versus mean differences of sage sparrow subspecies. *The Auk*, 119 (1): 26–35. https://doi.org/10.1093/auk/119.1.26

Patten, M. A. and Remsen, J. V. (2017). Complementary roles of phenotype and genotype in subspecies delimitation. *Journal of Heredity*, 108 (4): 462–464. https://doi.org/10.1093/jhered/esx013

[Downloaded from jad.lu.ac.ir on 2024-04-23]

[DOR: 20.1001.1.2676685.2022.4.2.5.7]

[DOI: 10.52547/JAD.2022.4.2.2]

Patterson, B. D. (2004). *The lions of Tsavo. Exploring the legacy of Africa's notorious man-eaters*. McGraw-Hill, New York City, New York, USA. 324 pp.

Patterson, B. D. (2007). On the nature and significance of variability in Lions (*Panthera leo*). *Evolutionary Biology*, 34 (1): 55–60. https://doi.org/10.1007/s11692-007-9003-6

Patterson, B. D., Kays, R. W., Kasisi, S. M. and Sebestyen, V. M. (2006.) Developmental effects of climate on the lion's mane (*Panthera leo*). *Journal of Mammalogy*, 87 (2): 193–200. https://doi.org/10.1644/05-MAMM-A-226R2.1

Peel, C. V. A. (1900). *Somaliland: an account of two expeditions into the far interior, together with a complete list of animals and birds known to inhabit that country, and a list of reptiles collected by the Author.* F.E. Robinson and Co., London, UK. 345 pp.

Pocock, R. I. (1931). The lions of Asia. *Journal of the Bombay Natural History Society*, 34 (3): 638–665.

Pusey, A. E. and Packer, C. (1987). The evolution of sex-biased dispersal in lions. *Behaviour*, 101 (4): 275–310. https://doi.org/10.1163/156853987x00026

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ricci, G. (1965). Esperienze pratiche col .300 Winchester Magnum. *Diana*, 65: 45–49.

Rosevear, D. R. (1974). *The Carnivores of West Africa*. Trustees of the British Museum (Natural History), London, UK. 548 pp.

Rothfels, N. (2002). *Savage and beasts. The birth of the modern zoo*. The John Hopkins University Press, Baltimore, Maryland, USA. 288 pp.

Scortecci, G. (1937). La fauna, *In*: Corni, G. (Ed.), *Somalia Italiana. Vol. 1*. Arte e Storia, Milan, Italy. pp. 207–243.

Smith, C. H. (1842). Mammalia. An introduction to the Mammalia, *In*: Jardine, W. (Ed.), *The Naturalist's Library. Vol. 15*. Chatto and Windus, London, UK. 313 pp.

Swayne, H. G. C. (1903). *Seventeen trips through Somaliland and a visit to Abyssinia*. Rowland Ward, London, UK.

Tamagnini, P. (1962). Sulle tracce del leone ferito. *Diana*, 62: 47–49.

Tedesco Zammarano, V. (1929). *Il sentiero delle belve. Impressioni di caccia in Africa Orientale*. Mondadori, Milan, Italy. 343 pp.

Tedesco Zammarano, V. (1930). *Fauna e caccia*. Ministero delle Colonie, Rome, Italy. 222 pp.

Tende, T., Bensch, S., Ottosson, U. and Hansson, B. (2014a). Dual phylogenetic origins of Nigerian lions (*Panthera leo*). *Ecology and Evolution*, 4 (13): 2668–2674. https://doi.org/10.1002/ece3.1116

Tende, T., Hansson, B., Ottosson, U., Åkesson, M. and Bensch, S. (2014b). Individual identification and genetic variation of lions (*Panthera leo*) from two protected areas in Nigeria. *PLoS ONE*, 9 (1): e84288. https://doi.org/10.1371/journal.pone.0084288

Trinkel, M. and Angelici, F. M. (2016). The decline in the lion population in Africa and possible mitigation measures, *In*: Angelici, F. M. (Ed.), *Problematic Wildlife. A Cross-Disciplinary Approach*. Springer, Berlin, Germany. pp. 45–68. https://doi.org/10.1007/978-3-319-22246-2_3

van Buuren, S. and Groothuis-Oudshoorn, K. (2011). Mice: Multivariate imputation by chained equations. R package version 2.9. Available at https://CRAN.R-project.org/package=mice

Venables, W. N. and Ripley, B. D. (2002). *Modern Applied Statistics with S*. Fourth Edition. Springer, New York City, New York, USA. 510 pp.

Yamaguchi, N., Cooper, A., Werdelin, L. and Macdonald, D. W. (2004). Evolution of the mane and group-living in the lion (*Panthera leo*): a review. *Journal of Zoology*, 263 (4): 329–342. https://doi.org/10.1017/S0952836904005242

Yamaguchi, N., Kitchener, A. C., Gilissen, E., and Macdonald, D. W. (2009). Brain size of the lion (*Panthera leo*) and the tiger (*P. tigris*): implications for intrageneric phylogeny, intraspecific differences and the effects of captivity. *Biological Journal of the Linnean Society*, 98 (1): 85–93. https://doi.org/10.1111/j.1095-8312.2009.01249.x

Ward, J. N. and Sorrell, D. S. (1950). The Fauna of Jubaland. *Oryx*, 1 (1): 26–34. https://doi.org/10.1017/s0030605300035651

Winker, K. (2010). Subspecies represent geographically partitioned variation, a gold mine of evolutionary biology, and a challenge for conservation. *Ornithological Monographs*, 67 (1): 6–23. https://doi.org/10.1525/om.2010.67.1.6

Wozencraft, W. C. (2005). Order Carnivora, *In*: Wilson, D. E. and Reeder, D. M. (Eds.), *Mammal species of the world: A taxonomic and geographic reference*. 3rd edition. Johns Hopkins University Press, Baltimore, Maryland, USA. pp. 532–628

Zukowsky, L. (1964.) Eine neue Löwenrasse als weiterer Beleg fur die Verzwergung der Wirbeltierfauna des afrikanischen Osthorns. *Milu, wissenschaftliche und kulturelle mitteilungen aus dem Tierpark Berlin*, 1: 269–273.

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Supplementary Table 1: Craniometric measurements (in mm) of all the male specimens used in the study. Estimated values are reported in **bold**.

Name	Putative subspecies	GLS	CBL	GLN	IOB	BZB	ML
C. 2131	*somaliensis*	332	302	94	67	233	223
C. 3476	*somaliensis*	293	271	89	58	209	202
IPUF	*somaliensis*	339	305	97	66	224	233
n H.I.P.U.F.	*somaliensis*	350	307	100	73	235	235
n G.I.P.UF.	*somaliensis*	331	**305**	100	66	235	230
174742	*massaica*	351	318	104	68	241	241
182297	*massaica*	373	322	110	71	248	257
182332	*massaica*	372	328	112	70	228	253
155443	*massaica*	373	335	118	70	234	256
163328	*massaica*	337	316	107	75	233	235
197944	*massaica*	345	309	97	78	261	248
199707	*massaica*	363	325	101	80	264	260
181568	*nyanzae*	334	295	102	67	216	233
181569	*nyanzae*	345	318	96	68	211	238
181571	*nyanzae*	368	324	114	71	243	255
181574	*nyanzae*	352	322	103	67	226	244
181577	*nyanzae*	356	318	103	70	235	245
162913	*nyanzae*	371	329	106	74	251	255
162919	*nyanzae*	356	321	104	66	235	242

Supplementary Table 2: Biometric measurements (in mm) of all the female specimens used in the study. Estimated values are reported in **bold**.

Name	Putative subspecies	GLS	CBL	GLN	IOB	BZB	ML
C. 1911	*somaliensis*	288	259	88	55	186	186
C. 1910	*somaliensis*	**290**	**262**	90	57	193	192
C. 3394	*somaliensis*	284	261	86	61	191	191
n.J. I.P.U.F.	*somaliensis*	297	267	88	61	190	201
n.4 Tozzi	*somaliensis*	264	255	82	55	195	190
174744	*massaica*	301	270	88	60	195	207
182308	*massaica*	290	259	90	58	195	202
182309	*massaica*	306	280	89	56	195	210
182311	*massaica*	285	262	88	57	195	204
182293	*massaica*	294	264	86	63	203	203
182324	*massaica*	299	266	90	57	185	200
182326	*massaica*	299	267	91	60	204	210
182421	*massaica*	292	262	88	58	192	203
182423	*massaica*	282	254	80	54	180	198
161914	*massaica*	291	258	86	58	192	196
163109	*massaica*	295	269	97	67	195	212
163329	*massaica*	307	273	100	60	193	209
163108	*massaica*	298	264	93	64	195	200
181589	*nyanzae*	296	269	87	62	202	208
181590	*nyanzae*	280	253	82	57	185	195
181592	*nyanzae*	306	273	94	64	205	210
181572	*nyanzae*	291	266	92	62	187	207
181930	*nyanzae*	300	264	92	61	206	206
181578	*nyanzae*	284	256	85	58	180	196
181583	*nyanzae*	309	278	98	63	202	211
162916	*nyanzae*	313	281	93	66	204	212
162914	*nyanzae*	277	254	79	56	185	199
162915	*nyanzae*	299	268	89	54	203	205
162917	*nyanzae*	302	272	89	60	196	208
162918	*nyanzae*	285	261	87	55	198	203

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