

# Examining the Extinction of the Barbary Lion and Its Implications for Felid Conservation

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## Abstract

Estimations of species extinction dates are rarely definitive, yet declarations of extinction or extirpation are important as they define when conservation efforts may cease. Erroneous declarations of extinctions not only destabilize conservation efforts but also corrode local community support. Mismatches in perceptions by the scientific and local communities risk undermining sensitive, but important partnerships. We examine observations relating to the decline and extinction of Barbary lions in North Africa. Whilst the extinction predates the era of the scientific conservation movement, the decline is relatively well documented in historical records. Recently unearthed accounts suggest Barbary lions survived later than previously assumed. We use probabilistic methods to estimate a more recent extinction date for the subspecies. The evidence presented for a much later persistence of lions in North Africa, including generations when sightings were nil, suggests caution when considering felid populations as extinct in the wild. The case raises the possibility that captive animals descended from the Moroccan royal collection are closer contemporaries to wild Barbary lions. Furthermore, our results highlight the vulnerability of very small lion populations and the significance of continued conservation of remnant lion populations in Central and West Africa.

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## Introduction

Several statements of extinction relating to felids have been proven unreliable, such as the recent rediscovery of the Barbary leopard [1] and the late persistence of the Caspian tiger, recognized as extinct since the early 1970s, yet later found present in Turkey where a local trade in hunted skins persisted into the 1980s suggesting survival into at least the early 1990s [2]. In both cases local people's observations remained unknown to science and therefore had no impact on conservation policy.

Wild populations of lion (*Panthera leo*), like other large mammalian carnivores, are suffering severe decline and in Africa have contracted sharply over the past 50 years [3], [4]. Outside East Africa, lion populations are fragmented, with remnants in Central and Western Africa threatened with extinction [5], [6]. The present-day status in sub-Saharan Africa mirrors the situation north of the Sahara a century ago where the once extensive lion distribution from North Africa to India was reduced to fragmented populations by the 20<sup>th</sup> century [7].

The North African 'Barbary lion' or 'Atlas lion' occupied the Maghreb, the region isolated from the rest of non-arid Africa by the Sahara [8]. Until the 18<sup>th</sup> century, Barbary lions ranged from the Atlas Mountains to the Mediterranean [7]. Extensive persecution in the 19<sup>th</sup> century reduced populations to remnants in Morocco in the west, and Algeria and Tunisia further east, all of which were extirpated during the 20<sup>th</sup> century [9], [10].

The Barbary lion (*P. l. leo*) is considered distinct from the six commonly defined sub-species in the rest of Africa [11], owing to

its geographic separation, morphology and unique montane habitat with cold winters. Although the phylogenetic status of lion populations remains unclear [12], [13], recent morphological and genetic studies consistently differentiate northern lions (India to North Africa) from sub-Saharan African lions [9], [14], [15].

The IUCN's assessments of species status, threats and extinctions have been established over the past four decades [4], which post-dates the extinction of the Barbary lion, so Red List declarations on the sub-species are based on reviews of literature [11]. The IUCN Wild Cats Status Survey and Action Plan recognized that certain captive lions may be descendants of the Barbary lion, designating the subspecies as 'extinct in the wild' [11]. Currently all extant African populations are grouped together as a single taxon, *Panthera leo*, with the species listed as 'regionally extinct' across its former northern range [16]. Only the Indian population is recognized as a distinct sub-species, *P. l. persica* [17], whilst North African populations (i.e. the Barbary lion) are mentioned in the context of both the IUCN's Indian and African lion accounts [4].

In the 16–18<sup>th</sup> centuries many accounts reported lions in the western Maghreb (northern Morocco) near the Atlantic and Mediterranean coasts [7], [18]. Up to the 1830s lions were still seen in these coastal areas, the Rif mountains and the Marmora forest [19], however records remain sparse throughout the 19<sup>th</sup> century [20]. By 1880 lions had retreated south of the Bou Regreg and Taza passes [19] into the Atlas Mountains and areas bordering the Sahara, where human populations were largely

nomadic. Previous commentators suggested Barbary lions were extirpated sometime between 1920 and 1930 [7], [19], [20]. Later sightings, however, have since been documented with the last in the High Atlas in 1942 [18].

In the eastern Maghreb (Algeria and Tunisia) lions frequented coastal-forested regions, the Tell Atlas and the Aurès mountain ranges. By the late 1800s, Tunisian sightings were confined to localities adjacent to the Algerian provinces of Souk Arras and Tebessa. Although no lions were shot in Tunisia after 1891 [7], rumors of their survival persisted in the 1900s in the Khmir Mountains and near Feriana [21]. The population was probably contiguous across the border, corresponding to home range sizes equivalent to those observed in present-day sub-Saharan Africa and India [22], [23], [24]. In Algeria, lions persisted into the 1890s and hunting accounts, the capture of wild cubs and photographs of tame lions were still widely reported [7], [20]. These observations, alongside interview evidence, suggest that a small population survived in Algeria well into the 20<sup>th</sup> century [25], long after 1893 when Algeria's supposedly last lion was shot [7].

Several reviews have considered the history of sightings [7], [19], [20], [26], [27] and the IUCN recognizes that lions persisted in Morocco into the 1940s [17]. Nevertheless these reviews have inadvertently missed, ignored or have lacked access to many local sources and literature accounts. A systematic evaluation of the last sightings in the Maghreb will provide more complete insights into persistence of remnant lion populations and the resilience of large mammalian carnivores to human pressure.

Several menageries in Europe held Barbary lions in medieval times [9] and they were popular exhibits in public zoological gardens in the 1800s [7], [20]. By the early 1900s zoos and circuses in Europe and North America often promoted their lions as “Barbary” [13], although true representatives were said to be only found in the collection of the Sultan of Morocco, derived from animals caught by local tribes [20]. The significance of this collection was not recognized until the 1970s after the lions were moved from the Royal Palace, Rabat, to a new zoo at Temara when a study identified animals with physical characteristics of the Barbary lion [20]. Despite several attempts, a formal scientific breeding program is yet to be established (Frey pers. comm.). Nevertheless, captive breeding has experienced a recent renaissance [28], [29] and a studbook for these animals (hereafter ‘Moroccan Royal lions’) has been developed [13].

Debate surrounds the authenticity of Moroccan Royal lions as descendants of wild Barbary lions [13]. One concern is that Moroccan Royal lions hybridized with sub-Saharan African lions potentially introduced to the collection before the 1970s [20]. Definitive genetic matches have not yet been established between Moroccan Royal lions and wild Barbary lions [13]. The few studies of Barbary lions that utilize museum samples [14] are limited by the scarcity of wild-origin reference specimens. Most recent genetic studies [30], [31], [32] rely on Royal lion samples from two zoos, covering at most 4 (possibly only 2) of the 12 maternal bloodlines [13]. In the absence of genetic data, owing to the lack of verified wild specimens, and working on the precautionary presumption that Barbary lions are taxonomically distinct from other lions, assessment of purity relies on ‘pedigree information’ which at best can be taken from the recently established studbook of lions of known ancestry arising from the Moroccan Royal Collection [13].

The North African-Asian population of lions [14] is only represented by today's Asiatic lion (*c.*350 wild individuals and *c.*100 zoo captives), so the potential significance of captive Moroccan Royal lions (*c.*90 individuals) is not trivial [13]. In the absence of definitive genetic comparisons we examine the

generational separation between lions surveyed in Temara Zoo in 1974 and wild-caught Barbary ancestors. This infers the degree of opportunity for hybridization had non-Barbary individuals bred within the Royal collection, and the potential purity and relevance of the extant captive population.

Our study re-examines the historical decline and extirpation of lions in North Africa. We calculate likely extinction dates for different populations and thus patterns of decline. We also examine new estimates of generation time in the captive population originally derived from wild North African ancestors and thus the likelihood of introgression with sub-Saharan individuals.

## Materials and Methods

### 2.1 Sightings Information

Existing literature was reviewed for accounts of sightings and kills by date and location, including documented interviews in addition to recent interviews by the authors (Tables 1–6). The collation includes sightings, photographs, accounts and recollections since 1839. Observations have been taken from recorded accounts from first-hand sources (written recordings of interviews), from direct interviews of eyewitnesses or a first-hand recollection of an eyewitness account; all sightings in the dataset are therefore from second-hand sources or better.

Morocco and the Morocco-Algeria border are considered as the western Maghreb, whilst the eastern Maghreb covers Tunisia and northern Algeria. The meridian bisects sightings west and east, the most proximal being separated by 220 km of desert and temporally by nearly 70 years. The nearest contemporaneous sightings across this divide occurred in 1912 and are separated by a distance of over 450 km. A small central population in the Saharan Atlas (observed in 1898, 1912, 1920 and 1935) possibly traversed both regions but, owing to the size of the dataset, exclusion of these 3 sightings made very little difference.

### 2.2 Inferring Extinction Dates

While the last sighting of a species is often used as the time of extinction, it rarely corresponds to the true extinction date [33].

Following Solow [33], let sighting times in years be order  $t_1 < t_2 < \dots < t_n$ , where  $t_1 = 0$ . Sampling from the uniform distribution, the unbiased estimate of extinction time is

$$\hat{T}_E = \frac{n+1}{n} t_n \quad (1)$$

and the expected year of extinction is  $\hat{T}_E$  plus the year of  $t_1$ . The upper bound,  $T_E^u$ , of  $1-\alpha$  CI for  $T_E$  is

$$T_E^u = t_n / \alpha^{1/n}, \quad (2)$$

where  $\alpha = 0.05$  (after [33]). Several other methods of inferring dates of extinction have been developed (see Solow [33] for a review). However, in a study of putatively extinct North American birds, Vogel et al. [34] showed that the simple Poisson process model, used here, had as good or better fit than other more complex models, such as the truncated exponential and Weibull.

Here we calculate the extinction dates for sightings of lions in the Western (Table 1;  $n = 16$ ) and Eastern Maghreb (Tables 2–6;  $n = 66$ ).

**Table 1.** The last sightings of lions in the Western Maghreb: Morocco to Western Sahara, 1830s–1940s (Rif Mountains, Anti Atlas, Middle Atlas and High Atlas).

|    | Location  | Season/Year | Observation Type                   | Solitary (0)/Group (1) | Original source          | Ref.       |
|----|---|-------------|------------------------------------|------------------------|--------------------------|------------|
| 1  | Guelaya (the region around Melilla)               | Before 1839 |                                    | 0                      |                          | [19]       |
| 2  | Cap Spartel-Tanger                                | Before 1839 | Shot, male                         | 0                      | Maalem Hamed             | [51]       |
| 3  | Mamora forest                                     | 1839        | Frequent lions                     | 1                      |                          | [51]       |
| 4  | Rif region  | Summer 1839 | Many observed and shot             | 1                      | Maalem Hamed             | [51]       |
| 5  | Jebel Kebir (Tanger)                              | 1846        | Shot, male                         | 0                      | Hooker and Ball          | [19]       |
| 6  | Megader pass (at 2300 m)                          | 1864        | Camp protected against lion attack |                        | Gerhard Rohlf            | [52]       |
| 7  | Rif mountains                                     | 1895        | Last lion killed in the Rif        | 0                      | de Planhol, 2004         | [53]       |
| 8  | M'Hamid, south of Zagora (Morocco-Algeria border) | c.1900      | Observations close to water points | 1                      | Local inhabitants        | [18]       |
| 9  | Djebel Ebrit (Ain Leuh-Timahdit)                  | c.1900      | Observations                       | 1                      |                          | [54]       |
| 10 | Budaa woods (Azrou)                               | 1901        | Observations, frequent lions       | 1                      | Marquis of Segonzac      | [19]       |
| 11 | Middle Atlas mountains                            | 1911        | Observations                       | 1                      | Engel                    | [19]       |
| 12 | Zaián forests, Beni Mgild (Khenifra)              | 1911        | Lions                              | 1                      |                          | [52]       |
| 13 | Oued Ifrane                                       | Winter 1917 | Observation, male                  | 0                      |                          | [54]       |
| 14 | Azrou vicinity                                    | 1920        | Observation of a single male       | 0                      |                          | [20], [55] |
| 15 | Middle Atlas mountains                            | 1922        | Shot                               | 0                      |                          | [56]       |
| 16 | Atlas Mountains (on the Casablanca-Dakar flight)  | 1925        | Male lion seen from the air        | 0                      | Photograph Flandrin, M.  | [57]       |
| 17 | Ouiouane area (Ain Leuh)                          | 1930        | Observations of few lions, tracks  | 1                      |                          | [58], [20] |
| 18 | Toubkal massif (now a NP)                         | Summer 1930 | Observations at 3000 m             | 1                      | Local residents          | [18]       |
| 19 | Hassi Aggou and Hassi Tighissit (Assa - TanTan)   | 1935        | Observations at water points       | 1                      | Bensalem, M.; Ennah, M.  | [18]       |
| 20 | Hassi Aggou vicinity                              | 1939        | Observations of 2 lions            | 1                      | Hunter told Monteil 1951 | [18]       |
| 21 | Tizi-n-Tichka pass (Marrakesh- Tadderte)          | 1942        | Shot                               | 0                      | Minet, J.                | [18]       |

NP = one of several National Parks established across the region since the 1940s. doi:10.1371/journal.pone.0060174.t001

### 2.3 Testing Behavioral Change

We tested whether lions appear to change their behavior as populations decreased in size to operate singly ('0') rather than in groups ('1') as a binary set of sightings [35].

In a series of  $N$  sightings,  $X_1, X_2, \dots, X_N$ , each sighting  $X_i$  is coded as  $X_i = 1$  or  $X_i = 0$ . Of the  $N$  sightings, let  $m$  equal the number of sightings of lions in groups and  $n$  equal the number of sightings of lions singly. Then

$$m = \sum_{i=1}^N X_i \tag{3}$$

and  $n = N - m$ . The cumulative number of group sightings at each point is then determined. This frequency is

$$S_j = \sum_{i=1}^j X_i \tag{4}$$

where  $j = 1, 2, \dots, N$ .

The statistic for testing the hypothesis of change is

$$D_{m,n} = \max_j \left| \frac{N}{mn} \left( S_j - \frac{jm}{N} \right) \right| \tag{5}$$

The expression is evaluated for all values of  $j$  from 1 to  $N-1$ .  $D_{m,n}$  is the largest absolute difference observed in the sequence. We may reject the  $H_0$  at 0.05 if  $D_{m,n} \geq 1.36\sqrt{N/mn}$

Here we test the null hypothesis that there has been no change in the probability of sightings of lions in groups over time in the Western and Eastern populations.

### 2.4 Estimation of Generations between Moroccan Royal Lions and Wild-caught Specimens

Hemmer [20] suggested that 20 generations separated Moroccan Royal lions surveyed in 1974 from wild lions captured c.1899, suggesting a 3.75-year generation time and multiple opportunities for hybridization with non-Barbary lions. The average age at which a wild female lion gives birth is 6.5–8 years [11], [36]. In the Moroccan Royal lion studbook, the mean generation time through to today's juveniles is 7.4 years (STD ± 3.2) in a range of 6.6–10 years [37]. The 30 breeding females since 1974 have a mean age at first surviving litter of 6.3

**Table 2.** Lion sightings in the eastern Maghreb of Algeria and Tunisia 1830–1850 (Ksour Mountains, Saharan Atlas, Tell Atlas, Ouled-Nail, Aurès Mountains).

|    | Location                        | Season/Year    | Observation Type                    | Solitary (0)/Group (1) | Original source      | Ref. |
|----|---------------------------------|----------------|-------------------------------------|------------------------|----------------------|------|
| 22 | Oued Khalaad, Tunisia           | 1832           | Observation of 16 lions             | 1                      | Greenville           | [59] |
| 23 | Djebel Guezoul (Tiaret)         | 1836           | Shot (100 shot during his life)     | 1                      | Mohamed Ben Esnoussi | [60] |
| 24 | Souk Tleta (Chelif region)      | Winter 1837    | Shot, male, female and 2 cubs       | 1                      | Agha Djendel         | [61] |
| 25 | Ain Sbaa (Bou Saada)            | 1840           | Male, attacking a sleeping man      | 0                      |                      | [62] |
| 26 | Djebel Mezioun                  | Spring 1840    | Observation of female and cubs      | 1                      |                      | [63] |
| 27 | Oued Tegedemt (South Tiaret)    | Summer 1840/42 | Observations 2                      | 1                      | Colonel Scott        | [64] |
| 28 | El Diss vicinity                | 1843           | Observed female, Shot male          | 1                      |                      | [65] |
| 29 | Theniet El Had (now a NP)       | Winter 1844    | Shot, 3 (14 lions in his life)      | 1                      | Mokhtar ben el Arbi  | [66] |
| 30 | Taza vicinity                   | 1844           | Lion attack                         | 0                      |                      | [66] |
| 31 | Miliana vicinity                | 1844           | Lions attack on livestock           | 1                      | Bugeaud              | [67] |
| 32 | Gaada (Djebel Amour)            | Before 1845    | Refuge place                        | 0                      |                      | [68] |
| 33 | Sidi Bel Abbés vicinity         | Winter 1845    | Shot, large lion                    | 0                      |                      | [69] |
| 34 | Sbeitla, Tunisia                | 1845           | Observations                        | 1                      | Bruce                | [59] |
| 35 | Kef vicinity (Tunisia)          | Spring 1845    | Skin female                         | 0                      |                      | [70] |
| 36 | Mahouna Gorges (near Guelma)    | Summer 1845    | Shot, 2                             | 1                      |                      | [71] |
| 37 | Bibans                          | Summer 1845    | Roaring                             | 0                      |                      | [72] |
| 38 | Saida                           | 1846           |                                     | 1                      | Berbrugger 1846      | [73] |
| 39 | Staouéli                        | 1846           | Attack, male                        | 0                      |                      | [74] |
| 40 | Guelma vicinity                 | Winter 1847    | Shot                                | 0                      |                      | [71] |
| 41 | Theniet El Had (actually NP)    | Winter 1847    | Shot                                | 0                      |                      | [66] |
| 42 | Djebel Guerioun (Aurès Mounts)  | Winter 1848    | Fresh faeces and an old male seen   | 0                      |                      | [71] |
| 43 | Montagne des lions (Oran-Arzew) | Winter 1849    | Observations                        | 1                      |                      | [75] |
| 44 | Saf Saf valley (Skikda region)  | Winter 1849    | Observations                        | 1                      |                      | [75] |
| 45 | Zerazer (Aurès Mounts)          | Winter 1850    | Shot, 2                             | 1                      |                      | [71] |
| 46 | Tebessa                         | Spring 1850    | Fresh male skin                     | 0                      |                      | [76] |
| 47 | Djebel Bouarif (Aurès Mounts)   | Summer 1850    | Winter refuge; 30 lions in the area | 0                      |                      | [77] |
| 48 | Fedjoudj (Aurès Mounts)         | 1850           | Winter refuge                       | 0                      |                      | [77] |

NP = one of several National Parks established across the region in the 1980s–1990s.  
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years ( $STD \pm 2.9$ ). These observations suggest that Moroccan Royal lions have a generation time similar to the birthing age for wild lions, 6.5 years [36]. We calculate the number of generations between the animals moved to Temara Zoo and the likely last wild-caught animals, based on a calculated inferred extinction date. We also calculate the number of generations occurring between sightings of wild Barbary lions as an indicator of persistence.

## Results

### 3.1 Sightings of Lions in North Africa

The list of recent historical lion sightings in North Africa includes data for the western Maghreb from 1840 to the 1940s (Table 1) and the eastern Maghreb from the 1830s to the 1950s (Tables 2–6). Sightings become infrequent in the eastern Maghreb after the 1890s and in the western Maghreb after the 1920s. Our examination of historical accounts reveals that lions occupied the Saharan Atlas (Fig. 1), much further south than previously reported by Schnitzler [27]. The precise location of the aerial

photograph on the Casablanca-Dakar route (Fig. 2) is unknown, however our research has identified that it was taken in 1925 when flights commenced [38]. A postcard edition of the image has recently been discovered with the caption “Un lion photographié en avion dans l’Atlas” (Fig. 3). Since this predates discussions on the extermination of lions in the region [19], its significance at that time was then unknown. The photograph by Flandrin is the last known image of a wild Barbary lion.

### 3.2 Recent Extinction of Lions in North Africa

In recent years it has become widely asserted that the animal shot in 1942 on the Tizi-n-Tichka pass in Morocco’s High Atlas Mountains [18] has been considered the last wild Barbary lion [4]. However, our analysis suggests that wild lions actually persisted longer in Algeria until 1958 ( $T_E$ ), with an upper bound for the 95% CI of  $T_E^u = 1962$ . This is 10 years after 1948 ( $T_E$ ), the estimated extinction date of the western (Morocco) population. However, the estimated 95% confidence intervals have a substantial overlap: with upper bounds ( $T_E$ ) of 1962 for the

**Table 3.** Lion sightings in the eastern Maghreb of Algeria and Tunisia, 1851–1860 (Ksour Mountains, Saharan Atlas, Tell Atlas, Ouled-Nail, Aurès Mountains).

|    | Location                            | Season/Year | Observation Type                                | Solitary (0)/Group (1) | Original source | Ref. |
|----|-------------------------------------|-------------|---|------------------------|-----------------|------|
| 49 | Ourten valley Khenchela (Aurès)     | Autumn 1851 | Observation, male, female                       | 1                      |                 | [71] |
| 50 | Drean                               | Spring 1852 | Frequent, Shot male                             | 1                      |                 | [78] |
| 51 | Baba Ali (Mitidja)                  | Summer 1852 | Observation, male                               | 0                      |                 | [79] |
| 52 | El Diss vicinity                    | 1852        | Shot, female                                    | 0                      |                 | [65] |
| 53 | Milianah vicinity                   | Spring 1853 | Observation                                     | 0                      |                 | [80] |
| 54 | Khenchela (Aurès Mounts)            | Summer 1853 | Shot, male (Shot 25 lions during his life)      | 0                      |                 | [71] |
| 55 | Djebel Onk Jemel (Aurès Mounts)     | Autumn 1853 | Shot, female                                    | 0                      |                 | [71] |
| 56 | Ferdjioua vicinity                  | Spring 1855 | SidiBou Akas                                    | 1                      | Vicomte de Noé  | [81] |
| 57 | Oued Tafna                          | 1855        | Tracks  | 0                      | Vicomte de Noé  | [81] |
| 58 | El Harrouch vicinity                | 1856        | Shot, male, female                              | 1                      |                 | [65] |
| 59 | Beni Salah forest                   | 1856–1857   | Shot male & female, (shot 39 lions in his life) | 1                      | Ahmed Ben Amar  | [82] |
| 60 | Medjerda vicinity, Tunisia          | 1856–1857   | Male, cubs, shot female                         | 1                      | Ahmed Ben Amar  | [82] |
| 61 | Ain Taoura (vicinity of Souk Ahras) | 1856–1857   | 2 cubs, shot female                             | 1                      | Ahmed Ben Amar  | [82] |
| 62 | El Kala vicinity (now a NP)         | 1856–1857   | 4 cubs, shot female                             | 1                      | Ahmed Ben Amar  | [82] |
| 63 | Ain Temouchent area                 | Spring 1858 | Observation                                     | 1                      |                 | [83] |
| 64 | El Kef region, Tunisia              | 1858        | Numerous lions                                  | 1                      |                 | [84] |
| 65 | Azzaba vicinity                     | 1858        | Shot, 2   | 1                      |                 | [83] |
| 66 | Skikda-Azzaba                       | 1858        | Observation                                     | 0                      |                 | [83] |
| 67 | Berrahal                            | Winter 1858 | Tracks, roaring, 3                              | 1                      |                 | [85] |
| 68 | Oued Saf Saf - Oued Zergua          | Winter 1858 | Numerous lions                                  | 1                      |                 | [85] |
| 69 | Skikda-Azzaba                       | Autumn 1859 | Observation, tracks                             | 1                      |                 | [86] |
| 70 | Boghar forest                       | 1860        | Observations                                    | 1                      |                 | [87] |
| 71 | Tiaret                              | 1860        |   | 1                      | Leroux          | [73] |
| 72 | Mascara                             | 1860        |   | 1                      | Leroux          | [73] |
| 73 | Tazoult-Hammam Essalihine           | Winter 1860 | Shot male, (Shot 30 lions during his life)      | 0                      | Chassaing, F.   | [85] |

NP = one of several National Parks established across the region in the 1980s–1990s.  
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Algerian population and 1965 for the western (Morocco) population.

### 3.3 Change in Behavior

The frequency of observations, particularly after the 1920s, which involves solitary animals rather than groups (Tables 1–6), may be entirely due to a dwindling population with lower density or a potential change in social behavior (from group to solitary living). Owing to the uncertainty surrounding some sightings, and therefore the order of occurrence of single and group sightings of lions, we analyzed the date at the two extremes; all groups occurring as late as possible and then as early as possible (only relevant to the eastern population). For the western population  $D_{m,n} = 0.351$  compared with a critical value of 0.658 ( $N = 18$ ), so that we cannot reject the  $H_0$ , and suggest that there has been no change in behavior. Likewise for the eastern population no change in behavior was detected even though the inhabited areas are adjacent to human settlements;  $D_{m,n}$  ranged from 0.235 to 0.249 compared to a critical value for both of 0.250 ( $N = 121$ ).

### 3.4 Persistence of Lions

If we consider the gap size between sightings, lions appear able to persist whilst unseen by humans for at least a generation, if not two. A more rigorous analysis of gaps sizes for sightings is not possible due to ambiguity in some sighting dates. In the western Maghreb lions went unseen for 10 years, reducing to 3–5 years towards the end of the record. In the eastern Maghreb the gap sizes between later sightings were generally greater than 5 years, although precision is difficult owing to uncertainty in some dates. In one case the gap could be >10 years (1900s to 1910–1912).

### 3.5 Generations between Moroccan Royal Lions and Wild-caught Specimens

Current breeding animals in the Moroccan Royal Lion studbook [13] are separated from the Royal Palace animals by just four generations (in one case, three generations) and recent cubs [39] are five generations removed. Hemmer's [20] estimate of generations between wild ancestors and the lions in the Royal collection in the 1970s, would suggest that today's surviving descendants stand 25 generations from wild ancestors (Fig. 4). However, assuming a generation time of 6.5 years [36], our

**Table 4.** Lion sightings in the eastern Maghreb of Algeria and Tunisia, 1861–1880 (Ksour Mountains, Saharan Atlas, Tell Atlas, Ouled-Nail, Aurès Mountains).

|     | Location                              | Season/Year | Observation Type                             | Solitary (0)/Group (1) | Original source | Ref. |
|-----|---------------------------------------|-------------|--|------------------------|-----------------|------|
| 74  | Miliana vicinity                      | Winter 1861 | Observations, many lions                     | 1                      | French man      | [88] |
| 75  | Djebel Chaambi (now a NP), Tunisia    | Spring 1862 | Frequent lions                               | 1                      |                 | [89] |
| 76  | Sahel (Algiers vicinity)              | Winter 1862 | Shot   | 0                      | Chassaing, F.   | [90] |
| 77  | Tebessa mountains, Kasserine, Tunisia | 1863        | Few lions left on the steppes                | 1                      | Citation        | [73] |
| 78  | Nechmeya vicinity                     | Autumn 1863 | Observation                                  | 0                      |                 | [91] |
| 79  | Ourten valley                         | Autumn 1863 | Observations, lion spot                      | 1                      |                 | [91] |
| 80  | Tazoult vicinity                      | Autumn 1863 | Observation, lion killing a cow              | 1                      |                 | [91] |
| 81  | Mouzaia vicinity (Chr a NP)           | 1864        | Observation, male                            | 0                      | Le Tell         | [92] |
| 82  | Tebessa border                        | 1864        | Fresh tracks, roaring                        | 0                      |                 | [91] |
| 83  | Beni Salah forest                     | Spring 1865 | Citation                                     | 1                      |                 | [93] |
| 84  | Oued Zenati vicinity                  | Spring 1865 | Shot   | 0                      |                 | [93] |
| 85  | Djebel Riless                         | Summer 1866 | Shot, 3                                      | 1                      |                 | [66] |
| 86  | Azzaba vicinity                       | 1866        | Shot, male, female                           | 1                      |                 | [65] |
| 87  | Djebel Tangout                        | 1866        | Observation, male after burning forest       | 0                      |                 | [65] |
| 88  | Ras El Ma (Azzaba)                    | 1866        | Observation, male                            | 0                      |                 | [65] |
| 89  | Oued Saida                            | 1867        | Observations                                 | 1                      |                 | [94] |
| 90  | Djurdjura (now a NP)                  | 1867        | Observations                                 | 1                      |                 | [95] |
| 91  | Fetzara lake                          | 1867        | Observations                                 | 1                      |                 | [95] |
| 92  | Feriana, Tunisia                      | 1868        |  |                        | Monchicourt     | [73] |
| 93  | Ouarsensis                            | 1869        |  |                        | Leroux          | [73] |
| 94  | Djebel Bouarif (Aur s Mounts)         | 1869        | Winter refuge, observed and tracks also seen | 1                      |                 | [74] |
| 95  | Souk Ahras vicinity                   | 1873        | Shot, 5                                      | 1                      |                 | [54] |
| 96  | Djebel Bissa                          | Winter 1874 | Observation                                  | 0                      | El Mobacher     | [96] |
| 97  | Annaba vicinity                       | Spring 1875 | Observations                                 | 1                      |                 | [59] |
| 98  | Ain Mimoun (Aur s Mounts)             | Spring 1875 | Observations, 2 lions roaring                | 1                      |                 | [59] |
| 99  | Skikda vicinity                       | 1875        | Shot 6 lions                                 | 0                      | Cheret, C.      | [97] |
| 100 | Souk Ahras vicinity                   | 1877        | Shot, 3                                      | 1                      |                 | [54] |
| 101 | Souk Ahras vicinity                   | 1878        | Shot, 4                                      | 1                      |                 | [54] |
| 102 | Souk Ahras vicinity                   | 1879        | Shot, 5                                      | 1                      |                 | [54] |
| 103 | Tebessa forest                        | 1879        | Twenty lions killed/year                     | 1                      |                 | [98] |
| 104 | Souk Ahras vicinity                   | 1880        | Shot, 3                                      | 1                      |                 | [54] |
| 105 | Northwest Tunisia                     | 1880        | Four shot, one photographed                  | 1                      |                 | [99] |

NP = one of several National Parks established across the region in the 1980s–1990s.  
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analysis places today's Moroccan Royal lions as much closer descendants; with the youngest breeders only 16 generations removed from wild ancestors (Fig. 4).

## Discussion

Our analysis suggests that relatively recent sightings of lions (1940s and 1950s) are not exceptional. Whilst we corroborate recognized sightings in Morocco in the 1940s, we also suggest that lions persisted in Algeria into the late 1950s, nearly seventy years later than considered in previous reviews. Barbary lions experienced a combination of factors of decline consistent with the

threats to modern-day felids; habitat availability, wild prey availability, livestock husbandry and management, human behaviour, land use and socio-economics [40], [41].

A more recent extinction date for Barbary lions raises several questions: (a) how lions managed to persist in degraded North African ecosystems; (b) whether later persistence in North Africa provides insights for conserving marginal lion populations in West and Central Africa; (c) whether wild Barbary lions were more recently taken into captivity, making current animals closer descendants than previously considered.



**Table 5.** Lion sightings in the eastern Maghreb of Algeria and Tunisia, 1881–1900 (Ksour Mountains, Saharan Atlas, Tell Atlas, Ouled-Nail, Aurès Mountains).

|     | Location                            | Season/Year | Observation Type              | Solitary (0)/Group (1) | Original source   | Ref.  |
|-----|-------------------------------------|-------------|-------------------------------|------------------------|-------------------|-------|
| 106 | Djurdjura (now a NP)                | 1880–95     | Shot by French man            | 0                      |                   | [52]  |
| 107 | Aurès Mounts                        | 1880–95     | Shot                          | 0                      |                   | [52]  |
| 108 | El Kala (vicinity NP)               | 1880–95     | Several shot                  | 1                      |                   | [52]  |
| 109 | Souk Ahras vicinity                 | 1881        | Shot, 1                       | 0                      |                   | [54]  |
| 110 | Ain Drahem, Tunisia                 | 1881        | Observation                   | 1                      |                   | [54]  |
| 111 | Feidja (now a NP), Tunisia          | 1881        | Observation                   | 1                      |                   | [54]  |
| 112 | Khang el Melah (Djelfa)             | Summer 1881 | Citation                      | 1                      | Guy de Maupassant | [100] |
| 113 | Djebel Chelia (Aurès Mounts)        | 1884        | Last lions in cedar forest    | 1                      |                   | [52]  |
| 114 | Zaccar (Djelfa)                     | 1884        | Isolated kills                | 1                      |                   | [52]  |
| 115 | Tebessa                             | 1885        | Shot, male                    | 0                      |                   | [101] |
| 116 | Ksenna forest                       | 1886        | Observations                  | 1                      |                   | [102] |
| 117 | Ghardimaou, Tunisia                 | 1887        | Lions in forest               | 1                      | Lataste, 1887     | [99]  |
| 118 | Feriana/Medjerda forest, Tunisia    | 1887        |                               | 1                      | Lataste, 1887     | [99]  |
| 119 | Djebel Mssid vicinity               | 1887        |                               | 1                      | Lataste, 1887     | [99]  |
| 120 | Ghardimaou/Souk Ahras (border area) | 1888        | Shot, male                    | 0                      |                   | [103] |
| 121 | Seraidji (Edough Mount)             | Summer 1890 | Shot, young female            | 0                      |                   | [103] |
| 122 | Djedeida, Tunisia                   | 1890        | Drowned young lion in dam     | 0                      |                   | [52]  |
| 123 | Babouch (South Tabarka), Tunisia    | 1891        | Shot, male                    | 0                      |                   | [104] |
| 124 | Souk Ahras vicinity                 | 1891        | Shot male                     | 0                      |                   | [104] |
| 125 | Edough Mount                        | 1892        | Observations, full grown male | 0                      | Werner            | [52]  |
| 126 | Ain Beida                           | Spring 1893 | Shot male                     | 0                      | Langelet, P.      | [105] |
| 127 | Batna vicinity                      | 1893        | Shot female                   | 0                      |                   | [104] |
| 128 | Oued Sahel valley                   | 1893        | Observations                  | 1                      |                   | [106] |
| 129 | Isser Valley                        | 1893        | Observations                  | 1                      |                   | [106] |
| 130 | Sebaou valley                       | 1893        | Observations                  | 1                      |                   | [106] |
| 131 | Thabourt Bouzgueur                  | 1893        | Observations, Winter refuge   | 1                      |                   | [106] |
| 132 | Aurès Mounts                        | 1894        | Lion hunting a horse          | 0                      | Germaine Tillon   | [107] |
| 133 | Djebel Amour                        | 1898        | Numerous lions                | 1                      |                   | [108] |

NP = one of several National Parks established across the region in the 1980s–1990s.  
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#### 4.1. Recent Persistence of Lions in North Africa

Previous assumptions that lions have been absent from North African ecosystems for most of the past century is challenged by our analysis. We suggest that small populations persisted largely undetected by humans for several generations, indeed many decades. In Morocco, an inhospitable interior always made encounters with lions rare, whilst in Algeria sightings across the population's range occurred on an almost annual basis up to 1894, although thereafter less frequently than every 1 lion generation (6–7 years). Our calculation of the time of extinction ( $T_E$ ) corresponds with the recent suggestion that the last Barbary lion was probably lost in the destruction of forests north of Setif in 1958 during the French-Algerian War [25].

#### 4.2. Adaptation of Lions in North African Ecosystems

Up to the late 1800s, hunters reported lions traversing from northwest Algeria, westwards into Morocco and from northeastern Algeria eastwards into Tunisia [19]. After the 1880s, the pattern of sightings suggest that lion populations retreated broadly in two

directions; in Morocco southwards away from coastal regions through the Rif, Middle and High Atlas Mountains and the Saharan fringes; and in Algeria eastwards into the Tell Atlas and the Aurès Mountains bordering Tunisia. In both regions small populations survived at low densities in remote areas for several generations. Literature and oral accounts suggest that lions persisted through certain behavioral adaptations (hunting domestic livestock, engaging in nocturnal activity, living in small groups or pairs) and shifts in range (leaving deforested localities, moving to outlying areas and higher altitudes, and following water points in arid regions). Many of these particular behavioral adaptations have since been observed in contemporary populations of lions in human-dominated landscapes in sub-Saharan Africa [42], [43] as well as in restricted available habitat in India [11].

Our analysis of historical records in the Maghreb suggests that lions appear not to adapt their social behavior as a response to human habitat pressure. There was no significant change from group to solitary living by lions in the remote western Maghreb regions, whilst importantly even the eastern Maghreb lion

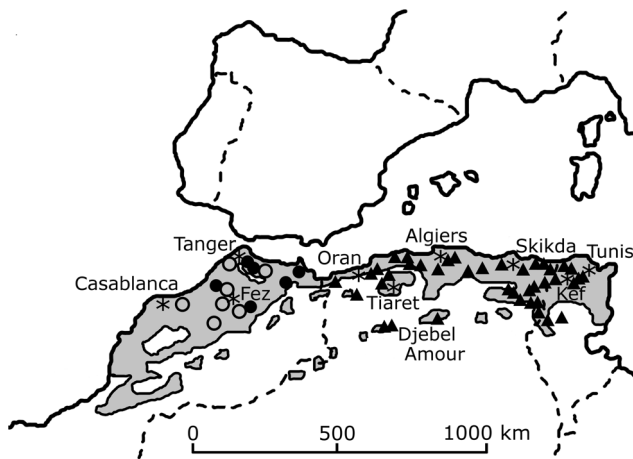
**Table 6.** Last lion sightings recorded in the eastern Maghreb of Algeria, 1900–1960 (Ksour Mountains, Saharan Atlas, Tell Atlas, Ouled-Nail, Aurès Mountains).

| Location                                      | Season/Year | Observation Type                    | Solitary (0)/Group (1) | Original source           | Citation Text S1      |
|---|-------------|-------------------------------------|------------------------|---------------------------|-----------------------|
| 134 Beni Salah (Chr ea NP vicinity)           | 1900's      | Observations                        | 1                      | Inhabitants of Beni Salah | [109]                 |
| 135 Zaccar-AinTorki                           | 1910–12     | Observations                        | 0                      | MrsDedreuil-Paulet        | Difallah, pers. comm. |
| 136 Aur s Mounts                              | 1911        | Shot, Male, female                  | 1                      | Sassorossi family         | [107]                 |
| 137 Bejaia vicinity                           | 1912        | Shot                                | 0                      |                           | [110]                 |
| 138 Ain Sefra                                 | 1912        | Shot                                | 0                      | Khazene, A,               | Fellous, pers. comm.  |
| 139 Biskra (lion probably from Aur s ranges)  | 1917        | Old lion                            | 0                      | Seen by the writer        | [111]                 |
| 140 Djebel Tameda, south of Boussemgghoun     | c.1920      | Last lion shot in the Saharan Atlas | 0                      | Gueniche Ahmed            | Bahmane L to Fellous  |
| 141 Between Ain Talawane and Ain Roua (Setif) | Late 1920s  | Observation (in spring)             | 1                      | Report by old man         | Difallah, pers. comm. |
| 142 Guenzet-Babor Mount (North Setif)         | 1930        | Observation                         | 0                      | Interview local people    | [112]                 |
| 143 North Setif                               | 1930        | Observations                        | 1                      | Interview local people    | [112]                 |
| 144 DjebelDirah (Sour El Ghozlane)            | 1930s       | Shot                                | 0                      | Kalem, pers. comm.        | Fellous               |
| 145 Boussam (Menaceur-Zaccar mounts)          | Winter 1935 | Male lion shot attacking a cow      | 0                      | Bounaceur Farid           | Fellous               |
| 146 Djebel es Somm (Djebel Amour)             | 1935        | Male lion attacked a camel          | 0                      | Hamami Bachir             | Fellous               |
| 147 Unknown location in Algeria               | 1943        | Shot                                |                        | Keeling, pers. comm.      | [113]                 |
| 148 North Setif                               | Late 1940s  | Observations                        | 1                      | Interview local people    | Difallah, pers. comm. |
| 149 Beni Ourtilane (North of Setif)           | 1956        | Observation                         | 0                      | People on a bus           | [112]                 |

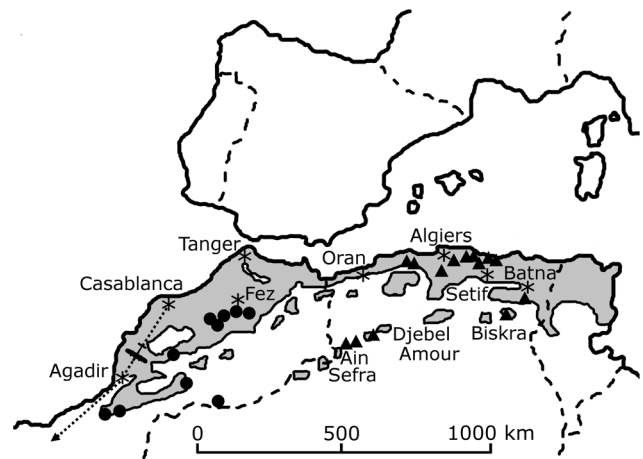
doi:10.1371/journal.pone.0060174.t006

populations did not exhibit a significant change in group living in the final decades of their existence, despite increasing encroachment by human populations. Although lion population density is typically lower in desert and semi-desert areas, pride size generally

remains comparable in desert ecosystems and moister ecosystems with higher lion density [22]. Interestingly, human presence has been shown to provide advantages to lion cub survival by



**Figure 1. Distribution of historical reports of lions in North Africa (AD 1500–1900).** Grey shading indicates Mediterranean scrubland ecosystems [8]. Earliest accounts in the western Maghreb from 16<sup>th</sup> to the 18<sup>th</sup> century are indicated as open circles [7], [19]. Documented sightings in known years from 1800 to 1900 are indicated as black circular markers in the western Maghreb (1–7 in Table 1); triangular markers indicate sightings in eastern Maghreb (22–133 in Tables 2–6). Asterisks (\*) denote locations of human population centers. Dashed lines indicate national boundaries.  
doi:10.1371/journal.pone.0060174.g001

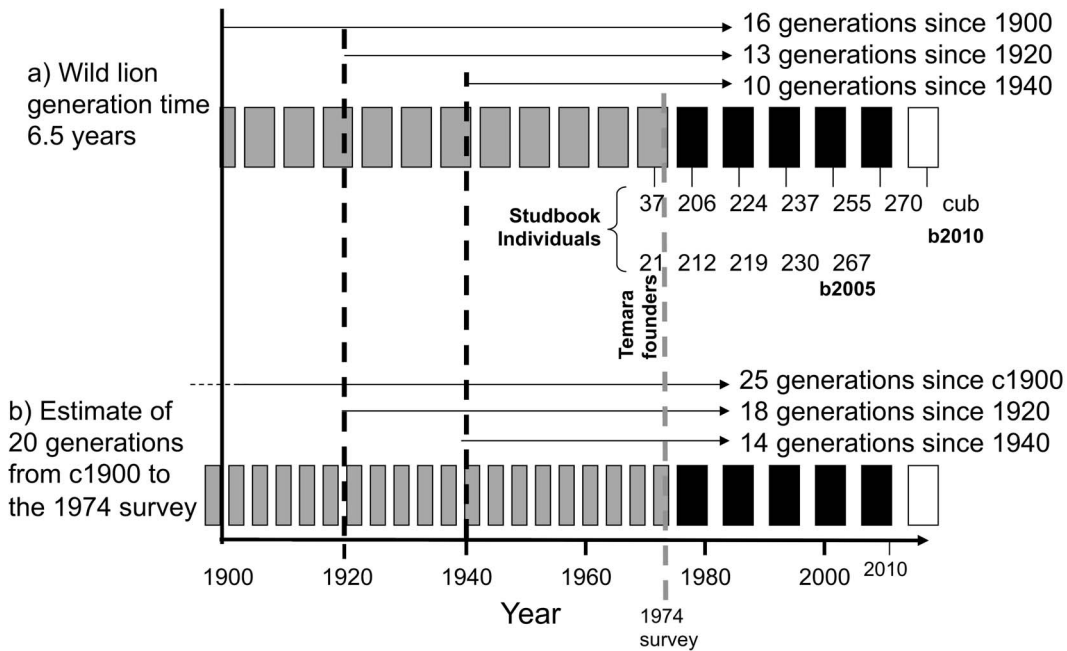


**Figure 2. Distribution of recent sightings of lions in North Africa (AD 1900–1960).** Grey shading indicates Mediterranean scrubland ecosystems [8]. Circular markers indicate sightings in western Maghreb (8–21 in Table 1); triangular markers indicate sightings in eastern Maghreb (134–149) from incidents described in Table 6. The dotted line indicates the air route across the Atlas Mountains (Casablanca–Agadir–Dakar) during which the last wild lion was photographed. Asterisks (\*) denote locations of human population centers. Dashed lines indicate national boundaries.  
doi:10.1371/journal.pone.0060174.g002





**Figure 3. A lion seen in the Atlas Mountains, during a flight on the Casablanca-Dakar air route.** The photograph taken by Marcelin Flandrin in 1925 is the last visual record of a wild 'Barbary' lion of North Africa.  
doi:10.1371/journal.pone.0060174.g003



**Figure 4. Estimates of captive generations since wild collection in North Africa for current Moroccan Royal lions.** Grey boxes indicate estimated lion generations based on suggestions by: (a) Packer et al. [38], and (b) Hemmer [20]. Black boxes are the five known generations in the European studbook [13] since the 1974 survey at Temara Zoo. Generational positions for two studbook maternal lines are illustrated for a female cub (white box) born to studbook female 270, and a young male (267) born to female 230, tracing to founder females 37 and 21 respectively.  
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removing secondary predators [44], and this may have enabled lion persistence in the Maghreb.

Final extirpation of lions through hunting was a response to livestock predation; a prey dependency probably driven by reduced habitat and fewer wild ungulates [18]. This final collapse may have been exacerbated by the species' behavioral need to remain in social groups with proportionally greater local resource requirements. Group living has been shown to be similarly maintained by lion populations in semi-arid environments such as the Kalahari and Etosha [45] [46]. In contrast, leopards (*Panthera pardus*) still persist at lower population densities in Morocco [1].

### 4.3 Heritage of Moroccan Royal Lions

Moroccan Royal Lions have been described as “an obvious relic of the original Barbary lion gene pool” [20]. Our analysis suggests fewer post-wild generations have occurred during the period where this population has existed solely in captivity. Today's lions, descended from the Moroccan Royal collection, could be closer relatives to wild ancestors than previously considered. In the absence of definitive nuclear DNA profiles from wild Barbary lion specimens, the precautionary principle suggests that Moroccan Royal lions should be conserved as descendants of the Barbary lion until science can tell us otherwise. The Moroccan Royal lions offer one of the few scenarios in which restoration of lions into regions where the species is long extinct could be envisioned as having useful conservation value [47].

### Conclusions

Insights from historical sightings are relevant to current lion conservation. We suggest that wild lions persisted in the Maghreb into the 1950s, much later than previously recognized. The lion is a well-known, visible and potentially threatening species, yet small populations survived in North Africa decades after being generally

considered extinct. This persistence reflects the recent rediscovery of a small population of Barbary leopard nearly 20 years after the last previous sighting and a decade since being declared extinct [1] [48]. Careful consideration should be given to mammalian carnivores currently presumed extinct or near-extinct in other regions, coupled with a greater understanding of extinction patterns and the conservation potential in relict populations.

Finally, we suggest caution when considering the current conservation status of lions. Although lions in the Maghreb adapted to reduced population density, prey availability and habitat encroachment, our analysis reveals that lion group-living behavior did not change significantly as human pressures increased. As a pride-forming species [45], *P. leo* populations are prone to collapse, whereas other felids may survive at lower local population densities by not living in social groups [49]. Lions in today's small populations in Central and West Africa persist [16] [50], even if rarely seen, in fragmented remnants, yet clearly exist at the edge of a precipitous drop into extinction. Continued, carefully considered conservation effort remains vitally important.

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### Author Contributions

Conceived and designed the experiments: SAB AF NY DLR. Performed the experiments: SAB AF DLR. Analyzed the data: SAB DLR. Contributed reagents/materials/analysis tools: SAB AF DLR. Wrote the paper: SAB AF NY DLR.

### References

- Henschel P, Hunter L, Breitenmoser U, Purchase N, Packer C, et al. (2008) *Panthera pardus*. In IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4. (Accessed 28 February 2011: <http://www.iucnredlist.org/details/15954/0>).
- Can OE (2004) Status, conservation and management of large carnivores in Turkey. Convention on the Conservation of European Wildlife and Natural Habitats, Standing Committee Meeting 24, 29<sup>th</sup> November-3<sup>rd</sup> December, T-PVS/Inf(2004) 8. Strasbourg: Council of Europe.
- Karanth KU, Chellum R (2009) Carnivore conservation at the crossroads. *Oryx* 43: 1–2.
- IUCN (2012) IUCN Red List of Threatened Species. Version 2012.1. (Accessed 26 June 2012: [www.iucnredlist.org](http://www.iucnredlist.org)).
- Tumenta PN, Kok JS, van Rijssel JC, Buij R, Croes BM, et al. (2009) Threat of rapid extermination of the lion (*Panthera leo leo*) in Waza National Park, Northern Cameroon. *Afr. J. Ecol.* 48: 888–894.
- Burton AC, Sam MK, Kpelle DG, Balangtaa C, Buedi EB, et al. (2011) Evaluating persistence and its predictors in a West African carnivore community. *Biol. Conserv.* 144: 2344–2353.
- Guggisberg CAW (1963) Simba: the life of the lion. London: Bailey Bros. and Swinfen.
- Dobson M (1998) Mammal distributions in the western Mediterranean: the role of human intervention. *Mammal Rev* 28: 77–88.
- Barnett R, Yamaguchi N, Shapiro B, Sabin R (2008) Ancient DNA analysis indicates the first English lions originated from North Africa. *Contributions to Zoology* 77: 7–16.
- Masseti M (2010) Holocene mammals of Libya: A biogeographical, historical and archaeozoological approach. *J Arid Env* 74: 794–805.
- Nowell K, Jackson P (1996) Wild cats, status survey and conservation action plan. Gland: IUCN/SSC Cat Specialist Group.
- Patterson BD (2007) On the nature and significance of variability in lions (*Panthera leo*). *Evol Biol* 34: 55–60.
- Black S, Yamaguchi N, Harland A, Groombridge J (2010) Maintaining the genetic health of putative Barbary lions in captivity: an analysis of Moroccan Royal Lions. *Eur J Wildl Res* 56: 21–31.
- Barnett R, Yamaguchi N, Barnes I, Cooper A (2006) The origin, current diversity and future conservation of the modern lion (*Panthera leo*). *Proc R Soc Lond B Biol Sci* 273: 2119–2125.
- Mazák JH (2010) Geographical variation and phylogenetics of modern lions based on craniometric data. *J Zool* 281: 194–209.
- Bauer H, Nowell K, Packer C (2008) *Panthera leo*. Gland, Switzerland: IUCN Red List of Threatened Species. Version 2010.4 (Accessed 16 November 2010: <http://www.iucnredlist.org/apps/redlist/details/15951/>).
- Breitenmoser U, Mallon DP, Ahmad Khan J, Driscoll C (2008) *Panthera leo ssp. persica*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1. (Accessed 23 August 2012: <http://www.iucnredlist.org/details/15952/0>).
- Cuzin F (2003) Les grands mammifères du Maroc méridional (Haut Atlas, Anti Atlas et Sahara): distribution, écologie et conservation. PhD thesis, Université Montpellier.
- Cabrera A (1932) Los mamíferos de Marruecos. *Seria Zoologica*. Madrid: Trabajos del Museo Nacional de Ciencias Naturales.
- Hemmer H (1978) Grundlagen und derzeitiger Stand des Zuchtprogrammes zur Rückerhaltung des Berberlöwen (*Panthera leo leo*). In: Seifurt S, Müller P, editors. Congress Report, 1st International Symposium on the Management and Breeding of the Tiger, 11<sup>th</sup> and 12<sup>th</sup> October 1978 in Leipzig, Abb. 1. Zoological Garden. Leipzig: International Tiger Studbook. 65–72.
- Johnston HH (1911) Tunisia. *The Encyclopedia Britannica*, 11<sup>th</sup> Edition, vol. 27. Cambridge: Cambridge University Press.
- Celesia GC, Peterson AT, Peterhans JCK, Gnoske TP (2009) Climate and landscape correlates of African lion (*Panthera leo*) demography. *Afr J Ecol* 48: 58–71.
- Jhala YV, Mukherjee S, Shah N, Chauhan KS, Dave CV, et al. (2009) Home range and habitat preference of female lions (*Panthera leo persica*) in Gir forests, India. *Biodivers Conserv* 18: 3383–3394.
- Visser HD, Müller L, Tumenta PN, Buij R, de Iongh HH (2009) Factors affecting lion (*Panthera leo*) home range, movement and diet in Waza National Park, Cameroon. *J Zool* 300: 131–142.
- Barnett R, Yamaguchi N, Shapiro B, 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: 87–94.
- Bartosiewicz L (2009) A lion's share of attention: archaeozoology and the historical record. *Acta Archaeologica Academiae Scientiarum Hungaricae*. doi 10.1556/AArch.59.2008.2.28

27. Schnitzler AE (2011) Past and present distribution of the North African-Asian lion subgroup: a review. *Mammal Rev* 41: 220–243. doi 10.1111/j.1365–2907.2010.00181.x.
28. Bowkett AE (2009) Recent captive-breeding proposals and the return of the ark concept to global species conservation. *Conserv Biol* 23:773–776. doi 10.1111/j.1523–1739.2008.01157.x.
29. Gippoliti S (2012) *Ex situ* conservation programmes in European zoological gardens: Can we afford to lose them? *Biodivers Conserv* 21: 1359–1364. doi 10.1007/s10531-012-0256-8.
30. Dubach J, Patterson BD, Briggs MB, Venzke K, Flamand J, et al. (2005) Molecular genetic variation across southern and eastern geographic ranges of the African lion, *Panthera leo*. *Conserv Genet* 6: 15–24.
31. Antunes A, Troyer JL, Roelke ME, Pecon-Slattery J, Packer C, et al. (2008) The evolutionary dynamics of the lion *Panthera leo* revealed by host and viral population genomics. *PLoS Genetics* 4: 11: e1000251.
32. Bertola LD, van Hooft WF, Vrieling K, Uit de Weerd DR, York DS, et al. (2011) Genetic diversity, evolutionary history and implications for conservation of the lion (*Panthera leo*) in West and Central Africa. *J Biogeogr* 38: 1356–1367.
33. Solow AR (2005) Inferring extinction from a sighting record. *Math Biosci* 195: 47–55.
34. Vogel RM, Hosking JRM, Elphick CS, Roberts DL, Reed JM (2009) Goodness of fit of probability distributions for sightings as species approach extinction. *Bull Math Biol* 71: 701–719 doi 10.1007/s11538-008-9377-3.
35. Siegel S, Castellan Jr NJ (1988) *Nonparametric statistics for the behavioral sciences*, 2<sup>nd</sup> Ed. New York: McGraw-Hill Book Company.
36. Packer C, Pusey AE, Eberly LE (2001) Egalitarianism in female African lions. *Science* 293: 690–693.
37. Black S, Harland A (2009) Moroccan Royal Lions: justification for a new EEP to support lion sub-species conservation. Paper presented at Felid TAG Meeting, Copenhagen, Denmark: Proceedings of the 26<sup>th</sup> Annual EAZA Conference, 17<sup>th</sup> September.
38. Davies RAG (1964) *A history of the world's airlines*. Oxford: Oxford University Press.
39. Zoo-Olomouc (2010) Přírůstky 6.8.2010 Lev berberský. Czech Republic: Olomouc Zoo (Accessed 21 March 2012: [http://zoo-olomouc.cz/app/sekce/23/prirustky?articles\[offset\]=40](http://zoo-olomouc.cz/app/sekce/23/prirustky?articles[offset]=40)).
40. Bauer H, de Iongh H, Sogbohossou E (2010) Assessment and mitigation of human-lion conflict in West and Central Africa. *Mammalia* 74: 363–367.
41. Inskip C, Zimmermann A (2009) Human-felid conflict: a review of patterns and priorities worldwide. *Oryx* 43: 18–34.
42. Mogensen NL, Ogutu JO, Dabelsteen T (2011) The effects of pastoralism and protection on lion behaviour, demography and space use in the Mara Region of Kenya. *African Zool* 46: 78–87.
43. Valeix M, Hemson G, Loveridge AJ, Mills G, Macdonald DW (2012) Behavioural adjustments of a large carnivore to access secondary prey in a human-dominated landscape. *J App Ecol* 49: 73–81.
44. Kissui BM, Mosser A, Packer C (2010) Persistence and local extinction of lion prides in the Ngorongoro Crater, Tanzania. *Popul Ecol* 52: 103–111.
45. Yamaguchi N, Cooper A, Wedelin L, Macdonald DW (2004) Evolution of the mane and group-living in the lion (*Panthera leo*): a review. *J Zool Lond* 263: 329–342.
46. Sunquist ME, Sunquist F (2002) *Wild cats of the World*. Chicago: University of Chicago Press.
47. Hunter TB, White P, Henschel P, Frank L, Burton C, et al. (2013) Walking with lions: why there is no role for captive-origin lions *Panthera leo* in species restoration. *Oryx* 47: 19–24.
48. Agencia EFE (2010) Hallan una población de leopardos que se daba por extinguida en el Magreb. (Accessed 28 February 2011: <http://www.telecinco.es/informativos/cultura/noticia/1274139/1274139>).
49. Courchamp F, Clutton-Brock T, Grenfell B (1999) Inverse density dependence and the Allee effect. *Trends Ecol Evol* 14: 405–410.
50. Henschel P, Azani D, Burton C, Malanda G, Saidu Y, et al. (2010) Lion status updates from five range countries in West and Central Africa. *Cat News* 52: 34–39.
51. Drummond-Hay JH (1861) *Morocco and the Moors*. Western: its tribes and savage animals. London: Murray.
52. Guggisberg CAW (1963) *Simba: the life of the lion*. London: Bailey Bros and Swinfen.
53. Schnitzler AE (2011) Past and present distribution of the North African-Asian lion subgroup: a review. *Mammal Rev* 41: 220–243.
54. Lavauden L (1932) Les grands félins de l'Afrique du Nord et leur disparition. *Le Chêne. Soc. Forestière Méditerranéenne et Coloniale*. N°4 Janvier: 208–234.
55. Grzimek B (1975) The lion, In Grzimek, B. (Ed.), *Grzimek's Animal Life Encyclopedia*, vol. 12, Mammals III. Van Nostrand Reinhold, New York, 353.
56. Yadav PR (2004) *Vanishing and endangered species*. New Delhi: Discovery Publishing House.
57. Black S (2008) Investigating the feasibility of reintroducing lions (*Panthera leo*) as a flagship for the Moroccan Atlas Mountains. MSc thesis, University of Kent.
58. Panouse JB (1957) Les mammifères du Maroc. *Trav Inst Sci Chérif Sér Zool* n°5. Rabat. 206 p.
59. Playfair RL (1877) *Travels in the footsteps of Bruce in Algeria and Tunis*. London: G. Kegan Parl & Co.
60. Dumas E (1855) *Moeurs et coutumes de l'Algérie*. Paris: Sind bad Bibliothethequearabe.
61. Roches L (1904) *Dix ans à travers l'Islam, 1834–1844*. Paris: Librairie Academique Didier.
62. Carette E (1844) *Exploration scientifique de l'Algérie pendant les années 1840–1841–1842*. Paris: Imp Roy Tome II: 355.
63. Gerard J (1864) *Chasse au lion*. Cie Editeurs. Québec: JN Duquest.
64. Scott KC (1842) *A journal of residence in the Esmaila of Abd-El-Kader*. London: Whittaker & Co.
65. Fenech EV (1867) *Récits et chasses d'Algérie*. Typographie Denis Aimé.
66. Marguerite A (1869) *Chasses de l'Algérie et notes sur les arabes du Sud*. 1ère édition. Paris: JouvettEditeurs.
67. Bloch A (2002) *Miliana par les textes*. Algiers, Editions Zyriab.
68. Dumas E (1845) *Le sahara Algérien*. Paris: Langlois & Leclercq.
69. Anon. (1845) *Journal des haras, des chasses et des courses de chevaux*. Imprimerie Parent Tome III. Bruxelles.
70. Kennedy JC (1846) *Algeria and Tunis in 1845*. Vols I & II. London: H Colburn Publisher.
71. Gerard J (1892) *Le tueur de lions*. Paris: Paris librairie Hachete & Cie.
72. Saint Marie C (1846) *Algeria in 1845. A visit to a French possessions in Africa*. London: R Bentley.
73. de Planhol X (2004) *Le paysage animal. L'homme et la grande faune: une zoogéographie historique*. Paris: Fayard.
74. Palisser G (1982) *Les lions et panthères dans le Sahel. L'Algérieniste* n°20, Décembre, Narbonne, France.
75. Lestiboudois T (1853) *Voyage en Algérie, ou études sur la colonisation de l'Afrique française*. Lille: Imp Danel.
76. Saint Arnaud AJL (1864) *Lettres du maréchal de saint Arnaud. 1832–1854*. 3 ème édition. Paris: M Levy frères.
77. Gerard J (1859) *La chasse au Lion*. Paris: Paris Librairie nouvelle.
78. Dufour L (1856) *Notice sur un lion tué en Algérie. Examen necroscopique*. Paris: H & C Noblet Imprimerie.
79. D'Esschavannes MJ (1852) *Revue de l'Orient, de l'Algérie et des colonies*. Paris: Rouvé J Tome XII: 221–222.
80. Bombonnel CL (1893) *Bombonnel, le tueur de panthères, ses chasses racontées par lui même*. 7eme édition, Paris: Librairie Hachette.
81. Anon. (1860a) *The hunting grounds of the Old World*. London: Sanders Otley & Co.
82. Gastineau B (1863) *Chasses au Lion et à la Panthère en Afrique*. Paris: Paris Librairie Hachette.
83. Blakesley JW (1859) *Four months in Algeria: with a visit to Carthage*. London: MacMillan & Co.
84. Dunant JH (1858) *Notice sur la régence de Tunis*. Genève: Imprimerie Jules Fick.
85. Anon. (1860b) *Journal des chasseurs*. Vol. 24, 2eme sem, mai-octobre: 239–248.
86. Thierry-Mieg C (1861) *Six semaines en Afrique, souvenirs de voyage*. Paris: M Levy frères.
87. Bernard A, Lacroix N (1906) *L'évolution du nomadisme en Algérie*. Alger: Edition Jourdan.
88. Windham WG (1862) *Notes in North Africa: guide to the sportsman and tourist in Algeria and Tunisia*. London: Ward & Lock.
89. Guerin V (1862) *Voyage archéologique dans la régence de Tunis*. Paris: TI Plon.
90. Baroli M (1967) *La vie quotidienne des français d'Algérie (1830–1914)* Paris: Librairie Hachette.
91. Ormsby J (1864) *Autumn rambles in North Africa*. London: Longman & Green.
92. Anon. (1936) *Revue Chasse et pêche Nord Africaines*. Mars n° 48: 7.
93. Carteron C (1866) *Voyage en Algérie*. Paris: J Hetzel Librairie.
94. Berard V (1867) *Indicateur general de l'Algérie*. Alger: Typo Bastide, 3eme edit. 600 p.
95. Loche V (1867) *Histoire naturelle des mammifères*. Paris: Arthis Bertrand Editeur.
96. Tounsi G (1998) *Un lion surgit dans la tribu des Sinfita à Tenès*. Evocation. *Journal Le Jeune Indépendant* N°14 du 25 au 31 mars. 24 p.
97. Simmonds PL (1877) *Animal Products: their preparation, commercial uses, and value*. London: Chapman & Hall. 416 p.
98. Bourde P (1880) *A travers l'Algérie*. Souvenirs de l'excursion parlementaire, septembre-octobre 1879. Paris: G Charpentier.
99. Gharaibeh BM (1997) *Systematics, distribution, and zoogeography of mammals in Tunisia*. PhD thesis, Texas Tech University, Lubbock.
100. Emmanuel J (2003) *Maupassant, guy, sur les chemins d'Algérie (1881–1890)*. Paris: Magella & Cie.
101. Lataste F (1885) *Étude de la faune des vertébrés de Barbarie (Algérie, Tunisie et Maroc)*. Actes de la Société Linnéenne de Bordeaux 39: 129–289.
102. Robert G (1891) *Voyage à travers l'Algérie: notes et croquis*. Paris: Imprimerie de G Rougier.
103. Seurat LG (1924) *Zoologie forestière de l'Algérie*. Alger: Direction des Forêts.
104. Lavauden L (1926b) *Les vertébrés du Sahara*. Tunis: Imp A Guénard.
105. Anon. (1893) *Rubrique annonce*. Le Chenil, n°12 du 23 mars: 137–138.
106. Hanoteau A, Lctourneau A (1893) *La kabylie et les coutumes kabyles*. Tome I. Paris: Imprimerie Nationale.
107. Anon. (1898) *La revue hebdomadaire*. Paris: Librairie Plon. 378 p.

108. Martin JP (2006) *Le Belezma: au forgeron de Batna*. Paris: L'Harmattan.
109. Desparmet J (1939) *Coutumes, institutions, croyances des indigènes de l'Algérie*. Tome I, Imprimerie Alger, La typo-litho and J Carbonel.
110. De Smet K (1982) La disparition des grands fauves en Algérie. *Bull Forest Conserv Nat Alger* 1: 23–25.
111. Ossendowski FA (1927) *The breath of the desert: the account of a journey through Algeria and Tunisia* (translated by Palen LS). London: George Allen and Unwin.
112. Haddadou MA (1994) *L'Algérie mystérieuse*. Alger.
113. Yamaguchi N, Haddane B (2002) The North African Barbary lion and the Atlas lion project. *International Zoo News* 49: 321.