

Inventory of free-ranging lions *Panthera leo* in Africa

H. Bauer and S. Van Der Merwe

Abstract The number of free ranging African lions *Panthera leo* has never been comprehensively assessed. We present an inventory of available information, covering most protected areas and ranging in quality from educated guesses to individually known populations. This gives a conservative estimate of 16,500–30,000 free ranging lions in Africa. The inventory shows that popu-

lations are small and fragmented in West and Central Africa, whereas the species still occurs widely in East and Southern Africa. The results concur with the current IUCN Red List categorization of the lion as Vulnerable.

Keywords Africa, inventory, lion, *Panthera leo*, Red List.

Introduction

Lions *Panthera leo* once roamed large parts of Africa, Europe, the Middle East and Asia. They disappeared from Europe during the first century AD and from North Africa, the Middle East and Asia between 1800 and 1950, except for one population of the subspecies *P. leo persica* in India. Lions are today found in savannah habitats across sub-Saharan Africa (Nowell & Jackson, 1996).

The African lion is classified as Vulnerable on the IUCN Red List, with agriculture, human settlement and poisoning indicated as the main threats (IUCN, 2002). This classification was partly based on an educated guess of between 30,000 and 100,000 free ranging lions (Nowell & Jackson, 1996). The large margin was justified by lack of information and the difficulty of conducting lion censuses (Loveridge *et al.*, 2001; Mills *et al.*, 2001). The African Lion Working Group, affiliated with IUCN, took the initiative to gather the available information for a more precise estimate, and this paper presents the results of this exercise.

Methods

Requests for information were sent to researchers, wildlife departments and conservationists, and an information sharing workshop for West and Central Africa was organized in Cameroon in 2001 (Bauer *et al.*, 2001). Information gaps were filled by specific requests to

individuals or conservation networks. In total nearly 100 people provided information. Information was also obtained from relevant literature, but data >10 years old were not included. The inventory is thus based on existing information, except for Zambia, which was surveyed especially for this inventory.

Individuals contacted were requested to indicate their method of estimation and an estimate of lion numbers (in 2001 or 2002 unless indicated otherwise) with an indication of minimum and maximum values. In a few cases these values were 95% confidence limits, but most sources could only indicate the lowest and highest conceivable estimate. For a few areas we had estimates from two or three equally authoritative sources; we included the mean estimate with the extreme values and indicated both sources. If minimum and maximum values were not provided, they were generated depending on the method of estimation, using a percentage of the estimate, viz:

1. Estimate $\pm 10\%$, based on a total count, with all lions in an area individually identified by features such as whisker spots, scars and nose colour (Pennycuik & Rudnai, 1970). This is the most accurate census method.
2. Estimate $\pm 20\%$, based on total or sample area inventory with the aid of calling stations, with or without bait, using hyaena and/or prey sounds to attract lions. Calling station methods and precision vary between areas and researchers; confidence limits were reported to be 3% in the Masai Mara National Reserve (Ogutu & Dublin, 1998), but these limits are expected to be higher under most conditions, and up to 90% depending on habitat (Mills *et al.*, 2001).
3. Estimate $\pm 30\%$, based on mark-recapture experiments, use of radio collars and tourist picture databases (Smuts *et al.*, 1977; Creel & Creel, 1997; Loveridge *et al.*, 2001); most studies in this category combine several of these methods. Spoor counts are included in this category, but the methodology has to be further developed to improve accuracy and precision (Stander, 1998).

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4. Estimate $\pm 40\%$, with estimate based on fieldwork and an informed guess by a resident researcher with intimate knowledge of an area, preferably based on prey censuses.

5. Estimate $\pm 50\%$, with a 'best guess' based on short visits and secondary data, such as prey or hyaena numbers, size of area, rainfall and other factors (East, 1984; Van Orsdol *et al.*, 1985).

6. Minimum and maximum values specified by the source, with other methods of estimation or information obtained under special circumstances.

Counts based on aerial, dung and roaring surveys were considered inappropriate methods and were not included. We present subtotals and totals under 5,000 rounded to the nearest 50 and over 5,000 to the nearest 500.

Results

The results for each protected area, ecosystem or region are presented in Table 1 and the geographical distribution of lions is illustrated in Fig. 1. The estimate for West and Central Africa together was 1,800, with all populations being small and fragmented over the region. As few systematic surveys have been carried out in this part of the continent the information is mostly based on best guesses. The estimate for East Africa was 11,000, with the continent's two largest populations in the Serengeti and Selous ecosystems of Tanzania. The estimate for

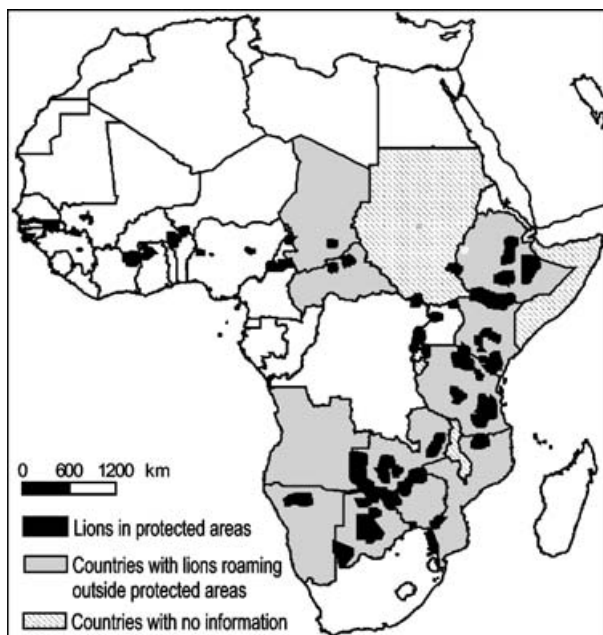


Fig. 1 Map of Africa illustrating the location of lion populations. Protected areas with lions, as listed in Table 1, are in black, and countries with substantial numbers of lions outside protected areas are in grey. Information in Table 1 that has no specific geographic denomination is not illustrated.

Southern Africa was 10,000, with the majority in Botswana and South Africa. Methods 1 to 3, with minimum and maximum values of 10–30% of the estimate, accounted for *c.* 30% of the total continental estimate of 23,000 lions, and 70% was established with methods 4 to 6, with minimum and maximum values of 40–50% or as specified by the source. The estimated minimum and maximum values of the total lion population were 16,500 and 30,000, respectively.

Discussion

Some figures in Table 1 are marked as disputed. In the case of Kruger National Park, the source stated that minimum and maximum values were inappropriate for the research conditions (G. Mills, pers. comm.). S. Creel (pers. comm.) provided an estimate for the Selous population, despite the paucity of data; C. Packer and J. Scott (pers. comm.) questioned the figure but did not propose an alternative and agreed that the estimate reflected the true order of magnitude. For the Central Kalahari area, P. Funston (pers. comm.) estimated the lion population at 517, higher than the estimate of the Botswana Department of Wildlife and National Parks. J. Anderson (pers. comm.) stated that the last two lions in Odzilla National Park, Congo, were shot in 1994, but C. Aveling (pers. comm.) reported that there could still be up to 25 individuals. Nowell & Jackson (1996) stated that lions were extinct in Gabon whereas some sources suggested that there may be lions on the Bateke Plateau. A recent survey in that area found that the last lion was shot in 1999. A few small savannah patches near Mpassa were not surveyed; these could theoretically contain 0–10 lions (P. Henschl, pers. comm.). For Niokolo Koba National Park, Senegal, the warden indicated that the only figure ever published, 120 in 1977, should be listed (Dupuy & Verschuren, 1977; I. Diop, pers. comm.). Another source, however, estimated the population at 20, based on extensive travel and interviews in 2001 (O. Burnham, pers. comm.). A third source used several methods and estimated 50–150 lions in 1996 (I. Di Silvestre, pers. comm.).

The results, based on extensive enquiries and estimates of differing degrees of precision, were obtained for all but a few areas, listed in Table 1 as "not available" or "present, not estimated". Of these areas, we expect the Ruaha and Tarangire ecosystems in Tanzania to contain substantial numbers of lions. The other areas have been described as depleted of natural resources (East, 1999) and therefore we expect their lion populations to have a marginal impact on the total estimate. Many rural non-protected areas in East and Southern Africa contain lions (G. Mills, pers. comm.), in contrast to West and Central Africa (Bauer *et al.*, 2003). Some of these areas were included but others have never been surveyed, although

Table 1 Estimates of lion populations in Africa, for 2001/2002 unless indicated otherwise, with minimum and maximum estimates, the method used for estimation (see text for details), and the data source (individuals or reference). Lions in conservation areas adjacent to National Parks were included in the figures for the Parks. Some contiguous protected areas were designated by the name of the most prominent area followed by 'ecosystem'.

Country or region	Ecosystem, location or National Park (NP) (area in km ²) ¹	Estimate	Min.	Max.	Estimation method (pers. comm. or reference)
North Africa	All ecosystems	0	0	0	6 (Nowell & Jackson, 1996)
Benin	Pendjari ecosystem (6,505)	45	39	52	2 (I. Di Silvestre, A. Tehou)
Benin	Remainder	20	12	28	4 (A. Tehou)
Burkina Faso	Arly-Singou ecosystem (6,388)	100	50	150	5 (P. Bouche, H. Bauer)
Côte d' Ivoire	Comoe NP (11,500)	30	15	45	5 (F. Fischer, H. Bauer)
Gambia	National	0	0	0	5 (H. Bauer)
Ghana	Gbele Reserve (1,226)	10	6	14	4 (Ghana Wildlife Society)
Ghana	Mole NP (4,921)	20	12	28	4 (Ghana Wildlife Society)
Guinea	Guinea-Mali Protected Area	120	60	180	5 (A. Oulare)
Guinea	Remainder	80	40	120	5 (A. Oulare)
Guinea-Bissau	Doulombi / Boe NP (1,500)	30	15	45	5 (D. Fai)
Liberia	National	0	0	0	5 (Garnett & Utas, 2000)
Mali	National	50	25	75	5 (Moriba)
Mauritania	National	0	0	0	6 (Nowell & Jackson, 1996)
Niger	"W" NP (2,977)	70	49	91	3 (Moussa & P. Gay)
Nigeria	National	200	100	300	5 (P. Jenkins)
Senegal	Niokolo Koba ecosystem ² (19,130)	60	20	150	6 (O. Burnham, I. Diop & I. Di Silvestre)
Sierra Leone	National	0	0	0	5 (Garnett & Utas, 2000)
Togo	National	0	0	0	6 (Nowell & Jackson, 1996)
<i>Subtotal</i>	West Africa	850	450	1,300	
Cameroon	Benoue ecosystem (30,000)	200	100	400	6 (P. Aarhaug & H. Bauer)
Cameroon	Waza NP (1,700)	60	42	78	3 (H. Bauer)
Central African Republic	National	300	150	500	5 (P. Scholte)
Chad	Zakouma ecosystem (3,000)	50	25	75	5 (P. Scholte)
Chad	Remainder	100	50	150	5 (P. Scholte)
Congo	Odzilla NP ² (2,848)	0	0	25	6 (J. Anderson & C. Aveling)
Democratic Rep. of Congo	Virunga NP (7,800)	90	60	125	5 (M. Languy)
Democratic Rep. of Congo	Garamba NP (12,477)	150	100	200	5 (F. Smith & M. Languy)
Equatorial Guinea	National	0	0	0	6 (Nowell & Jackson, 1996)
Gabon	National ²	0	0	0	6 (Nowell & Jackson, 1996)
<i>Subtotal</i>	Central Africa	950	550	1,550	
Burundi	National	Not available			
Djibouti	National	0	0	0	6 (Nowell & Jackson, 1996)
Ethiopia	Babile, Darkata. Webe Shebelle	300	180	420	4 (S. Williams & C. Sillero-Zubiri)
Ethiopia	Bale, Sof Omar	50	30	70	4 (S. Williams & C. Sillero-Zubiri)
Ethiopia	Borana, L. Stephanie, L. Turkana	100	60	140	4 (S. Williams & C. Sillero-Zubiri)
Ethiopia	Gambella	150	90	210	4 (S. Williams & C. Sillero-Zubiri)
Ethiopia	North East	250	200	300	6 (S. Williams & C. Sillero-Zubiri)
Ethiopia	Omo NP, Mago NP	Present, not estimated			6 (S. Williams & C. Sillero-Zubiri)
Ethiopia	Remainder	150	75	225	5 (S. Williams & C. Sillero-Zubiri)
Kenya	Aberdares NP (1,966)	7	5	15	6, 2000 (B. Heath)
Kenya	Amboseli NP (392)	20	20	20	4 (C. Packer)
Kenya	East of Rift Valley to the East of the Matthews, Ndotos, Mt Nyiru	Present, not estimated			6 (S. Williams)
Kenya	Galana Game Ranch	150	75	150	5 (B. Heath)
Kenya	Isiolo, Barsalinga, Wamba, Shaba	100	75	125	4 (S. Williams)
Kenya	Kora National Reserve	40	20	60	5 (M. Jenkins)
Kenya	Laikipia Plateau (10,000)	120	96	144	2 (L. Frank)
Kenya	Masai Mara NP (1,670)	547	492	602	1 (Ogutu & Dublin, 2002)
Kenya	Meru NP, Bisanadi Reserve (5,273)	80	40	120	5 (L. Frank)
Kenya	Nairobi NP (117)	22	22	22	2 (J. Cavanaugh & C. Packer)
Kenya	Nakuru NP (98)	28	17	39	4 (L. Hannah & J. Dawson)
Kenya	North of Tana, East of Rift Valley	650	325	1,300	5 (S. Williams)

Table 1 (Continued)

Country or region	Ecosystem, location or National Park (NP) (area in km ²) ¹	Estimate	Min.	Max.	Estimation method (pers. comm. or reference)
Kenya	Tsavu NP (40,000)	675	338	1,350	5 (C. Packer & B. Heath)
Kenya	Remainder	Present, not estimated			6 (S. Williams)
Rwanda	Akagera NP (1,500)	25	15	35	4 (S. Williams)
Somalia	National	Not available			
Sudan	National	Present, not estimated			6 (G. Steehouwer)
Tanzania	Manyara NP (325)	20	20	20	4 (C. Packer)
Tanzania	Ngorongoro Crater (4,081)	53	53	53	1 (C. Packer)
Tanzania	Selous Game Reserve ² (92,000)	3,750	3,000	4,500	5 (S. Creel)
Tanzania	Buffer zone around Selous	750	500	1,000	6 (S. Creel)
Tanzania	Serengeti ecosystem (40,000)	2,500	1,750	3,250	3 (C. Packer)
Tanzania	Tarangire and Ruaha ecosystem	Present, not estimated			6 (C. Packer)
Uganda	Kidepo Valley NP (1,340)	25	20	30	2 (L. Siefert & M. Dricuru)
Uganda	Murchison Falls ecosystem (5,198)	350	280	420	2 (L. Siefert & M. Dricuru)
Uganda	Queen Elizabeth ecosystem (3,233)	200	140	260	2 (L. Siefert & M. Dricuru)
<i>Subtotal</i>	<i>East Africa</i>	11,000	8,000	15,000	
Angola	National	450	270	630	4 (W. Van Hoven)
Botswana	Central Kalahari Game Reserve ² (52,000)	312	166	458	6 (P. Funston & Department of Wildlife and National Parks)
Botswana	Kgalagadi Transfrontier Park (38,000)	458	428	478	6 (P. Funston)
Botswana	Southern Kgalagadi Wildlife Management Areas ²	225	200	250	6 (P. Funston)
Botswana	Dry North	223	133	312	4, 2000 (C. Winterbach & L. Sechele)
Botswana	Kwando, Chobe River	213	149	277	3 (C. Winterbach & L. Sechele)
Botswana	Okavango Delta (80,000)	1,438	1,006	1,869	3 (P. Kat, C. Winterbach, H. Winterbach & L. Sechele)
Botswana	Makgadigadi Pans NP (2,836)	39	28	59	2 (G. Hemson)
Botswana	Nxai Pan (1,817)	Present, not estimated			6 (G. Hemson)
Botswana	Tuli Block	10	0	20	6 (C. Winterbach & H. Winterbach)
Lesotho	National	0	0	0	6 (J. Naude)
Malawi	National	Not available			
Mozambique	Manica Gaza	25	15	35	4 (J. Anderson)
Mozambique	Niassa, Cabo Delgado (15,000)	175	105	245	4 (J. Anderson)
Mozambique	Zambezi Valley	175	105	245	4 (J. Anderson)
Mozambique	Remainder	25	15	35	4 (J. Anderson)
Namibia	Etosha NP (22,270)	230	191	266	6 (P. Stander)
Namibia	Remainder	680	476	884	3 (P. Stander)
South Africa	Eastern Cape: Addo Elephant Park, Kwande, Shamwari	13	12	14	1 (R. Slotow & G. Van Dyk)
South Africa	Kruger ecosystem ² (23,700)	2,200	2,200	2,200	6 (G. Mills)
South Africa	Hluluwe-Umfolozi NP (965)	120	72	168	4 (R. Slotow)
South Africa	Phinda, St Lucia, Thembe, Ndumu	15	15	15	1 (R. Slotow & G. Van Dyk)
South Africa	Lowveld region	161	153	169	6 (S. Liversage, I. Sussens, T. Yule, L. van Losenoord, C. Jones, G. Thomson, R. Niemann, P. Owen, M. Pieterse)
South Africa	Venetia Limpopo Mine (400)	30	15	45	5 (J. Kruger)
South Africa	Ligwalagwala – near Malelane	13	13	13	1 (R. Slotow)
South Africa	Madikwe, Pilanesberg (550)	110	99	121	1 (G. Van Dyk)
South Africa	Kgalagadi Transfrontier Park	See Botswana			
South Africa	Tswalu	Not available			
South Africa	Waterberg Region	54	54	54	1 (R. Slotow & G. Van Dyk)
Swaziland	Hlane Royal NP (163)	15	15	15	1 (J. Naude)
Zambia	Kafue NP, Luangwa Valley and Lower Zambezi NP	1,500	1,000	2,000	6 (C. Stuart & T. Stuart)
Zimbabwe	Charara Safari Area (2,207)	40	24	56	4 (N. Monks)
Zimbabwe	Chete, Sijarira Safari Area	40	24	56	4 (N. Monks)
Zimbabwe	Chewore Safari Area (2,704)	100	60	140	4 (N. Monks)
Zimbabwe	Chirisa Safari Area (1,788)	40	24	56	4 (N. Monks)

Table 1 (Continued)

Country or region	Ecosystem, location or National Park (NP) (area in km ²) ¹	Estimate	Min.	Max.	Estimation method (pers. comm. or reference)
Zimbabwe	Chizarira NP (1,878)	60	36	84	4 (N. Monks)
Zimbabwe	Dande Safari Area (988)	50	30	70	4 (N. Monks)
Zimbabwe	Doma Safari Area (1,933)	35	21	49	4 (N. Monks)
Zimbabwe	Gonarezhou, Save, Chiredzi, Malilangwe, Beit Bridge, Tuli (5,200)	130	91	169	3 (C. Wenham)
Zimbabwe	Hurungwe Safari Area (2,606)	80	48	112	4 (N. Monks)
Zimbabwe	Hwange ecosystem (25,000)	120	72	168	4 (N. Monks)
Zimbabwe	Mana Pools NP (14,000)	97	83	112	6 (N. Monks)
Zimbabwe	Matetsi Safari Area (1,343)	60	36	84	4 (N. Monks)
Zimbabwe	Matusadona NP (16,000)	120	72	168	4 (N. Monks)
Zimbabwe	Sapi Safari Area (1,526)	40	24	56	4 (N. Monks)
Zimbabwe	Zambezi NP (865)	25	15	35	4 (N. Monks)
<i>Subtotal</i>	Southern Africa	10,000	7,500	12,500	
<i>Total</i>		23,000	16,500	30,000	

¹Area sizes, where available and as listed by East (1999), were not used for calculation of lion densities as most values do not include lion habitat adjacent to the area in question.

²Disputed or questioned, see text for details.

they may contain substantial numbers of lions. We believe that although surveys of lion populations for which no information is currently available will improve the precision of the estimate, it will not substantially increase the estimate of the current total. We conclude that this inventory represents the best possible conservative estimate of lion numbers at this time.

In West and Central Africa lion populations are generally small and isolated; they are declining in some protected areas and have virtually disappeared from non-protected areas, except southern Chad and northern Central African Republic (Bauer *et al.*, 2003). A few populations exist in savannah patches in the Central African forests, but most lions in this region are found in the Sahel savannah belt. This belt is also extensively used by livestock and thus human-lion conflict is common. Lion density is typically 0.01–0.03 km⁻² throughout the region, which is the low end of the density range in East and Southern Africa. This is due both to the naturally low biomass of mammals in the region (East, 1984), and to human influence (Oates, 1999; Fischer & Linsenmair, 2001).

In East and Southern Africa many large lion populations have been stable over the last 3 decades. The Serengeti population, which has recovered from a canine distemper virus epidemic that caused 30% mortality in 1994, is illustrative of their resilience (Roelke-Parker *et al.*, 1996). Conservation is bolstered by revenue from safari hunting and tourism, allowing conservation in lands outside National Parks. An important challenge for long-term conservation in this region is political stability (Dudley *et al.*, 2002). An example is the lion population in Akagera

National Park in Rwanda, currently estimated at 25, which before the recent civil war was estimated at 250 (Montfort, 1992).

This inventory supports the categorization of the lion as Vulnerable on the IUCN Red List, based on criterion C2a(i) (IUCN, 2001, 2002). For West and Central Africa our collation of data indicates that a categorization as Regionally Endangered (Gärdenfors *et al.*, 2001) may be appropriate. Our estimate overlaps with the low end of the educated guess by Nowell & Jackson (1996), but as their methodology of data collation was different from ours it is not possible to draw any conclusions concerning trends over time. This inventory is the first step towards a regularly updated African Lion Database for the monitoring of population trends. To this end, we recommend that areas with no or low quality information are surveyed in the near future and that other surveys are regularly updated.

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References

- Bauer, H., De Iongh, H.H., Princée, F.P.G. & Ngantou, D. (eds) (2001) *Status and Needs for Conservation of Lions in West and Central Africa*. IUCN Conservation Breeding Specialist Group, Apple Valley, USA.
- Bauer, H., De Iongh, H.H., Princée, F.P.G. & Ngantou, D. (2003) Research needs for conservation of lions in West and Central Africa. *Comptes Rendus Biologies*, **326**, S112–S118.
- Creel, S. & Creel, N.M. (1997) Lion density and population structure in the Selous Game Reserve: evaluation of hunting quotas and offtake. *African Journal of Ecology*, **55**, 83–93.
- Dudley, J.P., Ginsberg, J.R., Plumptre, A.J., Hart, J.A. & Campos, L.C. (2002) Effects of war and civil strife on wildlife and wildlife habitats. *Conservation Biology*, **16**, 319–329.
- Dupuy, A.R. & Verschuren, J. (1977) Wildlife and Parks in Senegal. *Oryx*, **14**, 36–46.
- East, R. (1984) Rainfall, soil nutrient status and biomass of large African savanna mammals. *African Journal of Ecology*, **22**, 245–270.
- East, R. (1999) *African Antelope Database 1998*. IUCN, Gland, Switzerland.
- Fischer, F. & Linsenmair, K.E. (2001) Decrease in ungulate population densities. Examples from the Comoé National Park, Ivory Coast. *Biological Conservation*, **101**, 131–135.
- Gärdenfors, U., Hilton-Taylor, C., Mace, G.M. & Rodriguez, J.M. (2001) The application of IUCN Red List criteria at regional levels. *Conservation Biology*, **15**, 1206–1212.
- Garnett, T. & Utas, C. (2000) *The Upper Guinea Heritage, Nature Conservation in Liberia and Sierra Leone*. Netherlands Committee for IUCN, Amsterdam, The Netherlands.
- IUCN (2001) *IUCN Red List Categories and Criteria: Version 3.1*. IUCN, Gland, Switzerland.
- IUCN (2002) *2002 IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland [http://www.redlist.org, accessed 16 September 2003].
- Loveridge, A.J., Lynam, T. & Macdonald, D.W. (compilers) (2001) *Lion Conservation Research, Workshop1: Survey Techniques*. Wildlife Conservation Research Unit, University of Oxford, Oxford, UK.
- Mills, M.G.L., Juritz, J.M. & Zuccini, W. (2001). Estimating the size of spotted hyena (*Crocuta crocuta*) populations through playback recordings allowing for non-response. *Animal Conservation*, **4**, 335–343.
- Montfort, A. (1992) Première liste commentée des mammifères du Rwanda. *Journal of African Zoology*, **106**, 141–151.
- Nowell, K. & Jackson, P. (eds) (1996) *Wild Cats, Status Survey and Conservation Action Plan*. IUCN, Gland, Switzerland.
- Oates, J.F. (1999) *Myth and Reality in the Rainforest: How Conservation Strategies are Failing in West Africa*. University of California Press, Berkeley, USA.
- Ogutu, J.O. & Dublin, H.T. (1998) The response of lions and spotted hyenas to sound playbacks as a technique for estimating population size. *African Journal of Ecology*, **36**, 83–95.
- Ogutu, J.O. & Dublin, H.T. (2002) Demography of lions in relation to prey and habitat in the Maasai Mara National Reserve, Kenya. *African Journal of Ecology*, **40**, 120–129.
- Pennycuik, C.J. & Rudnai, J. (1970) A method of identifying individual lions *Panthera leo* with an analysis of the reliability of identification. *Journal of Zoology London*, **160**, 497–508.
- Roeke-Parker, M.E., Munson, L., Packer, C., Kock, R., Cleaveland, S., Carpenter, M., O'Brien, S.J., Pospischil, A., Hofman-Lehmann, R., Lutz, H., Mwamengele, G.L.M., Mgas, M.N., Machange, G.A., Summers, B.A. & Appel, M.J.G. (1996) A canine distemper virus epidemic in Serengeti lions (*Panthera leo*). *Nature*, **379**, 441–445.
- Smuts, G.L., Whyte, I.J. & Dearlove, T.W. (1977) A mass capture technique for lions. *East African Wildlife Journal*, **15**, 81–87.
- Stander, P.E. (1998) Spoor counts as indices of large carnivore populations: the relationship between spoor frequency, sampling effort and true density. *Journal of Applied Ecology*, **35**, 378–385.
- Van Orsdol, K.G., Hanby, J.P. & Bygott, J.D. (1985) Ecological correlates of lion social organization (*Panthera leo*). *Journal of Zoology London*, **206**, 97–112.

Biographical sketches

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