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Panthera leo.

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***Panthera leo* (Linnaeus, 1758)**

Lion

Felis leo Linnaeus, 1758:41. Type locality "Africa," restricted to "Constantine, Algeria" by J. A. Allen (1924:222–223) and based on Cuvier's Lion de Barbarie (Geoffrey St. Hilaire and Cuvier 1819).

[*Felis leo*] *barbaricus* Meyer, 1826:6. Type locality "Barbarische" = Barbary, North Africa, vide G. M. Allen (1939:244).

[*Felis leo*] *persicus* Meyer, 1826:6. Type locality "Persische" = Persia, vide Ellerman and Morrison-Scott (1951:319).

[*Felis leo*] *senegalensis* Meyer, 1826:6. Type locality "Senegalische" = Senegal, vide G. M. Allen (1939:244); not *Felis senegalensis* Lesson, 1839:plate 10, or *Felis jubata senegalensis* Blainville, 1843.

Leo asiaticus Brehm, 1829:638. No type locality specified.

Leo africanus Brehm, 1829:638. No type locality specified.

Felis leo α *barbarus* Fischer, 1829:197. No type locality specified; based on Cuvier's Lion de Barbarie (Geoffrey St. Hilaire and Cuvier 1819).

Felis leo β *senegalensis* Fischer, 1829:197. No type locality specified; based on Cuvier and Geoffroy's (1819) Lion du Senegal. Preoccupied by [*Felis leo*] *senegalensis* Meyer, 1826:6 (Hollister, 1910:123). Not *Felis senegalensis* Lesson, 1839:plate 10, or *Felis jubata senegalensis* Blainville, 1843.

Felis leo bengalensis Bennett, 1829:1. Type locality "Bengal"; corrected to "Hurriana," = Harriana, northern India by Blyth (1863). Preoccupied by *Felis bengalensis* Kerr, 1792:151.

Felis leo ϵ *capensis* Fischer, 1830:565 [page mislabeled 365]. No type locality specified; based on Griffith's (1827) "South African Lion." Preoccupied by *Felis capensis* Forster, 1781:4, plate 1.

Felis leo var. *goojratensis* Smee, 1833(1834):165, 174. Type locality "Guzerat" = Gujerat, India; stated as "Ahmedabad" by Pocock (1930:660).

Leo asiaticus: Jardine, 1834:121. Name combination.

[?] *guzcratensis* Wagner, 1841:461. Incorrect subsequent spelling of *goojratensis* Smee, vide Pocock (1930:660).

Felis (*Leo*) *gougeratensis* H. Smith, 1842:178 and plate XI. Incorrect subsequent spelling of *Felis leo goojratensis* Smee.

Felis (*Leo*) *melanochaitus* H. Smith, 1842:177. Type locality "The Cape" vide Shortridge (1934:77) or "Cape of Good Hope" vide Roberts (1951:190); correct original spelling, by selection (Hollister 1910:123).

Felis (*Leo*) *melanochoetus* H. Smith, 1842:plate X. Incorrect original spelling of *Felis melanochaitus* H. Smith.

Leo gambianus Gray, 1843:40. Type locality "W. Africa, interior of Gambia"; renaming of *Felis leo senegalensis* Fischer, 1829: 197; nomen nudum.

F[*elis*]. *leo nubicus* Blainville, 1843:58. No type locality specified; stated as "Nubia" by G. M. Allen (1939:243).

Leo indicus Blainville, 1843:196. No type locality specified; presumably India (Ellerman and Morrison-Scott 1951:319; Pocock 1930).

Felis leo nigra Loche, 1858:7. Type locality not known, given as "Constantine, Algerien" vide Hemmer (1974:230).

Tigris leo: Severtzoff, 1858:388. Name combination.

L[*eo*]. *gozeratensis* Brehm, 1863:59. Incorrect subsequent spelling of *Felis leo goojratensis* Smee.

Leo nobilis Gray, 1867:263. Renaming of *Felis leo* Linnaeus, 1758; nomen nudum.

L[*eo*]. *goorgrattensis* Gray, 1867:263. Incorrect subsequent spelling of *Felis leo goojratensis* Smee.

Leo guzeratensis Fitzinger, 1868:443. Incorrect subsequent spelling of *Felis leo goojratensis* Smee.

[*Felis leo*] var. *somaliensis* Noack, 1891:120. Type locality "Somali-Halbinsel."

Felis leo kamptzi Matschie, 1900:92. Type locality "Yoko am oberen Sanaga," = Yoko, Upper Sanaga River, Cameroon.

Felis leo goojrattensis Matschie, 1900:94. Incorrect subsequent spelling of *Felis leo goojratensis* Smee.

Felis leo massaicus Neumann, 1900:550–551. Type locality "Kibaya, Massai-Land."

Felis leo sabakiensis Lönnberg, 1910:22. Type locality "Kilimandjaro: . . . Kibonoto in the cultavated zone, 1,500 m. above the sea" or "in the plains NW. of Kilimandjaro, Leitokitok; . . . " restricted to Kibonoto, Kilimanjaro, by J. A. Allen (1924:223).

Felis leo roosevelti Heller, 1913:2. Type locality "highlands of Abyssinia near Addis Ababa." Type locality explicitly questioned and stated more broadly as "Abyssinia" by Hollister (1918: 165).

Felis leo nyanzae Heller, 1913:4. Type locality "Kampala," Uganda.

Felis leo bleyenberghi Lönnberg, 1914:273–274. Type locality "Katanga," Belgium Congo.

Leo leo leo: J. A. Allen, 1924:223. Name combination.

Leo leo azandicus J. A. Allen, 1924:224. Type locality "Vankerckhovenville, northeastern Belgian Congo."

FIG. 1. Photograph of an adult male *Panthera leo*, Kenya, Africa. Used with permission of the photographer S. P. Goyal.

Leo leo hollisteri J. A. Allen, 1924:228. Type locality "Lime Springs, Sotik, British East Africa."
Leo leo krugeri Roberts, 1929:91. Type locality "Sabi Game Reserve (Kruger National Park)," southern Africa.
Panthera leo: Pocock, 1930:660. First use of current name combination.
Leo leo vernayi Roberts, 1945:65. Type locality "Matapa Pan, central Kalahari," southern Africa.
Felis leo blevenberghi Jobaert, 1954:479. Incorrect subsequent spelling of *Felis leo bleyenberghi* Lönnberg, 1914.
Leo maculates Heuvelmans, 1955:443. Nomen nudem.
Panthera leo webbiensis Zukowsky, 1964:270. Type locality "Somalilande."

CONTEXT AND CONTENT. Generic context given above. Hemmer (1974), Pocock (1930), and Meester et al. (1986) provided several synonyms without sufficient citation information for validation. These are listed above and in the "Literature Cited" with as much information as we could ascertain. The lion in North Africa, *Panthera leo leo* (Linnaeus), is extinct; *barbaricus* (Meyer), *barbarus* (Fischer), *leo* (Allen), and *nigra* (Loche) are synonyms. *P. leo* has 7 extant subspecies (Hemmer 1974).

P. l. azandicus (Allen, 1924:224), see above; *massaicus* (Neumann) partim and *somaliensis* (Noack) partim are synonyms.
P. l. bleyenberghi (Lönnberg, 1914:273–274), see above; *blevenberghi* (Jobaert) is a synonym.
P. l. krugeri (Roberts, 1929:91), see above; *vernayi* (Roberts) is a synonym.
P. l. melanochaitus (Smith, 1842:177), see above; *melanochaitus* (Smith) and *melanochætus* (Smith) are synonyms.
P. l. nubicus (Blainville, 1843:58), see above; *hollisteri* (Allen), *massaicus* (Neumann) partim, *nyanzæ* (Heller), *roosevelti* (Heller), *sabakiensis* (Lönnberg), *somaliensis* (Noack) partim, and *webbiensis* Zukowsky are synonyms.
P. l. persica (Meyer, 1826:6), see above; *asiaticus* (Brehm), *bengalensis* (Bennett), *goojratensis* (Smee), *goojrattensis* (Matschie), *goorgrattensis* (Gray), *gougeratensis* (Smith), *gozeratensis* (Brehm), *guzcratensis* (Wagner), *guzeratensis* (Fitzinger), and *indicus* (Blainville) are synonyms.
P. l. senegalensis (Meyer, 1826:6) see above; *gambianus* (Gray), *kamptzi* (Matschie), and *nobilis* (Gray) are synonyms.

DIAGNOSIS. The lion (Fig. 1) is the 2nd largest species of Felidae, slightly smaller than the tiger, *Panthera tigris* (Mazák 1981). Skull of *P. leo* (Fig. 2) is similar in appearance to that of the leopard (*Panthera pardus*) but is nearly twice the size. *P. leo* is digitigrade with sharp retractile claws; broad face, rounded ears, relatively short neck; and well-proportioned, muscular body more drawn in at belly compared with the tiger (Rudnai 1973a).

GENERAL CHARACTERS. Body is unicolor, lacking rosettes; color is light tawny, white on abdomen and inner side of legs, with black on back of ears (Smithers 1971). In size and general appearance, Asian and African subspecies are similar; the most obvious physical difference between Asian and African subspecies is a longitudinal fold of skin running along belly of Asian subspecies (Pocock 1930). Variations between African subspecies have been noted between and within geographic regions on the basis of size, coat color, and development and color of mane, with those from southern parts of continent being larger on average than those from eastern parts (Turner and Antón 1997).

Pelage varies across populations and between and within neighboring prides (Smuts et al. 1978). Color varies from light buff and silvery gray to yellowish red and dark brown; white lions have been reported from Kruger National Park and Umfolozi Game Reserve in South Africa (McBride 1977; Smuts 1982). Coat color results from a combination of shorter sandy-yellow hairs, mixed with and overlain by longer, black guard hairs (Rudnai 1973b). Juveniles are heavily spotted (Rosevear 1974).

Manes of adult males vary in color (from tawny to black) and size varies among populations and age classes (Rosevear 1974). Mane growth is influenced by testosterone, and mane color is usually light in young animals and darkens with age (Schaller 1972).

Head is rounded and bears prominent whiskers. For males, length of head and body ranges from 1,700 to 2,500 mm, length of tail is 900–1,050 mm, height at shoulder is ca. 1,230 mm (Nowak and Paradiso 1983), and mass is 150–225 kg (average =188 kg—

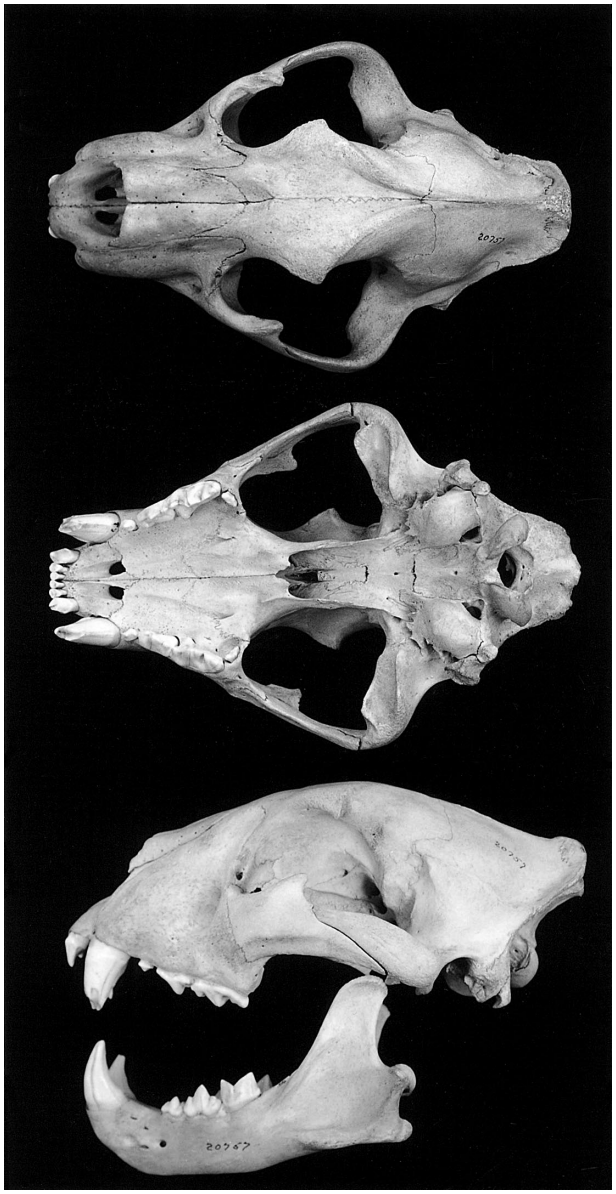

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of adult male *Panthera leo*, Chicago Field Museum no. 20757. Greatest length of cranium is 330 mm.

Smuts et al. 1980). In Kruger National Park, South Africa, 4 males >4 years old averaged 181 kg, 25 males 2–4 years old averaged 146 kg, and large male cubs averaged 77 kg (Smuts 1976). The largest male in Kruger National Park weighed 225 kg (Smuts 1982), but a male near Mount Kenya weighed 272 kg (Nowell and Jackson 1996). Males weigh 20–27% more than females. For females, length of head and body is 1,400–1,750 mm, length of tail is 700–1,000 mm, height at shoulder averages 1,070 mm, and mass is 120–182 kg (Nowak and Paradiso 1983). In Kruger National Park, South Africa, 25 females >4 years old averaged 126 kg, 11 females 2–4 years old averaged 103 kg, and large female cubs averaged 60 kg (Smuts 1976). The largest female weighed 152 kg (Smuts 1982).

Asian subspecies is slightly smaller than African subspecies; adult males weigh 160–190 kg and females weigh 110–120 kg (Nowell and Jackson 1996). Record total lengths for males are ca. 3,300 and 2,920 mm for African and Asian subspecies, respectively (Nowell and Jackson 1996).

Panthera leo has a muscular, deep-chested body with a rounded and shortened head and reduced dentition (Rudnai 1973b). Skull is wide and high compared with its length. Orbit is large, and its posterior border is slightly anterior to middle of skull. Postorbital processes are broad, blunt, and ligulate. Upper profile

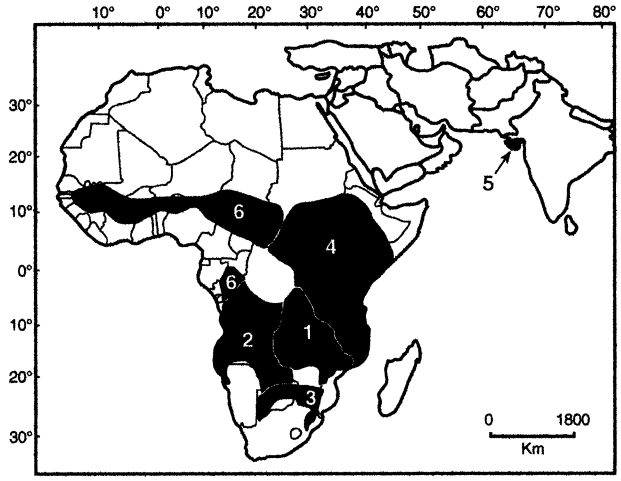

FIG. 3. Geographic distribution of *Panthera leo* in Africa and India (modified from Hemmer 1974; Nowell and Jackson 1996): 1, *P. l. azandicus*; 2, *P. l. bleyenberghi*; 3, *P. l. krugeri* and *P. l. melanochaitus*; 4, *P. l. nubicus*; 5, *P. l. persica*; 6, *P. l. senegalensis*.

of skull in lateral view is convex; muzzle is steeply sloped with nasal orifice set low. Temporal ridges meet on summit of sagittal crest, are short, and are restricted to posterior portion of crown (Pocock 1951). Sagittal crest, mastoid, and paroccipital processes are prominent (Smithers 1971). Ca. 50% of Asian subspecies have bifurcated infraorbital foramina, whereas African lions have only 1 foramen on either side (O'Brien et al. 1987a; Pocock 1939). Baseline of lower jaw is slightly convex. Carnassials are highly sectorial, and canines have a fine longitudinal groove (Ewer 1973). Averages or ranges for cranial measurements (in mm) are as follows: greatest length of skull, 250–460; condylobasal length, 316–345; basal length, 284; zygomatic breadth, 229; interorbital breadth, 69.5; braincase breadth, 106 (Rosevear 1974; Van Valkenburgh 1996). Mean length of 48 skulls was 277.1 (*SD* =22.9—Van Valkenburge and Ruff 1987). Ranges of cranial measurements for 5 males and 6 females, respectively, from eastern Africa are: greatest length, 353–401, 293–315; condylobasal length, 316–345, 264–280; mandibular length, 235–260, 196–212; width of mastoid, 133–144, 112–120 (Hollister 1918). Similar cranial measurements are presented by Roberts (1945).

Panthera leo is unique in having a horny spur that is separated from last caudal vertebra and that is covered by a tuft of black hair at tip of tail (Rudnai 1973b). Peculiarities of hair growth also distinguish lions from other felids. Pelage is composed of relatively sparse, fine underfur 6–8 mm long and of flattish-sectioned subbristles 10–14 mm long (Rosevear 1974). Lions have a large patch of reverse hair growing forward, starting with a vortex above lumbar vertebrae and continuing forward up to middorsal region where it forms a small transverse crest at interface with opposite-growing hair and extends laterally about one-third down side of body (Rudnai 1973b).

DISTRIBUTION. Ancestors of modern lions occurred throughout Europe and the Americas until Late Pleistocene (Harington 1996; Kurtén and Anderson 1980; Vereshchagin 1971). Ca. 2,000 years ago, lions became extinct in eastern Europe with the development of dense forests (Guggisberg 1961, 1975). Until ca. 1850, lions were distributed across the Indian subcontinent and were found in present-day states of Gujarat, Haryana, Madhya Pradesh, Punjab, Rajasthan, and Uttar Pradesh (Chellam and Johnsingh 1993). By early 1900s, the Asian subspecies was drastically reduced and today is confined to the Gir Sanctuary of Gujurat State in western India, where it was initially protected by the Nawab of Junagadh in his private hunting grounds (Kinnear 1920).

African subspecies occur along the southern fringe of the Sahara from western Africa to Sudan and Somalia then south through most of Africa excluding the Congo forest region (Fig. 3). Lions have disappeared in northern Africa and the Cape region. South of the Sahara, lions are rare in western Africa but survive in protected areas of eastern and southern Africa (Rosevear 1974). African parks are a refuge for free-ranging lions and within these areas their numbers increase (Orford et al. 1988). Countries in which lions are still relatively widespread include Botswana, Central African Republic, Ethiopia, Kenya, Tanzania, Zaire, and Zambia. Status in Angola, Mozambique, Somalia, and Sudan is uncertain but groups may be patchy and widespread (Fagotto 1985). Lions survived in the desert on the edge of Niger's Air Mountains up to ca. 1910 (Rosevear 1974). Lions may range into snowy mountainous regions of eastern Africa up to 3,600 m on Mt. Elgon, Mt. Kenya, and Mt. Ruwenzori and over 4,200 m in Ethiopia's Bale Mountains (Nowell and Jackson 1996).

FOSSIL RECORD. The earliest fossil record of the lion appears during the Late Pliocene at Laetoli in Tanzania ca. 3.5×10^6 years ago (Turner and Antón 1997). The 1st appearance of the lion in Europe occurred ca. 0.9×10^6 years ago at the French Mediterranean site of Vallonnet, and those European lions were larger than extant lions (Turner and Antón 1997). Fossil remains of the cave lion (*P. leo* cf. *spelaea*) were recovered from northern Israel dating to the Middle Pleistocene (Tchernov and Tsoukala 1997). Other areas in the Old World where fossil remains have been found include the upper beds of Olduvai Gorge in eastern Africa, Swartkrans and Kromdraai in South Africa, and the Mosbach gravels in Germany (Hemmer 1979a). Numerous finds in France, England, and Germany indicate that the lion was common during the Holstein and Ilford interglacials. During the Late Pleistocene, lions spread over North America into Central America (Hemmer 1978; Seymour 1983).

Various populations known from fossils by names *P. atrox*, *P. fossilis*, *P. spelaea*, and *P. vereshchagini* are now regarded as conspecific with *P. leo* (Burger et al. 2004; Harington 1977; Hemmer 1976, 1979a). In Europe and northern Asia, lion populations may have become isolated due to widespread ice sheets. American and cave lions became extinct ca. 10,000 years ago (Harington 1996).

FORM AND FUNCTION. Skull has short jaws. Backward-curved horny papillae cover surface of tongue (Pocock 1951). Although the sense of smell is well developed, vision and hearing are of greater importance in locating prey (Macdonald 1984). The mane serves as protection during intraspecific fighting, a signpost of gender distinguishable at a distance, an indicator of individual fitness, and insulation for the neck (Caputo 2002), but may have evolved recently (320,000–190,000 years ago—Yamaguchi et al. 2004).

Lions have an incompletely ossified hyoid apparatus with an elastic ligament measuring 15 cm when relaxed and 22.5 cm when stretched, allowing lions to move the larynx from palate and lengthen pharyngeal passage (Hast 1989). This elastic ligament makes roaring possible (Owen 1834; Pocock 1916).

Vertebral formula is 7 C, 13 T, 7 L, 3 S; number of caudal vertebrae not reported. Dental formula is i 3/3, c 1/1, p 3/2, m 1/1, total 30 (Groves 1982; Rosevear 1974; Smuts et al. 1978). Maxillary canines are ca. 43–52 mm tall, elongated, posteriorly recurved, conical, and somewhat longer than lower canines. P4 carnassials measure 38 mm long (Parker 1982; Rosevear 1974; Smuts et al. 1978). Lower carnassial has a deep, narrow carnassial notch and upper carnassial has a large protocone. Incisors are small, spatulate, and arranged in a compact transverse row; upper lateral incisors are larger than more mesial incisors (Rosevear 1974). Occiput is inclined posteriorly to upper toothrow and paramastoids and paraoccipitals are small and separate (Martin 1989).

Lions have sebaceous glands around chin, lips, cheeks, mystacial and genal whiskers, above tail, and between toes (Schaller 1972). Females have 2 pairs of mammae, rarely 3 (Ewer 1973). Anal glands of lions are ca. 25 mm long with ducts that open on either side of and close to anus (Ewer 1973). Penis is relatively short and baculum is 6.0–9.5 mm long (Didier 1949).

Lions drink after every meal when water is available, and drinking contributes significantly to water influx rates in hot weather (Eloff 1973; Green et al. 1984). Drinking comprises ca. 40% of the total water influx in lions in Etosha National Park (Clarke and Berry 1992). Lions can obtain water from prey and plants to a limited extent and can survive in very arid environments (Eloff 1973; Hanby et al. 1995). Asian lions frequently hunt within riverine forests near a water source (Chellam and Johnsingh 1993).

ONTOGENY AND REPRODUCTION. Lions have no fixed breeding season although birth peaks have been recorded in Kruger and Serengeti National Parks (February–April and March–

July, respectively) in relation to seasonal weather patterns and prey availability (Packer et al. 1990; Smuts et al. 1978). Lion productivity (measured in the number of surviving cubs) is limited by food. Four-cub litters survive best where prey is most abundant, and survival declines as the prey base declines (Packer and Pusey 1995). When the prey base is reduced, litter sizes are smaller.

Females come into estrus in response to within-pride mechanisms such as estrus of pridemates as well as loss of cubs from male infanticide at pride takeovers (Bertram 1975b; Packer and Pusey 1983a; Schaller 1972). Estrus lasts 4–7 days, with intervals between periods lasting from a few days to more than a year (Rudnai 1973a). During estrus, vaginal smears display flat, nonnucleated, cornified cells with a smaller number of cells whose nuclei are pycnotic (Asdell 1946). Ovulation is induced by copulatory stimuli or interaction with conspecifics during estrus (Schramm et al. 1994). Conception occurs on 4th day of estrus with a conception rate per estrous cycle of 38% (Cooper 1942; Rudnai 1973b). Copulation occurs up to 100 times per day with multiple males (Davies and Boersma 1984; Packer 1986). Intervals between matings range between 4 and 148 min with an average of 17 min (Rudnai 1973a).

Mean interbirth interval is 20 months if the previous litter survives to maturity and 4–6 months if the previous litter is lost (Pusey and Packer 1987). Gestation lasts 110 days. Litter size averages 1–4 (maximum of 6), and postpartum litter size is virtually identical to litter size in utero (Cooper 1942; Packer and Pusey 1987; Smuts et al. 1978). Sex ratio at birth is 1:1 (Rudnai 1973a). Females give birth in dens or areas of dense brush and keep litters hidden for at least a month while cubs are not very mobile and are vulnerable to predators (Hanby et al. 1995; Packer and Pusey 1997).

Eyes are open at birth or shortly thereafter. Mean weight at birth is 1,650 g, and cubs gain ca. 106 g per day in the first 4 weeks of life (Hemmer 1979b; Oftedal and Gittleman 1989). Newborns are marked with spots that persist on belly and legs until adulthood and may remain throughout life. Cubs may begin walking within 2 weeks of birth; eruption of milk teeth begins at 3 weeks of age, allowing the young to take solid foods at ca. 8 weeks (Oftedal and Gittleman 1989). Milk is high in fat (Ben Shaul 1962; De Waal et al. 2004). Cubs are weaned at ca. 8 months and eruption of permanent teeth begins between 9th and 12th months (Grzimek 1975).

Within a pride, cubs born <1 year apart constitute a cohort and are raised communally after 4–6 weeks of age (Hanby et al. 1995; Packer 1986; Packer and Pusey 1983b; Van Orsdol et al. 1985). Once cubs can move, mothers bring them out in the open to join the pride in a nursery crèche that will persist until they are ca. 2 years old and the mother resumes mating (Packer et al. 1990; Packer and Pusey 1997).

At 2 years of age, female lions are slightly shorter than adult females, whereas males may be slightly taller than adult females with initial mane growth evident around neck and on chest (Smuts et al. 1978). By 3 years of age, young females are difficult to distinguish from adults, and by 4 years, females cannot be distinguished from older females on the basis of body size (Smuts et al. 1978). For females, reproduction declines at 11 years of age and virtually stops at 15 years; although 16-year-old males can produce viable sperm, few old males have access to a pride (Packer et al. 1988; Smuts et al. 1978).

Sexual maturity occurs at ca. 24 months of age for both sexes, although males may not begin spermatogenesis until 30 months of age (Rudnai 1973b; Smuts et al. 1978). Males in the wild may not have an opportunity to reproduce before the age of 5 years (Smuts 1982). Four years is the median age when females have their 1st surviving litter and when males 1st become resident in a pride (Packer et al. 1988; Pusey and Packer 1987).

ECOLOGY. Lions prefer open woodlands, thick bush, scrub, and grass complexes (Kingdon 1977; Yalden et al. 1980) but will occur in semideserts, forests, and in mountains up to 5,000 m. The Gir Forests of India are dry, mixed deciduous forests dominated by teak (*Tectona grandis*) in the upper story with acacia thorn (*Acacia*) savanna in the eastern portion (Berwick 1976).

Prey selection of African lions is well studied (Elliott et al. 1976; Eloff 1984; Mills and Shenk 1992; Rudnai 1974; Ruggiero 1991; Scheel 1993a, 1993b; Smuts 1978a; Stander 1992b). In eastern Africa and parts of South Africa, wildebeest (*Connochaetes taurinus*) comprised the majority of the lion diet (Schaller 1972). Larger mammals, such as young African elephants (*Loxodonta africana*), buffalo (*Syncerus caffer*), eland (*Tragelaphus*), giraffe (*Giraffa camelopardalis*), and kudu (*Tragelaphus strepsiceros*) also may be captured (Pienaar 1969; Stander 1997). In Serengeti, 7 prey species that account for more than 90% of total meat intake are buffalo, kongoni (*Alcelaphus buselaphus*), Thomson's gazelle (*Gazella thomsonii*), topi (*Damaliscus lunatus*), warthog (*Phacochoerus aethiopicus*), wildebeest, and zebra (*Equus burchellii*—Scheel and Packer 1995). In Kafue and Manyara national parks of South Africa, buffalo make up 62% of lion kills (Ewer 1973; Schaller 1972). In Kalahari Gemsbok Park, lions survive on smaller prey such as gemsbok (*Oryx gazella*) and porcupines (*Hystrix*) because of the relative absence of large antelope (Eloff 1973, 1984; Turner and Antón 1997). In Kruger National Park, male lions prefer buffalo, whereas females prey upon smaller, more abundant ungulates such as wildebeest and zebra (Funston et al. 1998). Based on numbers killed in Nairobi National Park, kongoni, warthog, wildebeest, and zebra provide most of the prey (Rudnai 1974). Asian lions mainly prey upon smaller species than the African lions. The most common prey is chital (*Axis axis*), weighing ca. 50 kg, although sambar deer (*Cervus unicolor*), weighing ca. 166 kg, may be preferred (Chellam and Johnsingh 1993; Khan 1990).

Lions kill a greater proportion of males and young individuals of several prey species (Viljoen 1997). In Serengeti National Park in Tanzania, lions prey on cheetah (*Acinonyx jubatus*) cubs and may reduce cheetah density in that area (Durant 1998). Lions occasionally take small prey such as rodents, tortoises, fish in shallow ponds, termites, grass, and fruits such as the tsama melon (*Citrullus lanatus*). They also dig warthogs out of burrows (Ewer 1973; Van Orsdol 1984). Chimpanzee (*Pan troglodytes*) remains have been found in the feces of lions from Mahale Mountains National Park, Tanzania (Tsukahara 1993). Lions are opportunistic scavengers that readily displace other predators from their kills (Packer 1986; Schaller 1972). In Serengeti, ca. 40% of food items were scavenged, although scavenging is less common where prey animals are scarce (Packer et al. 1990; Stander 1992a).

Each pride has a territory of 20–500 km^2 (Van Orsdol et al. 1985). Average range sizes of prides in Africa were 26–226 km^2 but can be considerably larger (Stander 1992b; Van Orsdol et al. 1985; Viljoen 1993). Use of space within a territory is related to the availability of prey (Spong 2002). Variation in vibrissa spot pattern enables study of individual members of prides and group-level behaviors, and allows estimates of population size (Jhala et al. 1999; Pennycuick and Rudnai 1970).

In Serengeti, pride ranges may overlap but each pride maintains a core area where most activities are concentrated with little interaction with other groups (Schaller 1972). Serengeti lions maintain stable territories except during periods of extreme hardship (Packer et al. 1990). Studies on the impact of lion removal reveal that the opening of a territory (by removal of the current pride) is followed by an influx of competing new lions (Smuts 1978b). New prides are formed by the division of preexisting kin groups (Hanby and Bygott 1987; Pusey and Packer 1987). Although coalescence of unrelated females in a pride is rare, it occurred during prolonged drought in Botswana's Central Kalahari Game Reserve when original ranges expanded (Owens and Owens 1984).

Population densities (adults and subadults per 100 km^2) range from 0.08–0.13 in Selous Game Reserve, 0.17 in Botswana's Chobe National Park, 1.5–2.0 in Kalahari Gemsbok, to 3–10 and up to 18 in protected areas of eastern Africa and South Africa (Creel and Creel 1997; Nowell and Jackson 1996). Density of Asian lions is estimated at 1 lion/7 km^2, with mean home ranges for males and females of 110 km^2 and 50 km^2, respectively (Chellam 1993). Variation in population densities is the result of differences in resource availability and competition (Stander 1997). Adult sex ratio for African and Asian subspecies (1 male to 2.1 females) is skewed heavily in favor of females because of high male mortality, especially during subadulthood (Chellam and Johnsingh 1993; Smuts 1978b; Van Orsdol et al. 1985).

Home-range size of a pride correlates with lean-season prey biomass, but not with good-season prey biomass (Van Orsdol et al. 1985). In the dry season, lions hunt cooperatively more than during other seasons. During the wet season, groups of lionesses obtain more food than do solitary females (Stander 1991).

Prides allow greater protection for the individual lioness and her offspring and greater success in hunting effort (Packer 1986; Packer and Ruttan 1988). Coordinated group hunts allow for greater

capture and kill of prey (Packer 1986; Packer and Ruttan 1988; Stander 1992a, 1992b).

Lions and spotted hyenas (*Crocuta crocuta*) have similar prey preferences and often compete at kill sites (Cooper 1991; Schaller 1972). Lions are dominant to hyenas except when substantially outnumbered (1 or 2 lions per 20–40 hyenas); lions generally surrender the remnants of a kill to hyenas only after consuming most of the meat (Packer 1986). Lions are occasionally injured or killed by prey such as buffalo, rhinoceros (*Rhinoceros*), warthog, wildebeest, or zebra during failed hunting attempts (Bertram 1979; Rosevear 1974).

Tuberculosis has been diagnosed in lions from Kruger National Park and may be contracted directly or indirectly from buffaloes (Keet et al. 1996). An epidemic caused by a morbillivirus closely related to canine distemper virus emerged in a lion population of Serengeti National Park in 1994 and spread north in the Maasai Mara reserve. The fatal neurological disease was characterized by grand mal seizures and myoclonus (Roelke-Parker et al. 1996). Canine distemper virus has been documented in Serengeti lions and caused encephalitis, nervous disease, and pneumonia (Carpenter et al. 1998). Feline herpesvirus and feline immunodeficiency virus are endemic in Serengeti and Ngorongoro Crater populations (Packer et al. 1999). *Trichinella nelsoni* occurred in 3 lion carcasses from Serengeti (Pozio et al. 1997). Antibodies to the gram-negative bacteria *Bartonella* were found in 5% of 58 free-ranging lions (Molia et al. 2004). In captivity, feline immunodeficiency virus and canine distemper require individual isolation and treatment (Shoemaker and Pfaff 1997).

Lions are harassed by stable (*Stomoxys calcitrans*) and tsetse (*Glossina morsitans*) flies and other biting pests such as ticks (order Acarina) and fleas (order Siphonaptera). Lions generally have tapeworms from swallowing cysts with meat of their herbivore prey. *Sarcoptes scabiei* has been found on lion cubs in Kruger National Park and may result in mortality in severe cases (Young 1975). Various parasites, including *Ancylostoma paraduodenale*, *Cylicospirura*, *Dirofilaria sudanensis*, *Lagochilascaris major*, *Linguatula*, *Schistosoma mattheei*, and *Trichinella spiralis*, have been found in fecal samples of lions throughout Africa (Bjork et al. 2000). Twenty-eight parasites associated with lions include *Ancylostoma paraduodenale*, *A. tubaeforme*, *Cylicospirura subaequalis*, *Dipylidium*, *Diphyllobothrium theileri*, *Dirofilaria repens*, *D. sudanensis*, *Echinococcus granulosus*, *Filaria leonis*, *F. martis*, *Galoncus perniciosus*, *Gnathostoma*, *G. spinigerum*, *Lagochilascaris major*, *Mesocestoides*, *Ollulanus tricuspis*, *Pharyngostomum cordatum*, *Physaloptera praeputialis*, *Taenia*, *T. bubesi*, *T. gongyamia*, *T. hydatigena*, *T. regis*, *T. taeniaeformis*, *Toxocara canis*, *T. cati*, *T. leonina*, and *Trichinella spiralis* (Round 1968). Other fecal samples of wild lions had 15 parasite taxa, including *Ancylostoma*, Coccidia, *Giardia*, helminth larvae (*Ollulanus tricuspis* and *Aeluronstrongylus*), *Physaloptera*, *Sarcocystis*, *Spirometra*, Spirurida, Taeniidae (*Echinococcus* and *Taenia*), *Toxocara*, Trematoda, Trichostrongylidae, and *Trichuris* (Muller Graf 1995). Of the hosts sampled, 97.3% were infected with at least 1 parasite. Twelve previously undocumented parasites (*Aelurostrongylus*, Acanthocephala, Anoplocephalidae, *Capillaria*, *Denodex*, *Eimeria*, *Habronema*, *Isospora felis*, *I. rivolta*, *Isospora*, Trematoda, and *Trichuris*) occurred in fecal samples from Serengeti National Park and Ngorongoro Crater Conservation Area, northern Tanzania (Bjork et al. 2000). Cell and blood parasites such as *Eimeria* and *Babesia*, as well as gastric spiral bacteria and intramuscular sarcocysts, have been found in some individuals (Kinsel et al. 1998; Lopez-Rebollar et al. 1999). Endoparasites of the Asian subspecies from zoos are similar to parasites existing in African populations (Bjork et al. 2000). *Ancylostoma*, *Spirometra*, and *Toxascaris* have been found in both wild Gir Forest lions and those in captivity (Bjork et al. 2000). Antibodies to the abortifacient parasite *Neospora caninum* occur in lions (Ferroglio et al. 2003).

Mortality for lionesses declines at 3–4 years and then rapidly accelerates; no lioness has survived beyond 17 years in Serengeti National Park or Ngorongoro Crater, Tanzania (Packer et al. 1998). Males live an average of 12 years and up to 16 years (Hanby and Bygott 1991; Smuts et al. 1978). Cub mortality is high in lions and is linked to periods of prey scarcity and infanticide by male lions during pride takeovers; 27% of cub mortality is due to infanticide (Packer and Pusey 1983b; Schaller 1972; Van Orsdol et al. 1985; Whitman and Packer 1997). Cub survival is dependent on maternal survival, although juvenile survival is unaffected by maternal survival or subsequent reproduction (Packer et al. 1998). Disappearance of cubs 18 months or older is often due to death, but some young may disperse with the mother to a new area (Packer et al. 1988). In Serengeti, solitary females are less able to successfully rear large litters of cubs as compared with females in a pride (Packer and Pusey 1995). Survival of young remains constant with maternal age but litter size declines at 14 years (Packer et al. 1998).

Conflict with people on reserve borders is a major cause of mortality and may accelerate extinction in isolated areas (Woodroffe and Ginsberg 1998). Hunting is restricted to problem animals in Kenya and Uganda, with trophy hunting allowed in South Africa, Tanzania, and Zimbabwe. Lions are an important game animal for tourist hunting and generate ca. 12% of the hunting revenue in some parts of Africa (Creel and Creel 1997).

Lions are easily maintained in captivity, breed successfully, and survive for more than 20 years (Shoemaker and Pfaff 1997). In 1992, the International Species Information System reported ca. 715 lions in captivity throughout the world (Nowell and Jackson 1996). The anesthetics propofol, ketamine, and xylazine have been used successfully on lions (Epstein et al. 2002).

Relative amount of wear on P3, width of the pulp chamber of canine teeth, spot markings of cubs, prominence of nipples during lactation, number of incremental cementum lines, and certain behavioral characteristics can be used to determine age (David 1962; Rudnai 1973b; Schaller 1972; Smuts et al. 1978, 1980; Spinage 1976). Skull measurements provide the only means of assessing age of young lions <3 years of age more precisely than tooth eruption and replacement (Smuts et al. 1978). Shortly after 3 years of age, skull size increases and skull dimensions start to overlap those of older lions (Smuts et al. 1978).

Lions are individually recognized from scars, ear damage, and natural markings (e.g., whisker spot patterns—Pennycuick and Rudnai 1970). Lions can be immobilized by darting from a vehicle (Mills 1996). Death caused by capture is rare in lions, although severe stress due to human hunting has been linked with fatal capture myopathy (Joubert and Stander 1990).

BEHAVIOR. The pride is the primary fission–fusion social unit of lions (Gittleman 1996; Packer et al. 1991; Schaller 1972). Prides vary in size and structure, but typically contain 5–9 adult females (range, 1–18), their dependent offspring, and a coalition of 2–6 immigrant males (Heinsohn and Packer 1995; Packer et al. 1991). Observed groups may be much smaller (1.2–1.9 adults—Bauer et al. 2003). Pride sizes are smallest in arid environments with limited prey species (Elliott and Cowan 1977; Hanby and Bygott 1979; Ruggiero 1991; Schaller 1972; Stander 1992b; Wright 1960). On average, lionesses in a pride share one-seventh of their genes with other pride members. Number of lions in a pride varies across successive months because of synchrony of births and high mortality of cubs (Van Orsdol et al. 1985). Males reside in a pride for ca. 2 years before being replaced by another group of males (Packer et al. 1988). Pride membership is stable but pridemates are often scattered in subgroups throughout the range and each individual spends time alone (Pusey and Packer 1987; Schaller 1972).

The crèche is the social core of the pride and facilitates maternal defense of cubs and juveniles from predation and infanticide (Cairns 1990; Packer and Pusey 1997). Cubs attempt to obtain milk from any lactating female in the pride although females preferentially nurse their own offspring and cubs of close relatives; females with small litters give a higher proportion of their nursing to non-offspring compared with mothers of large litters (Pusey and Packer 1994).

Lions exhibit diverse patterns of behavior between and within prides, and different populations vary in feeding and hunting preferences and methods (Rosevear 1974). Most studies of lions are observational, and some exceed 40 years (Hanby et al. 1995). Other methods include censusing, DNA fingerprinting, immobilization (with ketamine hydrochloride–xylazine hydrochloride—Herbst et al. 1985), marking, and playback experiments.

Lions are mainly active at night. A large portion (ca. 80%) of the daily time budget (recorded in Tanzania during a 24-h period) is spent sleeping, lying down, or sitting (Hanby et al. 1995). Males use vocalizations (roaring) and scent marking to define boundaries, although these behaviors also function in communication between pridemates (Funston and Mills 1997; Grinnell et al. 1995; McComb et al. 1994; Schaller 1972). Roaring chorus by lions has a maximum

intensity of 114 dB at 1 m and may have an assembly function to which stray members respond and join the group in response to territorial defense against other prides (McComb et al. 1994; Peters and Wozencraft 1996). Lions use urine sprays or scrapes to define territories (Schaller 1972).

When active, lions engage in hunting, communal cub rearing, and territorial maintenance (Heinsohn and Packer 1995). Lions normally walk at ca. 4 km/h and can run for short distances at 50–60 km/h; activity in trees has been recorded, although lions are not adept climbers (Nowak and Paradiso 1983). Wrestling is most common in cubs but is rarely used by adults, whereas stalking was infrequently observed in play by cubs (Schaller 1972). Self and social grooming are frequent activities within a pride; forepaws, chest, and mane on the chest are most frequently groomed (Rudnai 1973b). Various behaviors and sounds that may be related to social maintenance and communication include clawing, crouching, ducking, grunting, headrubbing, rolling onto back, scratching, snarling, stretching, and tail flicking (Rudnai 1973b).

Territorial defense involves male, female, and juvenile lions (Grinnell and McComb 1996; Heinsohn 1997; Heinsohn et al. 1996; McComb et al. 1993). Males defend the pride against incursions by other males, thereby ensuring some exclusivity in mating, and females defend their young against infanticidal males and their territory against adjacent female prides (Packer et al. 1991). Male lions have territorial patrols that protect the pride from others (Packer and Pusey 1997). Females protect denning sites, hunting grounds, and water holes from other prides (Packer and Pusey 1997).

Members of adjacent prides usually remain several km apart (Hanby et al. 1995). When neighboring prides come into contact, lionesses typically attempt to expel intruders if they outnumber them (Heinsohn and Packer 1995; Schaller 1972). Some lionesses play a greater role in defending the territory than other females in the same pride (Heinsohn and Packer 1995). As they approach sexual maturity, juvenile lionesses become progressively more likely to join adult females in territorial defense (Heinsohn et al. 1996). Increased aggression in pride defense occurs with high lion density, such as in the Ngorongoro Crater (Heinsohn 1997; McComb et al. 1994). Territorial disputes often end with larger groups chasing off smaller groups (Hanby et al. 1995).

Males defend their area by using cooperative behavior that is not conditional on either kinship or behavior of the male's companions (Grinnell et al. 1995). Roaring may facilitate communication within prides as well as discourage the approach of nonpride members from a territory (McComb et al. 1994). Females with cubs can distinguish the roars of resident males from those of unfamiliar males that might pose a threat to their offspring (McComb et al. 1993).

A small proportion of lions are nomadic, including young and adult males without a pride. Nomadic lions follow the migrations of prey and hunt and scavenge cooperatively (Bertram 1975a; Bygott et al. 1979; Schaller 1968, 1969; Van Orsdol et al. 1985). Lionesses are highly philopatric, and few females are nomadic; a solitary female usually returns to or settles near her natal pride (Packer 1986). Nomadic lions, which have large ranges that may overlap with pride territories, are commonly found singly or in groups of as many as 5, with membership changing freely (Schaller 1972).

In a pride takeover, a coalition of males that generally are related either attack and kill or otherwise cause the deaths of small cubs (Hanby and Bygott 1987; Packer and Pusey 1997). Within a few days of cub mortality, females resume estrous cycles. Mating activity is quickly initiated by the newly resident males. A synchronous birth event within the pride is the result (Packer and Pusey 1983a). By removing cubs from a pride and stimulating female reproduction, males can father more offspring. Subadult males usually leave at takeovers; subadult females become peripheral or leave unless they mate with the incoming males (Hanby and Bygott 1987).

Cohorts of ≥3 males usually enter new prides as a group, but cohorts of only 1 or 2 males often team up with single males from other prides to achieve successful takeover of a pride (Packer et al. 1991). Bachelor groups are formed as coalitions of related and unrelated males; coalitions of unrelated males are not larger than 3 individuals, whereas coalitions of 4–9 animals are close relatives (Packer and Pusey 1997). A male's reproductive success is directly related to his length of tenure within a pride, which is dependent on the number of males in a coalition (Packer and Pusey 1997). Male pride tenure rarely exceeds 4 years before another coalition takes over (Bertram 1979; Packer et al. 1988; Stander 1992b).

In the absence of a pride takeover, males generally leave their natal pride when 2–4 years old (Bertram 1975b; Pusey and Packer 1987). Most females are incorporated into their natal prides, but some subadult females (33% in the Serengeti) emigrate when 2–4 years old (Pusey and Packer 1987; Van Orsdol et al. 1985). Evidence from Serengeti indicates that dispersal may be disadvantageous for females because of decreased survival of their 1st litter (Pusey and Packer 1987). Females that remain in their natal pride have a reproductive lifespan of ca. 12 years beginning at 4–5 years of age (Pusey and Packer 1987; Van Orsdol et al. 1985).

A lioness may attract a male during estrus by urinating and spraying scent from her anal glands along travel routes (Rosevear 1974). In the Luangwa Valley in eastern Zambia, copulation has occurred between females and males from different prides (Yamazaki 1996). The 1st male to find a female in estrus will guard her and attack any approaching male (Packer and Pusey 1997). However, lionesses will mate with several males during estrus (Bertram 1975a; Bygott et al. 1979; Packer and Pusey 1982; Schaller 1972). Mating occurs during day and night. The pair remain close together, and either sex may initiate copulation, with the male initiating ca. 40% of copulations during courtship (Rudnai 1973a). Ritualistic displays associated with mating include vocalizations, such as 'mating snarls,' social grooming, and following of the lioness by the male (Cooper 1942; Rosevear 1974; Rudnai 1973a). Crouching by the female generally indicates receptiveness, leading to the male mounting with his forelegs and copulating and ending with the male biting the neck of the lioness (Rosevear 1974; Rudnai 1973a). Copulation lasts for ca. 55 s (range, 30–154 s—Rudnai 1973a). After copulation, the lioness often rolls onto her back and remains prone (Rudnai 1973b).

Lions are opportunist carnivores that usually hunt in groups; males hunt less frequently than do females, but males are stronger and can gain access to kills made by females (Bertram 1975a; Scheel and Packer 1991). Prey selection is related to seasonal weather patterns and the migration of large herbivores in some parts of Africa (Hanby et al. 1995). Most species of prey are large, with a modal prey size of ca. 150 kg (Packer 1986). Average food acquisition ranges from 8.7 kg/day per lioness in the dry season to 14 kg/day per lioness in the wet season in Etosha National Park and 8.5 kg/day when prey animals are abundant in Serengeti National Park (Packer et al. 1990; Stander 1992b). Males may consume twice as much meat as females; cubs (<1 year old) consume one-third as much as adult females; subadults (1–2 years old) consume two-thirds as much as adult females (Packer et al. 1990).

Capture of prey includes searching, stalking, attacking, and subduing (Elliott et al. 1976). Cover, group size, prey-group size, and light (during nocturnal hunts) affect hunting success (Van Orsdol 1984). Lions stalk with their heads low to the ground, moving slowly and gradually toward prey (Rosevear 1974). Small prey are struck and stunned or killed from a single blow of the paw followed by a quick bite if necessary (Rosevear 1974). Larger prey are attacked typically at the shoulder or flank, the hind claws deeply embedded, forepaws at the neck, chest, or far side of the body with a seizing of the muzzle and twisting of the head (Rosevear 1974). Prey is dragged down rather than knocked over (Ewer 1973). At a kill, lions eat in the open or drag the carcass to a more protected location where blood is licked from the carcass; the belly is ripped open; and intestines, internal organs, connective tissue, muscle, bones, and skin are consumed (Rosevear 1974; Van Valkenburgh 1996).

In Africa, lions are more successful at capturing smaller prey, such as Thomson's gazelle, when attacks are launched at distances of ≤7.6 m than from further distances. For larger prey, such as wildebeests and zebras, hunting success is 50% at distances of 15.2 m (Elliott et al. 1976). Of 61 stalks, only 10 were successful (Rudnai 1973b). Variation in overall hunting success rates reflects quality of the hunting environment, such as open or short-grass plains, or food abundance (Elliot et al. 1976; Eloff 1984; Funston et al. 1998; Packer and Ruttan 1988; Schaller 1972; Stander 1992b; Van Orsdol 1984). One in 3 attacks on Thomson's gazelle was successful in long grass, but success rate fell to 1 in 6 in short grass (Schaller 1969). Hunting success generally increases asymptotically with increasing group size when individuals are expected to hunt cooperatively (Packer and Ruttan 1988). Success rate in capturing

Thomson's gazelle, wildebeest, and zebra is higher when >2 lionesses hunt together (Schaller 1972). However, the average biomass of kills made by groups of different sizes or the hunting rates of different-sized groups is not consistent (Bertram 1975a, 1976, 1979; Packer 1986; Packer and Pusey 1982, 1983a, 1983b).

Lions exhibit individual preferences in prey selection within and between prides in the same area (Rudnai 1973b; Van Orsdol 1984). Prey selection is based on sexual and social differences within a pride (Funston et al. 1998). A complex division of labor was found among lionesses hunting in Etosha National Park, with individuals repeatedly playing the same role during stalking, ambush, and kill (Stander 1992a, 1992b). Group hunts often involve spreading out around the intended victim, with each lion taking a different route to optimize catch success if the prey animal attempts escape (Bertram 1979). However, highly developed teamwork during hunting is not observed in Serengeti, where individual lionesses may refrain from hunting depending on the prey species being pursued (Packer and Pusey 1997). Lions do not adjust their stalking behavior according to vigilance of the prey (Scheel 1993b).

GENETICS. Lions have 38 chromosomes. Estimates of heterozygosity vary with method and genetic structure sampled, and includes values of 3.7% (Menotti-Raymond and O'Brien 1995), ca. 26% (Shankaranarayanan et al. 1997), and 0.75% (Spong et al. 2002). Isolation of lion populations causes a loss of genetic heterozygosity in some areas (Wildt et al. 1987). Low genetic variability may be characteristic of the Asian subspecies and not the consequence of inbreeding depression (Shivaji et al. 1998).

Lions of Ngorongoro Crater in Africa experienced a population crash after an outbreak of a biting fly (*Stomoxys calcitrans*) in 1962. The Ngorongoro population bottleneck caused loss of restriction fragment length variation in the class I genes of the major histocompatability complex. These genes play a critical role in the development of immune defenses (Packer et al. 1990). Decreased genetic variability of lions from Ngorongoro Crater did not affect the reproductive-endocrine system of females compared to outbred counterparts from Serengeti (Brown et al. 1993).

Asian lions are genetically distinct from sub-Saharan subspecies, although the difference is smaller than genetic differences between human racial groups. Based on genetic distance, the Asian subspecies separated from the African population ca. 100,000 years ago (O'Brien et al. 1987a, 1987b).

CONSERVATION STATUS. The Asian subspecies, *P. l. persica*, was listed in the Convention on International Trade in Endangered Species (CITES) Appendix I in 1977 and is fully protected in India. The United States Endangered Species Act (ESA) and the International Union for Conservation of Nature and Natural Resources (IUCN) recognize the Asian subspecies as endangered (Wilson and Reeder 1993). A census estimate for the Gir Forest population approximates 280 individuals in and around the reserve boundaries (Khan 1995). Other extant subspecies were listed in CITES Appendix II in 1977. No complete censuses for lions in Africa are available, although estimates range from 30,000 to 100,000; numbers are declining outside of protected areas throughout the continent because of increasing agricultural demands and urbanization (Shoemaker and Pfaff 1997).

Recent changes in the distribution of lions in Africa reflect the increasing rate of pastoralism adjacent to conservation areas (Anderson 1981; Schaller 1972; Stander 1990). In some areas of Africa, agro-pastoralists lose valuable livestock to predation by lions (Butler 2000). Hunting is regulated in countries where lions exist, but many are still killed illegally and sustainable harvest rates are difficult to manage. A more significant threat comes from loss of large areas of land required by the animals that comprise the lion food base (Macdonald 1984). Lion attacks on humans are not well documented on the African continent, with the exception of the killing numerous laborers at Tsavo, Kenya, in the late 1800s (Caputo 2002). Fatal attacks by lions may be linked to heavy poaching of wild ungulates near villages and livestock (Chellam and Johnsingh 1993; Nowell and Jackson 1996).

The Gir Forest in Saurashtra has been greatly reduced since the 1880s because of expansion of agriculture and habitat destruction (Singh 1997). Local attitudes toward lion conservation are strained because of threat of personal injury and economic hardship caused by lion predation on livestock (Saberwal et al. 1994). Satellite populations of lions that migrate outside of the Gir Forest may present new conservation challenges because of limited territorial space (Singh 1997). Lion–human conflict will continue to challenge management in the Gir Forest, where lion attacks on humans are associated with prolonged drought conditions (Nowell and Jackson 1996; Saberwal et al. 1994). Prohibition of lion baiting for tourist shows, consolidation of reserve boundaries, development of movement corridors between suitable areas, arresting the degradation of peripheral forests and wastelands, and more equitable compensation to villagers for livestock destroyed by lions could lessen lion–human conflict in the region and improve lion habitat (Saberwal et al. 1994; Singh 1997).

REMARKS. Variation in size of teeth, auditory bullae, and other cranial and dental features may not provide enough evidence for subspecific designation (Allen 1924; Hollister 1918). More than 20 subspecies of the lion were based on zoo specimens, but captivity influences skull shape (Hollister 1918), rendering zoo specimens useless for taxonomy (Smithers 1983). Genetic material from lions in eastern and southern Africa is sufficiently similar to warrant a single African subspecies, *P. leo leo*. If lions were to be classified as a unique subgenus or genus the name *Leo* would have precedence (Hershkovitz 1966). However, lions have been crossed with tigers and the hybrids have successfully mated (Guggisberg 1975). Sperm from wild and captive Asian subspecies have a high incidence of abnormalities (O'Brien et al. 1987a; Wildt et al. 1987). The etymology of *leo* is Latin for lion.

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