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# *Panthera pardus* (Carnivora: Felidae)

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***Abstract:*** *Panthera pardus* (leopard; Linnaeus, 1758) is the smallest of the 4 large felids in the genus *Panthera*. A solitary and adaptable species, *P. pardus* is the widest ranging of all wild felids, inhabiting rain forests, mountains, semiarid environments, and suburban areas throughout sub-Saharan Africa, the Middle East, and South Asia to the Russian Far East. Despite this distribution, *P. pardus* is listed as "Near Threatened" by the International Union for Conservation of Nature and Natural Resources and several Asian subspecies are listed as endangered. *P. pardus* primarily feeds on small to medium-sized ungulates, but has a varied diet including fish, reptiles, birds, and small mammals.

***Key words:*** Africa, Asia, felid, India, leopard, wild felid


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## *Panthera pardus* (Linnaeus, 1758)
## Leopard

*Felis pardus* Linnaeus, 1758:41. Type locality "Indiis" restricted to "Egypt" by Thomas (1911a:135) or "Algeria" by J. A. Allen (1924:249).
*Felis panthera* Schreber, 1775:plate XCIX; Schreber, 1777:384–385. Type locality "Africa," restricted to "Algeria" by Ellerman and Morrison-Scott (1951:316).
*Felis leopardus* Schreber, 1775:plate CI; Schreber, 1777:387. Type locality "Senegal."
*Felis leopardus varia* Schreber, 1777:387, plates CI and CIb. Vide Wagner 1841:479. Type locality unknown.
*Felis chalybeata* Schreber, 1775:plate CIc. Type locality unknown. Attributed to Hermann 1804. Possibly *Leptailurus serval* (Griffith et. al., 1827:175).
*Felis fusca* Meyer, 1794:394. Type locality "India orientali."
*Felis chalybeata* Hermann, 1804:36. Type locality unknown (Duvernoy 1834).
*Felis melas* G. Cuvier, 1809:152. Type locality "Java."
*Panthera vulgaris* Oken, 1816:1052. Unavailable name (International Commission on Zoological Nomenclature 1956: Opinion 417).
*F*[*elis*]. *pardus antiquorum* Griffith et al., 1827:165. Type locality unknown.
*Felis palearia* F. G. Cuvier, 1832:3 for plate of panthére male. Type locality "Alger."
*Felis nimr* Hemprich and Ehrenberg, 1833:plate xvii. Type locality "Arabia."
*F*(*elis*). *variegata* Wagner, 1841:483. Preoccupied (Pocock, 1930b:326).
*F*(*elis*). *pardus melas*: de Blainville, 1843:52. Name combination.
*F*(*elis*). *pardus sumatranus* de Blainville, 1843:186. Type locality "de Sumatra."
*F*(*elis*). *pardus barbarus* de Blainville, 1843:186. Type locality "d'Algérie."
*F*(*elis*). *varia*: Gray, 1843:40. Name combination.
*Felis poecilura* Valenciennes, 1856:1036. Type locality "Gabon."
*Felis longicaudata* Valenciennes, 1856:1036. Type locality "la côte de Malabar ou de Ceylan."

**Fig. 1.**—An adult male leopard (*Panthera pardus*) from Namibia. Used with permission of the photographer, Andrew Stein.

*Felis tulliana* Valenciennes, 1856:1039. Type locality "l'Asie Mineure."

*Felis orientalis* Schlegel, 1857:23, figure 13. Type locality "Korea."

*Leopardus japonensis* Gray, 1862:262, plate XXXIII. Alleged type locality "Japan."

*Leopardus varius*: Gray, 1863:3. Name combination.

*Leopardus perniger* Gray, 1863:3. Type locality "Sikim," Tibet (see "Nomenclatural Notes").

*Felis pardus melania* Gray, 1863:3. Type locality "Sikim," Tibet.

*Leopardus poliopardus* Brehm, 1863:108. Type locality unknown.

*Leopardus pardus*: Gray, 1867:263. Name combination.

*F*(*elis*). *palaeopardus* Gray, 1867:263. Type locality unknown; Gray attributed to Fitzinger.

*Leopardus chinensis* Gray, 1867:264. Type locality "Pekin, mountain-forests of the west," China; not *Felis chinensis* Gray, 1837.

*Felis fontanierii* Milne-Edwards, 1867:375. Type locality "environs de Pékin."

*Panthera pardus*: Fitzinger, 1868:457. First use of current name combination.

*Panthera nimr niger* Fitzinger, 1868:466. Type locality "Abyssinien."

*Panthera antiquorum* Fitzinger, 1868:466. Type locality "Ost-Indien."

*Panthera leopardus*: Fitzinger, 1868:468. Name combination.

*Panthera variegata*: Fitzinger, 1868:473. Name combination.

*Panthera variegata nigra* Fitzinger, 1868:475. Type locality "Java."

*Panthera orientalis*: Fitzinger, 1868:477. Name combination.

*Leopardus japonensis* Swinhoe, 1870:628. Type locality "North China and Manchuria." Preoccupied by *Leopardus japonensis* Gray, 1862:262.

*Felis leopardus* Sclater, 1878:289. Type locality "Persia," not *Felis leopardus* Schreber, 1775.

*Felis leopardus melanot*[*ica*]. Günther, 1885:plate xvi. Type locality "Grahamstown," clarified to "about 20 miles from Grahams-town" by Günther (1886:205).

*F*(*elis*). *antiquorum*: Matschie, 1895:194. Name combination.

(*Leopardus*) *pardus variegata*: Matschie, 1895:199. Name combination.

(*Leopardus*) *pardus tulliana*: Matschie, 1895:199. Name combination.

(*Leopardus*) *pardus panthera*: Matschie, 1895:199. Name combination.

(*Leopardus*) *pardus minor* Matschie, 1895:199. Nomen nudum.

(*Leopardus*) *pardus leopardus*: Matschie, 1895:199. Name combination.

*Felis pardus melas* de Pousargues, 1896:181. Type locality "Yun-nan." Not *Felis melas* Cuvier, 1809.

*Leopardus japanensis* Lydekker, 1896:71. Unjustified emendation of *Leopardus japonensis* Gray, 1862.

*Felis leopardus suahelicus* Neumann, 1900:551. Type locality "Tanga, am Manjara-See und in den Loita-Bergen ... in Nai (Nord-Ugogo), in Usandawe und in Uganda."

*Felis villosa* Bonhote, 1903:475. Type locality "Amur Bay, E. Siberia."

*Felis pardus chinensis*: Brass, 1904:6. Name combination.

*Felis pardus fontanieri*: Brass, 1904:6. Name combination and unjustified emendation of *Felis fontanierii* Milne-Edwards, 1867.

*Felis pardus nanopardus* Thomas, 1904:94. Type locality "40 miles west of Gorahai," Somaliland.

(*Felis* [*Leopardus*]) *grayi* Trouessart, 1904:268. Type locality "China."

*Leopardus pardus tullianus*: Satunin, 1905:152. Correction of gender agreement.

*Felis pardus ruwenzorii* Camerano, 1906:1. Type locality "Ruwenzori ... Bunjungolo."

*F*(*elis*). *pardus melanotica*: Pocock, 1907:677. Name combination.

*F*(*elis*). *pardus suahelica*: Lydekker, 1907:785. Name combination and inappropriate gender attribution.

*Panthera hanensis* Matschie, 1908:198. Type locality "Hing-an-fu," China.

*F*(*elis*). *pardus melanosticta* Lydekker, 1908:430. Unjustified emendation of *Felis melanotica* Günther, 1885.

*F*(*elis*). *pardus panthera*: Lydekker, 1910:385. Name combination.

*F*(*elis*). *pardus villosa*: Lydekker, 1910:385. Name combination.

*Felis fontanieri* Thomas, 1911b:688. Unjustified emendation of *Felis fontanierii* Milne-Edwards, 1867.

*Felis pardus panthera*: Brass, 1911:402. Name combination.

*Felis pardus variegata*: Brass, 1911:402. Name combination.

*Felis pardus tulliana*: Brass, 1911:403. Name combination.

*Felis pardus sinensis* Brass, 1911:403. Type locality "südlichen China."

*Felis pardus leopardus*: Brass, 1911:405. Name combination.

*Felis pardus variegata* G. M. Allen, 1912:235. Type locality "Yangtze valle, at Changyanghsien, Hupeh," China. Not *Felis variegata* Wagner, 1841.

*Felis pardus fortis* Heller, 1913:5. Type locality "Loita Plains, Southern Guaso Nyiro district, British East Africa."

*Felis pardus chui* Heller, 1913:6. Type locality "Gondokoro, northern Uganda."

*F*(*elis*). *p*(*ardus*). *variegata* Lydekker, 1914:498. Preoccupied by *Felis pardus variegata* G. M. Allen, 1912. Not *Felis variegata* Wagner, 1841.

*Leopardus pardus ciscaucasica* Satunin, 1914:159. Type locality "Kuban Provence, Caucasus" vide Ellerman and Morrison-Scott 151:317.

*Leopardus pardus orientalis*: Satunin, 1914:160. Name combination.

*Felis pardus centralis* Lönnberg, 1917:5, 49. Type locality "Kabare at Lake Albert," Belgian Congo, now Democratic Republic of the Congo.

*Panthera pardus reichenowi* Cabrera, 1918:481. Type locality "Yokó (Kámerun)."

*F*(*elis*). *p*(*ardus*). *ruvenzorii* de Beaux, 1923:275. Unjustified emendation of *Felis pardus ruwenzorii* Camerano, 1906.

(*Felis pardus*) *antinorii* de Beaux, 1923:276, 278. Type locality "Keren, paese dei Bogos," Somalia.

*Panthera pardus iturensis* J. A. Allen, 1924:259. Type locality "Niapu, Belgium Congo."

*Panthera pardus leopardus*: J. A. Allen, 1924:252. Name combination.

*Panthera pardus nimr*: J. A. Allen, 1924:252. Name combination.

*Panthera pardus melanotica*: J. A. Allen, 1924:252. Name combination.

*Panthera pardus suahelica*: J. A. Allen, 1924:252. Name combination.

*Panthera pardus nanopardus*: J. A. Allen, 1924:252. Name combination.

*Panthera pardus ruwenzorii*: J. A. Allen, 1924:252. Name combination.

*Panthera pardus fortis*: J. A. Allen, 1924:252. Name combination.

*Panthera pardus leopardus*: J. A. Allen, 1924:252. Name combination.

*Panthera pardus chui*: J. A. Allen, 1924:253. Name combination.

*Panthera pardus centralis*: J. A. Allen, 1924:253. Name combination.

*Panthera pardus reichenowi*: J. A. Allen, 1924:253. Name combination.

*Panthera pardus saxicolor* Pocock, 1927:213. Type locality "Asterabad, North Persia."

*Panthera pardus adusta* Pocock, 1927:214. Type locality "unknown."

*F*(*elis*). *p*(*ardus*). *saxicolor*: Dollman and Burlace, 1928:482. Name combination.

*Leopardus varius*: Pocock, 1930a:74. Name combination and unjustified emendation of *Felis leopardus varia* Schreber, 1777.

*Panthera pardus sindica* Pocock, 1930a:80. Type locality "Kirthar Range on the Sind-Baluchi boundary," Pakistan.

*Panthera pardus fusca*: Pocock, 1930b:307. Name combination.

*Panthera pardus millardi* Pocock, 1930b:316. Type locality "Kashmir."

*Panthera pardus japonensis*: Pocock, 1930b:320. Name combination.

*Panthera pardus bedfordi* Pocock, 1930b:323. Type locality "Shong Chou in S. E.. [sic] Shensi, 3,000 ft."

*Panthera pardus delacouri* Pocock, 1930b:325. Type locality "Hué in Annam."

*Panthera pardus melas*: Pocock, 1930b:326. Name combination.

*Panthera pardus jarvisi* Pocock, 1932a:33. Type locality "Sinai."

*P*[*anthera*]. *p*[*ardus*]. *adersi* Pocock, 1932a:33. Type locality "Zanzibar," restricted to "near Chuaka" (Pocock 1932b:563).

*P*[*anthera*]. *p*[*ardus*]. *shortridgei* Pocock, 1932a:33. Type locality "Damaraland," restricted to "Gangongo, 3560 ft. alt. on the Okavango River some 120 miles above the Okavango swamp in Western Caprivi" (Pocock 1932b:584).

*P*[*anthera*]. *p*[*ardus*]. *puella* Pocock, 1932a:33. Type locality "Kaokoveld," Namibia.

*Panthera pardus panthera*: Pocock, 1932b:544. Name combination.

*Panthera pardus antinori*: Pocock, 1932b:549. Name combination.

*Panthera pardus adusta*: Pocock, 1932b:549. Name combination.

*Panthera pardus brockmani* Pocock, 1932b:555. Type locality "Upper Sheikih in the Golis Range."

*Felis pardus fusca*: J. A. Allen, 1938:448. Name combination.

*Panthera pardus kotiya* Deraniyagala, 1956:116. Type locality "Ceylon."

*Panthera pardus dathei* Zukowsky, 1959:343. Type locality "Persiens," Iran.

*Panthera pardus brockmani*: Weigel, 1961:69. Name combination.

*Panthera pardus tulliana*: Weigel, 1961:70. Name combination.

*Panthera pardus ciscaucasica*: Weigel, 1961:70. Name combination.

*Panthera pardus pernigra*: Weigel, 1961:70. Name combination.

*Panthera pardus orientalis*: Weigel, 1961:70. Name combination.

*Panthera pardus transcaucasica* Zukowsky, 1964:158. Type locality "südkaukasischen," Armenia.

*Panthera pardus sexicolor* Ahmed et al., 1988:1341. Unjustified emendation of *saxicolor* Pocock, 1927.

*Panthera pardus fusea* Johnson et al., 1993:646. Unjustified emendation of *fusca* Meyer, 1794.

*P*[*anther*]. *p*[*ardus*]. *ciscaucasicus* Miththapala et al., 1996:1118. Correction of gender agreement.

Context and Content. Order Carnivora, family Felidae. *Panthera pardus* has 9 subspecies (Uphyrkina et al. 2001); 8 if *P. p. nimr* is included with *P. p. ciscaucasica* (Miththapala et al. 1996). Misspellings and gender changes are not included in the following subspecies synonymy.

*P. p. ciscaucasica* Satunin, 1914:159. See above; *ciscaucasica*, *dathei*, *leoparda* (Sclater), *saxicolor*, *sindica*, *transcaucasica*, and *tulliana* are synonyms.
*P. p. delacouri* Pocock, 1930b:325. See above; *sinensis* and *variegata* (Lydekker) are synonyms.
*P. p. fusca* (Meyer, 1794:394). See above; *antiquorum*, *centralis*, *chinenesis*, *chui*, *iturensis*, *longicaudata*, *melas*, *millardi*, *pernigra*, and *variegata* (Allen) are synonyms.
*P. p. japonensis* (J. E. Gray, 1862:262). See above; *bedfordi*, *chinensis*, *fontanierii*, *grayi*, and *hanensis* are synonyms
*P. p. kotiya* Deraniyagala, 1956:116. See above.
*P. p. melas* G. Cuvier, 1809:152. See above; *variegata* (Wagner) is a synonym.
*P. p. nimr* (Hemprich and Ehrenberg, 1833:plate xvii). See above; *jarvisi* is a synonym.
*P. p. orientalis* (Schlegel, 1857:23, figure 13). See above; *villosa* is a synonym.
*P. p. pardus* (Linnaeus, 1758:41). See above; *adersi*, *adusta*, *antinorii*, *barbara*, *fortis*, *leopardus* (Günther), *leopardus* (Schreber), *melanosticta*, *melanotica*, *minor*, *nanoparda*, *palearia*, *panthera*, *poecilura*, *puella*, *reichenowi*, *ruwenzorii*, *shortridgei*, *suahelicus*, *varia*, and *vulgaris* are synonyms.

Nomenclatural Notes. A thorough discussion of the type locality is in Pocock (1930a). The species name *pardus* is from the Greek *pardos* for male panther. Fitzinger (1868) provides pre-Linnean synonyms. The name *pernigra*/*perniger* is often attributed to Hodgson, but was published by Gray (1863) when cataloging Hodgson's specimens. Thus, following Ellerman and Morrison-Scott (1951), we have attributed the name to Gray. An alternative attribution would be Hodgson in Gray (1863). Other common names are graupanther (Brehm 1863); léopard, panther, panthère (Pocock 1930a, 1930b); chui, nsowä, steppenleopard, tui (Matschie 1895); ihwanqana, ingwe, nkoè, nkwê, nkwe, nngwe, yingwe (Roberts 1951); chita, harvard, ingwi, inkwi, ngo, nyalugwi, shabel, siveri, tijger (Ward 1910); chui, damissa, dumok, erith, lagho bagh, malilda, nimr, ol-owarukeri, osebo, terdwa (Dollman and Burlace 1928); and bars (Heptner and Sludskii 1992). "[T]he terms 'panther' and 'leopard' are used somewhat indiscriminately and inconsistently as synonyms. Leopard is the name by which the animal is commonly known amongst English-speaking people in Europe, America and Africa; but … panther … is more usually employed by Indian sportsmen" (Pocock 1930a:64). The generic synonymy for *Panthera* includes *Felis* and *Leopardus* as well as *Jaguarius*, *Leo*, *Pardus*, and *Tigris* (Mazák 1981).

## DIAGNOSIS

*Panthera pardus* (Fig. 1) is a large spotted cat distinguished from other members of the genus *Panthera* by its distribution throughout sub-Saharan Africa and Asia and its characteristic dark, rosette spots. In Africa, *P. pardus pardus* may be confused with cheetahs (*Acinonyx jubatus*), which also have been called "hunting leopards" in Asia (Sterndale 1884), but cheetahs are taller and more slender with circular, solid spots, unlike the robust *P. pardus* with rosettes. Cheetahs also have a diagnostic tearmark from the inside of the eye to the outside of the mouth, absent in *P. pardus* (Krausman and Morales 2005).

The coat pattern of *P. pardus* and the jaguar (*Panthera onca*) is similar, but *P. onca* often has a small spot within the rosette pattern, whereas *P. pardus* often does not. *P. pardus* and *P. onca* are not sympatric because *P. onca* inhabits Central and South America and *P. pardus* occurs in Africa, the Middle East, and Asia. *P. pardus* is marginally smaller than *P. onca* (length of head and body, 1.0–1.5 m, 1.1–1.8 m; mass, 30–90 kg, 61–132 kg, respectively), but *P. pardus* has a somewhat longer tail (0.8–1.0 m, 0.5–0.8 m, respectively—Nelson and Goldman 1933; Roberts 1951; Hall and Kelson 1959; Rosevear 1974; Eisenberg and Redford 1999; Stein 2008). *P. pardus* has a more slender head and smaller foot pads compared to the more robust skull and more evenly rounded foot pads of *P. onca* (Nelson and Goldman 1933).

## GENERAL CHARACTERS

Individual measurements can vary by geographic region with smaller individuals typically coming from Cape Province, South Africa, where adult male *Panthera pardus pardus* have a mean mass of 31 kg (range, 20–45 kg), whereas the more typical masses for an adult male *P. pardus* are reported from Zimbabwe as 60 kg (range, 52–71 kg) with individuals up to 90 kg on occasion (Kitchener 1991). Ranges of mean body mass (kg) for 34 females and 47 males from India, the Ivory Coast, Namibia, and South Africa were 21.2–54.0 and 30.9–62.6, respectively (Robinette 1963; Smithers 1983; Grimbeek 1991; Bailey 1993; Jenny 1996; Marker and Dickman 2005; Stein 2008). Ranges of mass (kg) without stomach contents for 9 females and 8 males were 26.8–36.4 and 33.6–60.0, respectively, in Zambia (Wilson 1968). Body mass of adults from the former Soviet Union ranged from 32 to 60 kg (Heptner and Sludskii 1992).

Mean length of head and body for 2 females and 2 males from Namibia were 106.5 and 132.0 cm, respectively (Stein 2008). Ranges of mean total length (cm) for 20 females and 23 males from South Africa and Namibia were 185.0–198.4 and 210.0–217.5, respectively (Grimbeek 1991; Bailey 1993; Marker and Dickman 2005; Stein 2008). Measurements (range; cm) of *P. p. orientalis* in the former Soviet Union (unknown sex and samples size) were: length of head and body, 120–171; length of tail, 75–102; length of hind foot, 24–26; length of ear, 7.5–8.0; height at shoulder, 50–78

(Heptner and Sludskii 1992). Measurements for 2 female *P. p. nimr* from the Judean Desert (mm) were: total length, 1,684–1,920; length of head and body, 930–1,130; length of tail, 754–790; length of hind leg from the hip to foot pad, 223–230; length of ear, 59–64; width of front interdigital foot pad, 52–52; width of hind interdigital foot pad, 48–49; mass, 22–23.5 kg (Ilani 1981). Mean and range of head and body lengths and length of tail (cm) for 10 *P. p. nimr* of unknown sex from Jordan, Sinai, Iraq, Oman, and Saudi Arabia were 197.11, 160.0–226.1; 78.12, 66.0–94.0 (Harrison and Bates 1991). Ear length of 1 animal was 44 mm (Harrison and Bates 1991).

Mean cranial measurements (cm; *n* in parentheses) for males and females, respectively, from Namibia were: greatest length, 17 (2), 15.6 (3); greatest width, 15.6 (2), 11.3 (3); upper canine length, 3.6 cm (3), 2.7 (5—Stein 2008; Fig. 2). Cranial measurements (mm, – indicates missing measurement) for 2 males and 2 females, respectively, from Gabon were: greatest length, 226.5, –, 171.5, –; condylobasal length, 202.0, –, 158.5, 166.0; zygomatic width, 148.8, 147.0, 106.7, 114.5; skull width, 91.7, –, 68.7, 73.1; I–M distance, 87.8, 83.0, 64.5, 67.0; C–M distance, 71.6, 68.1, 55.2, 57.0; palatal length, 101.0, 99.8, 75.7, 76.0; mandibular length, 149.8, 145.5, 114.2, 121.5 (Dobroruka and van Bree 1965). Mean cranial measurements (mm; range, *n*) for male and female *P. p. delacori*, respectively, from Southeast Asia were: greatest skull length, 212, 207–218, 4; 188, 180–196, 6; condylobasal length, 195, 186–202, 4; 172, 165–178, 5; zygomatic width, 139, 134–148, 4; 125, 116–130, 6; greatest skull width, 69.0, 67–71, 2; 65, 65, 1; interorbital width, 37.6, 36–41, 3; 31, 31, 1; postorbital width, 42.6, 42–43, 3; 37, 37, 1 (Dobroruka 1963). Mean cranial measurements (mm; range, *n*) for animals of unknown sex from Jordan, Sinai, Iraq, Oman, and Saudi Arabia were: greatest skull length, 193, 166–213, 6; condylobasal length, 177, 151–194, 6; zygomatic width, 121, 105–132, 7; mandibular length, 130, 111–142, 7 (Harrison and Bates 1991). Cranial measurements (mm; range) for males and females, respectively, from the former Soviet Union (no sample size) were: greatest skull length, 193–256, 180–218; condylobasal length, 186–224, 170–188; zygomatic width, 123–172, 116–135; muzzle width above canines, 53–65, 47–53; length of upper toothrow, 65–79, 60–68 (Heptner and Sludskii 1992). Canines average 34.4 mm in length (Christiansen 2007). The mandibular symphysis is not fused (Kalita et al. 2001).

Fur color varies from a pale yellow to rich ochre to black. Fur is generally soft and thick, with individuals living in colder climates having longer fur than those from warmer habitats (Turnbull-Kemp 1967). Fur along the ventral portion of the torso is generally lightly colored and long, regardless of the region. Fur is short and uniform in color on the rostrum and becomes spotted with solid dots along the muzzle and forehead. Whisker spots can be used for individual identification (Pennycuick and Rudnai 1970). The solid spots become irregular, rosette patterns along the neck and shoulders extending along the back and midsection to the rump and tail. Large, irregular spots are present along the limbs from the elbow and knee to the feet and along the ventral side of the torso. One of us (ABS) observed variation in eye color from golden yellow to a pale blue.

## DISTRIBUTION

*Panthera pardus* is the most widely distributed wild cat species in the world (Fig. 3), with a range extending from the Cape of Good Hope, South Africa, through the Middle East and Southeast Asia to the Amur Peninsula in the Russian Far East (Nowell and Jackson 1996). The population of *P. p. pardus* is distributed throughout sub-Saharan regions except for the Skeleton Coast of Namibia and most of South Africa outside of the Limpopo region, Eastern and Western Cape provinces. *P. p. adersi* is extinct (Goldman and Walsh 2002). In the Middle East, *P. p. nimr* occurs in Israel on the Arabian Peninsula (El-Mashjary 1995; Al-Johany 2007). *P. p. ciscaucasica* persists in protected areas and mountainous areas of the Russian North Caucasus, Georgia, Armenia, Azerbaijan, Nagorno-Karabakh Republic, Turkey, Turkmenistan, Afghanistan, Pakistan, and Iran in southwestern Asia (Henschel et al. 2008). *P. p. fusca* is pervasive throughout the protected area system within India. *P. p. kotiya* is present on Sri Lanka. *P. p. delacouri* is increasingly rare in China and Southeast Asia outside of protected areas. In northern China, *P. p. japonensis* also is rare. *P. p. melas* is still found in Malaysia, but not on the islands of Borneo or Sumatra (Nowell and Jackson 1996; Meijaard 2004).

*Panthera pardus pardus* is primarily distributed throughout sub-Saharan Africa with smaller isolated populations in the Atlas Mountains of Morocco, Ahaggar in southeastern Algeria, the eastern desert of Egypt, and Niger (Ray et al. 2005). The remaining populations of *P. p. pardus* are in West Africa extending from Nigeria to Senegal. The eastern and southern African population is more contiguous, although increasingly patchy, extending east to west from Somalia to Gabon and eastern Nigeria and south of the Sahel from Sudan to South Africa with an isolated population in the western Cape region (Nowell and Jackson 1996; Ray et al. 2005).

## FOSSIL RECORD

The origin of the modern *Panthera pardus* is between 470,000 and 850,000 years ago in Africa. Modern *P. pardus* migrated to Asia more recently, between 170,000 and 300,000 years ago (Uphyrkina et al. 2001). The earliest documented ancestral fossils of *P. pardus* were from Laetoli, Tanzania, along with lion (*Panthera leo*) fossils dated at approximately 3.5 million years ago (Turner and Anton

**Fig. 2.**—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult *Panthera pardus* (3996, University of Massachusetts Natural History Museum) confiscated by United States Fish and Wildlife. Greatest length of skull is 219 mm.

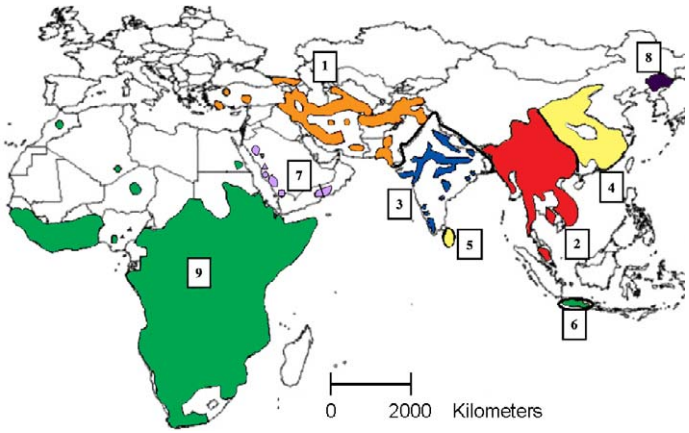


**Fig. 3.**—Geographic distribution of *Panthera pardus* (modified from Henschel et al. 2008). Subspecies are: 1, *P. p. ciscaucasica*; 2, *P. p. delacouri*; 3, *P. p. fusca*; 4, *P. p. japonensis*; 5, *P. p. kotiya*; 6, *P. p. melas*; 7, *P. p. nimr*; 8, *P. p. orientalis*; 9, *P. p. pardus*.

1997). The oldest fossil within Asia is from the Inain Siwaliks at approximately 2 million years ago (Hemmer 1976). This Asiatic *P. pardus* was similar in appearance to *P. onca* and the now extinct *P. gombazogensis* (Kitchener 1991).

## FORM AND FUNCTION

One of us (ABS) has observed that large male *Panthera pardus* may develop a dewlap extending from the lower jaw to the chest. *P. pardus* has large and well-defined musculature on the forelimbs, shoulders, and neck. *P. pardus* can drag a carcass more than double its body mass using its mouth and hoist the carcass into trees (Scheepers and Gilchrist 1991). A 39-kg *P. pardus* had a forelimb length of 57 cm, a hind-limb length of 76 cm, and an intergirdle distance of 74 cm (Day and Jayne 2007). In length, a humerus was 21 cm and a femur was 23 cm (Ray et al. 1996; 1997). Limb bone mean lengths and circumferences (mm) for 5 *P. pardus* were: humerus, 211.2, 90.1; radius, 263.6, 60.9; femur, 353.4, 87.0; tibia, 302.3, 83.4 (Christiansen 1999). Meniscal ossicles are present (Walker et al. 2002). Dental formula is i 3/3, c 1/1, p 3/2, m 1/1, total 30 (Stander 1997).

Hair of *P. p. nimr* is about 1.5–2.0 cm in length on dorsum and 4–5 cm in length on ventrum (Borner 1977). Hair on the distal part of the tail is longer than on the proximal region, thus the last one-third of the tail appears to have a larger diameter (Borner 1977). Hair density is about 3,000 hairs/cm$^2$ on dorsum with 1 guard hair for every 4 underfur hairs (Heptner and Sludskii 1992). Yellow guard hairs are "30 mm long and 121 microns thick but the black hairs [are] 40 mm long and 96 microns thick" (Heptner and Sludskii 1992:204). Similarly, yellow underfur is 20 mm long (21 μm thick) and black underfur is 24 mm long (32 μm

thick—Heptner and Sludskii 1992). Dark, smokey-gray dorsal underfur in a winter coat is up to 19 mm long (Pocock 1934). Winter hair (45–50 mm) is longer than summer hair (20–25 mm—Pocock 1934; Heptner and Sludskii 1992).

A 94-cm-long adult female had the following measurements (cm or g): height at withers, 67; height at hind limb, 69; length of head, 27; width of head, 15.5; mass of head, 2,000; mass of skull and mandible, 550; orbital cavity, 6 by 5; eyeball mass, 45; eyeball size, 3.4 by 3.2 by 3.3; cornea lateromedial by dorsoventral diameters, 2.2 by 1.8; mass of larynx, 105; thyroid size, 6.0 by 1.6 by 0.6; tracheal length, 26 (with 43 tracheal rings); lung mass with trachea, 405; heart mass, 175; heart circumference, 22.5; esophageal length, 42; mass of stomach, 250; lesser curvature of stomach, 24.5; greater curvature of stomach, 44; length of small intestine, 106; length of large intestine, 75.2; cecal length, 3.2; rectal length, 40; mass of intestines, 650; mass of spleen, 80; size of spleen, 21.5 by 4.5 by 1.8; mass of 5-lobed liver, 525; length of hepatic duct, 13.7 (Archana et al. 2006). An adult female had 13 ribs, a left lung with 2 lobes, a right lung with 5 lobes, and a gall bladder (Archana et al. 2006).

*Panthera pardus* has a digitigrade foot structure with the forefeet having 5 toes and the hind feet having 4. The 1st toe, set on the inside of the foot above the wrist, is only used when bringing down prey. The feet of adult male *P. pardus* are 70–90 mm in length and width, forming a near circular track for the forefoot (Stuart and Stuart 1994). The hind foot is often slightly longer than it is wide, but conforms to these measurements. The female feet are similar but are 55–70 mm in length and are 5–10 mm more slender (Stuart and Stuart 1994). The metacarpal–phalanx ratio is 1.87 (Iwanluk et al. 2001). Maximal speeds of 60 km/h, horizontal leaps of 6 m, and vertical leaps of 3 m are reported in the secondary literature (Nowak 1999).

Typically, feces of *P. pardus* are a cylindrical, sausage shape with a diameter between 20 and 30 mm (Stuart and Stuart 1994). Feces of *P. pardus* are primarily made up of undigested hair and bone (Keogh 1983).

Mean measurements (cm or g) of a pair of kidneys from an adult female were: length, 7.12; width, 5.12; thickness, 3.47; cortical thickness, 0.71; paracortical thickness, 0.96; medullary thickness, 1.08; mass, 158 (Sarma et al. 2004). A neonate had a cardiac foramen ovale (Macdonald and Johnstone 1995).

Acoustical compliances ($cm^3$ of air) were: middle-ear cavity, 4.3; tympanic membrane–ossicular, 2.15; total middle ear, 1.41 (Huang et al. 2000). Minimum frequency for acoustic reflectance was 0.77 kHz with an admittance-notch frequency of 3.12 kHz (Huang et al. 2000). Regarding the larynx, the longitudinal length of the vocal fold (at rima glottis) is 20 mm and the distance from the base of the cricoid cartilage to the superior border of the vocal fold is 50 mm (Hast 1989).

Ranges of heart rate (beats/min), respiration (breaths/min), and rectal temperature (°C) of immobilized *P. pardus* after 20 and 70 min, respectively, were: 70–88, 55–95; 6–28, 11–30; 39.1–40.6, 37.8–38.8 (Belsare and Athreya 2010). Hemoglobin of *P. pardus* has 2 forms, 80% of which is the major form (Abbasi and Braunitzer 1985; Ahmed et al. 1988). Mean hematological values were: blood clotting time, 5.29 min; hemoglobin 12.3–14.83 g/dl; hematocrit, 0.37–0.47; packed cell volume, 39–43%; red blood cells, 6.95–$10.26 \times 10^6$/μl; mean corpuscular volume, 45.5–61.6 $\mu m^3$; mean corpuscular hemoglobin, 14.0–21.4 pg (Hawkey and Hart 1986; Jain 1986; Pospíšil et al. 1987; Singh et al. 1999a). The differential counts (%) from $10.3–15.0 \times 10^6$/ml leukocytes were segmented neutrophils, 61–84; banded neutrophils, 4; basophils, 0–1; eosinophils, 0–11; monocytes, 1–3; lymphocytes, 9–23 (Hawkey and Hart 1986; Jain 1986; Pospíšil et al. 1987). Serum calcium and inorganic phosphorus (mg/dl) were 10.97 and 3.63, respectively, from 1 female (Singh et al. 1999b). Plasma protein and fibrinogen (g/dl) were 8.1 and 0.1, respectively (Jain 1986). Mean serum values for vitamins and lipids were: total cholesterol, 4.4–4.6 mmol/liter; high-density lipoprotein (HDL) cholesterol, 3.4 mmol/liter; low-density lipoprotein (LDL) cholesterol, 0.8 mmol/liter; triglycerides, 0.40–0.88 mmol/liter; retinol, 1,259 nmol/liter; retinyl palmitate, 267 nmol/liter; α-tocopherol, 24.2 μmol/liter (Crissey et al. 2003).

In females, baseline serum progesterone is 1.6 ng/ml and increases to 13–98 ng/ml during the luteal phase (Schmidt et al. 1988); fecal progesterone is 706–732 pg/g (De Haas van Dorsser et al. 2007). Progesterone stays at basal levels when animals are isolated (Schmidt et al. 1988). Basal concentrations (ng/ml) of luteinizing hormone and follicle-stimulating hormone in males and females, respectively, were: 1.9, 1.8; 28.7, 27.5 (Brown et al. 1989). Basal serum estrogen in females was 8.8 pg/ml (Brown et al. 1988) and peak fecal estrogen (1,433 ng/g) was twice basal levels (De Haas van Dorsser et al. 2007). The peak urinary relaxin concentration during 2 pregnancies was 3.6–4.6 ng/mg creatinine (De Haas van Dorsser et al. 2006). Sperm density, number of motile sperm, and number of normal sperm, respectively, were: $51.6–55.8 \times 10^6$/ml, 57%, and 72% (Jayaprakash et al. 2001; De Haas van Dorsser and Strick 2005). Total sperm length, head length, and head width (μm) are: 54.6, 4.2, and 2.5, respectively (De Haas van Dorsser and Strick 2005). Males over 8 years and under 3 years had lower sperm counts than males of intermediate ages and sperm counts were lower in summer than in winter (De Haas van Dorsser and Strick 2005).

Scats have the following bile acids: deoxycholic, chenodeoxycholic, and dehydrocholic (Khorozyan et al. 2007). Urine contains cauxin (McLean et al. 2007). Marking fluid contains 1.15 mg/ml lipids as well as the following: acids: acetic, butyric, heptanoic, hexanoic, isoheptanoic, isohexanoic, isooctanoic, isovaleric, octanoic, nonanoic,

propionic, and valeric; neutral compounds: 2-acetyl-1-pyrroline, acetaldehyde, and acetone; and basic compounds: cadaverine, dimethylamine, ethylenediamine, phenylethylamine, putrescine, and trimethylamine (Poddar-Sarkar and Brahmachary 2004).

## ONTOGENY AND REPRODUCTION

Mating occurs mid-January–mid-February in Iran (Farhadinia et al. 2009), January–February in Amur, and November–December in Nepal (Hayssen et al. 1993). Births occur February–March in India and Nepal, April–May in Amur, in the spring and early summer in Pakistan, during the rainy season in Angola, at the start of the rainy and start of the dry seasons in Zaire, and year-round in South Africa (Hayssen et al. 1993).

The mean length of estrus is 5–13 days; mean cycle length is 20–55 days and the follicular phase is 18–23 days (Hayssen et al. 1993; Cunningham and Gross 2000; De Haas van Dorsser et al. 2007). Gestation is 88–112 days (Acharjyo and Patnaik 1985; Hayssen et al. 1993; Cunningham and Gross 2000; De Haas van Dorsser et al. 2006, 2007). Lactation is 114–130 days with den emergence at 42 days (Hayssen et al. 1993) and independence at 13 months (Sunquist 1983; Le Roux and Skinner 1989). Lactating females may leave cubs alone for up to 36 h (Seidensticker 1977). Interbirth interval is 3.5–45 months with most intervals 8–12 months (Acharjyo and Patnaik 1985; Hayssen et al. 1993).

Females have 4 mammae. Litter size is 1–6, with a mode of 2, and litters of 5 or 6 are rare (Eaton 1977; Acharjyo and Patnaik 1985; Hayssen et al. 1993; Kumar and Luna 2005). Birth mass from secondary sources is 43–60 g (Kingdon 1977; Smithers 1983) but is 280–1,000 g from primary sources (Desai 1975; Acharjyo and Patnaik 1985; Shukla et al. 2003). Neonates have closed eyes, short fur, and pink skin on nose tip, paws, and perineal area (Desai 1975). From tip to tip neonates averaged 43.8 cm (Acharjyo and Patnaik 1985). Sex ratio at birth was 49 males to 41 females (Acharjyo and Patnaik 1985). Eyes open at 4–9 days, incisors erupt at 21–29 days, canines erupt at 30 days, and molars start to appear at 52 days (Desai 1975; Cunningham and Gross 2000; Shukla et al. 2003).

Females 1st mate at 23–32 months with a 1st birth from 27 to 52 months, whereas males can 1st sire young at 1.5 years (Hayssen et al. 1993). In Kruger National Park an average of 28% of adult females produced young each year (Bailey 1993). Infanticide may occur when territorial males are removed before cubs reach independence (Ilani 1990; Bailey 1993). Fully developed dentition is present at 2 years of age (Stander 1997). Incisors and canines show wear before premolars and molars (Stander 1997). A table of age and tooth wear from 8 months until 10 years is available (Stander 1997). Males have more enamel flaking and canine fractures than do females (Stander 1997).

## ECOLOGY

***Population characteristics.***—Populations of *Panthera pardus* in the Russian Far East are estimated at $< 60$ individuals (Miquelle and Murzin 2003). Smaller populations are present in Thailand and Malaysia (Grassman 1999). In Rajaji National Park, India, the population of *P. pardus* was estimated at 14.99 individuals/100 km$^2$ (Harihar et al. 2009). The stronghold of *P. p. pardus* is in Africa, where large, continuous populations still exist (Henschel et al. 2008). Density of *P. pardus* ranges from 2.49 to 11.11 individuals/100 km$^2$ in South Africa (Balme et al. 2010) and is 3.6 individuals/100 km$^2$ in north-central Namibia (Stein et al. 2011). Although a radiocollared female lived over 10 years in Thailand, at least 27 animals in zoos have lived 20–27 years (Grassman and Larney 2002; Weigl 2005).

***Space use.***—*Panthera pardus* occupies a variety of habitats where competitors are present, prey sizes vary, and cover is variable. Considering all of these influences on movements and habitat use of *P. pardus*, generally home ranges of *P. pardus* are largest where prey availability is relatively low, although ranges are smallest where prey availability is high and cover is available. In semiarid and arid environments with low prey density, ranges of *P. pardus* are the largest recorded, including the Kalahari Desert (male home range $\bar{X} = 2{,}182$ km$^2$—Bothma and Le Riche 1984) and the mountainous areas of Cape Province, South Africa ($\bar{X} = 388$ km$^2$—Norton and Lawson 1985). The ranges of *P. pardus* in northeastern Namibia were relatively large ($\bar{X} =$ 451 km$^2$ for males and 188 km$^2$ for females) in Kaudam National Park (Stander et al. 1997a). In north-central Namibia *P. pardus* had medium to large ranges; a male's range was 108 km$^2$ and 2 female ranges averaged 50 km$^2$ with the availability of desert warthogs (*Phacochoerus aethiopicus*) and greater kudu (*Tragelaphus strepsiceros* [currently *Strepsiceros strepsiceros*]—Stein et al. 2011). In rocky areas of eastern Botswana, ranges of *P. pardus* were 32.9 km$^2$ for females in Botswana (Steyn and Funston 2009) and 40–69 km$^2$ for males in the Cedarberg Wilderness Area, Cape Province, South Africa (Norton and Henley 1987). Ranges of *P. pardus* ranges within rain-forested areas vary from medium sized such as 86 km$^2$ for males and 25 km$^2$ for females in Tai National Park, Ivory Coast (Jenny 1996), to small range sizes of 32–46 km$^2$ for males and 14–26 km$^2$ for females in Huai Kha Kaeng National Park, Thailand (Rabinowitz 1989; Simcharoen et al. 2008). In Nepal, 2 males had home ranges of 47 and 48 km$^2$, whereas a female had a range of 17 km$^2$ (Odden and Wegge 2005). Ranges of *P. p. pardus* are smallest in forested and rocky areas such as Kruger National Park, where prey includes impala

(*Aepyceros melampus*; $\bar{X} = 38$ km$^2$ for males and 15 km$^2$ for females—Bailey 1993) and the Lolldaiga Hills, Kenya ($\bar{X} =$ 33 km$^2$ for males and 14 km$^2$ for females—Mizutani and Jewell 1998), but 1 female in the Serengeti, Tanzania, had a home range of 15.9 km$^2$ (Bertram 1982). However, the smallest ranges were in Sri Lanka (8–10 km$^2$—Eisenberg and Lockhart 1972).

Individual *P. pardus* that have larger ranges tend to have areas of overlap with neighbors, yet core areas or territories are exclusively maintained (Bothma and Le Riche 1984; Steyn and Funston 2009). Females typically share portions of their territories with their female offspring (Bailey 1993; Steyn and Funston 2009).

*Panthera pardus* feeding on large prey items may remain in a single location for several days (Bothma and Le Riche 1984; Bailey 1993), but will typically move through its entire home range over a period of 7–10 days (Mizutani and Jewell 1998). Human disturbances may influence the range use and activity patterns of *P. pardus* (Marker and Dickman 2005).

Typically *P. pardus* is nocturnal with peak activity during the hours of dawn and dusk (Eisenberg and Lockhart 1972; Chambers et al. 1984; Bailey 1993) or diurnal with peak activity during late morning and late afternoon–early evening (Norton and Henley 1987). The homing instinct is strong in *P. pardus* (Stander et al. 1997b), making translocation an impractical solution to conflict with people. Radiotagged *P. pardus* returned to their original range in proportion to the distance from the release site (Stander et al. 1997b).

Juveniles remain with their mother 12–18 months (Bailey 1993). Young males disperse, whereas young females often take over part of their mother's range (Bailey 1993).

***Diet.***—Diet selection of *Panthera pardus* is primarily driven by opportunity to catch and maintain possession of its prey. Although it prefers prey within the range of 10–40 kg, in the absence of larger competitors, it may feed on larger prey (Hayward et al. 2006; Stein 2008). The costs of attempting to kill larger prey ($> 150$ kg) may restrict the diet of *P. pardus*, although it has been recorded feeding on prey in this size range (Scheepers and Gilchrist 1991). As well, *P. pardus* can persist on a variety of smaller prey in environments of lean resources or an absence of larger prey (Stuart and Stuart 1993; Hayward et al. 2006). Most (69%) kills by *P. pardus* in southern India were $< 50$ kg (Johnsingh 1992). In Africa, *P. p. pardus* feeds on diverse species depending on ungulate species available. Primary prey are impala in Kruger National Park, South Africa, and Rhodes Matopos National Park, Zimbabwe (Smith 1978; Bailey 1993); impala, springbok (*Antidorcas marsupialis*), and small antelope in the Kalahari, South Africa (Mills 1990; Owen Smith and Mills 2008); impala, bush duiker (*Sylvicapra grimmia*), nyala (*Tragelaphus angasii*), red duiker (*Cephalophus natalensis*), southern reedbuck (*Redunca arundinum*), and desert warthog in the Phinda–Mkhuze complex, South Africa (Balme et al. 2010); rodents, bush-pig (*Potamochoerus larvatus*), and red-flanked duiker (*Cephalophus rufilatus*) in Lope National Park, Gabon (Henschel et al. 2005); rock hyrax (*Procavia johnstoni* [currently *P. capensis*]) and groove-toothed rat (*Otomys*) on Mt. Kenya (Roedel et al. 2004); chital (*Axis axis*) in Nepal (Odden et al. 2010) and India (Arivazhagan et al. 2007); cattle (*Bos taurus*), northern plains gray langur (*Presbytis entellus* [currently *Semnopithecus entellus*]), goral (*Naemorhedus goral*), and dogs (*Canis lupus familiaris*) in the Himalayas (Mukherjee and Mishra 2001); bezoar goats (*Capra aegagrus*) in Armenia (Khorozyan and Malkhasyan 2003); tufted deer (*Elaphodus cephalophus*) and bamboo rats (*Rhizomys sinense*) in the Wolong Reserve, China (Johnson et al. 1993); and sambar (*Cervus unicolor* [currently *Rusa unicolor*]), muntjac (*Muntiacus*), Gee's golden langur (*Trachypithecus geei*), goral, and livestock in Bhutan (Wang and Macdonald 2009). In mountainous and semiarid areas, *P. pardus* preys upon small prey such as rock hyrax, bush duiker, and crested porcupine (*Hystrix cristata*—Bothma and Le Riche 1984; Norton et al. 1986; Stuart and Stuart 1993; Stander et al. 1997a). In the absence of larger predators *P. pardus* may prey on slightly larger prey such as greater kudu (Karanth and Sunquist 1995; Stein 2008). Other prey include ungulates: hartebeest (*Alcelaphus*), bay duiker (*Cephalophus dorsalis*), Maxwell's duiker (*C. maxwellii* [currently *Philantomba maxwelli*]), black duiker (*C. niger*), red-flanked duiker, yellow-backed duiker (*C. sylvicultor* [currently *C. silvicultor*]), wildebeest (*Connochaetes taurinus*), common tsessebe (*Damaliscus lunatus*), *Equus*, roan antelope (*Hippotragus equinus*), sable antelope (*H. niger*), water chevrotain (*Hyemoschus aquaticus*), waterbuck (*Kobus ellipsiprymnus*), kob (*K. kob*), klipspringer (*Oreotragus oreotragus*), oribi (*Ourebia ourebi*), common warthog (*Phacochoerus africanus*), red river hog (*Potamochoerus porcus*), steenbok (*Raphicerus campestris*), Sharpe's grysbok (*R. sharpei*), mountain reedbuck (*Redunca fulvorufula*), bush duiker, African buffalo (*Syncerus caffer*), common eland (*Taurotragus oryx*), and bushbuck (*Tragelaphus scriptus*); primates: Campbell's mona monkey (*Cercopithecus campbelli*), Diana monkey (*C. diana*), mona monkey (*C. mona*), lesser spotted-nosed monkey (*C. petaurista*), vervet monkey (*Chlorocebus pygerythrus*), green monkey (*C. sabaeus*), ursine colobus (*Colobus vellerosus*), patas monkey (*Erythrocebus patas*), rhesus monkey (*Macaca mulatta*), bonobo (*Pan paniscus*), olive baboon (*Papio anubis*), chacma baboon (*P. ursinus*), and northern plains gray langur; rodents: African brush-tailed porcupine (*Atherurus africanus*), northern giant pouched rat (*Cricetomys gambianus*), montane African climbing mouse (*Dendromus insignis*), Gambian sun squirrel (*Heliosciurus gambianus*), red-legged sun squirrel (*H. rufobrachium*), Smith's bush squirrel (*Paraxerus cepapi*), forest giant squirrel (*Protoxerus stangeri*), roof rat (*Rattus rattus*),

greater cane rat (*Thryonomys swinderianus*), and striped ground squirrel (*Xerus erythropus*); and miscellaneous: domestic dog, African civet (*Civettictis civetta*), common genet (*Genetta genetta*), common dwarf mongoose (*Helogale parvula*), scrub hare (*Lepus saxatilis*), tree pangolin (*Manis tricuspis*), ground pangolin (*M. temminckii*), long-tailed pangolin (*M. tetradactyla*), banded mongoose (*Mungos mungo*), aardvark (*Orycteropus afer*), birds, reptiles, fish, dung beetles (Fey 1964; Pienaar 1969; Eisenberg and Lockhart 1972; Le Roux and Skinner 1989; Edgaonkar and Chellam 1998; Zuberbühler 2001; Roedel et al. 2004; D'Amour et al. 2006; Bodendorfer et al. 2006; Odden and Wegge 2009), and perhaps the Indian giant squirrel (*Ratufa indica*—Mehta 1997). The probability of a kill is greatest in areas with intermediate cover (Balme et al. 2007). *P. pardus* will eat grass (*Isachne beuttneri* and *Streptogyna crinite*—Hoppe-Dominik 1988) and drink water every 2.7 days in the Kalahari, South Africa (Bothma 2005).

Cannibalism can occur (Pienaar 1969; Bodendorfer et al. 2006; Steyn and Funston 2006). *P. pardus*, in general, does not target domestic stock or humans, but particular individuals may develop the habit of raiding livestock or human settlements (Sterndale 1884; Corbett 1947; Turnbull-Kemp 1967; Mizutani 1999). A *P. pardus* killed 51 sheep and lambs in a single event (Stuart 1986). In Kashmir, 48.5% of 35 attacks by *P. pardus* on humans were fatal (Nabi et al. 2009), whereas in Uganda, 32.5% of 114 attacks were fatal (Treves and Naughton-Treves 1999).

***Diseases and parasites.***—External parasites include flies: *Lipoptena chalcomelaena* and *Wohlfahrtia magnifica*; ticks: *Amblyomma hebraium*, *A. nuttali*, *A. thaolloni*, *A. variegatum*, *Haemaphysalis aciculifer*, *H. bispinosa*, *H. concinna*, *H. dentipalpis*, *H. elliptica*, *H. hystricis*, *H. konigsbergeri*, *H. leachi*, *H. papuana*, *H. parmata*, *Ixodes cavipalpus*, *I. cumulatimpuctatus*, *I. moreli*, *I. muniensis*, *I. oldi*, *I. pilosus*, *I. rasus*, *I. vanidicus*, *Rhipicentor bicornis*, *R. nurrali*, *Rhipicephalus appendiculatus*, *R. armatus*, *R. capensis*, *R. compositus*, *R. haemaphysaloides*, *R. pravus*, *R. sanguineus*, *R. senegalensis*, *R. simus*, *R. sulcatus*, *R. tendeiroi*, *R. tricuspis*, and *R. ziemanni*; fowl and pig fleas: *Echidnopahaga gallinacea* and *E. larina* respectively; chiggers: *Gahrliepia rustica*; and mange-causing ear mites: *Notoedres cati* (Turnbull-Kemp 1967; Bailey 1993; Rosen et al. 1998; Apanaskevich et al. 2007). Mange increased during the early dry season (Bailey 1993).

Endoparasites include acanthocephalans: Acanthocephala, *Cucullanorhynchus constrictruncatus*; cestodes: Hymenolepididae, *Mesocestoides*, Pseudophyllidae, *Spirometra*, and Taeniidae; protozoa: *Babesia*, *Coccidia*, *Cryptosporidium*, *Giardia*, *Sarcocystis*, and *Toxoplasma gondii*; nematodes: *Aelurostrongylus*, *Ancylostoma braziliense*, *An. canimum*, *Brugia pahangi*, *Capillaria*, *Dirofilaria immitis*, *Dracunculus*, *Galoncus perniciosus*, *Gnathostoma*, *Mammomonogamus*, *Molineus*, Spiruroidea, *Strongyle*, *Toxocara*, *Toxascaris leonina*, *T. mystax*, and *Trichinella britovi*; sporocysts of *Isospora felis*; tapeworms: *Dibothriocephalus latus*, *Diphyllobothrium latum*, *Dipylidium*, *Taenia ingwei*, and *T. pisiformes* but not *Echinococcus felidis*; and trematodes: Dicrocoeliidae, Echinostomatidae, *Nanophyetus salmincola*, and *Paragonimus westermanii* (Strauss and Sivanandam 1966; Turnbull-Kemp 1967; Somvanshi et al. 1987; Bailey 1993; Pythal et al. 1993; Patton and Rabinowitz 1994; Tehsin 1996; Upadhye and Dhoot 2000; Dhoot et al. 2002; Penzhorn et al. 2002; Gawande et al. 2007; Amin et al. 2008; Hüttner et al. 2009; Mowlavi et al. 2009; Fayer 2010).

Some *P. pardus* were seropositive for feline immunodeficiency virus (Troyer et al. 2005) and for type 2 feline coronavirus (Kennedy et al. 2002). The yeast *Malassezia symphodialis* was isolated from the ear canal of 2 *P. pardus* (Coutinho et al. 2006). The bacteria *Salmonella enteritidis* and *S. typhimurium* occur in *P. pardus* (Babu et al. 1993). Pyometra in a captive, 14-year-old female was treated by ovariohysterectomy and systemic antibiotics (McCain et al. 2009). Adenocarcinoma (Ranganath et al. 2008), uterine leiomyoma (Siegal-Willott et al. 2005), histiocytoma (Nath et al. 2006), lymphosarcoma (Sujatha et al. 2005), squamus cell carcinoma (Sabapara et al. 2003), avian influenza H5N1 (Keawcharoen et al. 2004), bovine tuberculosis (Renwick et al. 2006), *Clostridium perfringens* enterotoxicosis (Neiffer 2001), degenerative spinal disease (Kolmstetter et al. 2000), feline enteritis (Singh et al. 1983), hepatitis (Gupta 1978), hiatal hernia (Kearns et al. 2000), neoplasia (Owston et al. 2008), pulmonary anthracosis (Sujatha et al. 2007), and rabies (Jayakumar et al. 1989) occur in *P. pardus*.

***Interspecific interactions.***—Although they coexist, tigers (*Panthera tigris*) restrict the distribution of *P. pardus* in Nepal (Seidensticker 1976; Odden et al. 2010); 5 *P. pardus* were killed by *P. tigris* in Nepal (McDougal 1988). In Rajaji National Park in India, with the displacement of human communities and the increased population, densities of *P. pardus* declined sharply and diet of *P. pardus* showed a pronounced shift (Harihar et al. 2011). Diet of *P. pardus* can be an indicator of the presence of intraguild competitors, where dietary shifts signaled the decline of a *P. tigris* population in India (Ramakrishnan et al. 1999). In Cameroon evidence of changes in the population of *P. pardus* were not always tied to the presence of one larger competitor, however, because reduced lion (*Panthera leo*) numbers did not signal an increase in the population of *P. pardus* where spotted hyenas (*Crocuta crocuta*) were still present (Croes et al. 2011). Dietary overlap of *P. pardus* with cheetahs (*Acinonyx jubatus*) is 68.7%, with wild dogs (*Lycaon pictus*) is 65.7%, and with *P. leo* is 39.1% (Hayward and Kerley 2008). *P. leo*, spotted hyenas, wild dogs, and *P. tigris* will opportunistically kill *P. pardus* or their cubs, just as *P. pardus* will kill the unprotected cubs of intraguild members. These larger predators also take kills

from *P. pardus* (Schaller 1972; Mills 1990; Creel and Creel 2002). *P. pardus* tends to select smaller prey when inhabiting areas with larger competitors (Karanth and Sunquist 1995, 2000). In Bandipur, India, *P. pardus* accounted for 15% of 379 kills, whereas dholes (*Cuon alpinus*) took 80%, and *P. tigris* took 5% (Johnsingh 1983). Human agropastoralists regularly scavenge the prey of *P. pardus* (Treves and Naughton-Treves 1999).

## HUSBANDRY

*Panthera pardus* can be anesthetized with a mixture of tiletamine hydrochloride and zolazepam hydrochloride at dosages of 4–5 mg/kg (Swanepoel et al. 2010) or a xylazine hydrochloride (1.4 mg/kg)–ketamine hydrochloride (5 mg/kg) mixture (Belsare and Athreya 2010). When mass is not estimated an initial dose of 50 mg xylazine–150 mg ketamine can be supplemented with 50–75 mg of ketamine only (Belsare and Athreya 2010). Odden and Wegge (2005) also suggests using 3.6–5.9 mg/kg of ketamine and 0.07–0.12 mg/kg of medetomidine. Other drugs and dosages are: diazepam (0.17–0.18 mg/kg), ketamine (6–12 mg/kg), xylazine (0.5–2.0 mg/kg), and telazol (2–7 mg/kg—Sabapara 1995).

Novel odors have short-term (3-h) effects on behavior of captive *P. pardus* (Yu et al. 2009). *P. pardus* in structurally enriched enclosures is more active than those in unenriched enclosures (Mallapur et al. 2002).

## BEHAVIOR

***Reproductive behavior.***—Adult *Panthera pardus* are solitary with the exception of females rearing cubs and during mating when males and females associate for several days before separating again (Eisenberg and Lockhart 1972).

Females attract mates through the release of scent marks and vocalizations that attract a male, which associates with her for 1–4 days (Bailey 1993). In mating, the male mounts the female and holds the skin on the nape of her neck (De Haas van Dorsser et al. 2007). Males often leap off the female as she aggressively snarls and occasionally strikes at the male (Seidensticker 1977). The female rolls "on her back in front of the male and presents herself. She sits with her forelimbs extended fully on the ground, her hind limbs remaining half bent" (Desai 1975:297). Insertion occurs 4–8 s after mounting and coitus is 10–50 s; 5–60 copulations occurred during a 9-h period in peak estrus (Desai 1975), whereas 13 copulations occurred during a 1.5-h period, with a mean duration of copulation of 3 s and an average interval between copulations of 6.5 min (Laman and Knott 1997). A female associated with a male 11 days after her cubs were killed (Bailey 1993).

***Communication.***—"Cubs emit low cries when hungry or uncomfortable" (Desai 1975:299). Guttural sounds accompany coitus and at the peak of copulation both males and females make a high-pitched sound (Desai 1975). "A leopard call consists of a repeated pattern of strokes sounding much like the sawing of wood" (Eisenberg and Lockhart 1972:71). Average number of strokes per call is 13–16 with a range of 2–30 with an intercall interval of 6 min and a range of 1–10 min (Ulmer 1966; Eisenberg and Lockhart 1972). Duetting may occur (Eisenberg and Lockhart 1972). Both males and females roar (Ulmer 1966). Marking behavior includes tree scratching and soil scrapes (Eisenberg and Lockhart 1972). Scent marking, roaring, and conspicuous behaviors maintain spacing distances (Muckenhirn and Eisenberg 1971).

***Miscellaneous behavior.***—In Kenya and South Africa, 66% of activity of *Panthera pardus* is nocturnal (Hayward and Slotow 2009). In the rain forests of West Africa, *P. pardus* is diurnal with strong individual prey preferences (Jenny and Zuberbühler 2005). In Oman, *P. p. nimr* was most active at 0200–0700 h and least active at 1200–1500 h (Spalton et al. 2006).

*Panthera pardus* attacks its prey in a variety of ways, but primarily stalks to within a short distance of its target before pouncing (Stander et al. 1997a). Females with cubs increase foraging efficiency by killing smaller prey (Bothma and Coertze 2004a). *P. pardus* kills smaller prey by biting the nape of the neck or puncturing the skull with its canines, whereas larger prey are bitten on the throat, avoiding the horns and antlers of antelope and deer. In the Kalahari, *P. pardus* exhibited a flexible hunting strategy that did not regularly include the typical stalk–chase–kill sequence, but rather involved longer stalking periods at further distances related to the target prey species and reduced available cover (Bothma and Le Riche 1989).

After making a kill *P. pardus* will either eat a small prey item immediately or cache the kill for feeding in safety (Bothma and Le Riche 1984; Bailey 1993). *P. pardus* may drag its kills several hundred meters to specific types of trees or bushes of a prescribed height, trunk thickness, and foliage density (Bothma and Le Riche 1984; Bailey 1993). In Kruger National Park, *P. pardus* hoisted 84% of its kills into trees (Bailey 1993). In the Kalahari Desert, Tsavo National Park, Kenya, or the commercial farmlands of north-central Namibia, where larger predators are less common, *P. pardus* cached its kills under bushes (Hamilton 1976; Bothma and Le Riche 1984; Stein 2008). In northern Botswana, male *P. pardus* tended to take prey to trees more than females (Stein et al. 2010). *P. pardus* also will cache kills in caves (de Ruiter and Berger 2001).

In northeastern Namibia, *P. pardus* staggered its activities in different parts of its shared range when another animal was occupying the area (Stander et al. 1997a). *P. pardus* fights on rare occasions, usually when a newcomer

challenges the resident animal (Corbett 1947; Hamilton 1976; Bailey 1993).

In the Kalahari, adult males scent marked 2.3 times more than adult females without cubs and 5.9 times more often than females with cubs (Bothma and Coertze 2004b). The frequency of scent marking increased during courting and bouts of mating. Tree scratching also is used to mark territory, but less frequently than scent marking (Bothma and Coertze 2004b). Scrapes in Iran had a mean length of 39.3 cm and a mean width of 22.7 cm (Ghoddousi et al. 2008). *P. pardus* prefers specific tree species for scratching, for example *Acacia erioloba* in the Kalahari or water berry (*Syzygium cordatum*) in the Soutpansberg mountains of South Africa, but may not scratch trees in other parts of its range (Hamilton 1976; Stuart and Stuart 1994; Bothma and Le Riche 1995).

## GENETICS

Diploid chromosome number (2n) is 38 with a fundamental number (FN) of 72 and includes 5 metacentric, 7 submetacentric, 4 acrocentric, and 2 telocentric pairs (Hsu et al. 1963; Tanomtong et al. 2008). The X chromosome is a small submetacentric and the Y chromosome is the smallest metacentric (Tanomtong et al. 2008).

The most genetically diverse (expected heterozygosity, 0.77–0.80) population of *Panthera pardus pardus* is found in sub-Saharan Africa, whereas the lowest genetic variation (expected heterozygosity, 0.340–0.356) occurs in the isolated Amur peninsula, *P. p. orientalis*, of the Russian Far East (Spong et al. 2000; Uphyrkina et al. 2001, 2002). For *P. p. kotiya*, percent polymorphism and percent average heterozygosity for wild-caught, captive-born, and melanistic *P. pardus*, respectively, were 4.0, 1.2; 4.0, 1.4; 4.0, 2.0 (Miththapala et al. 1991). Two of 12 loci were polymorphic in *P. pardus* (Newman et al. 1985). Inbreeding coefficients for captive *P. pardus* ranged from 0 to 0.5 (Shoemaker and Wharton 1984). Y-chromosome, mitochondrial, and autosomal DNA suggest that *P. leo* and *P. pardus* are sister taxa (Davis et al. 2010).

Melanism is inherited as a recessive trait (nonagouti) of the agouti locus in *P. pardus* (Robinson 1969, 1970; Roychoudhury and Acharjyo 1984) and is not the result of the 2-base pair deletion in the *ASIP* gene or either of 2 "in-frame" deletions in the *MC 1R* gene (Eizirik et al. 2003). Albino *P. pardus* have been seen (Divyabhanusinh 1993). Hybrids between *P. pardus* and *P. leo*, *P. onca*, *P. tigris*, and cougars (*Puma concolor*) have been reported (Gray 1971).

Microsatellite DNA from scats can individually identify *P. pardus* (Perez et al. 2006; Mondol et al. 2009), as can spot patterns (Miththapala et al. 1989). Artificial insemination can be successful (Dresser et al. 1982). Cytochrome *b* from fecal genetic material can distinguish sympatric tigers and *P. pardus* (Nagata et al. 2005).

## CONSERVATION

*Panthera pardus* is listed in the Convention for the International Trade of Endangered Species of Wild Fauna and Flora (CITES) *Appendix I* (2013). In 2005, only 11 African countries could export skins of *P. pardus* under the Convention for the International Trade of Endangered Species of Wild Fauna and Flora, representing 2,590 specimens (Ray et al. 2005). The range of *P. pardus* has been drastically reduced worldwide and reduced approximately 37% throughout Africa (Ray et al. 2005). As of 1964, only 10–15 *P. p. orientalis* were estimated to live in the former Union of Soviet Socialist Republics (Bannikov 1964). Conservation efforts and the regulation of the distribution of trophy hunting permits can reduce mortality (Balme et al. 2009). Efforts to distribute financial benefits from trophy hunting and photographic tourism may also mitigate conflicts with farmers (Stein et al. 2010).

On the International Union for Conservation of Nature and Natural Resources (IUCN) *Red List of Threatened Species*, *P. p. melas*, *P. p. orientalis*, and *P. p. nimr* are "Critically Endangered" (Ario et al. 2008; Jackson and Nowell 2008; Mallon et al. 2008), whereas *P. p. kotyi* and *P. p. ciscaucasica* are "Endangered" (Khorozyan 2008; Kittle and Watson 2008). In 2011, the total captive population of *P. p. nimr* consisted of 42 males, 32 females, and 3 unsexed individuals derived from 14 founders (Budd and Leus 2011).

## REMARKS

The earliest writings of *Panthera pardus* were recorded in Sumeria dating back to 3100 BC (Turnbull-Kemp 1967). In Sumerian culture, the god Nin-urta used cyclone winds as a weapon, in the form of the *P. pardus*–headed Shargaz. The Chinese believe *P. pardus* to be 1 of 4 beasts of power (Turnbull-Kemp 1967). *P. pardus* is present on ancient Egyptian hieroglyphics and drawings (Budge 1978). Ancient Rome used *P. pardus* for gladiatorial fighting.

In East Africa, killing a *P. pardus* can assist a young Maasai male achieve warrior status (Hazzah et al. 2009). Skins of *P. pardus* are used in the ceremonial dress of cultures throughout Africa, and consuming meat or genitalia of *P. pardus* is thought to transfer the power and stealth of the *P. pardus* (Turnbull-Kemp 1967).

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