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Crocuta crocuta (Carnivora: Hyaenidae)

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Abstract: *Crocuta crocuta* (Erxleben, 1777), the spotted hyena, is a large, widespread, terrestrial carnivore with a female-dominant social system. It ranges from about 17°N to 28°S and lives in diverse habitats from savannas to swamps (but not rain forests) and up to 4,000 m in elevation. As assessed in 2014, *C. crocuta* is listed as "Least Concern" (LC) by The International Union for Conservation of Nature and Natural Resources Red List of Threatened Species version 2016.1.

Key words: canid, carnivore, sexual dimorphism, spotted hyena

Crocuta Kaup, 1828

Canis Erxleben, 1777:578. Part. Type species *Canis crocuta*, by subsequent designation Kaup, 1828.

Hyaena Schreber, 1777:Plate LXXXXVI B. Type species *Hyaena crocuta*, by subsequent designation Kaup, 1828.

Hyana part Desmarest, 1820:216. Incorrect subsequent spelling of *Hyaena*.

Crocuta Kaup, 1828:column 1145. Type species *Canis crocuta* Erxleben, 1777, by original designation.

Crocotta Kaup, 1829:78, 189. Incorrect subsequent spelling of *Crocuta* Kaup, 1828.

Content and Context.   Order Carnivora, family Hyaenidae, subfamily Caninae. *Crocuta* is monotypic.

Fig. 1.—A sated adult female *Crocuta crocuta*. Photograph by Marie Lemerle used with permission.

Crocuta crocuta (Erxleben, 1777)

Spotted Hyena

Canis crocuta Erxleben, 1777:578. Type locality "Guinea, Aethiopia, ad caput bonae spei in terrae rupiumque caueis," restricted to "Senegambia" by Cabrera (1911a:95).

Hyaena crocuta: Schreber, 1777:Plate LXXXXVI B. Name combination.

Hyaena maculata Thunberg, 1811:302. Type locality "Africes australis."

Hyaena capensis Desmarest, 1817:499. Type locality "aux environs du Cap de Bonne Esperance, … au midi de l'Afrique."

Hyaena rufa Desmarest, 1817:499. Type locality not given; stated as Cape of Good Hope by Ellerman et al. (1953).

Hyana capensis Desmarest, 1820:216. Type locality "Le midi de l'Afrique, aux environs du Cap de Bonne Esperance."

Hyana rufa Desmarest, 1820:216. Type locality not given, "inconnues."

Hyaena croacuta A. Smith, 1826:12. Incorrect subsequent spelling of *crocuta* Erxleben, 1777.

Hyaena encrita A. Smith, 1827:461. Misprint (Ellerman et al. 1953).

Hyaena cuvieri Boitard, 1842 (1845):233. Type locality "au Cap," Cape of Good Hope.

H[*yaena*]. *crocuta capensis*: de Blainville, 1844:82. Name combination.

H[*yaena*]. *crocuta habessynica* de Blainville, 1844:82. Type locality not given, Ethiopia implied.

Hyaena (*Crocotta*) *wissmanni* Matschie, 1900a:22. Type locality "Epikuro in Deutsch-Südwest-Afrika" Namibia (Jenks and Werdelin 1998).

Hyaena (*Crocotta*) *gariepensis* Matschie, 1900a:25. Type locality "Bambusbergen im Oranje-Gebiet" refined to "Bamboos Mountains … 31º 30'S., 26º 20'E." by Ellerman et al. (1953).

Hyaena (*Crocotta*) *germinans* Matschie, 1900a:26. Type locality "Rukwa-See" (Lake Rukwa), Tanzania.

Hyaena (*Crocotta*) *thierryi* Matschie, 1900a:30. Type locality "Sansanne Mangu, in Nord-Togo."

Hyaena (*Crocotta*) *togoensis* Matschie, 1900a:31. Type locality "Volta, West-Togo," restricted to "Kete Krachi, Togo," by Jenks and Werdelin (1998).

Hyaena (*Crocotta*) *noltei* Matschie, 1900b:211, 215. Type locality "Yoko, Kamerun" refined to "Yoko, upper Sanaga, south Cameroon," by Jenks and Werdelin (1998).

Crocotta weissmanni: Trouessart, 1904:243. Name combination and incorrect subsequent spelling of *wissmanni* Matschie 1900a.

Hyaena (*Crocuta*) *leontiewi* Satunin, 1905:556. Type locality "Abyssinia" = Ethiopia and Eritrea.

Crocotta kibonotensis Lönnberg, 1908 (1910):16. Type locality "Kibonoto Steppe," Kilimanjaro, Tanzania.

Crocotta germinans: Lönnberg, 1908 (1910):16. Name combination.

Crocotta panganensis Lönnberg, 1908 (1910):18. Type locality "Kibonoto," Kilimanjaro, Tanzania.

Crocuta crocuta: Cabrera, 1911a:95. First use of current name combination.

Crocuta wissmanni: Cabrera, 1911a:95. Name combination.

C[*rocuta*]. *gariepensis*: Cabrera, 1911a:95. Name combination.

C[*rocuta*]. *germinans*: Cabrera, 1911a:95. Name combination.

C[*rocuta*]. *thierryi*: Cabrera, 1911a:95. Name combination.

C[*rocuta*]. *togoensis*: Cabrera, 1911a:95. Name combination.

C[*rocuta*]. *noltei*: Cabrera, 1911a:95. Name combination.

C[*rocuta*]. *kibonotensis*: Cabrera, 1911a:95. Name combination.

C[*rocuta*]. *panganensis*: Cabrera, 1911a:95. Name combination.

Crocuta capensis: Cabrera, 1911a:96. Name combination.

Crocuta leontiewi: Cabrera, 1911a:97. Name combination.

Crocuta rufopicta Cabrera, 1911a:97. Type locality "Odueina, Boran Country."

Crocuta thomasi Cabrera, 1911a:98. Type locality "Ankole, Uganda."

Crocuta nyasae Cabrera, 1911a:99. Type locality "Mount Milanji, South Nyasaland."

Crocuta nzoyae Cabrera, 1911b:199. Type locality "Meseta de Uasingishu, Africa Oriental Inglesa" = Guas Ngishu Plateau, Kenya.

Crocuta crocuta fisi Heller, 1914:5. Type locality "Merelle Waterholes, Marsabit Road, British East Africa" = Kenya.

Crocuta crocuta fortis Allen, 1924:214. Type locality "Faradje, northeastern Belgian Congo."

C[*rocuta*]. *c*[*rocuta*]. *Germinans*: Allen, 1924:214. Name combination.

Hyaena (*crocotta*) *wismanni* Matthews, 1939a:256. Incorrect subsequent spelling of *wissmanni* Matschie 1900a.

Hyaena (*crocotta*) *leontiewi*: Matthews, 1939a:256. Name combination.

Crocotta kibotonensis Matthews, 1939a:256. Incorrect subsequent spelling of *kibonotensis* Lönnberg 1908.

Crocuta nyassae Matthews, 1939a:256. Incorrect subsequent spelling of *nyasae* Cabrera 1911a.

Crocuta croucta Wilson and Reeder, 2005:1795. Incorrect subsequent spelling of *crocuta* Erxleben, 1777.

CONTENT AND CONTEXT. Context as for genus. *Crocuta crocuta* has no currently recognized subspecies.

NOMENCLATURAL NOTES. The genus name was used for an insect by Meigen (1800), but Meigen's pamphlet was suppressed for the purposes of zoological nomenclature by the International Commission on Zoological Nomenclature (1963). Synonymy is modified from Matthews (1939a), Jenks and Werdelin (1998), and Wozencraft (2005).

Crocuta is a Latinized version of the Greek "krokúttas" or "krokottas," which itself comes from a Sanskrit word that references a female golden jackal (Funk 2010). Ancient texts often referred to any of the three hyenas as jackals. The first recorded association of the spotted hyena with the designation *crocuta* was in 1681 (Funk 2010:55). An additional common name in English is tiger wolf, and a list of common names from over 95 languages is available online via Wikipedia (2019).

DIAGNOSIS

Crocuta crocuta (Fig. 1) is sympatric with the brown hyena (*Hyaena brunnea*) in the southern parts of its range and the striped hyena (*H. hyaena*) in the east (Kruuk 1972). The genus *Crocuta* has rounded ears (pointed in *Hyaena*), lacks a dorsal mane (present in *Hyaena*), and has a spotted pelage (striped or uniform in *Hyaena*—Ellerman et al. 1953). The sagittal crest of the *Crocuta* skull (Fig. 2) is largest in the middle region (more posterior in *Hyaena*), and the origin of the temporalis is more anterior than in *Hyaena* (Buckland-Wright 1969:19, figure 1). Small differences in the occipital, squamosal, condylar, nuchal crest, otic, basis cranii, zygomatic arch, and orbital regions as well as the axis and atlas vertebrae have been detailed (Buckland-Wright 1969).

Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult (115 months of age) female *Crocuta crocuta* from the Masai Mara National Reserve, Talek Region, Kenya (Michigan State University, Mammal Research #36083, collected by Kay Holekamp). Greatest length of skull is 267 mm. Images by Barbara Lundrigan used with permission.

GENERAL CHARACTERS

Crocuta crocuta is a large (40–80 kg) carnivore with a female-dominant social system. Ground color of pelage varies widely from light gray through yellows to reds, with dark brown to black spots (Allen 1924). Spots fade with age (Kruuk 1972). The adult pelage is rough to the touch; younger individuals have

soft and fluffy fur (Matthews 1939b; K. E. Holekamp, pers. comm.). The round ears are erect with short, dirty-white and gray hair inside (Deanne 1962). The nose is black and smooth (Deanne 1962). Four toes, with nonretractable claws, are present on each foot (Deanne 1962).

The well-developed neck and forequarters relative to the hindquarters give *C. crocuta* a sloping back most obvious when the animal runs away from a perceived danger (Fig. 3). The body shape also allows the animal to carry off large clumps of meat well above the ground and drag heavy carcasses away from kill sites (Kruuk 1972).

Mean external measurements (mm; parenthetical range if available, *n*) of northern *C. crocuta* from Ethiopia, Kenya, Tanzania, and Uganda for females, males, and specimens of unknown sex, respectively, were: total length, 1,515 (NA, 23), 1,477 (NA, 24), and 1,494.5 (1,475.0–1,501.0, 28); length of head and body, 1,333 (NA, 1), 1,295 (NA, 1), and 1,204.5 (1,191.0–1,209.0, 28); length of tail 233.8 (231.0–296.0, 23), 233.4 (232.0–267.0, 25), and 330.2 (NA, 2); length of hind foot, 235.9 (234.0–236.0, 24), 237.8 (234.0–238.0, 25), and 230.0 (NA, 28—Allen 1924; Matthews 1939a; Deanne 1962; Hamilton et al. 1986). Mean external measurements (mm; *n*) for females and males, respectively, from Namibia were: height at shoulder, 767 (21) and 775 (19); girth, 888 (17) and 845 (16); neck diameter, 533 (21) and 521 (20—Hamilton et al. 1986). Mean external measurements (mm) of two female *C. crocuta* from the Faradje, Democratic Republic of the Congo were: total length, 1,665; length of head and body, 1,340; length of hind foot, 257 (Allen 1924). Measurements (mm) of a specimen of unknown sex from Chad were: total length, 1,676; length of tail, 317.5 (Deanne 1962). Mean mass (kg; parenthetical range, *n*) for females, males, and specimens of unknown sex, respectively, were 55.0 (50.0–55.6, 22), 48.7 (NA, 25), and 54.8 (NA, 1—Deanne 1962; Neaves et al. 1980; Hamilton et al. 1986). In the Serengeti eight adult females averaged 55.3 kg (range 44.5–63.9) and 12 adult males averaged 48.7 kg (range 40.5–55.0—Kruuk 1972). To detect female-biased sexual-size dimorphism a sample needs 71 individuals of each sex (McElhinny 2009).

Mean external measurements (mm; parenthetical range if available, *n*) of southern *C. crocuta* from Botswana, Malawi, Namibia, South Africa, Zimbabwe, and Zambia for females, males, and specimens of unknown sex, respectively, were: total length, 1,590.1 (1,440.0–1,794.0, 20), 1,569.8 (1,439.0–1,735.0, 19), and 1,625 (NA, 1) and length of tail, 254.6 (130.0–315.0, 20), 242.2 (208.0–290.0, 17), and 311 (NA, 1—Deanne 1962; Skinner and Chimimba 2005). Mean measurements (mm; parenthetical range, *n*) for females and males, respectively, were: height at shoulder 822 (735–885, 22) and 809.2 (700–870, 24); length of ear, 111.8 (80–127, 25) and 114.9 (80–138, 25); length of the hind foot with claw, 247.6 (200–270, 17) and 246.9 (230–270, 15); and length of the hind foot without claw, 228 (215–250, 5) and 230 (220–245, 9—Skinner and Chimimba 2005).
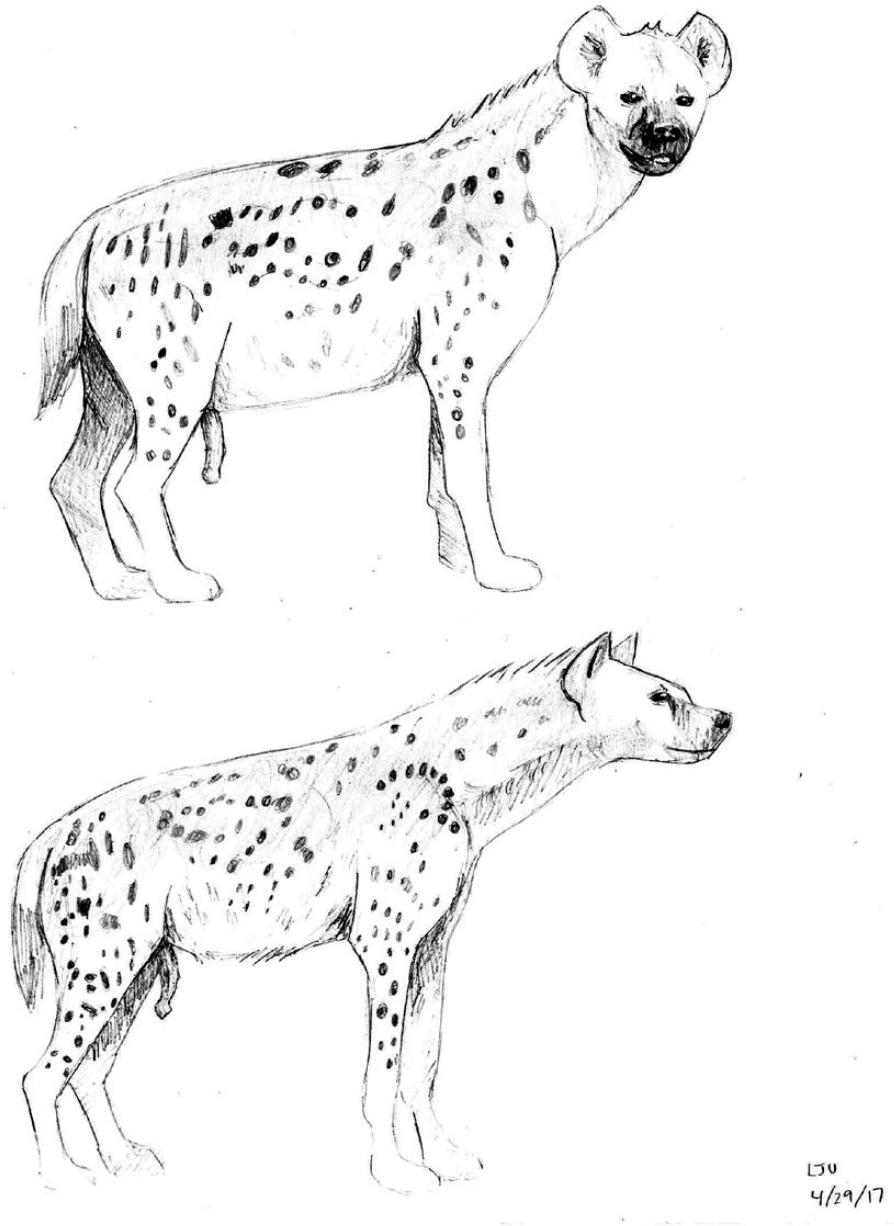
Fig. 3.—Lateral view of a female (top) and male (bottom) *Crocuta crocuta* illustrating the more robust neck and torso of females. Drawing by Lily Johnson-Ulrich used with permission.

Mean mass (kg; parenthetical range, *n*) for females, males, and specimens of unknown sex, respectively, were 68.4 (55.0–77.1, 46), 60.9 (49.0–79.0, 50), and 62.4 (47.0–78.2, 24—Deanne 1962; Wilson 1968; Smuts 1973; Racey and Skinner 1979; Mills 1984; van Jaarsveld et al. 1984; Skinner and Chimimba 2005). Mean measurements (mm or kg, parenthetical range) of 12–13 females and 11–13 males, respectively, from Natal were: length of head and body, 1,327 (1,220–1,440) and 1,339 (1,250–1,420); heart girth, 938 (850–1,040) and 924 (860–1,010); mass, 70 (56–80) and 66.6 (55–79—Whateley 1980).

Cranial and dental measurements of *C. crocuta* are provided here roughly from north to south. Condylobasal length

of a specimen of unknown sex from Sudan was 255 mm (Matthews 1939a). Cranial and dental measurements (mm) for an individual of unknown sex from Ethiopia were: interorbital breadth, 55.5; lower carnassial length, 26.0; lower carnassial width, 10.0; length of lower tooth series, 103.0; distance from condyle to mandible, 172.0; postorbital constriction, 41.0; rostral breadth on canines, 58.0; upper carnassial length, 36.0; upper carnassial width, 19.0; length of upper tooth series, 98.0; width of palate across the carnassials, 99.0; zygomatic breadth, 153.0 (Cabrera 1911a).

Cranial and dental measurements (mm) for a female from Odueina, Somalia, were: condylobasal length, 240.0; interorbital

breadth, 53.5; lower carnassial length, 28.0; lower carnassial width, 11.0; length of lower tooth series, 106.5; distance from condyle to mandible, 178.0; postorbital constriction, 40.0; rostral breadth on canines, 59.0; upper carnassial length, 36.0; upper carnassial width, 20.0; length of upper tooth series, 103.0; width of palate across the carnassials, 97.0; zygomatic breadth, 159.0 (Cabrera 1911a).

Cranial and dental measurements (mm) for a male from Ankole, Uganda, were: condylobasal length, 245.0; interorbital breadth, 54.0; lower carnassial length, 26.0; lower carnassial width, 10.5; length of lower tooth series, 107.0; distance from condyle to mandible, 175.0; postorbital constriction, 41.0; rostral breadth on canines, 58.0; upper carnassial length, 35.0; upper carnassial width, 18.0; length of upper tooth series, 100.0; width of palate across the carnassials, 101.0; zygomatic breadth, 165.0 (Cabrera 1911a). Zygomatic breadth of a specimen of unknown sex from Uganda was 182 mm (Matthews 1939a).

Mean cranial and dental measurements (mm; parenthetical range) of 38 *C. crocuta* from Kenya with sexes combined were: breadth at base of canines, 59.0 (54–65); condylobasal length, 232.0 (221–254); greatest length of nasals, 56.7 (47–67); interorbital breadth, 53.6 (48–60); length of lower tooth series, 104.7 (101–109); mastoid breadth, 94.9 (90–100); postorbital constriction, 43.6 (37–49); upper carnassial length, 35.0 (32.0–37.6); upper carnassial width, 19.8 (17.9–21.7); length of upper tooth series, 97.0 (94–106); zygomatic breadth, 162.3 (147–175—Allen 1924).

Mean cranial and dental measurements (mm; parenthetical *n*) of *C. crocuta* from the Balbal plains in Tanzania were: P2 length, 14.38 (97); P3 length, 21.11 (97); P4 length, 34.97 (97); c length, 14.47 (7); d2 length, 8.62 (4); d3 length, 13.48 (4); d4 length, 17.85 (4); m1 length, 26.67 (95); p2 length, 14.49 (96); p3 length, 19.86 (98); p4 length, 21.66 (91); prosthion to basion length, 228.3 (9—Kurtén 1956). Zygomatic breadth and condylobasal length (mm) of one female and one male, respectively, from the Balbal plains in Tanzania were 176, 247 and 177, 242. Condylobasal length of a specimen of unknown sex from Tanzania was 254 mm (Matthews 1939a).

Mean cranial and dental measurements (mm; parenthetical range, *n*) for females, males, and specimens of unknown sex, respectively, from Faradje, Democratic Republic of the Congo were: breadth at base of canines, 62.2 (61.0–63.4, 2), 63.2 (60.0–65.7, 3), and 65.0 (63.5–67.0, 4); condylobasal length, 250.0 (242.0–258.0, 2), 248.7 (242.0–252.0, 3), and 251.0 (245.0–257.0, 4); greatest length of nasals, 63.5 (61.0–66.0, 2), 59.3 (56.6–63.4, 3), and 62.8 (54.2–67.7, 4); greatest length of skull, 281.0 (270.0–292.0, 2), 282.0 (275.0–291.0, 3), and 284 (278.0–288.0, 4); interorbital breadth, 56.5 (55.0–58.0, 2), 57.3 (54.8–58.7, 3), and 58.6 (58.0–59.0, 4); upper carnassial length, 35.7 (35.5–35.9, 2), 37.8 (37.4–38.1, 3), and 36.6 (35.0–38.2, 4); upper carnassial width, 19.2 (18.9–19.4, 2), 21.7 (21.0–22.5, 3), and 19.8 (19.1–21.0, 4); length of upper tooth series, 101.2 (99.5–102.8, 2), 102.6 (100.6–105.4, 3), and 100.6 (95.0–103.0, 4);

length of lower tooth series, 108.4 (105.4–111.4, 2), 110.7 (109.4–112.0, 3), and 110.3 (108.0–111.2, 4); mastoid breadth, 104.0 (102.0–106.0, 2), 103.3 (100.0–108.0, 3), and 105.0 (102.0–108.0, 4); postorbital constriction, 45.8 (44.0–47.5, 2), 47.8 (46.0–49.0, 3), and 47.0 (43.0–51.2, 4); zygomatic breadth, 178.5 (174.0–183.0, 2), 182.0 (177.0–191.0, 3), and 181.3 (179.0–184.0, 4—Allen 1924).

Cranial and dental measurements (mm) for a female from Mount Mulanji, Malawi, were: condylobasal length, 260.0; interorbital breadth, 61.0; upper carnassial length, 38.0; upper carnassial width, 20.0; length of upper tooth series, 111.0; lower carnassial length, 32.0; lower carnassial width, 12.0; length of lower tooth series, 119.0; distance from condyle to mandible, 190.0; postorbital constriction, 48.0; rostral breadth on canines, 69.0; width of palate across the carnassials, 110.0; zygomatic breadth, 179.0 (Cabrera 1911a).

Mean greatest skull length (mm, parenthetical range) of five females and three males, respectively, from Zimbabwe were 226.0 (214.2–243.8) and 224.7 (210.0–254.5—Skinner and Chimimba 2005).

Cranial and dental measurements (mm) for an individual of unknown sex from Linyanti, Botswana, were: condylobasal length, 256.0; interorbital breadth, 64.0; upper carnassial length, 35.0; upper carnassial width, 20.0; length of upper tooth series, 113.0; lower carnassial length, 32.0; lower carnassial width, 11.0; length of lower tooth series, 117.0; distance from condyle to mandible, 190.0; postorbital constriction, 53.0; rostral breadth on canines, 66.0; width of palate across the carnassials, 112.0; zygomatic breadth, 185.0 (Cabrera 1911a). Condylobasal length of one specimen of unknown sex from Linyanti, Botswana, was 256 mm; the zygomatic breadth of another specimen from the same location was 185 mm (Matthews 1939a).

Mean cranial and dental measurements (mm; parenthetical range, *n*) of *C. crocuta* from South Africa were: breadth across zygomatic arches, 175.9 (146.0–188.0, 13); C breadth, 12.1 (10.7–12.9, 8); C length, 16.7 (15.5–17.5, 8); M1 breadth, 5.2 (4.7–5.5, 3); P1 breadth, 6.9 (6.1–8.2, 13); P2 breadth, 12.0 (10.5–13.0, 12); P2 length, 16.5 (14.7–19.2, 13); P3 breadth, 17.2 (15.8–18.0, 13); P3 length, 22.8 (21.0–24.5, 13); P4 length, 37.3 (35.0–39.7, 13); breadth of blade of P4, 11.3 (10.9–12.0, 13); length of metastyles of P4, 16.4 (15.2–17.8, 12); length of paracone of P4, 13.4 (12.0–14.5, 11); greatest anterior breadth across protocone of P4, 21.1 (19.9–22.5, 12); height of coronoid process, 85.6 (66.0–91.8, 14); c breadth, 12.4 (11.3–13.6, 10); c length, 16.1 (14.7–17.4, 10); m1 breadth, 12.0 (10.9–13.1, 14); m1 length, 27.6 (27.5–31.2, 14); m1 length of talonid, 2.9 (2.4–3.8, 14); p2 breadth, 11.0 (10.1–12.0, 12); p2 length, 16.1 (15.1–18.1, 14); p3 breadth, 15.2 (14.2–16.2, 14); p3 length, 20.8 (19.4–22.0, 14); p4 breadth, 13.3 (12.5–14.0, 14); p4 length, 22.6 (21.3–23.9, 14); p4 length of protoconid, 12.2 (11.0–13.6, 13); minimum dorsoventral depths of mandible anterior to p2, 37.3 (32.7–42.7, 14); minimum dorsoventral depths of mandible posterior to m1, 45.7 (35.0–49.7, 14); buccal-lingual breadth of mandibular corpus below the center of p3, 19.4 (17.9–21.4,

14); distance from anterior face of p2 to posterior margin of m1, 83.9 (79.0–88.7, 14); distance from anterior face of lower canine to the midpoint of posterior face of lower mandibular condyle, 177.5 (149.0–189.0, 14—Turner 1984). Condylobasal length of one specimen of unknown sex from South Africa was 258 mm; zygomatic breadth of another specimen from the same location was 179 mm (Matthews 1939a).

Cranial and dental measurements (mm) for an individual of unknown sex from the Cape Peninsula of Africa were: condylobasal length, 236.0; interorbital breadth, 57.0; upper carnassial length, 35.0; upper carnassial width, 22.0; length of upper tooth series, 100.0; lower carnassial length, 30.0; lower carnassial width, 12.0; length of lower tooth series, 111.0; distance from condyle to mandible, 180.0; postorbital constriction, 42.0; rostral breadth on canines, 64.0; width of palate across the carnassials, 114.0; zygomatic breadth, 176.0. Cranial and dental measurements (mm) for an individual of unknown sex from West Africa were: length of lower tooth series, 109.3; length of upper tooth series, 99.8; width of palate across the carnassials, 107.1 (Cabrera 1911a).

Mean cranial and dental measurements (mm; parenthetical range, *n*) of *C. crocuta* with sexes combined from unknown locations were: breadth across zygomatic arches, 166.3 (154.0–173.0, 4); C breadth, 11.8 (10.6–13.0, 4); C length, 16.6 (16.0–17.4, 3); P1 breadth, 6.5 (5.7–7.4, 3); P2 breadth, 11.3 (10.5–11.9, 4); P2 length, 15.6 (14.8–16.4, 4); P3 breadth, 16.9 (15.9–18.1, 4); P3 length, 21.8 (20.0–22.7, 4); P4 length, 37.4 (35.9–38.3, 4); breadth of blade of P4, 11.43 (10.4–11.9, 4); length of metastyles of P4, 16.4 (15.0–17.3, 4); length of paracone of P4, 13.4 (13.2–14.0, 4); greatest anterior breadth across protocone of P4, 20.5 (19.6–21.3, 4); height of coronoid process, 81.2 (71.2–86.0, 4); c breadth, 12.2 (11.5–12.7, 4); c length, 15.8 (15.1–16.4, 3); m1 breadth, 11.7 (11.2–12.6, 4); m1 length, 28.2 (26.4–29.6, 4); m1 length of talonid, 2.8 (2.4–3.2, 4); p2 breadth, 10.7 (10.0–11.4, 4); p2 length, 15.5 (14.7–16.5, 4); p3 breadth, 14.4 (14.2–14.6, 4); p3 length, 20.9 (19.6–22.2, 4); p4 breadth, 12.7 (12.1–13.0, 4); p4 length, 22.8 (21.9–23.2, 4); p4 length of protoconid, 11.9 (11.2–12.6, 3); minimum dorsoventral depths of mandible anterior to p2, 34.5 (33.2–36.4, 4); minimum dorsoventral depths of mandible posterior to m1, 44.2 (37.0–49.3, 4); buccal-lingual breadth of mandibular corpus below the center of p3, 17.8 (16.5–19.0, 4); distance from anterior face of p2 to posterior margin of m1, 83.5 (80.2–85.8, 4); distance from anterior face of lower canine to the midpoint of posterior face of lower mandibular condyle, 173.3 (159.0–185.0, 4); nasals length, 42.8 (39.0–47.0, 10—Turner 1984).

Mean cranial and dental measurements (mm; parenthetical *n*) of *C. crocuta* of unknown sex from an unknown location (probably Ethiopia) were: P2 length, 18.48 (4); P3 length, 24.22 (5); P4 length, 41.8 (5); d2 length, 10.20 (1); d3 length, 14.10 (1); d4 length, 20.00 (1); m1 length, 32.78 (6); p2 length, 16.00 (1); p3 length, 23.33 (6); p4 length, 24.60 (6); prosthion to basion length, 232.0 (2—Kurtén 1956); alveolar length of lower canine, 25.7 (24.5–26.5, 3); alveolar length of the upper

canine, 33.5 (33.0–34.0, 3); basilar length, 192.8 (186.5–204.0, 3); greatest breadth of the "hindhead," 87.8 (84.0–91.5, 3); width of palate at upper border of palate-pterygoid suture, 31.3 (31.0–32.0, 3); midline length of basisphenoid, 25.7 (25.0–27.0, 3); infraorbital foramen distance at upper inner margin, 50.3 (46.5–53.0, 3); nasal width, 23.8 (23.0–25.0, 3); smallest interorbital width, 46.9 (44.0–52.3, 3); narrowest zygomatic arch measured at upper border of zygomatico-temporalis suture, 16.9 (15.5–19.0, 3); total midline length from front edge of premaxilla to rear edge of sagittal crest, 231.8 (218.0–245.5, 2); zygomatic breadth, 142.0 (133.0–156.0, 3—Satunin 1905).

Cranial and dental measurements are also available for fossil remains of *C. crocuta*. Mean lower carnassial lengths (mm; parenthetical range, *SD*, *n*) of late Pleistocene *C. crocuta* from various locations in Britain were: Kirkdale Cave, 31.505 (30.0–34.4, 1.013, 21); Barrington, 31.770 (30.3–33.7, 1.1148, 10); Torcourt Cave, 31.376 (29.5–33.6, 1.186, 17); Tornewton Cave, 31.596 (28.7–34.6, 1.304, 90); Joint Mitnor Cave, 31.350 (31.0–31.7, 0.495, 2); Pin Hole, 32.766 (30.0–40.7, 2.212, 44); Coygan Cave, 32.137 (29.5–34.8, 1.585, 16); Picken's Hole, 32.288 (30.0–34.7, 1.419, 25); Badger Hole, 32.762 (30.7–34.0, 1.054, 8); Hyaena Den, 32.310 (31.1–34.5, 1.195, 8); Kent's Cavern, 32.493 (26.9–36.3, 1.404, 118); Brixham Cave, 32.240 (31.4–34.0, 1.101, 5—Klein and Scott 1989).

Mean dental measurements (mm; parenthetical range, *n*) of late Pleistocene *C. crocuta* from Fouvent-Saint-Andoche were: C breadth, 13.2 (12.0–14.9, 15); C length, 17.5 (17.0–18.0, 13); P1 breadth, 7.6 (6.0–9.0, 20); P1 length, 7.7 (7.0–9.0, 21); P2 breadth, 13.5 (12.0–14.8, 26); P2 length, 17.7 (16.0–19.0, 16); P3 breadth, 17.5 (15.0–19.0, 22); P3 length, 24.5 (23.0–26.0, 20); P4 breadth, 21.6 (19.0–23.0, 19); P4 length, 39.7 (35.5–42.0, 16); D2 breadth, 7.6 (7.0–9.0, 8); D2 length, 12.5 (11.6–14.0, 8); D3 breadth, 13.5 (13.0–15.0, 6); D3 length, 22.6 (21.3–23.7, 13); D4 breadth, 12.6 (12.0–15.0, 7); D4 length, 10.2 (9.0–11.0, 6); c breadth, 13.7 (12.0–16.0, 41); c length, 16.3 (14.4–19.0, 40); p2 breadth, 12.2 (10.5–13.7, 20); p2 length, 16.5 (14.0–18.5, 21); p3 breadth, 16.4 (15.0–17.3, 41); p3 length, 22.5 (21.0–24.0, 44); p4 breadth, 14.9 (12.0–17.4, 62); p4 length, 24.0 (21.5–26.0, 64); m1 breadth, 13.4 (12.0–14.5, 46); m1 length, 31.7 (27.5–34.0, 42); d2 breadth, 6.3 (5.0–7.2, 11); d2 length, 10.8 (9.5–12.0, 11); d3 breadth, 7.1 (5.4–8.0, 15); d3 length, 13.9 (12.7–15.0, 15); d4 breadth, 8.0 (7.0–9.0, 21); d4 length, 19.6 (19.0–21.0, 17—Fourvel et al. 2015).

Mean dental measurements (mm; parenthetical *n*) of late Pleistocene *C. crocuta* from Kent's Cavern were: P2 length, 14.38 (97); P3 length, 21.11 (97); P4 length, 34.97 (97); c length, 14.47 (7); p2 length, 14.49 (96); p3 length, 19.86 (98); p4 length, 21.66 (91); m1 length, 26.67 (95); d2 length, 9.19 (10); d3 length, 13.74 (11); d4 length, 19.91 (34); prosthion to basion length, 249.6 (5—Kurtén 1956).

Mean cranial and dental measurements (mm; parenthetical range if available, *n*) of *C. crocuta* fossils from Sterkfontein Valley, South Africa, were: breadth across zygomatic arches, 156.0 (NA, 1); C breadth, 10.2 (NA, 1); C length, 15.9 (14.3–17.5,

2); M1 breadth, 7.4 (NA, 1); P1 breadth, 7.2 (6.0–8.3, 2); P2 breadth, 12.5 (11.5–13.9, 5); P2 length, 17.1 (16.0–18.4, 5); P3 breadth, 17.1 (15.0–19.5, 6); P3 length, 23.3 (21.1–25.7, 6); P4 length, 37.9 (35.0–41.4, 4); breadth of blade of P4, 12.4 (11.2–13.0, 3); length of metastyles of P4, 16.2 (14.6–19.2, 3); length of paracone of P4, 13.4 (12.6–14.0, 4); greatest anterior breadth across protocone of P4, 22.0 (19.1–25.0, 5); c breadth, 12.9 (11.1–14.6, 2); c length, 15.4 (14.5–16.2, 2); m1 breadth, 12.0 (11.1–12.4, 5); m1 length, 28.3 (27.8–29.5, 4); m1 length of talonid, 3.7 (3.4–3.8, 4); p2 breadth, 10.7 (9.7–12.1, 7); p2 length, 15.9 (13.9–17.6, 6); p3 breadth, 15.4 (13.0–24.7, 8); p3 length, 20.1 (18.8–21.7, 8); p4 breadth, 13.1 (12.0–14.0, 7); p4 length, 22.4 (19.5–24.2, 7); p4 length of protoconid, 12.3 (11.5–12.8, 6); minimum dorsoventral depths of mandible anterior to p2, 35.4 (31.5–38.0, 4); minimum dorsoventral depths of mandible posterior to m1, 40.0 (38.0–42.0, 2); buccal-lingual breadth of mandibular corpus below the center of p3, 18.3 (15.6–20.1, 7); distance from anterior face of p2 to posterior margin of m1, 84.1 (83.0–85.2, 2—Turner 1984).

DISTRIBUTION

Geographically (Fig. 4) *Crocuta crocuta* is widespread across sub-Saharan Africa except rain forests in the Congo basin and much of southern Africa, thus from about 17°N to 28°S (Kruuk 1972; Holekamp and Dloniak 2010). It occurs from sea level to near the snow line of Kilimanjaro and up to 4,000 m (Matthews 1939b; Kruuk 1972).

FOSSIL RECORD

The fossil record of *Crocuta* is extensive especially in Eurasia and Africa, but the interpretation of that record is in flux. The extant African *Crocuta crocuta* is closely related to extinct Eurasian, late Pliocene, and Pleistocene cave hyenas (Rohland et al. 2005; Sheng et al. 2014). The origin and evolutionary diversity of *Crocuta* is complex and not resolved with evidence of bidirectional gene flow between Eurasian and African *Crocuta* (Sheng et al. 2014; Westbury et al. 2020).

FORM AND FUNCTION

Form.—The adult dental formula is i 3/3, c 1/1, p 4/3, m 1/1, total 34 (Fig. 2; Pournelle 1965). The neonatal dental formula is i 3/3, c 1/1, p 0/0, m 0/0 (Pournelle 1965). Bone-crushing teeth include the third upper and lower premolars, whereas the carnassial shear (upper fourth premolar and lower first molar) can slice thick pieces of hide or tendon (Kruuk 1972). Bite force increases up to 5 years of age; thus, subadults when weaned cannot crush the same bones as adults (Binder and Van Valkenburgh 2000).

Crocuta crocuta has a thick hide (Kruuk 1972). Descriptions and inventory of the muscles of the head, neck, back, thorax, abdomen, forelimb, and hind limb are available (Watson and Young 1879:plates V, VI). Muscles of the thorax, forelimb, and associated synovial sheets have been detailed (Gomerčić 1985). Masses of > 50 individual limb muscles from an adult female are available (Spoor and Badoux 1989).

The dissection of an adult male provides the best description of the major anatomical features of *C. crocuta* (Watson and Young 1879). The dorsally papillated tongue is elongate, flattened, and thin with a central oval surface of blunted papillae and a marginal surface of recurved papillae. The tonsil is oval with oblique glandular ridges; the short, soft palate lacks a uvula. The thickly muscular esophagus can be dilated and has a dense, tough mucous coat with longitudinal rugae. An empty stomach measured 23 by 18 cm, length by breadth, with thick walls and internal rugae of various robustness and orientations (Watson and Young 1879:82, figure 1). The small pyloric opening was 0.3 cm in diameter. The small intestine (82 cm in length) has constrictions at irregular intervals, and the internal mucous surface is covered in villi. Eight Peyer's patches increase in size from the stomach to the lower ilium. The 15-cm cecum marks the entrance to the 67-cm-long, well-muscled large intestine. The two segments of the liver are each divided into lobes (Watson and Young 1879:85, figure 3). A pyriform gallbladder is present, as is a long, narrow pancreas (3 by 3 cm), and an elongate, tongue-shaped spleen (41 cm long, 3–8 cm in width—Watson and Young 1879).

The epiglottis guards the cartilaginous larynx, which merges into the 28-cm-long trachea that has 49 cartilaginous rings of varying breadth. The two unconnected halves of the thyroid extend from the cricoid cartilage of the larynx to the sixth tracheal ring. The right lung has six lobes, whereas the left lung has only three (Watson and Young 1879:figure 4). The heart has a clearly defined fossa ovalis. The kidneys are globular with no lobes (Watson and Young 1879). The pyriform bladder is 7 cm long when empty (Matthews 1939c).

Weight of the left adrenal of five adult females (mean body mass 51.6 kg) was 6.9 g (± 1.2 *SE*) and of the left gonad 2.7 g (± 0.3 *SE*), whereas five adult males (mean body mass 43.6 kg) had smaller left adrenals, 4.8 g (± 0.4 *SE*) and larger left gonads, 6.3 (± 1.2 *SE*—Neaves et al. 1980). Subcutaneous fat is primarily in the axilla and groin. Abdominal fat is prominent on the omentum and mesenteries, whereas retroperitoneal fat is primarily around the kidneys (Matthews 1939b).

The brain lacks a central sulcus between motor and somatosensory cortex (Sakai et al. 2011). The hemispheres of the brain of one adult were each 8 cm in length and together 7 cm in breadth (Watson and Young 1879:90, figure 5). Mean endocranial volume of 32 *C. crocuta* was 160.06 ml (± 9.353 *SD*) with mean regional volumes as follows: anterior cerebrum, 39.18 ml (± 8.671 *SD*), posterior cerebrum, 90.88 ml (± 8.735 *SD*), and cerebellum plus brain stem, 26.47 ml (± 1.831 *SD*); mean basal length of the skulls was 217.91 mm (± 6.81 *SD*—Sakai et al. 2011). Endocranial volumes for 88 *C. crocuta* were
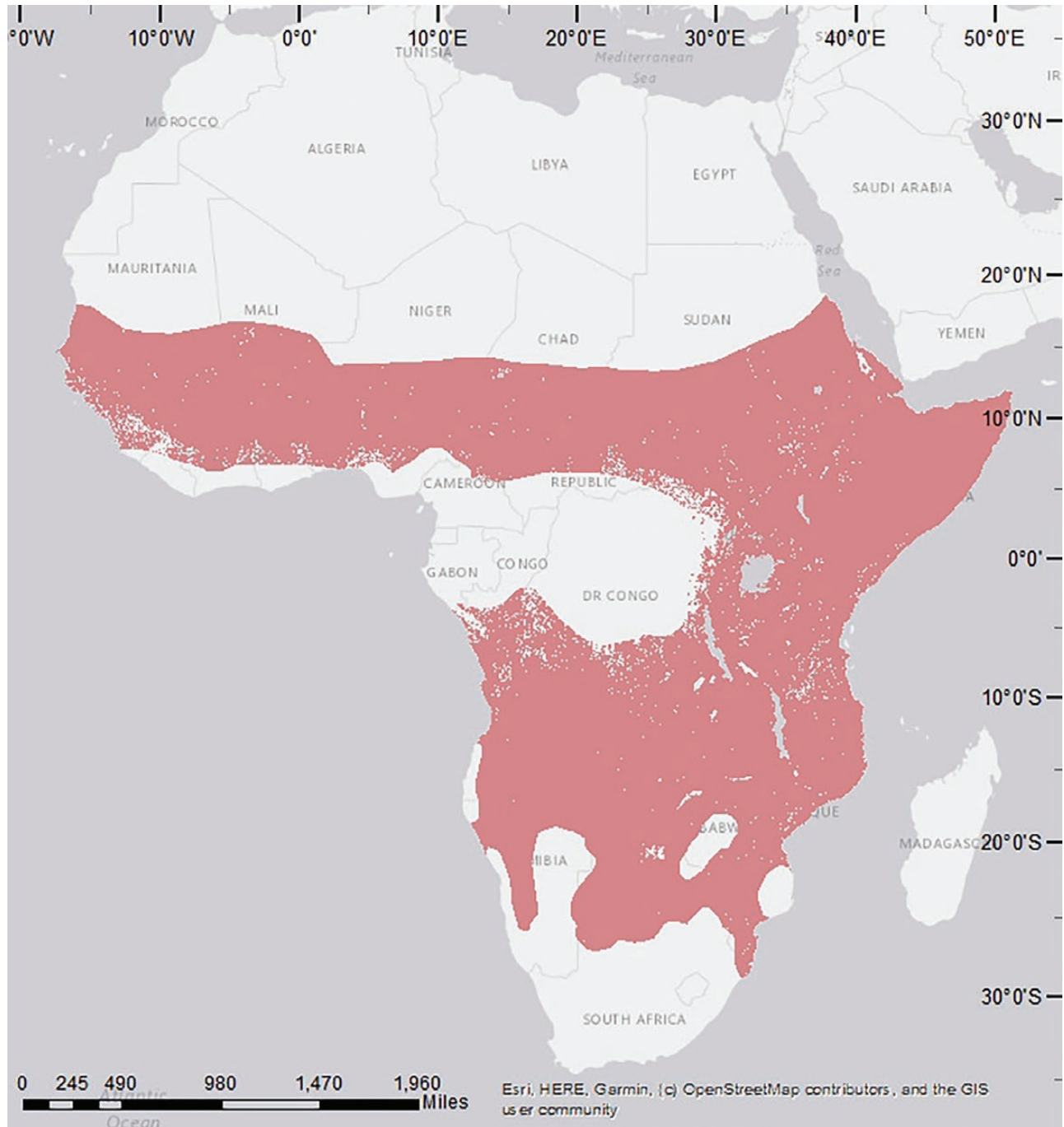
Fig. 4.—Geographic distribution of *Crocuta crocuta*. Modified from International Union for the Conservation and Nature and Natural Resources (Bohm and Höner 2015) to eliminate elevation and habitat areas unsuitable for *C. crocuta*.

155–220 ml (Mann et al. 2018). In six adult females the hSDN nucleus in the medial preoptic area and anterior hypothalamus is one-half the size of that in four adult males (Fenstemaker et al. 1999). Extensive brain images and atlases of *C. crocuta* (catalog # 64-352) are part of the online Comparative Mammalian Brain Collection (Welker et al. 2019).

Crocuta crocuta has a zonary, hemochorial placenta that has received histological, ultrastructural, and genomic study (Matthews 1954; Morton 1957; Oduor-Okelo and Neaves 1982; Enders et al. 2006; Funk et al. 2019). Females have paired ovaries, oviducts, and uterine horns (Watson 1877). Ovarian capsules, whose walls are "heavily loaded with fat," surround

each of the ovoid ovaries and have a 2- to 3-cm slit that opens to the fimbria of the oviducts (Matthews 1939c:22). Two fat pads encase the ovaries and the oviducts on each side (Cunha et al. 2003:206, figure 5). The coiled oviduct has a complexly folded, vascularized mucosa with both ciliated and nonciliated epithelial cells as well as a musculature (Cunha et al. 2003). Histological evidence indicates ovulation can occur from alternate ovaries and that follicular development may occur during lactation (Matthews 1939c; van Jaarsveld et al. 1992a). Females with 1–2 embryos had 2–4 recent corpora lutea, and up to 13 corpora lutea may be present in the ovaries of old females (Matthews 1939c).

Uterine horns are 7–8 cm in length in nonpregnant females with layers of longitudinal and circular muscle with associated vasculature and connective tissue around the endometrium (Cunha et al. 2003). The lumen of the uterine horns is coiled, and uterine glands are embedded in the endometrium (Cunha et al. 2003). The muscular portions of the uterine horns fuse to form the body of the uterus that connects to the vagina and urogenital sinus (Cunha et al. 2003). The indistinct cervix is a histological transition between vagina and uterine horns, and paired bulbourethral glands are situated at the junction of the vagina and the urogenital sinus (Cunha et al. 2003). A number of internal longitudinal folds line the 6- to 13-cm-long vagina as well as the bicornuate uterus (Matthews 1939c).

The urogenital canal runs from the tip of the elongate clitoris (~17 cm) to the vagina after passing the junction with the urethra (Matthews 1939c). The urethra runs along the ventral aspect of the reproductive tract (Cunha et al. 2003). A large fold of tissue may prevent urine from entering the vagina (Matthews 1939c).

In prepubertal females and adult males the base of the clitoris (2.5–3.0 cm in diameter) or penis (2.5–3.5 cm in diameter) is 20–28 cm anterior to the root of the tail and 15–20 cm anterior to the center of the anus. Both the clitoris and the penis are pendulous with an anterior and downward direction and contain erectile tissue (Matthews 1939c; Cunha et al. 2003). The proximal portion of the elongate, ovoid, dark gray-black glans has backward-directed small protuberances but is smooth distally. The meatus is a longitudinal, slit opening on the dorsal tip. Covering most of the glans is a much wrinkled black prepuce. Posterior to the glans and anterior to the anus are two shallow pouches, each divided into hairy anterior and smooth posterior parts that appear as low eminences on the perineum. In females the pouches contain fibrous and adipose tissue and are formed from fused labia (Matthews 1939c; Cunha et al. 2003). In males, the testes may occupy the scrotal sac or lie under the perineal skin. Minor sex differences exist in the abdominal hair pattern around the external genitalia. Both prepubertal females and adult males have a pair of 3–5 mm in diameter nipples on the abdomen centered in 1.3-cm-diameter areolae (Matthews 1939c).

The prepuce of sexually mature, nulliparous females is enlarged and becomes slack and baggy after the first birth; its opening is also increased. The glans, itself, also hypertrophies as does the tip meatus. The distal shape of the glans becomes more truncated and rounded as the enlarged meatus (1.5 cm) becomes

more ventral (Matthews 1939c). Glans measurements (mean and parenthetical *SE*, in g or mm) for five adult females, five adult males, and three juvenile females, respectively, were: mass, 49 (2), 56 (4), 59 (5); meatus width, 58 (6), 5(1), 16 (7); total length, 171 (2), 193 (4), 163 (8); glans diameter, 17 (1), 17 (1), 18 (2); shaft diameter, 22 (2), 21 (1), 24 (3—Neaves et al. 1980). Photographs, drawings, and detailed text of the internal anatomy and external genitalia of adults are available (Matthews 1939c; Davis and Story 1949; Cunha et al. 2003; Cunha et al. 2014).

For parous females the gray-black prepuce (diameter at base 3.75–5.25 cm) hangs in slack, baggy folds that reach maximum size near parturition and through lactation and then tighten up. Parturition often results in lacerations of the prepuce opening (Fig. 5). Nipples in parous females are black, about 2.5 cm long by 1.0–1.8 cm in diameter, and centered on conical areolae that are 5.0–5.5 cm in diameter (Matthews 1939c). One of 116 females had four nipples; the remainder had two (Kruuk 1972). If supernumerary nipples are present, they enlarge during lactation. At peak lactation, each mammary gland is 26 cm long,
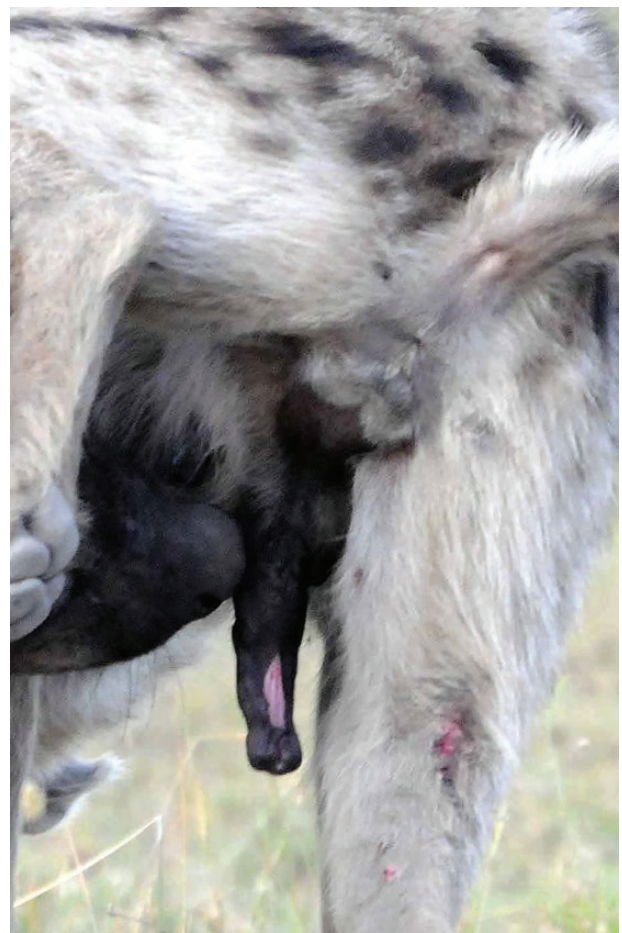

Fig. 5.—Detail of the genitalia of a parous female *Crocuta crocuta* illustrating the healed (pink) parturition scar. Photograph by Kay Holekamp used with permission.

10 cm wide, and 5 cm thick. Mammary tissues and associated structures regress after lactation but seldom completely (Matthews 1939c).

The neuroanatomy of the clitoris and penis is similar with a single opening at the tip. The glans is wide and blunt in females and tapered in males. In both sexes, the dorsal nerves track along both sides of the corporeal body at the 5 and 7 o'clock positions. In females the dorsal nerves fan out laterally on the clitoral body (Baskin et al. 2006). Females have fewer spinal motoneurons innervating the bulbocavernosus and ischiocavernosus perineal muscles (Forger et al. 1996).

Males have pyriform Cowper's glands and a highly variable prostate but no seminal vesicles. Testes of adults are 4 cm long and 2 cm wide (Matthews 1939c). Mean testes volume (mm^2) varies; 1,685.58 (± 55.27 *SE*) for 16 immigrant males and 1,200.3 (± 127.89 *SE*) for four adult natal males, but the volume for 30 immigrant males (940, ± 57 *SE*) did not differ from that for 12 adult natal males (1,030, ± 86 *SE*—Holekamp and Smale 1998; Curren et al. 2013). Ejaculate and sperm characteristics (mean and parenthetical *SE*) of 16 immigrant and four natal males, respectively, are concentration (sperm/ml × 10^6), 18.52 (5.96), 2.23 (1.24); percent motile, 56.47 (7.78), 25.75 (15.10); sperm length (μm), 45.97 (0.33), 40.25 (2.63); sperm midpiece length (μm), 5.81 (0.09), 5.50 (0.20); sperm head length (μm), 3.75 (0.10), 3.50 (0.29); ejaculate volume (ml), 6.40 (0.76), 2.38 (0.92—Curren et al. 2013). No baculum is present (Estes 1991).

Both sexes have extensive anal glands including a pair of large glands, one on either side of the rectum with numerous smaller median glands. The ducts open to the dorsal part of the anal pouch (Matthews 1939b, 1939c). The pasty secretion is semisolid (Matthews 1939b).

Function.—Vision during the day appears similar to humans but at night is far superior (Kruuk 1972). Hearing is acute; *Crocuta crocuta* can hear conspecific vocalizations at a carcass up to 10 km distant (mean 4.2 km—Mills 1990). They can also use contact calls to distinguish individuals (Benson-Amram et al. 2011).

Stomachs rarely contain soft tissues but primarily hold bones, hair, and feathers (Matthews 1939b). *C. crocuta* can completely digest bones, hair, and teeth, but may also regurgitate slimy masses of hair and bone slivers (Kruuk 1972). Regurgitation of these remains attracts other individuals, who, along with the regurgitator will roll in the expelled material (Kruuk 1972). Feces are primarily minerals from bones with some hair or feathers and are often deposited in latrine areas (Matthews 1939b). Fresh scat is green and turns white as it dries (Matthews 1939b).

Mass-specific total body water was 66.3% (± 4.3 *SD*) for six free-living *C. crocuta*. Water flux was 64.4 (± 30.0 *SD*) ml/kg-day in and 63.9 (± 29.1 *SD*) ml/kg-day out (Green et al. 1984). Mean serum sodium was 139 (± 4.0 *SD*) mmol/l with an influx of 3.47 (± 1.66 *SD*) mmol/kg-day and an efflux of 3.43 (± 1.59 *SD*) mmol/kg-day (Green et al. 1984).

Mean plasma cortisol levels were about 100 ng/ml (van Jaarsveld and Skinner 1992) and did not differ between immigrant and natal males (Holekamp and Smale 1998). Mean fecal glucocorticoid (fGC) levels for four clans were 103–185 ng/g (Van Meter et al. 2009). Intense anthropogenic disturbance (not tourism) and social instability, but not ecological factors, elevate fGC levels (Van Meter et al. 2009). Young juveniles (< 6 months) have higher mean fGC levels (37 females, 35.4 ng/g; 50 males, 45.2 ng/g) than older (6–24 months) juveniles (28 females, 19.2 ng/g; 31 males 17.7 ng/g—Benhaiem et al. 2012). Lactating females (*n* = 76, 112.6 ng/g, ± 35.5 *SE*) had higher levels of fGC than 34 nonlactating females (40.0 ng/g, ± 9.3 *SE*) with 20 pregnant females intermediate (59.5 ng/g, ± 17.3 *SE*—Goymann et al. 2001b).

ONTOGENY AND REPRODUCTION

Ontogeny.—The genital tubercle of *Crocuta crocuta* enlarges by day 31 of gestation, but the reproductive tract has not differentiated (Cunha et al. 2005). Fetal ovaries begin to differentiate by day 45 of gestation, and testicular differentiation is apparent by day 30 (Browne et al. 2006). At day 50 of gestation the Müllerian ducts are well-developed in females and absent in males, and the Wolffian ducts are beginning to degenerate in females (Lindeque and Skinner 1982a). From at least 60 days, fetal gonads and adrenal glands synthesize androgens (Lindeque and Skinner 1982a; Browne et al. 2006). Although steroid hormones have complicated roles in the development of the external genitalia, growth of both the clitoris and the penis is largely independent of androgens (Drea et al. 1998; Cunha et al. 2014).

Gestational age can be estimated by femur length using transabdominal ultrasound (Place et al. 2002). *C. crocuta* can be roughly aged by the closure of the frontoparietal and basilar sutures in the skull and the amount of tooth wear (Matthews 1939c; Lindeque and Skinner 1984; van Jaarsveld et al. 1987). Ages of subadults may be estimated by tooth-eruption models (Van Horn et al. 2003).

Cubs are born in isolated underground dens where they spend their first weeks of life before being carried to a communal den (White 2007; Holekamp and Dloniak 2010). At birth, the dark brown neonates can walk, react to sound and movements, and have open eyes and erect ears, as well as erupted incisor (2–4 mm long) and canine (6–7 mm long) teeth (Matthews 1939c; Pournelle 1965; Golding 1969; Frank et al. 1991). Cheek teeth begin to erupt at 31 days, and adult dentition is present by 15–18 months (Pournelle 1965; Kruuk 1972; Mills 1990; Van Horn et al. 2003). Cubs can move rapidly at 10 days (Kruuk 1972). At 6–11 weeks molting to the adult pelage starts at the head and forequarters and is nearly complete by 9–18 weeks except for a middorsal stripe (Pournelle 1965; Golding 1969), although the legs may remain dark for a year (Kruuk 1972). Average mass of six neonates was 1.49 kg (Pournelle 1965; Golding 1969).

A 1.6 kg captive neonate was 3.2 kg at 25 days, 4.8 kg at 37 days, and 14.5 kg at 100 days (Pournelle 1965), but two other 1.6 kg captive neonates grew at a slower rate, being only 8.6–10.9 kg at 3 months (Golding 1969). Fetal growth curves are available from 30 days to near term and postnatal curves from birth to 25 years (van Jaarsveld et al. 1988).

An ethogram of behavior during the first month of life includes aggressive, dominance and submissive, play, and exploration behaviors (Drea et al. 1996). Littermates establish relative dominance rank as early as the first day of life (Smale et al. 1995). During the first week mother–cub interactions predominate (Drea et al. 1996), and vocalizations are apparent (Kruuk 1972). The "giggle" (rarely called "chuckle") vocalization is "sharper and higher pitched" than that of adults (Pournelle 1965:503). Social and interactive play between cubs begins the second week of life, with locomotor and object play emerging in weeks 3 and 4 (Drea et al. 1996). Adult behavioral displays, such as leg lifting with genital erections, begin at 1 month (Kruuk 1972).

First solid food is at 3 months, but only rarely do juveniles under 6 months eat from a kill (Kruuk 1972). Juveniles begin following their mothers at a few months of age, gain independence from the communal den at 8.9 months (*n* = 22 juveniles from 11 litters), and begin to hunt at 8–10 months of age (Kruuk 1972). Typically weaning is 12–18 months but can last up to 2 years and, rarely, may be as short as 7 months (Hofer and East 1995; Holekamp et al. 1996). In Kenya, females are larger than males for many traits because females grow faster after weaning (Swanson et al. 2013). Development of the massive skulls needed for bone cracking is not complete until 35 months, well after weaning and sexual maturity (Watts et al. 2009; Tanner et al. 2010). For the first 2 years of life, females and males do not differ in their use of space (Boydston et al. 2005).

Females are sexually mature at 2–3 years, and the first estrus may result in pregnancy (Matthews 1939c; Kruuk 1972). Age at first birth is 30–45 months (Mills 1990), but varies with dominance rank, 2–3 years for high-ranking females versus 5–6 years for low-ranking females (Holekamp et al. 2012). Males are sexually active at 2 years (Kruuk 1972). Females rarely disperse, but in their third year (30–45 months) nearly all males leave their natal clan and move into another clan (~8–10 km distant) where they initially assume a low rank as immigrants (Mills 1990; Van Horn et al. 2003; Boydston et al. 2005). Consequently, for females rank has stronger effects on social networks than does rank for males (Turner et al. 2018). Rarely, males may be nomadic for short periods (Mills 1990).

Reproduction.—The female urogenital sinus traverses the clitoris and functions in urination, copulation, and birth (Cunha et al. 2003). *Crocuta crocuta* anatomy gives females complete control over mate choice (Holekamp and Dloniak 2010). Copulation lasts 8–12 min (Matthews 1939c) and requires the coordinated efforts of females and males to align the flaccid forward-projecting clitoris and the erect penis (Cunha et al. 2003). A "male must squat behind the female and hop around

while thrusting blindly upward and backward" until intromission occurs (Holekamp and Dloniak 2010:196). Swelling of both clitoris and penis may result in a partial lock during coitus (Cunha et al. 2003). Reproductive females mate with multiple males during estrus, and males can mate with multiple females (Engh et al. 2002; East et al. 2003; Holekamp and Dloniak 2010). At least 20–35% of cubs from twin litters have different sires (Engh et al. 2002; East et al. 2003). In 24 observed copulations, females copulated only with immigrant males (Holekamp and Smale 1998); in addition, paternity tests indicated that only one of 71 cubs conceived over 13 years was sired by a natal male (Engh et al. 2002; Holekamp et al. 2012).

Ovarian hormones facilitate the "development of a large clitoral canal and a highly elastic urogenital meatus" (Cunha et al. 2003:207). For one nulliparous female, 3–4, 10-s contractions occurred in bouts about every 78 s, 1–5 h before birth, whereas in the hour before birth contractions occurred singly about every 44 s (Frank and Glickman 1994).

For birth to occur the fetus "moves along an exceptionally tortuous route, first following a caudal-ventral path from the uterus through the bony pelvic outlet, and then making a sharp turn in an anterior direction to traverse the clitoral canal to emerge through the meatus of the glans clitoris" (Cunha et al. 2003:207). The meatus tears during delivery of primiparous mothers; thus, subsequent deliveries are easier. However, first-term births have higher neonatal mortality (~60% in one captive colony), especially if the placenta detaches early in labor and the cub becomes anoxic (Frank and Glickman 1994; Cunha et al. 2003). Also, both mother and offspring may die if a cub becomes wedged during labor (Morton 1957). Births from a single litter may occur within an hour (Henschel and Skinner 1990; Frank et al. 1991) or up to days apart (Matthews 1939c). Placentophagia occurs (Henschel and Skinner 1990; Frank and Glickman 1994).

Birth typically occurs at the entrance to the natal den, with only the posterior portion of the female plugged into the narrow opening (K. E. Holekamp, pers. comm. to VH). A photo essay of the birth of a cub at Kruger National Park is available (Adams and Cox 2019).

Overall cub mortality is inversely related to rank as low-ranking mothers lose more cubs from birth to 1 month of age (Holekamp et al. 1996; White 2002; Watts et al. 2009; Swanson et al. 2011). Causes of cub mortality are infanticide (including facultative siblicide), starvation, disease, weather, injury, humans, and predation (Hofer and East 1997; Smale et al. 1999; White 2005; Wahaj et al. 2007).

Crocuta crocuta does not have seasonal births in equatorial regions (Matthews 1939b), but births may be restricted to winter in southern latitudes (Pournelle 1965; Lindeque and Skinner 1982b), although conceptions are positively correlated with food abundance (Holekamp et al. 1999b). Gestation is 110 days. Stillbirths and in utero resorption of embryos are common in captivity and in the wild. Approximately 27–33% of litters have higher litter size in utero than at birth (Wahaj

et al. 2007). Mean litter size declines from pregnancy to den emergence: 78 in utero litters, mean 1.90; 70 litters at birth, mean 1.63; 1,117 litters at den emergence, mean 1.55 (Zuckerman 1952; Reitz 1972; van Jaarsveld et al. 1988; Holekamp and Dloniak 2010). Singletons are common for first litters (~80% captive—Frank et al. 1991; ~50% wild— White 2005), and triplets are rare (Smale et al. 1999; Wahaj et al. 2007). Litter composition is biased toward mixed-sex litters (van Jaarsveld et al. 1988), in part due to sibling aggression in same-sex litters (Frank et al. 1991; Golla et al. 1999). However, at 1–2 months, fighting rates did not differ between 26 mixed- and 20 same-sex litters (Wahaj and Holekamp 2006), and "mothers endeavor to keep all offspring alive for as long as possible" (White 2008:353). Males provide no parental care (Holekamp and Dloniak 2010).

The minimum inter-litter interval is 9–10 months (Matthews 1939a, 1939b) if offspring survive, but in the wild the average inter-litter interval is 14–19 months (Mills 1990; Holekamp et al. 1996). Estrus may occur as early as 2 weeks after the loss of a litter (Matthews 1939c), but in the wild litters are produced 3–5 months after the loss of cubs (Mills 1990).

Sex steroids as well as reproductive protein hormones vary by sex, age, reproductive condition, and social status. Plasma estrogens and progesterone (nmol/l) are higher in females (estradiol: four females, mean 1.38, no *SE*, five males, mean 0.41 ± 0.04 *SE*; estrone: four females, mean 1.00, no *SE*, five males mean 0.11 ± 0.008 *SE*; progesterone: four females, mean 96.9, no *SE*, five males, mean 6.42 ± 3.21 *SE*—Racey and Skinner 1979). In females, progesterone levels vary from 4 to 92 ng/ml with some correlation to reproductive state in some females (Racey and Skinner 1979; Gombe 1985; van Jaarsveld et al. 1992a). Estrogen patterns are even less clear (van Jaarsveld et al. 1992a). Lactating females have 25–33% lower prolactin levels than other age, sex, or reproductive classes (van Jaarsveld et al. 1992b). Mean plasma gonadotropins (ng/ml) are similar for females and males (luteinizing hormone: five females, 8.40 ± 5.12 *SE*, five males, 3.22 ± 0.29 *SE*; follicle-stimulating hormone: five females, 29.04 ± 1.36 *SE*, five males, 25.08 ± 1.36 *SE*—Racey and Skinner 1979).

Plasma androgen levels vary across studies (Goymann et al. 2001a). Reported levels of androgens use different units that are not directly comparable (ng/100 ml plasma, ng/g gonadal or adrenal tissue—Racey and Skinner 1979; nmol/l plasma— Lindeque et al. 1986; ng/ml plasma—Frank et al. 1985; ng/g feces—Dloniak et al. 2004). Androgen levels vary with age (Glickman et al. 1992) and, in adults, variation occurs both with reproductive state in females (highest during pregnancy) and with residency in males (highest in immigrant males—Dloniak et al. 2004). Androgen levels are also positively correlated with social rank in multiparous females (Jones 2019). In males, androgen levels vary with dispersal status and may increase with age or tenure within a clan (van Jaarsveld and Skinner 1991; Holekamp and Smale 1998; Goymann et al. 2001a). In adrenal glands, amounts of testosterone and androstenedione are similar in females and males (Racey and Skinner 1979). Gonadectomy

reduces plasma androgen levels to near zero in both sexes (Frank et al. 1985). Androgen binding in plasma is greater for females than males (van Jaarsveld et al. 1992c). Fecal androgen levels follow the same patterns (sex and reproductive differences) as plasma levels (Dloniak et al. 2004).

ECOLOGY

Population characteristics.—Population density varies widely, 0.004–1.65 individuals/km^2 (compilation of 50 studies—Holekamp and Dloniak 2010). The lowest density is in the Namib Desert, Namibia, and the highest in the Amboseli National Park and the Ngorogoro Crater, Tanzania (Holekamp and Dloniak 2010). Clan territories in the Namib Desert are 383–816 km^2 (Tilson and Henschel 1986). One clan in the Kruger National Park had a 130 km^2 territory, but individuals within the clan ranged only 9–16 km^2 (Henschel and Skinner 1991). Overall, clan home ranges vary from 13 to 1,065 km^2 (Holekamp et al. 2012).

Sex-ratio data come primarily from adults. Of 103 adults collected while they were scavenging, 40 (39%) were female (Matthews 1939c). In contrast, of 234 adults captured during a behavioral study, 116 (50%) were female (Kruuk 1972), and the Serengeti has a 1.17:1 female to male bias (Hofer and East 1993a). Juvenile sex ratios may be correlated with clan dynamics and be male-biased before clan fission and female-biased after fission (Holekamp and Smale 1995). Across nine studies, adult sex ratio had a mean of 1.8 females to males, range 1.0–3.1 (Holekamp et al. 2012). Sex ratio (F:M:unknown) of 100 cubs (< 3 months old) was 36:44:20 (White 2002).

Clans of up to 126 individuals are composed of several matrilines of females and their offspring plus multiple adult immigrant males (Kruuk 1972; Frank 1986a; Holekamp et al. 2012; Green et al. 2018). Smaller social groups (3–8 individuals) occur in the Namib Desert (Tilson and Hamilton 1984). Number of matrilines varies from 1 to over 10 per clan (Holekamp et al. 2012). On average 55% of individuals in a clan are adults, range 36–73% (Holekamp et al. 2012).

Relatedness is higher within than between matrilines, and clan members overall are not closely related due to male-mediated gene flow across clans (Van Horn et al. 2004a). As males emigrate from their natal clans 1–38 months after puberty, clans have two classes of adult males, natal and immigrant (Holekamp and Smale 1998). Immigrant males comprise 60–75% of adult males in a clan (Holekamp et al. 2012).

In captivity, several individuals have lived 27–29 years, and one individual lived 41 years 1 month (Jones 1982; Weigl 2005). In the wild, *Crocuta crocuta* can live up to 26 years (Holekamp and Smale 1995, K. E. Holekamp, pers. comm.).

Space use.—*Crocuta crocuta* tolerates diverse habitats from "dry and arid semi-deserts to the thickest tropical forest" (Matthews 1939a:44). During the day it rests in thick bush, long grass, rock crevices, dens, or natural cavities (Matthews 1939b; Gasaway et al. 1989). *C. crocuta* extensively modifies earthen

dens originally excavated by other animals such as aardvarks (*Orycteropus afer*) or warthogs (*Phacochoerus*—Kruuk 1972; Henschel and Skinner 1990); warthogs may share burrows with *C. crocuta* (Deanne 1962).

Cubs rather than adults alter most of the tunnels which are too narrow for adults and large predators (Kruuk 1972; East et al. 1989). A warren of dens measured 15 by 30 m on the Ol Balbal Plain, Tanzania (Matthews 1939b). The 1.5- to 3-m-long burrows are often oval (more wide than high) with entrances up to 1 m in diameter but sometimes < 25 cm (Kruuk 1972). On average, *C. crocuta* move their communal dens monthly (Boydston et al. 2006), but dens may be used and reused for years (Hill 1980; Boydston et al. 2006). Less commonly used are granite or limestone calcrete dens (Skinner et al. 1986).

Diet.—*Crocuta crocuta* is a carnivorous predator whose main prey are 56–182 kg hoofed mammals and their offspring (Hayward 2006). Zebra (*Equus*) are variously reported as preferred or avoided prey. A meta-analysis suggests that buffalo (*Syncerus*), giraffe (*Giraffa*), and zebra are avoided (Hayward 2006), but in the Serengeti, wildebeest, (*Connochaetes*), gazelle (*Gazella*), and zebra may account for 95% of its prey (Kruuk 1972). In the Namib Desert, gemsbok (*Oryx gazella*) account for 80% of prey with mountain zebra (*Equus zebra*) a distant second (12%—Tilson et al. 1980). In the Kalahari, juvenile gemsbok, blue wildebeest (*Connochaetes taurinus*), common eland (*Taurotragus oryx*), and Cape springbok (*Antidorcas marsupialis*) account for 65% of kills (Mills 1990). Other ungulates in its diet include Cape buffalo (*Syncerus caffer*), common duiker (*Sylvicapra grimmia*), impala (*Aepyceros melampus*), hartebeest-kongoni (*Alcelaphus buselaphus*), Cape klipspringer (*Oreotragus oreotragus*), greater kudu (*Tragelaphus strepsiceros*), steenbok (*Raphicerus campestris*), kirrugum (*Damaliscus korrigum*), warthog, Defassa waterbuck (*Kobus defassa*), and domestic livestock (e.g., cattle, *Bos*, goat, *Capra*—Kruuk 1972; Tilson et al. 1980; Mills 1990). Besides ungulates, *C. crocuta* will eat termites, fish, tortoises, puff adder (*Bitis arietans*), pythons (*Python sebae*), ostrich (*Struthio camelus*), calves of other large mammals (black rhino, *Diceros bicornis*, common hippopotamus, *Hippopotamus amphibious*, and African savanna elephant, *Loxodonta africana*); other carnivores (lion, *Panthera leo*, golden jackal, *Canis aureus*, dog, *Canis familiaris*, bat-eared fox, *Otocyon megalotis*, genet, *Genetta genetta*, mongoose, either *Mongos* or *Helogale*), hyrax (*Procavia capensis*), aardvark, primates (*Cercopithecus*, *Chlorocebus*, *Colobus*), lagomorphs (*Lepus*), and rodents (e.g., mice [no scientific name], springhare, *Pedetes capensis*, porcupine, *Hystrix africaeaustralis*—Kruuk 1972; Tilson et al. 1980; Mills 1990; Sillero-Zubiri and Gottelli 1992). A secondary source of food is opportunistic scavenging, including eating conspecifics which may be killed in clan fights or by lion predation (Kruuk 1972; Tilson et al. 1980; Mills 1990; Watts and Holekamp 2008). *C. crocuta* will consume, or at least chew, other items, such as tail-lights, wood, or grass. It will also snap up flying termites, forage for fish in shallow water, and eat fruit (Kruuk 1972; Stuart 1976; Mills 1990; Sillero-Zubiri and Gottelli 1992).

Crocuta crocuta can live up to 30+ km away from fresh water (Kruuk 1972). A radiocollared female drank nine times in 12 days (Kruuk 1972). Drinking bouts seldom last > 30 s (Kruuk 1972). When water is scarce, it may rely on fluids from ingested prey (Cooper 1990; Mills 1990; Gasaway et al. 1991).

Diseases and parasites.—External parasites hosted by *Crocuta crocuta* include flies (*Hippobosca capensis*), especially in the axilla and groin; fleas (*Ctenocephalus felis*, *Echidnophyaga*); ticks (*Haemaphysalis leachi*, *Rhipicephalus simus*), especially on the ears; and a leech (*Hirudo hildebrandti*) on the hard palate (Loveridge 1923; Matthews 1939b).

Internal helminths (from liver, intestines, stomach, or muscle) include tapeworms (*Diphyllobothrium*, *Dipylidium*, *Echinococcus*, *Sparganum* [larval form of *Spirometra*], *Taenia* [*Cysticercus* is the larval *Taenia*]), nematodes (*Cylicospirura subaequalis*, *Dipetalonema dracunculoides*, *Toxocara canis*, *Uncinaria*), and roundworm larvae (*Trichinella*—Baylis 1937; Sachs and Taylor 1966; Round 1968). A 1.5 m, not fully grown, *Taenia crocutae* occurred in the intestine of a *C. crocuta* (Mettrick and Beverley-Burton 1961). The following taxa, in order of abundance, were found in feces and considered to be parasites: *Ancyclostoma* (hookworm), *Spirometra* (cestode, larvae known as *Sparganum*), *Isospora* (coccidian), *Dipylidium* (tapeworm), Spirurida (nematode), Taeniidae (tapeworm), *Mesocestoides* (cestode), *Toxocara* (roundworm), *Nematodirus* (nematode); two other taxa (*Moniezia*, *Trichuris*) were considered to be parasites of prey items and not hosted by *C. crocuta* (Engh et al. 2003). Microfilariae of *D. dracunculoides* are known from blood (Lightner and Reardon 1983). *C. crocuta* also hosts the following protozoan parasites: *Hepatozoon*, *Trypanosoma congolense* (Baker 1968; McCully et al. 1975).

Bacterial infections of the bile duct and liver are present, and diseased spleens are common (30% of specimens examined) with large nodules filled with cheesy pus (Matthews 1939b). The abdominal wall may have small white patches of fibrous tissue that are easily peeled off (Matthews 1939b). No skin disease (e.g., mange) was found (Matthews 1939b). *C. crocuta* may die from rabies (Mills 1990; Sabeta et al. 2018). It may also be infected with *Brucella*, *Anaplasma*, and the rinderpest virus (a paramyxovirus) via its prey (Sachs and Staak 1966). Individuals with antibodies to the canine distemper virus were not clinically ill, but low-ranking individuals had higher titers (Alexander et al. 1995). Similarly, *C. crocuta* with antibodies to coronavirus had no severe clinical symptoms (East et al. 2004).

Broken bones, broken teeth, and tooth abscesses are common (Matthews 1939b; Henderson et al. 1984). Uterine cancer (leiomyoma) and metastatic mammary cancer (adenocarcinoma) have been recorded in captive *C. crocuta* (Hubbard et al. 1983). In 1912–1930 and again in the 1950s disease decimated populations of *C. crocuta* in South Africa (Pienaar 1963). *C. crocuta* may starve to death (Kruuk 1972; Henschel and Skinner 1987).

Interspecific interactions.—Main competitors for food are lions and wild dogs (*Lycaon pictus*), and vultures of various genera (Kruuk 1972; Watts and Holekamp 2008). *Crocuta crocuta* will yield a carcass to a pack of wild dogs (Matthews 1939b) but will follow vultures to locate carcasses (Matthews 1939b). Lions will kill *C. crocuta* when competing over a carcass (Matthews 1939b; Kruuk 1972; Mills 1990). In areas with livestock grazing, lion population sizes decrease and *C. crocuta* populations increase eliciting trophic cascades with both top-down and bottom-up effects (Green et al. 2018).

Symbiotic bacteria may play an important role in communicating sex and reproductive state (Theis et al. 2013).

Crocuta crocuta shares parasites with its herbivore prey, often at different stages of the life cycles of the parasite, such as the tapeworm, *Taenia hyaenae*, found as an adult in *C. crocuta* but in larval stages in the muscles of large antelopes (Sachs 1966).

Miscellaneous.—*Crocuta crocuta* can be immobilized with succinylcholine chloride and is more susceptible to adverse side effects during the wet season (Kruuk 1972). A combination of equal parts tiletamine and zolazepam can be administered (2–6.5 mg/kg) via a CO_2-powered rifle (or by injection) to immobilize or anesthetize *C. crocuta* (van Jaarsveld 1988; Van Horn et al. 2004a). Phencyclidine hydrochloride has been used to capture animals, as has ketamine hydrochloride, whereas a combination of xylazine hydrochloride (0.5 mg/kg) and ketamine hydrochloride (5 mg/kg) has been used for anesthesia (Smuts 1973; Lindeque et al. 1986). Tolazoline hydrochloride (4 mg/kg) via an intramuscular injection will antagonize the effects of xylazine (Stander and Gasaway 1991). Anesthesia has been maintained with halothane or a combination of 9% alphaxolone and 3% alphadolone (van Jaarsveld et al. 1984). Ears may be clipped for individual identification, but natural pelage variation can also be used (Kruuk 1972; Frank 1986a).

Crocuta crocuta has successfully reproduced in 12 by 5.5 m outdoor cages with 3 by 3 m indoor dens. Individuals were fed raw meat on the bone, milk with raw eggs, and vitamin supplements (Reitz 1972).

BEHAVIOR

Grouping behavior.—*Crocuta crocuta* forms complex social groups (clans) composed of matrilineal kin groups and immigrant males (Frank 1986a). Clans "are fission-fusion societies in which individual members travel, rest, and forage in subgroups that frequently change composition" (Smith et al. 2008:619). Clans defend group territories. Adult females initiate most cooperative territorial behaviors (e.g., patrolling and scent-marking), but some groups of resident males also patrol territory boundaries. Most intruders are males. Residents are more likely to attack same-sex intruders (Boydston et al. 2001). Fission of clans has occurred when mid- or low-ranking females dispersed as a group into neighboring vacant habitat when food availability was low, and high-ranking conspecifics were in abundance (Holekamp et al. 1993). Fission has also occurred over the course of a few years through regular anthropogenic disturbance (cattle grazing) that split a single hyena clan and its territory into two (Holekamp and Dloniak 2010). *C. crocuta* most often traverses its territory alone, but often moves in small groups of two or three; however, packs up to 25 individuals also occur (Kruuk 1972; Holekamp et al. 2000) and larger aggregations (over 50) may assemble at buffalo kills (K. E. Holekamp, pers. comm.). Communal activities include hunting zebra, fighting other clans, pasting (scent-marking), social defecating, and social sniffing (Kruuk 1972). The latter activity involves a group of animals in close proximity actively and repeatedly sniffing the ground and each other (Kruuk 1972). Clans that range over large areas with few available prey do not exhibit territorial behavior (Gasaway et al. 1989).

Within clans "dominance relationships are organized along matrilineal lines and female dominance over males is the norm among adults" (Smale et al. 1993:467). Dominance rank is "inherited" by successful maternal intervention by high-ranking mothers as well as coalitionary support (Frank 1986b; Engh et al. 2000; East et al. 2009). Gestational androgens may also influence rank acquisition (Dloniak et al. 2006). Within a juvenile cohort dominance relations correlate with maternal rank by 6–8 months, and after 8 months juveniles outrank their older siblings (Holekamp and Smale 1993). Juveniles are subordinate to all adult females until about 6 months when challenges to adults in lower-ranking matrilines start to be successful (Smale et al. 1993). Juveniles are nearly always dominant to immigrant males (Smale et al. 1993). Rank order of immigrant males follows their tenure in the clan, with the most recent arrivals being the lowest-ranking (East and Hofer 2001).

Rank influences most aspects of *C. crocuta* biology. High-ranking females have priority of access to food, need to devote less time to hunting, give birth earlier in their lives, have shorter inter-litter intervals, wean cubs earlier (and at a lower maternal mass), have higher cub survival, and live longer (Hofer and East 2003; Holekamp and Dloniak 2010; Holekamp et al. 2012). Cubs of high-ranking females grow faster as they have greater access to carcasses and can dominate cubs of lower-ranking females (Holekamp and Dloniak 2010). High-ranking females also associate more with their offspring as well as adult female kin than do low-ranking females (Holekamp et al. 1997). Overall, reproductive rates increase with rank, with up to a 5-fold difference in lifetime reproductive success between high- and low-ranking females (Hofer and East 2003; Holekamp and Dloniak 2010; Holekamp et al. 2012).

Social interactions are of three major types, meeting ceremonies, aggressive fights, and sexual encounters. Meeting, or greeting, ceremonies occur frequently, are usually initiated by the lower-ranking individual, and involve olfactory exchanges of mouth and genitals as well as specific postures (Kruuk 1972; East et al. 1993). These multimodal greeting displays promote social bonding and cooperation within a shifting social

milieu (Smith et al. 2011). Aggression usually occurs in three contexts: over food, near the den, or in specific female and male interactions (Kruuk 1972). Aggression is influenced by relatedness; for example, cubs are less aggressive toward their sires than other males (Van Horn et al. 2004b). Also *C. crocuta* directs significantly less aggression toward maternal half-siblings than toward paternal half-siblings (Wahaj et al. 2004). Female–female aggression and male–male aggression occur at similar rates (Curren et al. 2015), but aggression by females is more intense than that of males (Curren 2012; Yoshida et al. 2016). Play behavior occurs among adults, among cubs, and among cubs and adults together (Kruuk 1972).

Reproductive behavior.—In *Crocuta crocuta*, male courtship behavior includes persistently following a female, and both approaching and fleeing from her (Szykman et al. 2001). Occasionally, coalitions of males (two or more) may repeatedly attack a female as they try to sniff and bite her while she crouches and defends herself (Szykman et al. 2003). Affiliative interactions are initiated mostly by males, and males associate more with those females likely to be near estrus (Szykman et al. 2001).

Copulation is seldom observed in the wild; it requires exact coordination of the sexes with a series of positions to achieve a link between the clitoris and the penis (Matthews 1939c). Two observed copulations were 5 and 6 min in duration (Kruuk 1972).

Females often give birth in solitary burrows or dens and then move their cubs to a communal location 2–6 weeks later (Matthews 1939b; Kruuk 1972; Frank et al. 1991). Average age at transfer was 2 weeks for 14 litters including one cub moved at 9 weeks (East et al. 1989). Birth dens may be 0.1–25.6 km distant from the communal den (East et al. 1989). Occasionally, the birth den may become the communal den (East et al. 1989). When cubs are small, mothers may sleep near the den and remain there for long periods, but as the cubs age mothers usually visit the den morning and evening to nurse (Kruuk 1972; East et al. 1989; Henschel and Skinner 1990). If cubs are not outside the den, a mother will call for them (Kruuk 1972). Females lie on their side to nurse, and cubs also lie on their side to suckle. One cub lies parallel to the mother with its tail toward her head; the second cub, if present, lies at right angles (Kruuk 1972). One nursing bout with two cubs lasted just over 4 h (Kruuk 1972).

Depending on foraging conditions, mothers may be away from their cubs for three or more days (Hofer and East 1993c). Upon return their mammary glands have swollen to the point where they have chafed the skin on the hind legs and caused bleeding (Kruuk 1972). Mothers of singletons attend to their cubs at the same rate as mothers of twins, and growth rates of singletons are higher than those of twins (Hofer and East 1993c).

Over 10 years, allosuckling was observed only in a single reproductive season (Knight et al. 1992). At the communal den, higher-ranking females may actively prevent lower-ranking mothers from accessing their cubs for nursing (White 2007).

Food provisioning is rare (Hill 1980; Mills 1990). Lactating females will occasionally (18 incidents over 14 months) bring food to their cubs at communal dens, but that food may be usurped by higher-ranking females. At kills, low- and high-ranking mothers will usually share food with their cubs and less theft occurs than at communal dens (Holekamp and Smale 1990). At the den and at kills, mothers protect their cubs from aggression by conspecific adults (Kruuk 1972).

Communication.—Vocal, olfactory, and visual communication is extensive and can be used for individual recognition among clan members (Holekamp et al. 2007). The vocal repertoire of *Crocuta crocuta* includes whoops, groans, growls, lows, yells, screams, rumbles, and giggles (Kruuk 1972). The acoustic complexity of vocalizations, especially whoops and giggles, codes information about location, age, and sex as well as individual identity and kinship (East and Hofer 1991a, 1991b; Holekamp et al. 1999a; Matthews 1939b; Mathevon et al. 2010). An extensive catalog of 11 vocalizations is available, tabled with body postures and the situations in which the vocalization is used (Kruuk 1972:D. 8; Mills 1990:180–181, table 5.6).

Olfactory communication (pasting, scraping, and fecal deposition) is used for defining territory boundaries and for greetings among clan mates (Kruuk 1972; Henschel and Skinner 1991). Resident females scent-mark (paste) more frequently than males (Boydston et al. 2001). Pasting involves secreting a thin layer of exudate from the anal glands onto a 2–3 cm length of a grass stalk (or the side of a cage). A brief eversion of a short section of the rectum exposes the openings of the anal gland to allow release of the secretion (Kruuk 1972). Anal gland secretions allow identification of sex and reproductive state (Theis et al. 2013). Pasting may be done at dens or kills as well as at territorial boundaries (Kruuk 1972). *C. crocuta* also repeatedly scrapes the ground leaving a scent from the interdigital glands of its forefeet (Kruuk 1972). In addition, feces are often deposited in latrine areas at the boundaries of a clan's territory (Kruuk 1972). Pasting, scraping, and fecal deposition may occur contemporaneously (Kruuk 1972). Although defecation has a communicatory function, urination does not and may occur anywhere and at any time, even when an animal is lying down (Kruuk 1972).

Olfactory cues stimulate specific responses. *C. crocuta* rolls in carrion and the odor of carrion attracts conspecifics, whereas the odor of camphor does not (Drea et al. 2002a). In addition, anal secretions convey "information about the sex, familiarity, and even identity of conspecifics" (Drea et al. 2002b).

Postures including body, ear, and tail position as well as the shape of the mouth are used in dominance interactions and also indicate the probability an animal will approach or withdraw (flee) from a situation (Kruuk 1972:217–219, figures 56–58). Changes in clitoris and penis positions are also used in communication (Kruuk 1972).

Miscellaneous behavior.—*Crocuta crocuta* uses olfactory, visual, and auditory cues to identify prey (Matthews 1939b; Mills 1990). It varies hunting techniques to suit different prey items, from seemingly random chases by one or two individuals for small prey to coordinated pack hunting for

large prey (details in Kruuk 1972; Cooper 1990; Mills 1990; Gasaway et al. 1991). *C. crocuta* may entirely consume a gazelle (*Gazella*) fawn in < 2 min, whereas 25 individuals ate an adult wildebeest (*Connochaetes*) in over an hour (Kruuk 1972). In the Serengeti solitary hyenas may leave their home ranges and social groups when prey are scarce and travel up to 40 km to hunt where prey abundance is high due to the presence of migratory ungulates (Hofer and East 1993b).

Crocuta crocuta uses different teeth for different purposes: "soft meat is pulled out of the carcass with the front incisors and canines, bones are crunched farther back in the mouth (for this, they often hold single bones with their forelegs, or stick the head of the male gazelle upright in the ground by the horns); pieces of skin and so on are cut far back in the mouth with the carnassials" (Kruuk 1972:107).

Intelligence and learning have been studied. Problem solving is facilitated by teamwork and cooperation (Drea and Carter 2009). The "audience effect" is evident, and experienced individuals modify their behavior to accommodate naïve companions (Drea and Carter 2009). Also, 14 of 19 individual *C. crocuta* were able to open a puzzle box (Holekamp et al. 2015). Learned aversions to food may be attenuated by feeding in groups (Yoerg 1991). Another form of social learning, response facilitation, influences feeding, scent-marking, coalition formation, greeting, and cooperative hunting (Glickman et al. 1997). Rank acquisition is via associative learning accompanied with aggression by coalitions (Holekamp et al. 2007). *C. crocuta* has a long-term memory of past interactions of conspecifics and rank relations (Holekamp et al. 2007). It can recognize the relationships between clan mates even when the observer is not directly involved (third-party relationship—Engh et al. 2005). *C. crocuta* may employ tactical deception (Holekamp et al. 2007). Affiliative conciliatory behavior occurred within 5 min after 14.6% of 698 fights (Wahaj et al. 2001).

Frequent gaits include a walk, slow lope (10 km/h), fast lope (13–16 km/h), and a run (at least 50 km/h—Matthews 1939b; Mills 1984). The track of the lope yields a series of double impressions in the ground with the hind foot slightly behind the opposite forefoot (Matthews 1939b). Longer forelimbs than hind limbs necessitate using a transverse gallop rather than a trot or pace (Spoor and Belterman 1986). An additional gait occurs when a submissive animal may approach a dominant one by crawling on the carpal joints of their forelegs "with hind legs bent, ears flat, mouth slightly open, and tail straight up or bent forward"; this is the same locomotion that cubs use within their burrows (Kruuk 1972:220).

In the Masai Mara National Reserve, Kenya, 96.2% of activity occurred from 1800 to 0900 h, but animals were not continually active (Kolowski et al. 2007). Females tended to be less active than males during from 0700 to 1100 h, but over 24 h, both sexes spent 65% (males) to 75% (females) of the time resting (Kolowski et al. 2007). In other areas of Kenya and Tanzania, *C. crocuta* is also active primarily at night (1700–0700 h), but it also hunts during the day (Matthews 1939b;

Kruuk 1972; Gasaway et al. 1991). Similarly, in the Kalahari, *C. crocuta* is active from 1730 to 0730 h with a long peak from 1930 to 0630 h (Mills 1990). In the Kalahari, the breakdown of activity is 69.0% inactive, 23.6% foraging, 5.1% eating, and 2.3% socializing (Mills 1990). In the Addo Elephant National Park, *C. crocuta* was crepuscular (Hayward and Hayward 2007).

GENETICS

The diploid chromosome number (2n) of *Crocuta crocuta* is 40 with 20 meta- and submetacentric and 18 acro- and subtelocentric autosomes. The X chromosome is metacentric; the Y is submetacentric; and small submetacentric chromosomes have satellites (Wurster and Gray 1967; Hsu and Benirschke 1968; Wallace and Fairall 1970). Photos of C- and G-banded karyotypes are available (Perelman et al. 2005). From chromosome banding patterns, *Crocuta* shares 11 homologous or partially homologous chromosomes with felids; three homologs with viverrids alone; two homologs with procyonids and viverrids; and one homolog with mustelids, procyonids, and viverrids; two chromosomes are unique (Wurster-Hill and Centerwall 1982). The *Crocuta* karyotype differs from the ancestral feliformid karyotype by two chromosome fissions, four fusions, and three inversions and differs from the ancestral carnivore karyotype by an additional fission (Perelman et al. 2005; Nash 2006). *C. crocuta* has zinc finger X and Y genes (Schwerin and Pitra 1994).

Microsatellite DNA from 11 loci can be used to estimate relatedness in *C. crocuta* (Wilhelm et al. 2003; Van Horn et al. 2004a). Relatedness 1) is 0.44–0.46 for parents and cubs as well as for half sibs, 2) declines across generations within a matriline, and 3) was not related to social rank across matrilines (Van Horn et al. 2004a). As entire matrilineal lineages may become extinct in under 10 generations, selection may operate on kin groups as well as on individuals (Holekamp et al. 2012). Dispersal of males maintains genetic variation even after a bottleneck (Watts et al. 2011) but does not overwhelm the genetic influence of female philopatry (Holekamp et al. 2012).

Paleogenomes from extinct *Crocuta* and genomes from modern *Crocuta* suggest African and Eurasian population split about 2.5 Ma, but with bidirectional gene flow after the lineages split (Westbury et al. 2020). The mitochondrial genomes of both the Pleistocene and extant *C. crocuta* have been sequenced (Bon et al. 2012). Seven nuclear gene segments have also been delineated (Koepfli et al. 2006). The *C. crocuta* genome has not been sequenced, but the placental transcriptome has (Funk et al. 2019) as has the cDNA for placental aromatase cytochrome P450 (Conley et al. 2007). As of January 2021, GenBank had 1,327 genomic DNA/RNA and 23 mRNA entries for *C. crocuta* (www.ncbi.nlm.nih.gov/genbank). As of January 2021 iDigBio had over 500 records including 80 fossil specimens and one audio recording (www.idigbio.org).

CONSERVATION

Crocuta crocuta is widespread in Africa and is listed on The International Union for Conservation of Nature and Natural Resources Red List as "Least Concern" (LC) with a world population of 27,000–47,000 that is decreasing (Bohm and Höner 2015).

Persecution and habitat loss have put many populations in decline (Bohm and Höner 2015). In areas of human disturbance, *C. crocuta* has more difficulty maintaining proximity to the communal den and to areas of high prey density (Kolowski and Holekamp 2009); it also has higher vigilance rates when resting (Pangle and Holekamp 2010). In protected area where livestock invade, humans are the major source of mortality for *C. crocuta* (Pangle and Holekamp 2010; Green et al. 2018). Tourism had no effect on vigilance in the Masai Mara National Reserve (Pangle and Holekamp 2010), and passive management practices are effective in maintaining population densities (Farr et al. 2019). As recently as 1962, in Zululand, *C. crocuta* was in demand for magic medicines (Deanne 1962).

Hominids have been killing *C. crocuta* since the Pleistocene (Hidalgo 2010). *C. crocuta* may have competed with Neanderthals for den sites in caves (Fosse 1999); it is present in a 20,000-year-old cave painting in France and other Paleolithic rock art (Spassov and Stoytchev 2004).

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