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Canis aureus (Carnivore: Canidae)

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Abstract: *Canis aureus* (Linnaeus, 1758), the golden jackal, is a medium-sized, wide spread, terrestrial carnivore. It is 1 of 7 species found in the genus *Canis.* It ranges from Africa to Europe, the Middle East, Central Asia, and Southeast Asia. Due to its tolerance of dry habitats and its omnivorous diet, *C. aureus* can live in a wide variety of habitats. It normally lives in open grassland habitat but also occurs in deserts, woodlands, mangroves, and agricultural and rural habitats in India and Bangladesh. It ranges from sea level in Eritrea to 3,500 m in the Bale Mountains of Ethiopia and 2,000 m in India. *C. aureus* is listed as "Least Concern" by the International Union for Conservation of Nature and Natural Resources Red List of Threatened Species version 2016.1.

Key words: canid, carnivore, cooperative breeder, golden jackal, opportunistic omnivore

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Canis aureus Linnaeus, 1758

Golden Jackal

Canis aureus Linnaeus, 1758:40. Type locality "oriente;" restricted to "Benná Mts., Laristan, S. Persia" by Thomas (1911:135).
Lupus aureus Linnaeus, 1758:40. No type locality. From a pre-1758 name.
Vulpes indiae orientalis Linnaeus, 1758:41. No type locality. From a pre-1758 name.
[*Canis*] *anthus* F. Cuvier, 1820:plate. Type locality "Senegal."
Canis variegatus Cretzschmar, 1826:31, plate 10. Type locality "Nubien. Oberes Egypten;" preoccupied.
Canis syriacus Hemprich and Ehrenberg, 1830:sig z, plate 16. Type locality "e monte Lebano."
Canis lupaster Hemprich and Ehrenberg, 1833:sig ff. Type locality "Fayum, Egypt" (not seen cited in Allen 1939:194).
Canis sacer Hemprich and Ehrenberg, 1833:sig ff. Type locality "Fayum, Egypt" (not seen cited in Allen 1939:194).
Canis riparius Hemprich and Ehrenberg, 1833:sig ff. Type locality "Coast of Abyssinia, near Arkiko" (not seen cited in Allen 1939:195).
Canis aureus indicus Hodgson, 1833:237. Type locality "Himalaya."
Canis aureus var. *moreotica* I. Geoffroy Saint-Hilaire, 1835:plate 1. Type locality "de Morée."
Thous anthus: Hamilton Smith, 1839:195. Name combination.
Thous variegatus: Hamilton Smith, 1839:198. Name combination.
Thous sengalensi Hamilton Smith, 1839:201, plate 13. Type locality "Gambia and Senegal."
Sacalius aureus: Hamilton Smith, 1839:214. Name combination.

Fig. 1.—Adult *Canis aureus* in the Serengeti, Tanzania, © Patricia D. Moehlman.

Sacalius barbarus Hamilton Smith, 1839:218. Type locality "Tunis;" preoccupied by *Canis barbarus* Shaw, 1800:311 synonym for *Vulpes vulpes.*

Sacalius indicus: Hamilton Smith, 1839:219. Name combination.

C[*anis*]. *dalmatinus* Wagner, 1841:383. No type locality; Dalmatia implied.

Canis graecus Wagner, 1841:383. Type locality "Europaei." Renaming of *C. aureus moreotica* I. Geoffroy Saint-Hilaire, 1835.

C[*anis*]. *aureus vulgaris* Wagner, 1841:383. No type locality.

Canis aureus algirensis Wagner, 1841:384. Type locality "d'Alger" from 'chacal d'Alger' I. Geoffroy Saint-Hilaire, 1835:22.

C[*anis*]. *aureus tripolitanus* Wagner, 1841:384. No type locality; Tripoli, Tunis implied.

Canis aureus typicus Kolenati, 1858:96. No type locality; Persia, Georgia, Turkey implied.

Canis aureus typicus var *caucasica* Kolenati, 1858:96. No type locality; Caucasus implied.

Canis aureus var *syriaco* Kolenati, 1858:96. Unauthorized emendation of *syriacus* Hemprich and Ehrenberg, 1830.

Canis aureus var *indica* Kolenati, 1858:96. Unauthorized emendation of *indicus* Hodgson, 1833.

Canis aureus var *nubica* Kolenati, 1858:96. Renaming of *Canis variegatus* Cretzschmar, 1826 but Kolenati attributes the name to Rüppell without giving a date.

Canis aureus var *algira* Kolenati, 1858:96. Unauthorized emendation of *algirensis* Wagner, 1841.

Canis aureus var *senegalensis*: Kolenati, 1858:96. Name combination.

Canis aureus var *barbarus*: Kolenati, 1858:96. Name combination.

Canis aureus balcanicus Brusina, 1892:317. Type locality "Nardu — nadomak Valpova — na obali Drave, Slavonija."

Canis hadramaticus Noack, 1896:356. Type locality "Hadramaut in Arabien." A jackal-wolf composite. The jackal was chosen as the lectotype (Morrison-Scott 1939)

Canis mengesi Noack, 1897:518. Type locality "Ostafrikanische."

Canis lupus minor Mojsisovico, 1897:202, 241, 244. Preoccupied by *Canis spelaeus minor* Wagner, 1829 according to Kretzoi, 1947.

Canis cruesemanni Matschie, 1900:145. Type locality "Siam."

Canis anthus soudanicus Thomas, 1903:295. Type locality "El Obeid," Kordofan, Sudan.

Canis somalicus Lorenz, 1906:306. Type locality "Ireso bei Agada."

Canis gallaënsis Lorenz, 1906:307. Type locality "Ginea (Arussi)."

Canis doederleini Hilzheimer, 1906a:116. Type locality "Oberägypten."

Canis thooides Hilzheimer, 1906b:364. Type locality "Sennaar."

Canis lupaster grayi Hilzheimer, 1906b:367. Type locality "Nordafrika."

Canis studeri Hilzheimer, 1906b:368. Type locality "Tunis."

C[*anis*]. *mengesi lamperti* Hilzheimer, 1906b:371. No type locality.

Thos aureus bea Heller, 1914:5. Type locality "Loita Plains, British East Africa," Kenya.

Canis indicus kola Wroughton, 1916:651. Type locality "Palanpur," India.

Canis naria Wroughton, 1916:651. Type locality "Coorg," west coast of India.

Canis lanka Wroughton, 1916:652. Type locality "Mankeni," Sri Lanka.

Thos lupaster maroccanus Cabrera, 1921:263. Type locality "Mogador (Marruecos)."

Th[*os*]. *l*[*upaster*]. *Algirensis*: Cabrera, 1921:263. Name combination.

Th[*os*]. *a*[*ureus*]. *Riparius*: Cabrera, 1921:264. Name combination.

Th[*os*]. *aureus nubianus* Cabrera, 1921:264. Renaming of *variegatus* Cretzschmar, 1826.

Canis aureus hungaricus Éhik, 1938:11. Type locality "Tyukod (Marshy-land Ecsed), Comitat Szatmár, Hungary;" Preoccupied according to Kretzoi, 1947.

Canis aureus minor: Éhik, 1938:13. Name combination; preoccupied.

Thos aureus algirensis: Allen, 1939:194. Name combination.

Thos aureus anthus: Allen, 1939:194. Name combination.

Thos aureus lupaster: Allen, 1939:194. Name combination.

Thos aureus maroccanus: Allen, 1939:195. Name combination.

Thos aureus soudanicus: Allen, 1939:195. Name combination.

Thos gallaensis: Allen, 1939:195. Name combination.

Thos lamperti: Allen, 1939:195. Name combination.

[*Canis aureus*] *moreoticus* Kretzoi, 1947:287. Unjustified emendation of *moreotica* I. Geoffroy Saint-Hilaire, 1835.

Thos aureus ecsedensis Kretzoi, 1947:287. Renaming of *C. a. hungaricus* Éhik, 1938.

Canis lupaster doederleini: Saleh and Basuony, 2014:49. Name combination.

Canis aureus qattarensis Saleh and Basuony, 2014:49. Type locality "northern region of the Egyptian Western Desert."

CONTENT AND CONTEXT. Order Carnivora, family Canidae, subfamily Caninae, genus *Canis*. As many as 13 subspecies of *C. aureus* are distinguished through Europe and Africa (Allen 1939; Ellerman and Morrison-Scott 1951; Coetzee 1977). However, these subspecies may be part of a 3-species complex (see "Nomenclatural Notes"). Unfortunately, much of the literature does not specify geographic location or subspecies. Here, *C. aureus* is used for the global range from Africa into Eurasia (Wozencraft 2005). Therefore, we list the historical 13 subspecies of *C. aureus* (Heller 1914; Allen 1939; Ellerman and Morrison-Scott 1951; Coetzee 1977; Wozencraft 2005). The newly named subspecies, *qattarensis* Saleh and Basuony, 2014, is tentatively treated as a synonym of *syriacus*. Subspecies designations for the *orientalis* Linnaeus, 1758 and *studeri* Hilzheimer, 1906b are not known.

C. a. algirensis Wagner, 1841. See above; synonyms are *algira* Kolenati, 1858; *barbarus* (Hamilton Smith, 1839); *grayi* Hilzheimer, 1906b; *tripolitanus* Wagner, 1841.

C. a. anthus F. Cuvier, 1820. See above; synonym is *senegalensis* (Hamilton Smith, 1839).

C. a. aureus Linnaeus, 1758. See above; synonyms are *balcanicus* Brusina, 1892; *caucasica* Kolenati, 1858; *hadramauticus* Noack, 1896; *maroccanus* (Cabrera, 1921); *orientalis* (Linnaeus, 1758); *typicus* Kolenati, 1858; *vulgaris* Wagner, 1841.

C. a. bea (Heller, 1914). See above.

C. a. cruesemanni Matschie, 1900. See above.

C. a. ecsedensis (Kretzoi, 1947). See above; synonyms are *hungaricus* Ehik, 1938; *minor* Mojsisovico, 1897 (preoccupied).

C. a. indicus Hodgson, 1833. See above; synonyms are *indica* Kolenati, 1858; *kola* Wroughton, 1916.

C. a. lupaster Hemprich and Ehrenberg, 1833. See above; synonym is *sacer* Hemprich and Ehrenberg, 1833.

C. a. moreotica I. Geoffroy Saint-Hilaire, 1835. See above; synonyms are *dalmatinus* Wagner, 1841; *graecus* Wagner, 1841.

C. a. naria Wroughton, 1916. See above; synonym is *lanka* Wroughton, 1916.

C. a. riparius Hemprich and Ehrenberg, 1833. See above; synonyms are *gallaënsis* Lorenz, 1906; *hagenbecki* Noack, 1897; *lamperti* Hilzheimer, 1906b; *mengesi* Noack, 1897; *somalicus* Lorenz, 1906.

C. a. soudanicus Thomas, 1903. See above, synonyms are *doederleini* Hilzheimer, 1906a; *nubianus* (Cabrera, 1921); *nubica* Kolenati, 1858; *thooides* Hilzheimer, 1906b; *variegatus* Cretzschmar, 1826 (preoccupied).

C. a. syriacus Hemprich and Ehrenberg, 1830. See above, synonym are *qattarensis* Saleh and Basuony, 2014; *syriaco* Kolenati, 1858.

Nomenclatural Notes. The above-named list may represent 3 taxa of canids: *Canis anthus* (African wolf), *C. aureus*, and *C. lupus* (gray wolf). Genetic analyses of *C. aureus* and *C. lupus* suggest that *C. aureus* from Africa and Eurasia are distinct clades and should be considered to be separate species, that is *C. anthus* (Africa) and *C. aureus* (Eurasia—Koepfli et al. 2015). As noted above, the literature does not distinguish these species and we include both as *C. aureus*.

In addition, large *C. aureus* in Egypt (*lupaster*) may be a cryptic subspecies of *C. anthus* (Rueness et al. 2011; Gaubert et al. 2012). *Canis aureus lupaster* (Hemprich and Ehrenberg 1833) is classified as a golden jackal; however Ferguson (1981) suggested that the taxon *C. aureus lupaster*, which is present in arid areas of Egypt and Libya (Osborn and Helmy 1980), may actually represent a small *C. lupus* rather than a large jackal. Mitochondrial DNA analyses suggest that *C. a. lupaster* represents an ancient wolf lineage that may have colonized Africa prior to the northern hemisphere radiation (Rueness et al. 2011). Mitochondrial DNA analyses assigned individuals from Algeria, Mali, and Senegal to *C. lupus lupaster* (Gaubert et al. 2012) and identified *C. lupus lupaster* mtDNA haplotypes in *C. aureus* from Senegal questioning the genetic differentiation between the proposed *C. anthus* and *C. aureus*. We retain *C. aureus lupaster* as a form of the golden jackal not as a subspecies of *C. lupus* following Wozencraft (2005—Qumsiyeh 1996; Ferguson 2002).

The specific name is Latin for golden. Common names include Asiatic jackal, common jackal, ibn awa or ibn awee (classic Arab), wa wie (spoken Arab), cakalli (Albanian), čagalj (Croatian), šakal obecný (Czech), sjakal (Danish, Swedish), jakhal (Dutch), šaakal (Estonian), sakaali (Finnish), Sjakalur (Faeroese), chacal doré (French), Goldschakal (German), τσακαλ (Greek), aranysakál (Hungarian), sciacallo dorato (Italian), chagal, turg (Kurdish), zeltainais šakālis (Latvian), xakali (Maltese), gullsjakal (Nowegian), shoghal (Persian), szakal złocisty (Polish), chacal-dourado (Portuguese), şakal (Rumanian), šakal obyčajný (Slovakian, Slovenian), chacal (Spanish), çakal (Turkish—Hatt 1959; P. D. Moehlman, in litt.). Indigenous names include Amharic: tera kebero (Ethiopia); Fulani: sundu; Hausa: dila; Hindi: Giddhad; Kanada: nuree; Kiswahili: bweha wa mbugani, bweha dhahabu (Tanzania); Marathi (India): kolha; Nepali (Nepal), Bengali, Gujarati and Kutchi (India): shiyal; Singhelese: nariya; Songhai: nzongo; Tamil (India): peria naree; Wolof: Tili (P. D. Moehlman, in litt.).

DIAGNOSIS

Canis aureus occurs sympatrically with the silver-backed jackal (*Canis mesomelas*) and the side-striped jackal (*Canis adustus*) in parts of East Africa. All have skull lengths of 141–147 mm with minimal divergence in size (van Valkenburgh and Wayne 1994). *C. mesomelas* is distinguished by reddish flanks and limbs, and the skull may have a less developed parietal crest (Clutton-Brock et al. 1976), the angle of its ears which are more upright, and, usually, the prominent dark "silver" saddle composed of black and white hairs (Walton and Joly 2003). *C. aureus* may have a dark saddle seasonally, which is not prominent. *C. adustus* characteristically has shorter ears set more to the side of the skull, a pale side-stripe, and a white-tipped tail (Moehlman and Jhala 2013). *C. lupus* is much larger with a heavier body and variable pelage coloring. The skull is much larger with a well-developed interparietal crest, strong jaw, and large canine and carnassial teeth (Clutton-Brock et al. 1976).

GENERAL CHARACTERS

Canis aureus (Fig. 1) is a medium-sized canid, considered the most typical representative of the genus *Canis* (Clutton-Brock et al. 1976). Basic coat color is golden but varies from pale creamy yellow to a dark tawny hue on a seasonal basis. The pelage on the back is often a mixture of black, brown, and white hairs, such that they can appear to have a dark saddle similar to the *C. mesomelas* (Walton and Joly 2003; Moehlman and Jhala 2013). The long contour hairs have an extensive black tip and a wider penultimate white band (Pocock 1938). In winter, a copious under wool is present (Pocock 1938). *C. aureus* inhabiting rocky, mountainous terrain may have a grayer coat shade (Sheldon 1992). The belly and underparts are a lighter pale-ginger to cream. The tail is bushy with a tan to black tip. Females have 7–8 mammae (Poché et al. 1987), comprising 4 pairs (Sheldon 1992). Eye color varies from pale yellow to amber (Lewis et al. 1968).

Means and parenthetical ranges of external measurements (mm) from 6 males and 3 females, respectively, in Gujarat, India (Y. V. Jhala, in litt.) were: length of head and body, 793 (760–840), 760 (740–800); length of tail, 220 (200–240), 205 (200–210); length of ear, 76 (68–90), 80 (75–85); body mass (kg) of 6 male and 4 females was 8.8 (7.6–9.8) and 7.3 (6.5–7.8), respectively. In Tanzania, the external measurements (mm or kg) from 2 males in the Serengeti (Moehlman and Jhala 2013) were: length of head and body, 740, 785; length of tail, 270, 280; length of ear, 110, 110; mass, 6.3, 7.7. In Egypt, means and parenthetical ranges (mm) for 9 adult *C. a. lupaster* of unknown sex were: length of head and body, 872 (822–893); length of tail, 312 (290–347); length of hind foot, 200 (190–212); length of ear, 112 (104–121); and body mass (kg) of 4 adults was 13 (10–15—Osborn and Helmy 1980). In Lebanon, external measurements (mm) of 3 adult *C. a. syriacus* were: total length, 988.3 (950–1015); length of tail, 275 (265–290); length of head and body, 713.3 (680–750); length of hind foot, 156 (140–170); length of ear from notch, 74.7 (70–80—Lewis et al. 1968). In Bangladesh, mean measurements (mm, *SD*, *n*) of females and males, respectively, were: total length, 1009.3 (33.67, 6), 1058.6 (20.30, 7); length of tail, 220.1 (17.16, 7), 245.0 (21.41, 6); length of hind paw, 58.0 (4.93, 7), 56.3 (4.83, 7); length of hind foot, 146.2 (24.66, 5), 162.6 (8.52, 7); length of ear, 69.4 (4.80, 5), 74.1 (5.49, 7); mass (kg), 8.5 (0.73, 7), 10.3 (0.95, 7—Poché et al. 1987). Mean adult mass (kg) of 5 females and 3 males, respectively, was 10.0 and 12.0 (Palmqvist et al. 2002). On average, females are 12% lighter than males: 5.8 kg versus 6.6 kg (Moehlman and Hofer 1997).

Mean cranial measurements (mm, *SD*; Fig. 2) on 10 mandibles and upper jaws of adult *C. aureus* in Iran were: length of skull, 169, 31.9; length of cranium, 101, 23.7; nasal length, 67, 16.6; cranial width, 72, 4.4; length of mandible, 112, 34.6; lateral alveolar root to mental foramen, 25, 1.7; mental foramen to caudal mandibular border, 87, 3.8; mandibular foramen to base of mandible, 12, 0.4; caudal border of mandible to below mandibular foramen, 11, 0.8; maximum mandibular height, 60, 5.8 (Mofared 2013). Mean measurements (mm, range) for 3 Lebanese adults were: greatest length of skull, 148.6 (135.2–157.4); condylobasal length, 142.9 (131.9–149.1); zygomatic breadth, 83.9 (73.3–90.2); breadth of braincase, 48.8 (46.0–50.3); interorbital constriction, 29.4 (25.5–32.7); maxillary toothrow, 62.9 (60.4–65.0); mandibular toothrow, 72.2 (58.2–74.9); mandibular length, 114.1 (104.1–121.0—Lewis et al. 1968). Mean cranial measurements (mm; with range and *n*) of Egyptian adult *C. a. lupaster* were: condyloincisive length, 185.2 (173.5–196.0, 13); zygomatic width, 101.4 (93.5–111.3, 14); rostral width, 33.8 (31.2–37.8, 14); postorbital width, 34.8 (31.8–38.9, 13); basioccipital width at tempoparietal suture, 54.4 (51.8–59.1, 13); nasal length, 72.0 (65.9–84.8, 14); width across upper molars, 58.2 (54.2–63.0, 14); distance from anterior most surface of canine to posterior of 2nd molar, 80.3 (75.6–86.8, 14); skull height, 66.8 (62.0–74.0, 9—Osborn and Helmy 1980). In Bulgaria, mean cranial and tooth measurements (mm) for 92 males and 56 females, respectively, were: total skull length, 166, 161; neurocranium length, 89, 86.5; greatest length of nasals, 59.7, 57.9; greatest neurocranium breath, 52.5, 52.6; total length of mandible, 121.9, 118.6; height of vertebral ramus, 48.6, 46.7; length of P1 to P4, 33.9, 33.4; length of M1 to M3, 31.8, 31.0 (Stoyanev 2012). Mean mandible length and depth at 2nd molar (mm)

Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male *Canis aureus aureus* (Field Museum of Natural History, Chicago, Illinois, [FMNH] #103909) from Maimana, Fariab, Afghanistan, 2,900 feet. Greatest length of skull is 177 mm. Photograph by Bruce Patterson used with permission.

for 5 females and 3 males, respectively, was f: 102.8, 14.3; m: 108.9, 15.3 (Palmqvist 2002). Condylobasal length (mm) from 10 males was 154, whereas it was 140 from 7+ female skulls (Pocock 1938).

DISTRIBUTION

Canis aureus is widespread in North and East Africa, Europe, the Middle East, Central Asia, and Southeast Asia (Fig. 3). They range from sea level in Eritrea to 3,500 m in the Bale Mountains of Ethiopia and 2,000 m in India (Prater 1971; Admasu et al. 2004).

In Greece and Dalmatia, *C. aureus* is documented from the Holocene (Sommer and Benecke 2005; Malez 1984 in Rutkowski et al. 2015) and the ancient Mediterranean populations have persisted and merged with jackals coming from Asia (Fabbri et al. 2014; Rutkowski et al. 2015). The expanding population of *C. auerus* in Europe is due to natural long-distance dispersal (Arnold et al. 2012; Rutkowski et al. 2015). *C. aureus* expanded from southeastern Europe to Hungary in the late 1800s (Tóth et al. 2009). In the late 20th century, the expansion was rapid and is still ongoing (Kryštufek et al. 1997; Arnold et al. 2012).

FOSSIL RECORD

The fossil record of *Canis aureus* is limited with many fossils that are controversial as to their specific attribution. A right lower carnassial from a Paleolithic Lebanon cave may be *C. aureus* (Hooijer 1961). Fossil remains attributed to *C. aureus* dating from the Upper Pleistocene were found in North Africa (Savage 1977). Palestinian fossils attributed to this species have been reattributed to *C. lupaster* (Kurten 1974) and hence might be a separate species (Spassov 1989). Reliable fossils of *C. aureus* have not been found in the Pleistocene of Europe (Spassov 1989). *C. aureus* appears to have arrived in sub-Saharan Africa after *C. mesomelas* and *C. adustus*, which have a fossil record in eastern and southern Africa from 500,000 to 2.5 million years (Ewer 1956; Savage 1977).

FORM AND FUNCTION

The dental formula is i 3/3, c 1/1, p 4/4, m 2/3, total 42 (Fig. 2). Of 31 *Canis aureus* skulls, 13% had broken teeth (van Valkenburgh 2009). Baculum length is 62.7 mm (Dixson 1995), but 2 bacula of *C. a. lupaster* were 70 and 73 mm (Osborn and Helmy 1980).

Male and female skulls can be differentiated but cranial measures overlap (Stoyanev 2012). Differentiation was not dependent on age or collection site. Only juveniles below the age of 6 months could be differentiated from adults. *C. aureus* from Bulgaria did not differ from European or Asian skulls and encompassed both African and Dalmatian jackals, but skulls from *Canis aureus lupaster* were larger, longer, and broader (Stoyanev 2012). Croatian skulls were of a shorter length and broader (Stoyanev 2012). In Bulgarian skulls, age could be assessed in 223 of 228 from craniometrics differences (Stoyanev 2012). Across 7 populations, sexual dimorphism in skull length

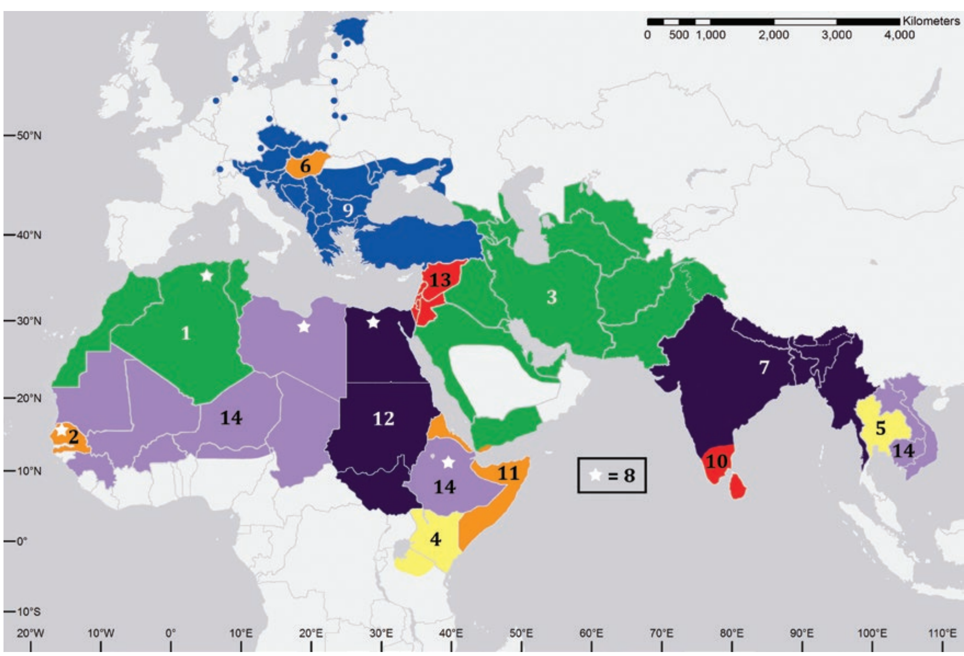

Fig. 3.—Geographic distribution of *Canis aureus* includes subspecies that may belong to *C. anthus* or *C. lupus*. The map shows the likely ranges of the following subspecies, 1, *C. a. algirensis*; 2, *C. a. anthus*; 3, *C. a. aureus*; 4, *C. a. bea*; 5, *C. a. cruesmanni*; 6, *C. a. ecsedensis*; 7, *C. a. indicus*; 8, *C. a. lupaster* (dispersed stars on map); 9, *C. a. moreotica* (isolated records presented as blue dots on map); 10, *C. a. naria*; 11, *C. a. riparius*; 12, *C. a. soudanicus*; 13, *C. a. syriacus*; 14, *C. a.* subspecies undetermined.

and canine diameter was significant for East African and northern Indian *C. aureus* but not north African, north central African, Middle Eastern, Pakistani, or southern Indian animals (Van Valkenburgh and Wayne 1994). In Bangladesh, mean organ weights (g, *SD*, *n*) for adult females and males, respectively, were: heart, 71.0 (7.35, 3), 79.2 (14.02, 4); liver, 297.7 (14.52, 3), 365.5 (72.06, 4); paired kidneys, 45.7 (8.73, 3), 64.0 (4.37, 4); spleen, 75.3 (21.1, 3), 43.0 (10.61, 3); lungs, 64.7 (11.47, 3), 85.7 (18.87, 3—Poché et al. 1987).

Adult *C. aureus* can be immobilized for handling up to 55 min with 130 mg ketamine hydrochloride and 15 mg promazine hydrochloride (Fuller et al. 1989). For 3 female and 4 male *C. aureus*, doses of 15–80 mg/kg of ketamine hydrochloride generated recovery times of 32–300 min with no apparent side effects (Poché et al. 1987). Time to immobilization was 2–3 min (Poché et al. 1987). Trapped jackals were anesthetized with an intramuscular injection of a mixture of medetomide 0.09 mg/kg and ketamine 2.8 mg/kg and time to immobilization was an average of 5.0 min (Admasu et al. 2004).

ONTOGENY AND REPRODUCTION

Ontogeny.—The estimated weight from a captive born litter of 2 female and 2 male *Canis aureus* neonates was 189 g (Moehlman and Hofer 1997). A male pup weight at day 8 was 249 g, day 13: 500 g, and at day 15: 590 g. A female pup at day 5 weighed 295 g, and at day 21 weighed 670 g (Seitz 1959). Pups are blind at birth with eye opening at 8–11 days and tooth eruption at 11 days (Seitz 1959; Wandry 1975). In captivity, canine teeth erupted at 28 days (Seitz 1959) and pups emerged from the den box at approximately 4 weeks (Wandry 1975). At 13 months of age a female had her 1st litter and hence was reproductively mature at 11 months of age (Seitz 1959).

In the Serengeti, Tanzania, the pups are born and remain in underground dens until they are 3 weeks old during which time their mother spends most of her time with them (Moehlman 1983). Pups emerge at approximately 3 weeks of age and in addition to nursing, eat regurgitated food (Moehlman 1986). Some families have helpers which are offspring from the previous year's litter. During pregnancy, the female is provisioned by her mate and while she is lactating she is provisioned by her mate and the "helpers" which are her older offspring (Moehlman and Hofer 1997). One of us (PDM) has observed that helpers also provision the pups which are their full siblings. They are weaned at 8–10 weeks of age and stay within several hundred meters of the den until they are 10 weeks old. At 14 weeks of age they are well coordinated and start to forage with the adults. They will continue to receive some food from their parents until they are 8 months old. Even when they are helpers (11–18 months) they may infrequently receive food from their parents (Moehlman 1986).

Adults can be distinguished from juveniles by frontoparietal ridges that are fused posteriorly to the frontoparietal suture creating a high sagittal ridge (Osborn and Helmy 1980). Tooth wear can be used to age *C. aureus* (Raichev 2011).

Reproduction.—In the Serengeti mating typically occurs from October to December (Moehlman 1983, 1986) and birth from December to March (Moehlman 1983). In Egypt, litters have been observed in March, April, and May (Flower 1932). In India reproductive behavior begins in February–March (Jhala and Moehlman 2004) and in Israel between October and March (Golani and Keller 1975; Ginsberg and Macdonald 1990). In Bangladesh, pups are present year-round (Poché et al. 1987). Gestation is about 63 days (Sheldon 1992). Litter size ranges from 1 to 9, average 5.7 (Moehlman and Hofer 1997). In Tanzania, an average of 2 pups emerged from the natal den at 3 weeks (Wyman 1967). Lactation lasts for 8–10 weeks (Moehlman 1986). Six females captured in Kenya in June to August were not lactating (Fuller et al. 1989).

ECOLOGY

Population characteristics.—In Tanzania, densities up to 2 adults per km^2 may occur (Moehlman 1983, 1986, 1989). In northern Dalmatia, Croatia, territory density was 0.61–1.15 groups per 10 km^2 (Krofel 2008), whereas in southern Dalmatia density was 6–7 groups per 10 km^2 (Krofel 2007). In Kenya, juveniles comprised 47% of captured *Canis aureus* (Fuller et al. 1989). In the Serengeti, maximum longevity is about 14 years (Moehlman and Hofer 1997). In captivity, individuals have lived up to 18 years 10 months (Weigl 2005). Sex ratio at approximately 3 weeks when pups emerge from the den is 1:0.8 (n = 33), surviving at age 14 weeks (1:0.8, n = 44), helping as juveniles at approximately 52 weeks (1:1, n = 16), and reproductive adults (1:1, n = 46—Moehlman 1986). The sex ratio is equal for all age groups and sex ratio is equal for helpers.

Space use.—Tolerance of dry habitats and an omnivorous diet allow *Canis aureus* access to a wide variety of habitats (Jhala and Moehlman 2008). They normally live in open grassland habitat but also occur in deserts, woodlands, mangroves, and agricultural and rural habitats in India and Bangladesh (Jhala and Moehlman 2008)

In the Serengeti, *C. aureus* maintains year-round exclusive territories of 0.5–7.0 km^2 (Moehlman 1983) and 2–5 km^2 in Ngorongoro (van Lawick and van Lawick-Goodall 1970), but will make excursions beyond these territorial boundaries to gain access to fresh carcasses. In Algeria, seasonal territories as may be as small as 0.39 km^2 (Khidas 1990). Territories are within larger home ranges. Home range size of radiocollared individuals in some locales can vary according to habitat and age. An adult pair in *Acacia* woodland in Kenya had a home range of 2.4 km^2 and 2 juvenile females had home ranges of 5.6 and 21.7 km^2 (Fuller et al. 1989), although range size over a 16-month period in the Bale Mountains of Ethiopia varied from 7.9 to 48.2 km^2 for adults and from 24.2 to 64.8 km^2 for subadults (Admasu et al. 2004). Subadults may have larger home ranges as they explore and search for a mate and a territory. Home ranges of individuals within a social group tend to overlap (van Lawick and van Lawick-Goodall 1970; Khidas 1990; Admasu et al. 2004). In Bangladesh, breeding pairs defend an average of 37.3 ha of cover but not the peripheral foraging areas (Jaeger et al. 1996, 2007) and a male and female had home ranges of 1.1 and 0.6 km^2, respectively (Poché et al. 1987). In Israel, home and core ranges (km^2) of *C. aureus* near villages were about one-third of those in more natural areas (mean, *SD*): home, 6.6 (4.5) versus 21.2 (9.3); core, 1.2 (0.9) versus 3.5 (1.6—Rotem et al. 2011).

In the Serengeti, territories are maintained for up to 8 years albeit with changes in boundaries and size through time. Both members of the pair mark and defend the territory (Moehlman 1986).

Diet.—In Bangladesh, rodents are the most common food (Jaeger et al. 2007). Similarly, in Bulgaria, rodents comprise 59.3% of the diet with brown hares (*Lepus europaeus*, 20.1%) and plants (primarily fruit, 19.7%) as the next most common components (Markov and Lanszki 2012). In Rajasthan, India, rodents make up 45% of the diet (Mukherjee et al. 2004). In Algeria, mammals comprise about a one-third of the diet with 17–24% poultry and 12–27% insects depending on location (Amroun et al. 2006). In Israel, domestic carrion may form a significant component of the diet along with fruit, birds, small mammals, and invertebrates (Borkowski et al. 2011). In Bangladesh, 12 stomachs contained primarily carrion, poultry, and vegetation but no rodents (Poché et al. 1987).

Single *C. aureus* typically hunt smaller prey like rodents and birds, using their hearing to locate rodents in the grass and then pouncing on them by leaping through the air, or digging out rodents from their burrows. However, single animals will also hunt Thomson's gazelle (*Eudorcas tomsonii*) fawns. They have been observed to hunt young, old, and infirm ungulates that are sometimes 4–5 times their body weight (van Lawick and van Lawick-Goodall 1970; Eisenberg and Lockhart 1972). *C. aureus* in Bale, Ethiopia, may be more solitary than elsewhere in the range, with individuals having been observed foraging alone on 87% of occasions (Admasu et al. 2004). This is likely because food resources were widely dispersed and rarely concentrated enough for jackals to forage in groups (Admasu et al. 2004).

In the Serengeti, mated pairs will hunt cooperatively and regularly kill Thomson Gazelle fawns and occasionally adults; pairs have a higher kill rate than individuals (Wyman 1967; Kruuk 1972; Rosevear 1974). Cooperative hunting permits them to harvest much larger prey in areas where they are available Temu et al. 2017. In the Ngorongoro Crater, *C. aureus* pairs cooperatively killed Thomson's gazelle fawns and occasionally killed adult Thomson's gazelle. Individuals successfully hunted Abdim's storks (*Ciconia abdimii*) and during Wildebeest calving season consumed the abundantly available placentas. There was one observation of *C. aureus* cooperatively killing and eating a bat-eared fox (*Otocyon megalotis*) (Temu et al. 2017). Golden jackals consumed significantly more grams of food per hour of foraging when compared with sympatric Silver-backed jackals (Temu et al. 2016). In some areas, particularly where food resources are clumped, aggregations of *C. aureus* may occur, such as 14 jackals on a carcass in Ngorongoro (van Lawick and van Lawick-Goodall 1970) and aggregations of 5–18 jackals scavenging on carcasses of large ungulates in India (Y. V. Jhala, in litt.). *C. aureus* will cache excess food (van Lawick and van Lawick-Goodall 1970). In India, they will kill poultry as well as young and weak sheep and goats (Jhala and Moehlman 2004), and will venture into human habitation at night to feed on garbage (Poché et al. 1987). In the Golan Heights, 1.5–1.9% of domestic calves are killed by predators, primarily *C. aureus* (Yom-Tov et al. 1995).

In the Serengeti, *C. aureus* scavenges the kills of spotted hyenas (*Crocuta crocuta*) and lions (*Panthera leo*) and leopards (*Panthera pardus*—van Lawick and van Lawick-Goodall 1970; Moehlman 1986). In the Serengeti during the dry season, *C. aureus* does not have access to free standing water and can tolerate dry habitats (Moehlman and Jhala 2013).

Diseases and parasites.—In the Serengeti, blood of 2 *Canis aureus* males was negative for leptospirosis, canine distemper, canine brucellosis, rabies, rinderpest, African horse sickness, and rift valley fever. Both individuals had titers for canine adenovirus and canine coronavirus. The older male was positive for canine parvovirus (Karesh 1990 in litt.). In 1994 during an outbreak of distemper, one *C. aureus* tested positive for canine distemper virus (Roelke-Parker et al. 1996). In 2011, samples collected from *C. aureus* pups were positive for canine distemper virus, but only 1 death was observed (Olarte-Castillo et al. 2015). In Kenya (1987–1988) testing for canine parvovirus (CPV-2), canine distemper virus, *Ehrlichia canis*, and rabies indicated that 9 of 16 individuals were positive for CPV-2; all were negative for canine distemper virus, *E. canis*, and rabies (Alexander et al. 1994).

In Israel, a serological survey indicated the presence of canine distemper virus, *E. canis*, and *Leshimania infantum.* Blood smears in one individual revealed *Hepatazoon canis* (Shamir et al. 2001). *Leshimania tropica* is also known from Israeli jackals (Talmi-Frank et al. 2010). Six of 8 *C. aureus* were positive for *Toxoplasmosis gondii* in the United Arab Emirates (Dubey et al. 2010).

Canis aureus in Serbia had an infection rate of 46 out of 447 jackals (10.3%) of at least one helminth species and in total 12 species were identified: 2 trematodes, *Alaria alata* and *Pseudamphistomum truncatum*, 3 nematodes, *Toxocara canis*, *Ancylostoma caninum*, and *Gongylonema*, and 7 cestodes, *Taenia pisiformis*, *Taenia hydatigena*, *Multiceps multiceps*, *Multiceps serialis*, *Mesocestoides lineatus*, *Macrocanthorynchus hirudinaceus*, and *Onicola canis* (Ćirović et al. 2015). In Israel, fecal samples had *A. caninum* and *Dipylidium caninum* (Shamir et al. 2001). In Tanzania, fecal samples from *C. aureus* had *Coccida*, *Ancyclostoma*, *Psoroptes*, and *T. canis* (W. B. Karesh, in litt.). In Rumania, the roundworm, *Trichinella britovi* occurs in *C. aureus* (Blaga et al. 2008). In Uzbekistan and Turkmenistan, the Ministries of Health (Berdyeva 1998; L. M. Isaev Institute of Medical Parasitology 1998) reported that *C. aureus* may be infected with the guinea worm, *Dracunculiasis medinensis*; thus, *C. aureus* potentially can infect water sources. In Italy, a subadult male had 2 ectoparasitic species, *Dermacentor reticulatus*, *Isodes ricinus*, and 1 endoparasitic species, *Metagonimus yokogawai* (Lapini et al. 2009). One *C. aureus* from Tunisia had 72 tapeworms, *Echinococcus granulosus* while 4 others had fecal evidence of the species (Lahmar et al. 2009). The protozoan, *Babesia gibsoni*, may use *C. aureus* as a host (Patton 1910).

Interspecific interactions.—In East Africa, *Canis aureus* is sympatric with *C. mesomelas* and *C. adustus*. Skull characters indicate that *C. aureus* are more carnivorous than *C. adustus* and less carnivorous than *C. mesomelas* (van Valkenburgh and Wayne 1994). In Hungary, dietary overlap between sympatric *C. aureus* and red foxes (*Vulpes vulpes*) is high at 73% as both primarily eat small mammals < 50 g (Lanszki et al. 2006).

In East Africa, spotted hyenas will kill and feed on *C. aureus* (Kruuk 1972; Kingdon 1977). In the Serengeti, *C. aureus* give a "warning yowl" when spotted hyenas approach their dens. The adult jackals then chase the hyenas and bite them on the rump or genitals. Honey badgers (*Mellivora capensis*) have been observed near *C. aureus* dens, but have always been chased away by the parents and helpers. In India, striped hyenas (*Hyaena hyaena*) may prey on *C. aureus* (Y. V. Jhala, in litt.) and pythons (*Python molurus*) can be major predators (Singh 1983). In India, when *C. aureus* approaches human habitation it may be killed by feral domestic dogs and death due to road kills increased during its breeding season (Y. V. Jhala, in litt.). *C. aureus* may be killed as a side effect of predator control programs when it scavenges poisoned carcasses (Moehlman and Jhala 2013).

Miscellaneous.—Capture methods include rubber-padded, steel, foot-hold traps, cage-type live traps, large box traps, and Victor steel traps with off-set jaws (Poché et al. 1987; Fuller et al. 1989; Admasu et al. 2004; Rotem et al. 2011). Differences in white markings on throat and chest may allow individual identification (Macdonald 1979). Unique facial scars and naturally notched ears can be used to identify individuals (Moehlman 1983, 1986).

HUSBANDRY

As of March 2000, approximately 193 *Canis aureus* were in Indian zoos (Jhala and Moehlman 2004). *C. aureus* have been raised in captivity for behavioral studies (Seitz 1959; Wandry 1975). Individuals were housed in a kennel of 225 m^2 which included 5 separate and interconnected areas/cages. Each cage had a large box with a tunnel-like entrance (Wandry 1975).

BEHAVIOR

Grouping behavior.—*Canis aureus* are typically monogamous but can potentially be socially flexible depending on demography and food resources (Macdonald 1979; Moehlman 1983, 1986, 1989; Fuller et al. 1989; Moehlman and Hofer 1997; Admasu et al. 2004). The basic social unit is the breeding pair and some offspring from the previous year's litter may remain with the parents and help to raise the current littler of pups (Moehlman 1983, 1986, 1989). In Tanzania, *C. aureus* usually form long-term pair bonds which can last for up to 6 years. The bonded pair is territorial and both male and female mark within and on the boundaries of their territory and defend their territories against intruders. Same sex aggression is the norm with the territorial male attacking intruding males and females attacking intruding females. The pair hunt together, share food, and cooperatively rear their young (Moehlman 1983, 1986, 1989). Moehlman and Hofer (1997) give average group size as 2.5 (Serengeti, Tanzania), similar to average group size (3; $n = 7$) in Velavadar N. P., India (Y. V. Jhala, in litt.).

Reproductive behavior.—*Canis aureus* has a strong pair bond which normally lasts for its lifetime (Moehlman 1983, 1986, 1989). Mating involves a copulatory tie that lasts for several minutes (Golani and Mendelssohn 1971; Golani and Keller 1975). Pups are born in an underground den and normally emerge at about 3 weeks of age. Once pups emerge from the den they are fed solid food by adults regurgitating to them in addition to nursing. The origin of the dens can vary. Some authors (e.g., Rosevear 1974) report the use of existing aardvark *Orycerопus afer* or warthog *Phacochoerus* burrows, but in the Serengeti this is unlikely as *C. aureus* den openings are too small for either of these species (Jhala and Moehlman 2004). Earthen dens may have 1–3 openings and are typically about 2–3 m long and 0.5–1 m deep (Jhala and Moehlman 2004). Pups may be moved to different dens 2–4 times during their first 14 weeks of development (Moehlman 1983, 1986, 1989).

In Tanzania, *C. aureus* typically produces litters once a year during the wet season (December to February) when the large migratory herds of wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*), and Thomson's gazelles are present on the short-grass plains (Maddock 1979). Thus, when *C. aureus* has pups, food items ranging in size from dung beetles to Thomson's gazelle fawns are abundant. *C. aureus* also scavenges at carcasses of wildebeest and zebra that are killed by larger predators, mainly spotted hyenas (van Lawick and van Lawick-Goodall 1970; Moehlman 1983, 1986).

In the Serengeti since mated pairs are monogamous with long-term bonds, sequential litters are full siblings as confirmed by genetic analysis of microsatellite DNA (P. D. Moehlman, in litt.). The male provisions the female while she is pregnant and both the male and the helpers (the previous years pups) provide the female with food while she is lactating (Moehlman 1983, 1986, 1989; Moehlman and Hofer 1997). The presence of helpers correlates significantly with a higher pup survival (Macdonald and Moehlman 1983; Moehlman 1986, 1989).

Communication.—Territories are maintained indirectly by scent marking and vocalizations. Both members of a pair use a raised-leg urination posture to scent mark grass tufts, bushes, and trees at nose height. Urination with a raised rear leg instead of squatting is considered to be a 'marking posture' and indicates that the individual is a territory holder and on its territory. Marking, for example "raised-leg" urinations indicate that an individual is a territory holder and on its territory. When a territorial male or female leaves their area they do not "mark." Both the boundary and the area within a territory are "marked." When foraging with their mate, territorial individuals mark at twice the frequency as when they are foraging alone. When travelling together they mark the same spot in tandem (Moehlman 1983, 1986). The presence of scent from both members of the pair may advertise to potential intruders that they are both actively in residence (Moehlman 1983). Such scent marks are considered to play an important role in territorial defense (Rosevear 1974).

Affiliative behaviors like greeting ceremonies, grooming, and group vocalizations are common in *C. aureus* social interactions (Van Lawick and van Lawick-Goodall 1970; Golani and Keller 1975). Vocalization consists of a complex howl repertoire beginning with 2–3 simple low-pitch howls and culminating in a high-pitched staccato of calls. In the Serengeti, individuals give reciprocal howls to locate their mates and family members. Families also occasionally group howl in response to neighboring family howls (Moehlman 1983). Similar functions accrue to howling in Bangladesh, for territory maintenance and advertisement of dominance (Jaeger et al. 1996). *C. aureus* has a "rumble growl" and "predator bark" when potential predators like spotted hyenas approach a den with pups. Pups respond to these vocalizations by running into the den (Moehlman 1983).

Miscellaneous behavior.—In Kenya, *Canis aureus* was active during the day, as well as at dawn and dusk but not in the middle of the night (Fuller et al. 1989). In Bangladesh, it preferred the cover of sugarcane during the day (Jaeger et al. 2007).

GENETICS

The diploid chromosome number (2N) of *Canis aureus* is 78 (Wurster and Benirschke 1968). A total of 12–24 microsatellite loci from Israeli *C. aureus* generated expected levels of heterozygosity (Cohen et al. 2013). In Serbian *C. aureus*, mitochondrial DNA has no variation and nuclear variability is low (Zachos et al. 2009). The mitochondrial DNA control regions are variable across *C. aureus* from Bulgaria, Serbia, Croatia (Dalmatia and Slavonia), and Italy and most genetically distinct in the population from Dalmatia (Fabbri et al. 2014).

A melanistic individual occurred in Turkey (Ambarli and Bilgin 2012). Other melanistic and piebald forms are known (Muller-Using 1975; Jerdon 1984). Hybridization with domestic dogs may occur in Croatia (Galov et al. 2015) but not in India (Yumnam et al. 2015).

Genetic data suggest that *C. a. lupaster* represents an ancient wolf lineage that most likely colonized Africa prior to the northern hemisphere radiation (Rueness et al. 2011). A combined analysis of nuclear and mitochondrial DNA (Bardeleben et al. 2005) indicates that *C. aureus* is in a wolf-like clade that includes *Canis adustus*, *C. mesomelas*, *C. familiaris*, *C. lupus*, *C. latrans*, *Cuon alpinus*, and *Lycaon pictus.* A phylogeny of living canids based on 22 nuclear and 3 mitochondrial loci produced a similar wolf-like clade (Perini et al. 2010).

CONSERVATION

Canis aureus is fairly common throughout its range and is listed on the International Union for Conservation of Nature and Natural Resources Red List as "Least Concern" with at least 80,000 individuals on the Indian continent and an unknown number in Africa (Jhala and Moehlman 2008). This species is not listed in CITES. In the European Union, *C. aureus* is listed as an Annex V species and should be legally protected (Rutkowski et al. 2015; Trouwborst et al. 2015). As the expansion of *C. aureus* is a natural long-range dispersal, it should not be considered an alien invasive species (Rutkowski et al. 2015).

In the Serengeti–Ngorongoro ecosystem the population may be in decline (Durant et al. 2011) but it is still at a relatively high density (0.5 individuals per km^2). In Greece, the population has been declining from at least 1975 (Giannatos et al. 2005). In areas where *C. aureus* is perceived as a threat to livestock, it is often killed in indiscriminate predator control programs (Moehlman and Jhala 2013).

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